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Quantifying Tropical Dry Forest Type and Succession: Substantial Improvement with LiDAR

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ABSTRACT

Improved technologies are needed to advance our knowledge of the biophysical and human factors influencing tropical dry forests, one of the world's most threatened ecosystems. We evaluated the use of light detection and ranging (LiDAR) data to address two major needs in remote sensing of tropical dry forests, *i.e.,* classification of forest types and delineation of forest successional status. We evaluated LiDAR-derived measures of three-dimensional canopy structure and subcanopy topography using classification-tree techniques to separate different dry forest types and successional stages in the Guánica Biosphere Reserve in Puerto Rico. We compared the LiDAR-based results with classifications made from commonly used remote sensing data, including Landsat satellite imagery and radar-based topographic data. The accuracy of the LiDAR-based forest type classification (including native- and exotic-dominated forest classes) was substantially higher than those from previously available data (kappa = 0.90 and 0.63, respectively). The best result was obtained when combining LiDAR-derived metrics of canopy structure and topography, and adding Landsat spectral data did not improve the classification. For the second objective, we observed that LiDAR-derived variables of vegetation structure were better predictors of forest successional status (*i.e.,* mid-secondary, late-secondary, and primary forests) than was spectral information from Landsat. Importantly, the key LiDAR predictors identified within each classification-tree model agreed with previous ecological knowledge of these forests. Our study highlights the value of LiDAR remote sensing for assessing tropical dry forests, reinforcing the potential for this novel technology to advance research and management of tropical forests in general.

Abstract in Spanish is available in the online version of this article.

Key words: ALS; biodiversity; land-use legacy; secondary forests; vegetation structure.

REMOTE SENSING IS AN IMPORTANT TOOL FOR SUPPORTING RESEARCH AND MANAGEMENT OF TROPICAL DRY FORESTS (Sánchez-Azofeifa *et al.* 2003), one of the world's most threatened ecosystems (Janzen 1988). Current limitations in remotely sensed assessments of forest types and succession, however, hamper efforts to quantify important ecosystem characteristics such as those related to biodiversity and carbon storage (*e.g.,* Quesada *et al.* 2009, Sánchez-Azofeifa *et al.* 2009). Improved technologies are therefore needed to advance our knowledge of the biophysical and human dimensions of these ecosystems (Sánchez-Azofeifa *et al.* 2005, see Krishnaswamy *et al.* 2009). In particular, hyperspectral and LiDAR remote sensing hold a special interest because they can add a great deal of dimensionality to the spectral and structural information available to make ecological inferences (Kalacska & Sánchez-Azofeifa 2008, Sánchez-Azofeifa *et al.* 2009). The process of applying these technologies in tropical dry forests is just beginning within the scientific community. In this study, we evaluated the utility of LiDAR relative to other commonly used remote sensing data sets to: (1) classify forest types; and (2) identify successional status in a tropical dry forest of Puerto Rico.

LiDAR (*i.e.,* light detection and ranging) uses a laser to directly measure canopy height, subcanopy topography, and the vertical distribution of intercepted surfaces, opening new opportunities for assessing forest structure and function (see Hill & Suarez 2010). LiDAR data are becoming increasingly common and they are part of the next generation of satellite and airborne-based systems for ecological observations (*e.g.,* Carnegie Airborne Observatory [Asner *et al.* 2007], National Ecological Observatory Network [NEON; Keller *et al.* 2008], NASA ICESat2, http://icesat.gsfc.nasa.gov/icesat2).

As different vegetation types support different groups of organisms, maps of forest types derived from remote sensing data are commonly used to assess biodiversity and wildlife habitats (Turner *et al.* 2003). In this sense, the combination of Landsat satellite imagery with environmental GIS layers is one of the most common approaches for classifying vegetation (Cohen & Goward 2004); however, accurately delineating tropical dry forest

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types has been problematic. Frequent confusion has been reported between semi-deciduous forests and shrublands/woodlands, semi-deciduous forests and evergreen forests, and scrub forest, shrublands and pastures, among others (*e.g.,* Helmer *et al.* 2002, 2008, Kennaway & Helmer 2007, Gould *et al.* 2008, Martinuzzi *et al.* 2008, see also Krishnaswamy *et al.* 2004, 2009 using other optical sensors). Further classification challenges may arise by the presence of forest types in different successional stages, as well as by introduced species creating novel forest types (Lugo 2009).

Recent studies in temperate zones found that LiDAR-derived information of canopy height can be powerful predictor of vegetation types, either alone or in combination with spectral imagery (Hill & Thomson 2005, Antonarakis *et al.* 2009). In particular, LiDAR data can improve the delineation of forest classes that are spectrally similar, but structurally different (Neuenschwander *et al.* 2009), a problem that confounds accurate classification in tropical dry forests. In addition, because topography influences the distribution of tropical forest types at a local scale (Lugo 2005), the use of topographic information from LiDAR may prove useful for further discriminating forest types.

Understanding succession and land-use legacy is important for managing tropical forests, as they affect the structure, function, and services of these ecosystems (Chazdon *et al.* 2009, Quesada *et al.* 2009). Today, tropical dry forests occur in a dynamic mosaic of different human land uses and forest patches in different stages of development (Quesada *et al.* 2009). In this context, the delineation of successional stages (*i.e.,* young, mature, and primary forests) is a topic of major research interest, but also of major technological challenges (Sánchez-Azofeifa *et al.* 2003, 2009, Quesada *et al.* 2009). Previous studies were able to separate successional stages in forests up to 30 yr of age (*i.e.,* in young to mid-secondary forests) using the Landsat-derived Normalized Difference Vegetation Index (NDVI; Arroyo-Mora *et al.* 2005, Hartter *et al.* 2008). In these studies, the value of the NDVI resides in its sensitivity to tree canopy cover (Feeley *et al.* 2005), and the fact that tree canopy cover —and the proportion of deciduous species— change within the first 20–30 yr (see Arroyo-Mora *et al.* 2005, Hartter *et al.* 2008). After that, however, the overall horizontal structure of the forest (including canopy cover) tends to stabilize (Lugo 2005), limiting the use of NDVI to further track succession. As a result, assessing succession in tropical dry forests of >30 yr old has been difficult (Sánchez-Azofeifa *et al.* 2003, 2009). As the vertical structure of tropical dry forests can further change after the horizontal structure stabilizes (Lugo 2005), LiDAR data may be helpful for tracking successional changes in more mature stands. This includes, for example, the identification of mature secondary forests and primary forests, which are of key value for biodiversity and conservation (Chazdon *et al.* 2009).

