NERC Open Research Archive
*sharing our research*

Centre for Ecology & Hydrology
NATURAL ENVIRONMENT RESEARCH COUNCIL

# Article (refereed) - postprint

Contact CEH NORA team at
noraceh@ceh.ac.uk

**Land-use history augments environment–plant community relationship strength in a Puerto Rican wet forest**

Running headline (45 characters): Land-use legacies and the abiotic environment

Authors: J. Aaron Hogan[*1], Jess K. Zimmerman[1], Maria Uriarte[2], Benjamin L. Turner[3], Jill Thompson[1,4]

Institutions:

[1] Department of Environmental Sciences, University of Puerto Rico Río Piedras, San Juan, Puerto Rico 00925, USA

[2] Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027, USA

[3] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama

[4] Centre for Ecology & Hydrology (Edinburgh), Midlothian, EH26 0QB, UK

*Correspondence author. E-mail: jamesaaronhogan@gmail.com

**Summary (350/350 words)**

1. Environmental heterogeneity influences the species composition of tropical forests, with implications for patterns of diversity and species co-existence in these hyper-diverse communities. Many studies have examined how variability in soil nutrients and topography influence plant community composition, with differing results. None have quantified the relative contribution of environmental heterogeneity vs. endogenous

processes to variability in forest community composition over time and with respect to successional recovery.

2. Using five consecutive trees censuses of a forest plot in Puerto Rico, conducted between 1990 and 2011, we evaluated the influence of edaphic and topographic variability on community composition. The plot has a well-documented land-use history and is subject to periodic hurricane disturbance. Using multiple canonical distance-based Redundancy Analyses, we studied how spatial heterogeneity in soil nutrients and topography structure community composition over time, as the forest recovers from long-term land-use effects and two major hurricanes in 1989 and 1998.

3. For the entire plot, spatial variables (principle coordinates of neighborhood matrices), representing the autocorrelation of tree species in the community, explained the majority (49-57 percent) of the variability in tree community composition. The explanatory power of spatial variables decreased over time, as forest structure recovered from hurricane damage and the stems in the understory died. Soil nutrients and topography, collectively, explained a moderate portion (33-37 percent) of the species compositional variation, and were slightly more robust in explaining compositional differences in areas of more-intense past land use.

4. Areas of less-intense past land-use showed weaker community–environmental trends overall, illustrating a tendency for stronger resource competition (i.e., light, water, and soil nutrients) between species in these areas. This illustrates how environmental-plant community interactions are strengthened by the lasting effects of human land-use legacies, which persist for decades to centuries.

5. *Synthesis.* Our findings confirm past land-use to be a fundamental driver of the structure and composition of secondary forests through its impacts on the tree community, the abiotic terrestrial environment, and their interaction. Since the extent of second-growth tropical forests continues to increase, our findings highlight the importance of understanding the processes that determine the rate and nature of their succession.

**Key-words:** beta-diversity maps, land-use legacies, Luquillo, plant–soil (below-ground) interactions, soil resources, spatial autocorrelation, terrain ruggedness, topography, tropical forest, variance partitioning.

## Introduction

A number of theories exist regarding how such high levels of tree species diversity are maintained in tropical forests, from negative density dependent mechanisms (e.g., Janzen-Connell processes; Janzen 1970; Harms *et al.* 2000; Jansen *et al.* 2014) to dispersal-limited stochasticity (Hubbell 2001; see Wright 2002 for a complete review of theories). Studies also support local resource variation (i.e., soil nutrients, light and water), and other niche-related processes as key in maintaining diversity, especially in highly-diverse tropical ecosystems (Hutchinson 1957; Hutchinson 1978; Ricklefs 1977; Booth *et al.* 1988; Paoli *et al.* 2006).

These processes shape observed forest communities by operating at multiple scales, over varying time periods, and in conjunction with natural or anthropogenic disturbance regimes.

Natural disturbances (e.g., hurricanes, floods and fire) and human land use (e.g., logging) induce changes in species composition and abiotic resource availability, accelerating ecosystem transformation (Sousa 1984; White 1979; Legendre and Fortin 1989). A number of studies have demonstrated that forest responses to human and natural disturbance depend on species-specific life-history trade-offs. Differences in survival and reproductive strategies among tropical tree species, specifically the initial competitive advantage and subsequent high mortality of early-successional pioneer species as the forest canopy recovers, determines the trajectory and rates of forest succession (Pacala and Rees 1998; Uriarte *et al.* 2012; Wright *et al.* 2010; Comita *et al.* 2010). As human activities continue to simplify and modify ecosystems (Chapin *et al.* 1997; Hautier *et al.* 2015), it is crucial to understand how land-use legacies influence the abiotic environment of tropical forests and how the impacts of these legacies play out over time.

Time since land-use abandonment, the land-use intensity, and its duration are the main factors affecting soils and subsequent vegetation recovery rate and quality (e.g., forest structure, canopy height, and biomass). For example, disturbance intensity was found to be more important than environmental variation in soil resources in determining structure and composition of regenerating forests in Hainan Island, China (Ding *et al.* 2012). Human land use reduced total organic carbon and nitrogen concentrations of soils in Mexican forests, with increases after land-use abandonment, but at different rates (Cram *et al.* 2015). Nitrogen and phosphorus have long been thought to trade-off as limiting nutrients in terrestrial systems, and together may be used as indicators of soil fertility in the tropics (Tateno and Chapin III 1997). The recovery of soil fertility and the organic humus layer in tropical forest, clay-derived soils (e.g., Oxisols vs. Ultisols) that have been strongly affected by past land use are likely to take decades to recover, illustrating the long-term effects of soil-based alteration via land-use on vegetation composition and structure (Zimmermann *et al.* 2010).

Environmental heterogeneity in resources reflects the complex interaction of many biotic (e.g., herbivory and vegetation turnover) and abiotic processes (e.g., decomposition, lithology, and climate) that operate at a variety of spatial and temporal scales (Canham *et al.* 1994; Zimmerman *et al.* 1996; Wilson 2000; Tylianakis *et al.* 2008). Specifically, highly-diverse tropical forests are known for their large spatial variability in soil chemical and texture, soil moisture, elevation, topography and temporal dynamism in soil moisture (related to rainfall and soil characteristics) and light conditions (e.g., light dynamics associated with canopy structure and gap creation or hurricane disturbance and recovery; Terborgh 1992; Holdridge *et al.* 1971; Brokaw and Busing 2000; Davies *et al.* 1998; Cleveland *et al.* 2011).

Soil properties can influence tree canopy height, productivity, and the rate of recovery of tropical forests following disturbance, especially in terms of species community richness (Ellis and Pennington 1992). High soil C: N, sand: clay, Al and P concentrations were associated with a more complex forest structure and increased diversity associated across a successional gradient in Brazil (Martins *et al.* 2015). Similarly, higher soil organic matter,

higher nitrogen availability, and lower bulk density of soils were the main factors facilitating forest regrowth and succession in highly-degraded areas of China (Duan *et al.* 2