Scientists are using LiDAR to characterize forest succession. Previous work in temperate and tropical moist forests showed that LiDAR data were sensitive to successional changes (see Drake *et al.* 2002 and Hill & Thomson 2005). Recently, Weber and Boss (2009) successfully separated young, intermediate, and mature stages in a broadleaf temperate forest. In a conifer forest, Falkowski *et al.* (2009) mapped six successional stages (from stand initiation to old growth) with an accuracy of >95 percent. In a tropical dry forest, Castillo-Nuñez *et al.* (2011) used LiDAR to delineate mechanisms of forest regeneration.

We investigated two major objectives in this study. First, we evaluated the use of airborne-based LiDAR data for classifying tropical dry forest types in an area exhibiting varied composition, including different native forest formations and a class dominated by an exotic species. Second, we explored the value of LiDAR data for identifying successional status in forests of >30 yr old. An overarching goal in both objectives was to compare the performance of LiDAR with similar classifications made from available Landsat imagery and non-LiDAR topographic data.

METHODS

STUDY AREA.—This study was conducted in the Guánica Biosphere Reserve in Puerto Rico (17°58′ N, 66°52′ W; Fig. S1). Guánica is considered to be one of the best examples of subtropical dry forests because it has been protected since the 1930s and is a local biodiversity hotspot (Gould *et al.* 2008). It is also a core site for the NEON program (Keller *et al.* 2008). The reserve comprises two main areas covering nearly 4000 ha from the shoreline of the Caribbean Sea to an elevation about 230 m, and our study area corresponds to the largest of these portions (approx. 3000 ha; Fig. S1). Annual rainfall is 860 mm with a major dry period from December to March and a minor one between June and August (Medina & Cuevas 1990). The substrate is derived from limestone with common presence of exposed rock outcrops.

VEGETATION AND LAND-USE HISTORY.—Dry forests in the Caribbean islands are typically shorter than in other parts of the world (Murphy & Lugo 1986). Three intergrading and edaphically determined forest types occupy most of Guánica, including: semi-deciduous forest (the most common type) in the internal hills and coastal areas, semi-evergreen forest in valleys and ravines with well-developed soils, and scrub forest in coastal areas and limestone outcrops. A narrow fringe of dwarf forest occurs along coastal rocky areas exposed to the ocean winds. Finally, a distinctive stand of the exotic *Prosopis pallida* (*i.e.,* mesquite) occurs along an alluvial fan in the southern part of the reserve (see Table 1 for a description of the forest types). Forested wetlands (*i.e.,* mangroves) were not considered in this study.

Guánica is a mosaic of mature forests dominated by secondary forests that have recovered after land-use abandonment occurring between the 1930s and the 1950s. The area was previously used for charcoal and fence-post production (involving logging and harvesting of stems and branches from trees), with smaller areas used for agriculture and forest plantations. Studies in the semi-deciduous forests revealed that the vegetation has recovered significantly (Murphy *et al.* 1995, Lugo 2005). After 45 yr of land-use abandonment, for example, Molina Colón and Lugo (2006) found that stands previously used for charcoal pro-

TABLE 1. *Forest types in Guánica based on Lugo et al. (1978), Lugo 2005, Murphy & Lugo (1986), Farnsworth (1993), and Gould et al. (2008). The number of field samples used by this study (N) is included.*

Class name	*N*	Description
Semi-deciduous forest	28	Covers about 60 percent of Guánica. Average tree height is 4.3 m with tallest trees between 7 and 12 m. Most trees are <10 cm in diameter, with up to 14,000 trees per hectare and basal area about 20 m^2/ha. Canopy cover fluctuates from 97 percent in the wetter month to 77 percent in the drier month, and leaf area index from 4.3 to 2.1.
Semi-evergreen forest	21	About 20 percent of the area; in moist ravines and valleys with thicker soils, abundant leaf litter, and springs or runoff catchments. Trees are taller with some species reaching 10–15 m, and high species diversity. Includes evergreen forests.
Scrub forest	19	Covers about 15 percent of Guánica, also known as shrubland/cactus. Open shrubland with cactus and widely spaced stunted trees found in areas with poor soil development and much exposed bedrock.
Dwarf forest	8	Along coastal rocky areas exposed to ocean winds and salt spray, and composed by gnarled and twisted trees with horizontal stem and canopy growing close to the ground. Believed to support the oldest trees in Puerto Rico.
Mesquite forest	7	Relatively homogenous stand of *Prosopis pallida* with a dense herbaceous understory.

duction or agriculture recovered in >75 percent of the original levels of tree height, basal area, stem density, and crown area index, with slightly higher recovery values observed in those used for charcoal production. The height of mature trees may be reached after 60–70 yr (Agosto Diaz 2008). In addition, past agricultural lands are today dominated by the exotic tree *Leucaena leucocephala*. Despite decades of recovery, past land use still explains most of the structural and compositional variations of the semi-deciduous forests in Guánica (Agosto Diaz 2008).

REMOTE SENSING AND VEGETATION DATA.—The data for this study consisted of airborne LiDAR data, location samples for the different forest types, historic land-use information, Landsat ETM+ satellite imagery, and non-LiDAR topographic data from the Shuttle Radar Topography Mission (SRTM).

For the first objective (*i.e.,* classifying forest types), we obtained location samples for the different forest classes based on previous studies plus additional field visits. Most samples for the semi-deciduous forest class were based on field plots established by Agosto Diaz (2008). These plots were designed using a stratified random sample technique with the objective of identifying the human and environmental factors explaining variations in forest structure, and therefore they represented an ideal training data set for our study. We visited the area during 2009 to geolocate additional vegetation plots. We used GPS surveys and visual interpretation of 1-m spatial resolution color aerial photos supported by expert knowledge, for a total of 83 sample locations. All samples represented an area of at least 30 m by 30 m of the same forest type (to coincide with the geospatial grain size used

TABLE 2. *Remote sensing-based explanatory variables.*

Variable name	Description
LiDAR variables of canopy structure	
CDENSITY1	Canopy density 1; percent of returns >0.3 m
CDENSITY2	Canopy density 2; percent of returns >1.0 m
CDENSITY3	Canopy density 3; percent of returns >2.0 m
STRAT1	Stratum 1; percent of vegetation returns between 0.3 and 3 m
STRAT2	Stratum 2; percent of vegetation returns between 3 and 8 m
STRAT3	Stratum 3; percent of vegetation returns >8 m
H10th	10th percentile of vegetation heights
H25th	25th percentile of vegetation heights
HMEDIAN	Median height of vegetation returns
H75th	75th percentile of vegetation heights
H90th	90th percentile of vegetation heights
HMEAN	Mean height of vegetation returns
HMAX	Maximum height of vegetation returns
HMAD	Median absolute deviation of vegetation heights
HSD	Standard deviation of vegetation heights
HSKEW	Skewness of vegetation heights
HKURT	Kurtosis of vegetation heights
HIQR	Interquartile range of vegetation heights
Landsat ETM+ spectral variables	
B1	Band 1
B2	Band 2
B3	Band 3
B4	Band 4
B5	Band 5
B7	Band 7
NDVI	Normalized difference vegetation index
TCAP-B	Tasseled cap brightness
TCAP-G	Tasseled cap greenness
TCAP-W	Tasseled cap wetness
(Note: The suffix 'wet' or 'dry' before the variable's name is added to identify the image season when needed [*e.g.,* $NDVI_{dry}$]. Similar, the symbol 'Δ' before the variable's name is added to denote multi-temporal change [*e.g.,* ΔNDVI]).	
Topographic variables	
ELEV	Elevation
SLP	Slope
ASP	Aspect
CURV	Curvature
SRAD	Area Solar Radiation
IMI	Integrated Moisture Index (Iverson *et al.* 1997)
CTI	Compound Topographic Index (Gessler *et al.* 1995)
(Note: Derived from both 30-m LiDAR and SRTM DEMs)	
Other	
DIST	Distance to the coast

by this study), and were separated by >60 m (consistent with Agosto Diaz 2008). Finally, Agosto Diaz (2008) and E. Medina (pers. comm.) facilitated sample locations for the scrub forest and dwarf forest.

The second objective (*i.e.,* classification of successional stages) was conducted in the semi-deciduous forest. We utilized historic land-use information for 25 plots derived from aerial photos from the 1930s, 1950s, and 1970s (Agosto Diaz 2008). We identified four different successional classes based on the year of land-use abandonment and the type of past land use. These successional classes included: (1) mid-secondary forests with a logging past (*i.e.,* ~40 yr old stands previously logged and harvested for charcoal and fence-post production, $N = 5$); (2) late-secondary forests with a logging past (*i.e.,* ~60 yr old stands previously logged and harvested for charcoal and fence posts, $N = 6$); (3) late-secondary forests with an agricultural past (*i.e.,* ~60 yr old stands previously cleared for agriculture, $N = 3$); and (4) primary forests (*i.e.,* undisturbed, ≥ 90 yr old stands, $N = 11$). Although small in sample size, the class with a history of agriculture allowed us to explore the potential separability of different historic land uses (*i.e.,* agriculture or charcoal production) within the same successional stage (*i.e.,* late-secondary forest).

The airborne LiDAR data were collected during January and February 2004 by 3001 Inc. and the US government, covering Puerto Rico and the U.S. Virgin Islands. The sensor recorded up to three return height values per laser pulse (*i.e.*, first, last, and intermediate returns), and with varied pulse density. The Western half of Guánica was acquired at a density of 0.20 pulses/m^2 and the Eastern half at 0.05 pulses/m^2. These are very low data densities relative to more recent acquisitions (*e.g.,* >1 pulse/m^2). The reported mean vertical error was 9.27 cm.

The satellite imagery consisted of 30-m pixel Landsat ETM+ scenes from October 2002 (*i.e.,* wet season) to January 2003 (*i.e.,* dry season), with precision and terrain correction (*i.e.,* Level 1T). The reported horizontal error was 2.3 m for the 2002 scene and 2.6 m for the 2003 scene.

Finally, auxiliary topographic information came from the SRTM. We used the 30-m gridded digital elevation model (DEM). The reported mean horizontal and vertical errors are <12 and 10 m, respectively, although they may vary locally (Rodríguez *et al.* 2006).

DATA PREPROCESSING.—We first thinned the Western portion of the data (0.20 pulses/m^2) to the same point density of the

TABLE 3. *Forest type classification models (N = 11), including the source of predictor variables included in each model (marked with 'X'; top section), classification accuracy (i.e., error rates for each forest type and for the entire classification, and the kappa value; in the center) and variables included in the final models (bottom). Models 1–5 were developed from single sources of predictor variables; models 6–9 from multiple sources, and models 10–11 after adding elevation (ELEV) and curvature (CURV).*

Model	1*	2†	3‡	4§	5¶	6**	7††	8‡‡	9§§	10¶¶	11***
LiDAR canopy	X					X			X	X	
ETM+ wet season		X					X	X	X		X
ETM+ dry season			X				X	X	X		X
LiDAR DEM				X		X			X	X	
SRTM DEM					X			X			X
ELEV and DIST										X	X
Scrub forest	0.16	0.21	0.37	0.68	0.58	0.16	0.21	0.21	0.11	0.05	0.11
Semi-deciduous forest	0.21	0.46	0.43	0.25	0.46	0.14	0.46	0.21	0.14	0.07	0.25
Dwarf forest	0.13	0.38	0.38	0.50	0.75	0.13	0.38	0.38	0.13	0.13	0.25
Semi-evergreen forest	0.29	0.86	0.67	0.05	0.57	0.14	0.76	0.67	0.14	0.10	0.57
Mesquite forest	0.43	0.57	0.43	0.14	0.29	0.14	0.29	0.43	0.14	0.00	0.00
Overall error rate	0.23	0.51	0.47	0.31	0.53	0.14	0.46	0.36	0.13	0.07	0.28
Kappa	0.69	0.32	0.37	0.58	0.30	0.81	0.39	0.51	0.82	0.90	0.63

*HMAD, H90th, CDENSITY2, HMAX, H75th, CDENSITY3, STRAT2.

†NDVI, TCAP-W, TCAP-G.

‡NDVI, TCAP-W, TCAP-G, TCAP-B.

§CURV, IMI, CTI, SRAD, SLP.

¶SRAD, CURV, SLP, ASP.

**CURV, CDENSITY2, HMAD, H90th, CTI, CDENSITY3, SLP, HMAX, H75th, STRAT2, HMEDIAN, CDENSITY1, STRAT1.

††NDVI(wet), TCAP-W(dry), TCAP-G(wet), TCAP-W(wet), ΔTCAP-B, NDVI(dry), TCAP-G(dry), ΔB2, ΔB5.

‡‡NDVI(wet), TCAP-G(wet), TCAP-W(dry), NDVI(dry), TCAP-W(wet), ΔB2, ΔTCAP-B, TCAP-G(dry), CURV, ΔB5, TCAP-B(wet), SLP, ASP, ΔB1, CTI.

§§CURV, HMAD, H90th, CDENSITY2, CTI, HMAX, H75th, CDENSITY3, B2(wet), STRAT2, TCAP-G(wet), SLP, HMEDIAN, TCAP-W(wet).

¶¶CURV, ELEV, DIST, HMAD, CDENSITY2, H90th, CTI, CDENSITY3.

***ELEV, DIST, NDVI(wet), TCAP-W(dry), TCAP-G(wet), TCAP-W(wet), NDVI(dry), ΔTCAP-B, ΔB2, CURV, TCAP-G(dry), SLP, ΔB5, TCAP-B(wet), CTI, ASP.

Eastern portion (0.05 pulses/m^2). We then used an algorithm (Evans & Hudak 2007) to classify the LiDAR data into ground versus canopy returns, and calculated a suite of canopy metrics at a 30-m grid size (see Table 2). We considered any return >30 cm above the ground to be vegetation, avoiding confusion with limestone outcrops. As most vegetation returns (*i.e.,* 95%) were first or single returns, the metrics of canopy density by this study (calculated as # of vegetation returns above a specific height × 100/total number of returns, within each 30 × 30 m grid cell) can be used also as a physical measure of canopy cover (*i.e.,* horizontal structure).

We calibrated the Landsat data to reflectance values and then applied a radiometric normalization method Canty and Nielsen (2008) using ENVI 4.5 (ITT Visual Information Solutions®, Boulder, Colorado, U.S.A.). We calculated the NDVI and the Tasseled Cap transformation for the two scenes. The Tasseled Cap (Kauth & Thomas 1976) reduces the image data to three ecologically meaningful bands or indices of brightness, greenness, and wetness, which have been shown useful for separating successional stages and forest types (*e.g.,* Cohen *et al.* 1995, Helmer *et al.* 2000, Song *et al.* 2007). Finally, we calculated differences in the band spectral values and indices between the two image dates (Table 2).

We horizontally co-registered the 30 m SRTM DEM to the 30 m LiDAR DEM and calculated a suite of topographic variables from both DEMs using ArcGIS 9.2 (ESRI®, Redlands, California, U.S.A.) Spatial Analyst (Table 2). Finally, we created a GIS layer quantifying the distance from the coast.

DATA ANALYSIS.—We used classification-tree techniques, which have been successfully applied in tropical deciduous ecosystems (Krishnaswamy *et al.* 2004). For the first objective, we used the Random Forest (RF) algorithm (Breiman 2001), implemented in R (Liaw & Wiener 2002, R Development Core Team 2005), which is a bootstrap-based extension of classification-tree methods that has shown excellent results in ecological and remote sensing studies (*e.g.,* Lawrence *et al.* 2006, Cutler *et al.* 2007, Martinuzzi *et al.* 2009). Classification rules are developed by combining hundreds to thousands of classification trees, constructed from random subsets of the training data and explanatory variables. The algorithm provides an internal measure of misclassification error (using observations that are randomly withheld in each tree development), eliminating the need for a secondary data set for accuracy assessment (Breiman 2001, Lawrence *et al.* 2006, Falkowski *et al.* 2009). The algorithm provides also measures of variable importance (derived from the permutation of the independent variables), which can be used to compare with ecological expectations based on literature (Cutler *et al.* 2007). We identified the most parsimonious model using a RF-based method by Murphy *et al.* (2010), which iteratively reduces the number of variables using the variable's importance measure.

We classified forest types in two ways, first using single sources of remotely sensed explanatory variables (*e.g.,* LiDAR canopy alone) and then by combining multiple data sources (*e.g.,* LiDAR canopy plus LiDAR DEM). The variables Elevation (ELEV) and Distance to the coast (DIST) were added at the end, in a separate new model. This is because the importance of these variables appears to be too specific to Guánica (*i.e.,* they explain much of the distribution of the mesquite and dwarf forest). Therefore, creating classification models with and without

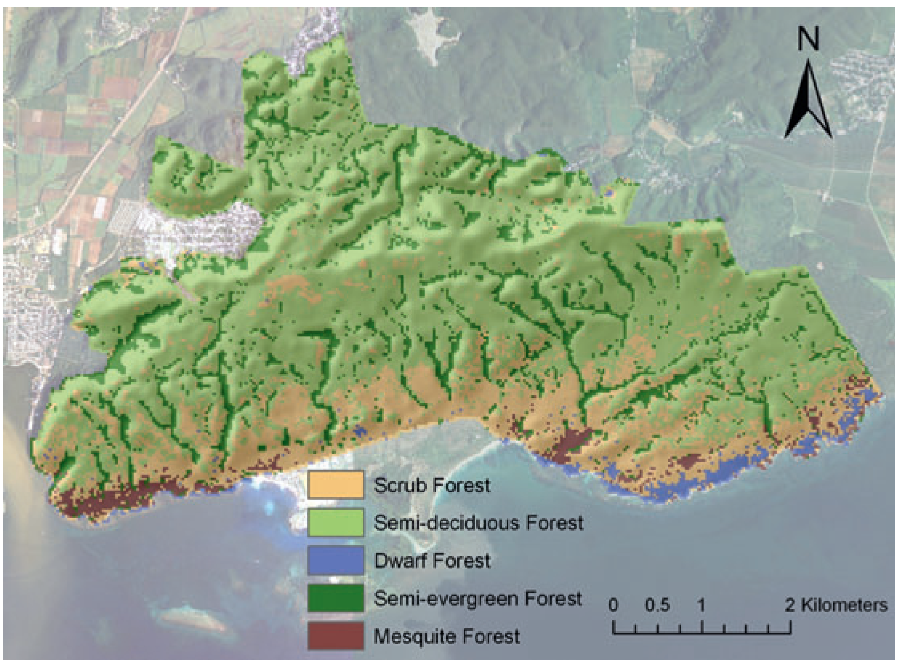

FIGURE 1. Map of five forest types for the Guánica Biosphere Reserve (Puerto Rico) derived from LiDAR data (spatial resolution = 30 m).

ELEV and DIST allowed us to better transfer our findings to other areas.

Classification trees were applied differently in classifying forest succession. As the sample size was smaller ($N = 25$ and restricted to semi-deciduous forests), we were able to partition the data manually. We developed decision trees using the smallest number of binary partitions possible to explain the data (three splits; *i.e.* # of land-use history classes − 1). We compared the results of using LiDAR canopy metrics versus Landsat multi-season imagery. Topography was not included because it is not a major variable explaining variations in forest structure within semi-deciduous forests (Agosto Diaz 2008). For all the classifications made, we reported global and class-level errors rates (ranging from 0 to 1) and the kappa statistic (Landis & Koch 1977), which measures overall classification accuracy compensating for agreement due to chance (where a value of 1.0 denotes perfect agreement and 0.0 no agreement other than that which would be expected by chance alone). Kappa values ranging between 0.41–0.60, 0.61–0.80, and 0.81–0.99 describe moderate, substantial, and almost perfect accuracies, respectively (Landis & Koch 1977).

RESULTS

We first classified forest types using one source of remotely sensed explanatory variables. The classification using LiDAR canopy metrics alone yielded the highest accuracy (kappa = 0.69), followed by the LiDAR DEM metrics (kappa = 0.58; Table 3). The classifications using Landsat or STRM DEM data, on the other hand, had kappa values ranging between 0.30 and 0.37. The classification from the LiDAR DEM had a higher accuracy than the classification from SRTM DEM (kappa values of 0.58 and 0.30, respectively). In these two models, the semi-evergreen forest showed the largest error difference, with a misclassification rate of 0.05 from the LiDAR DEM versus 0.57 from the SRTM DEM. Finally, classification accuracies from the two Landsat scenes were very similar (kappa values of 0.37 and 0.32).

The most important predictors in the LiDAR canopy model included the median absolute deviation of vegetation heights (HMAD), the 90th percentile of vegetation heights (H90th), and the percent of returns >1.0 m (CDENSITY2; Table 3). The NDVI and the wetness and greenness indices were important in the Landsat-based models. Finally, the variable curvature (CURV) appeared among the most important variables in the classifications using topographic data.

The combination of the two different sources of LiDAR explanatory variables (*i.e.,* canopy and topographic metrics) reduced the error from 0.23 (observed using LiDAR canopy metrics alone) to 0.14, resulting in a kappa statistic of 0.81 (Table 3). The class-level errors ranged between 0.13 and 0.16. On the other hand, combining the two Landsat seasons did not substantially improve the classification accuracy over the dry season

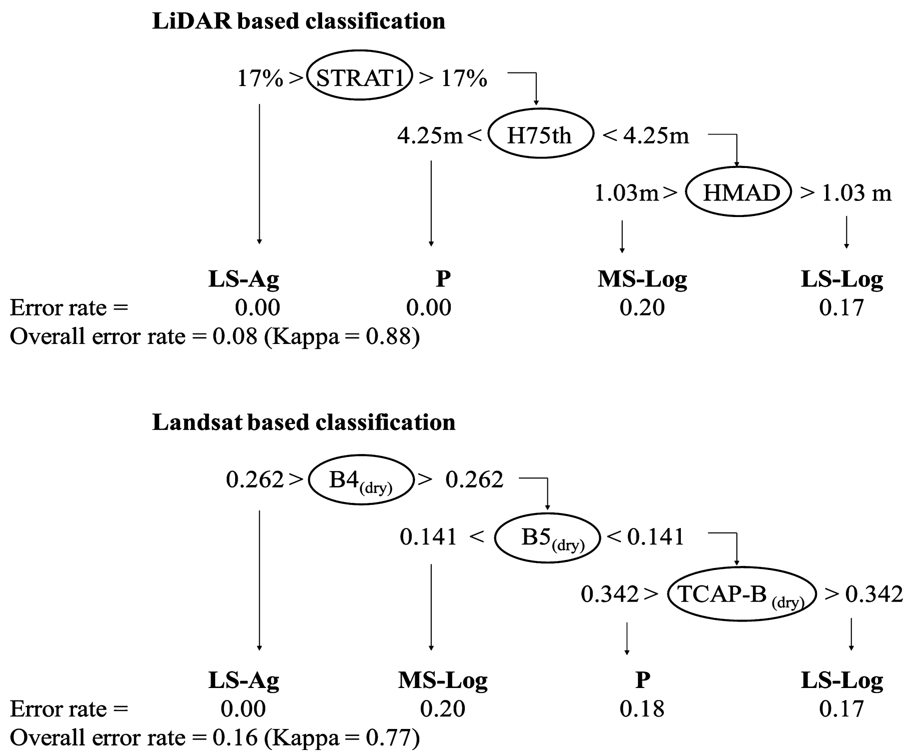

FIGURE 2. Classification-tree decisions and resultant accuracy statistics for forest successional classification using LiDAR (top) or Landsat ETM+ (bottom) data. Mid-secondary forest with logging past (MS-Log); late-secondary forest with logging past (LS-Log); late-secondary forest with agricultural past (LS-Ag); primary forest (P).

imagery alone (kappa values of 0.39 and 0.37, respectively). The class-level errors for the Landsat multi-season classification ranged between 0.21 and 0.76, with two of the three most extensive forest types in Guánica (*i.e.,* semi-deciduous and semi-evergreen) >0.40.

The addition of SRTM topographic variables to the multi-date Landsat model increased the classification accuracy from a kappa of 0.39 observed in the Landsat-only model to 0.51 (Table 3). The class-level error ranged between 0.21 and 0.67, with the largest error found in the semi-evergreen forest. Finally, the addition of Landsat variables did not improve the accuracy observed using LiDAR explanatory variables (canopy plus DEM; *i.e.,* kappa 0.82 vs. 0.81). The variables included in the models developed from multiple sources of remotely sensed based explanatory variables were typically a combination of the most important variables observed in the models using one source at a time.

Adding the variables elevation (ELEV) and distance to the coast (DIST) improved the classification accuracy. The kappa value increased from 0.81 to 0.90 in the LiDAR-based model, and from 0.51 to 0.63 in the Landsat-SRTM one (Table 3). The final models included ELEV and DIST in addition to other variables that were important in the previous classifications. The resultant LiDAR-based map of forest types for Guánica is shown in Figure 1.

In addressing our second objective, we classified past land use within the semi-deciduous forest using LiDAR (canopy) versus Landsat variables (Fig. 2). The model constructed from LiDAR had the highest accuracy (kappa values of 0.88 and 0.77, respectively), and both models separated the mid- and late-secondary forest classes equally. The LiDAR-based model, however, separated the primary forests perfectly (*i.e.,* error rate = 0.00) while the Landsat- based models produced some confusion (error rate = 0.18). The three explanatory variables included in the LiDAR-based model included the percentage of vegetation returns between 0.3 and 3 m (STRAT1), the 75th percentile of vegetation heights (H75th), and the median absolute deviation of

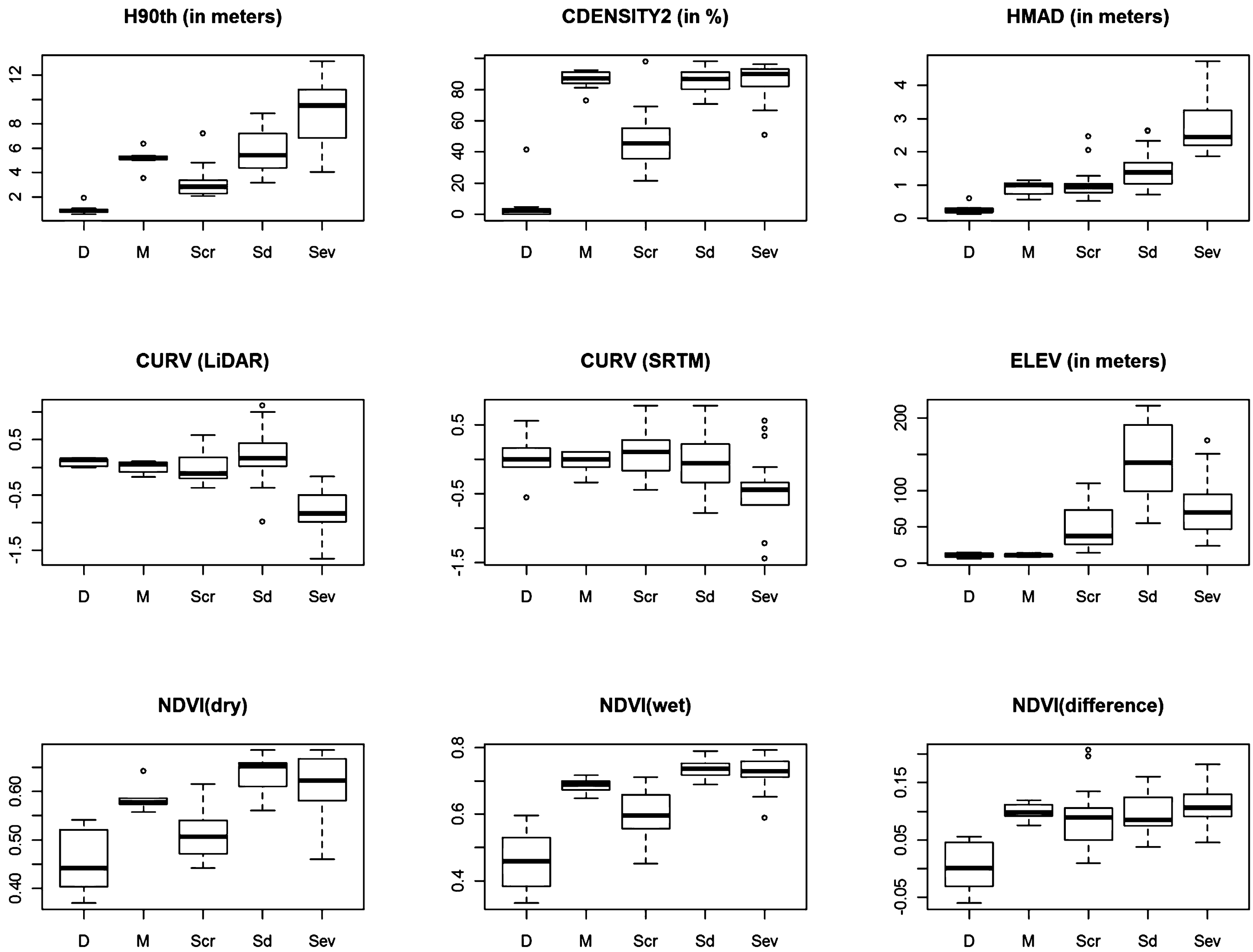

FIGURE 3. Remotely sensed predictor variables in different forest types, including: semi-deciduous forest (Sd), semi-evergreen (Sev), scrub forest (Scr); mesquite (M), and coastal dwarf forest (D).

vegetation heights (HMAD; Fig. 2). On the other hand, the Landsat-based model included Band 4, Band 5, and the Brightness index, all from the dry season.

DISCUSSION

Our study explored the use of LiDAR data to classify tropical dry forest types and succession. We found that LiDAR data were powerful predictors of tropical dry forest types, achieving higher accuracies than classifications made from previously available remote sensing data (*i.e.,* Landsat and SRTM). The best results were obtained when combining LiDAR-derived information of canopy structure and topography. As a result, forest types that have been difficult to separate in previous efforts using Landsat imagery (*e.g.,* Helmer *et al.* 2002, 2008, Gould *et al.* 2008, Martinuzzi *et al.* 2008) were possible to separate using LiDAR.

In addition, we detected no enhanced value for classifying forest types in Guánica after integrating Landsat with LiDAR data. In fact, a misclassification rate of 0.14 when using LiDAR data alone (and 0.07 when adding the variables elevation and distance to the coast; Table 3) yields little room for improvement. Expanding to other land cover types is important to better understand the role of LiDAR in tropical dry forest regions.

Scientists have long shown that Guánica forests vary in terms of canopy height, canopy cover and vertical complexity, and that their geographic distribution is profoundly affected by soil conditions (see Lugo 2005). The most important LiDAR-derived predictors seem to reflect those variations, providing a novel picture of the vegetation (Fig. 3). The metric H90th, for example, tends to correspond well with the mean tree height of a stand (Hopkinson *et al.* 2006, Li 2009). We likewise observed an increase in canopy height from dwarf forest to the scrub forest, semi-deciduous and mesquite, and finally to the semi-evergreen forest, with median values of about 1, 3, 5, and 10 m that match the general descriptions found in the literature (see Lugo 2005, Agosto Diaz 2008). The metric CDENSITY2, a surrogate of canopy cover in this study, showed that well-developed forests such as the semi-deciduous, semi-evergreen, and mesquite have high canopy cover (*e.g.,* >70% for the semi-deciduous and consistent with Murphy and Lugo [1986]), whereas the naturally open scrub forest reported much lower values, as expected (Fig. 3). The fact that the dwarf forest appeared with little or no canopy cover is an artifact of the threshold established at >1 m, above which little or no vegetation exists for this forest type. Finally, the metric HMAD (median absolute deviation of vegetation heights) seems to reflect known patterns of vertical heterogeneity. In this sense, the semi-evergreen is the most structurally diverse forest type in Guánica because it supports the largest variations in tree height and diameter, followed by the semi-deciduous forest (Lugo 2005). In our study, the semi-evergreen and semi-deciduous forest types showed the first and second largest HMAD values, respectively (see Fig. 3).

Distinctive characteristics of the invasive mesquite forest also related to the HMAD LiDAR metric. Our study showed that the mesquite forest is similar to the semi-deciduous forest in terms of horizontal structure and height (*i.e.,* Wilcoxon Test [W] = 87.5, *P*-value = 0.68 for CDENSITY2; W = 107.5, *P*-value = 0.71 for H90th). This exotic-dominated forest, however, appeared less vertically diverse (in HMAD values) than the semi-deciduous forest (W = 167, *P*-value = 0.005; see Fig. 3). This might be a result of the different number of tree strata naturally present in these two forest types, *i.e.,* one for the mesquite (Stromberg 1993) versus one to three for the semi-deciduous (Lugo 2005). This difference in the number of strata might cause the laser returns to be more scattered along the vertical dimension, resulting in different HMAD values. Our findings agree with Asner *et al.* (2008a, b) who found that exotics can transform the 3D structure of the forest, and that LiDAR can be sensitive to those transformations. Furthermore, we observed little variation in H90th values within the mesquite stand (Fig. 3), suggesting a tree cohort established likely after a single disturbance event (*e.g.,* agricultural abandonment) rather than

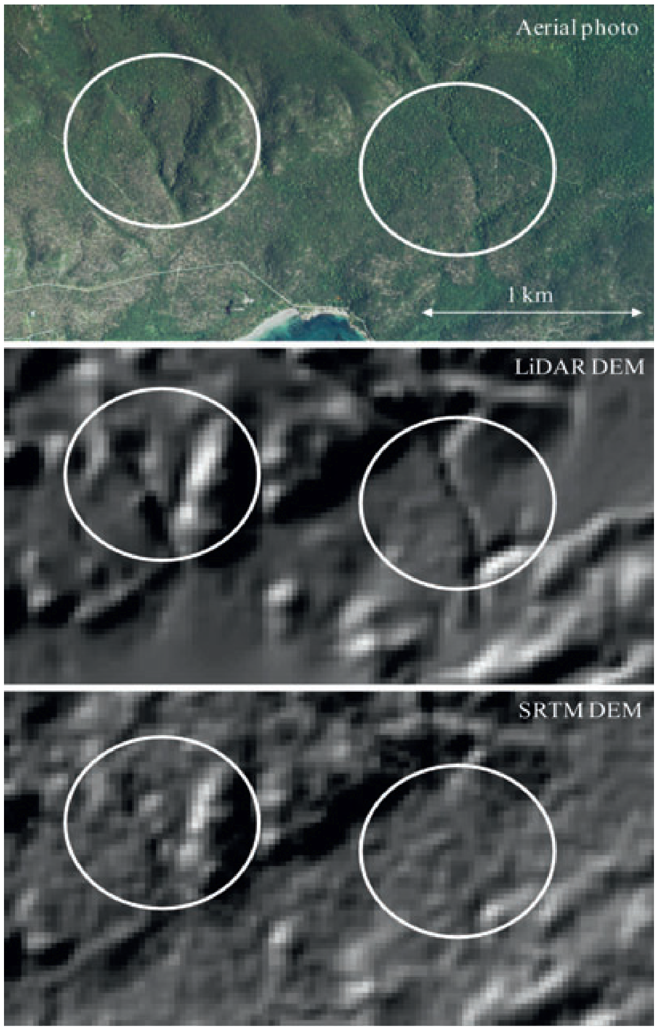

FIGURE 4. Topographic detail captured by the 30-m pixel digital elevation models from LiDAR versus SRTM. Examples of small valleys and ravines as highlighted with circles.

gradual recruitment over time (therefore providing insights about the processes of invasion). Finally, a recent field visit to other areas mapped as mesquite forests revealed the presence of mixed mesquite/semi-deciduous forest patches in the eastern part, and some level of overestimation in the west.

Topographic (*i.e.,* DEM-based) variables were important for refining the classification of tropical dry forest types, agreeing with Helmer *et al.* 2008, Martinuzzi *et al.* 2008, and Sesnie *et al.* 2008. Although both LiDAR and SRTM DEMs added predictive power to the classifications, the LiDAR DEM did a better job in discriminating forest types. This difference was largely attributed to the semi-evergreen forest, which was better separated using the LiDAR DEM. We believe that this is a result of a lower ability of SRTM data to depict topographic changes under forest canopies. Although LiDAR returns can reach the true ground even under very dense forest canopies (Hofton *et al.* 2002), elevations retrieved from SRTM are located somewhere between the canopy top surface and the ground (Hofton *et al.* 2006). As a result, valleys and ravines, which are the distinctive locations of semi-evergreen forests, were better defined in the LiDAR DEM than in the SRTM DEM (see Fig. 4). In these areas, the lower surface elevations might be canceled by the simultaneous presence of taller forests, resulting in a final SRTM elevation that is not very different from the nearest cells. The better separation of semi-evergreen forests with the LiDAR-derived curvature (*i.e.,* CURV, which describe convexity and concavity of slope profiles with positive and negative values, respectively) reinforces the previous point (Fig. 3).

LiDAR metrics of canopy structure were useful for separating mid- and late-secondary forests, as well as primary forests. Identifying these habitats is critical for conservation and management, yet has been difficult in previous studies. We observed that the LiDAR variables that best classified succession were those describing vertical canopy structure (rather than horizontal, *i.e.,* STRAT1, H75th, and HMAD). This supports the idea that horizontal structure might have stabilized in these mature forests,

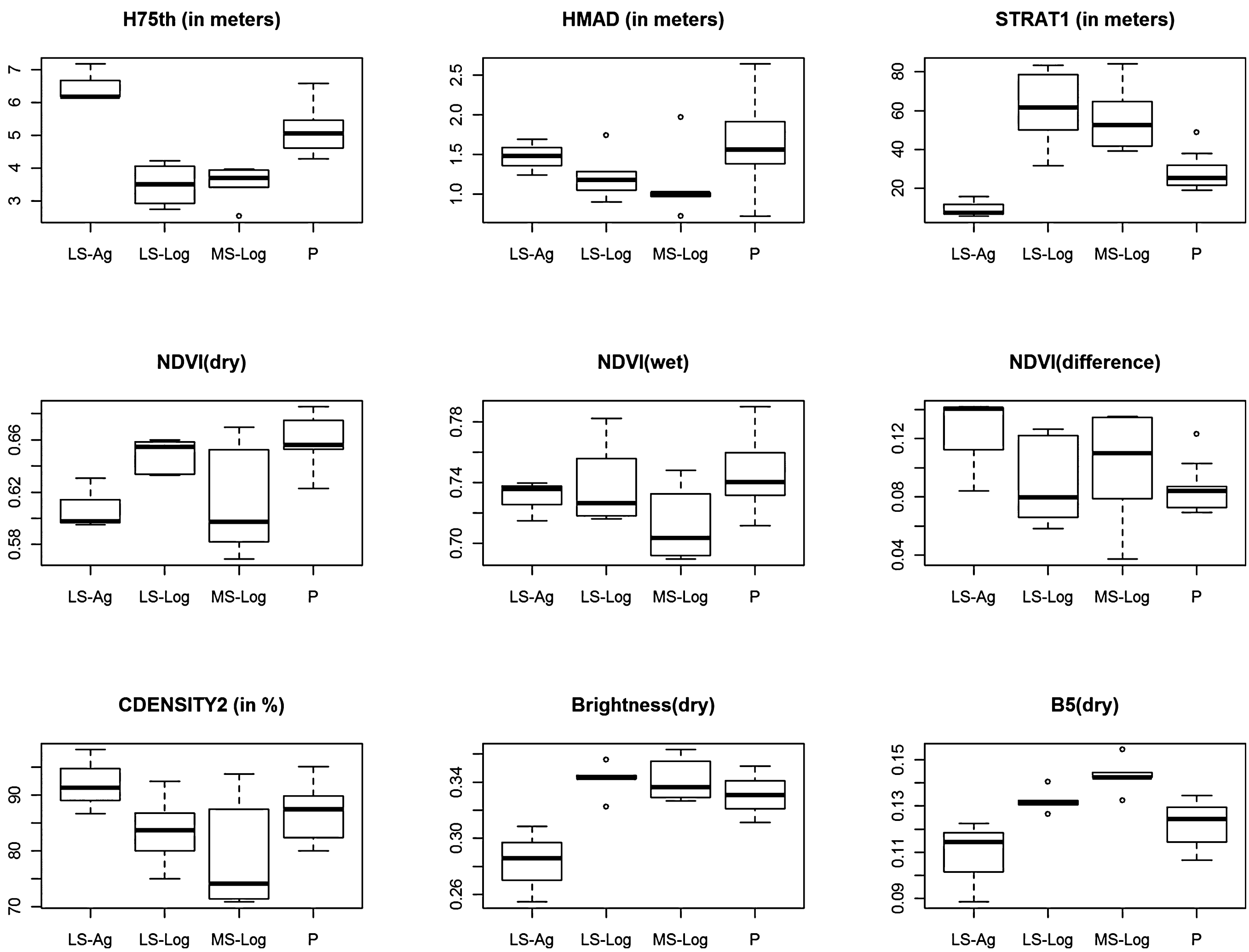

FIGURE 5. Remotely sensed predictor variables in different succesional classes, including: mid-secondary forest with logging past (MS-Log); late-secondary forest with logging past (LS-Log); late-secondary forest with agricultural past (LS-Ag); and primary forest (P).

whereas changes in the vertical dimension might still be occurring as forest ages (Lugo 2005). Although more research is needed to better understand the biophysical meaning of these metrics, our findings reinforced the value of LiDAR to assess succession and land-use legacy (Falkowski *et al.* 2009). Finally, the fact that an exotic species (*Leucaena leucocephala*) dominates forest recovery in one of the past land uses perfectly classified (*i.e.,* the one with agricultural history), adds further value to use of LiDAR for assessing novel forests. Expanding and testing succession assessments in other tropical dry forest types and land-use histories are warranted.

Our findings provide also valuable information for further applications using optical imagery (*e.g.,* Landsat). For instance, our study supported the use of dry season imagery to assess succession in tropical dry forests, similar to Arroyo-Mora *et al.* (2005) and Kalacska *et al.* (2007). We found that the variables that appeared useful for classifying succession in our mature forests (*i.e.,* Landsat bands 4, 5, and brightness, achieving a kappa of 0.77), however, were different to those identified previously in younger forests, *i.e.,* NDVI (see Arroyo-Mora *et al.* 2005 and Hartter *et al.* 2008). This might be related to the fact that NDVI captures differences in horizontal structure between successional stages, but these are more evident in younger forests than in mature ones (Kalacska *et al.* 2005, Lugo 2005). As a result, the successional classes investigated in this study showed very similar NDVI and canopy cover values (CDENSITY2; Fig. 5). Finally, the variables identified by this study were consistent with Helmer *et al.* (2002), assessing succession in other tropical forests. Recently, advances have been made with the use of high-spatial resolution imagery and multi-scale approaches (see Gallardo-Cruz *et al.* 2012).

Our study highlights the value of LiDAR data —even low density LiDAR— for assessing tropical dry forests, and complements recent findings by Kennaway *et al.* (2008), Castillo-Nuñez *et al.* (2011), and Castillo *et al.* (2012). Our results are in agreement with work from a wide variety of forested ecosystems indicating that LiDAR data provide predictor variables that afford unique explanatory power to describe landscape patterns and processes (*e.g.,* Kellner *et al.* 2011). For example, in a growing number of studies, LiDAR canopy and topography metrics have been shown to afford predictive power that is either on par with, or exceeds, that of conventional passive multi-spectral remote sensing data (*e.g.,* Hyde *et al.* 2005, Goetz *et al.* 2007, Vogeler *et al.* in review, this study) and field-collected data (*e.g.,* Vierling *et al.* 2011a) in explaining ecological attributes of forest biodiversity, animal species' habitats (Vierling *et al.* 2008), and vegetation structure. However, passive data remain indispensable for ecological study: continued advances in spectral, spatial, and temporal resolution of passive remote sensing data, in addition to time series analysis of existing archival data (*e.g.,* Kennedy *et al.* 2007, Krishnaswamy *et al.* 2009), will continue to provide a rich set of products that can be merged with LiDAR-based analyses. As LiDAR data sets become more prevalent and widely employed in a variety of scientific, management, and other contexts (Stoker *et al.* 2008, Vierling *et al.* 2011b), such fusion between LiDAR and passive remote sensing data is becoming more feasible to not only analyze the status of ecosystems for a single date, but to quantify dynamic change through time (Dubayah *et al.* 2010, Hudak *et al.* 2012).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Location of the study area in Southwestern Puerto Rico.

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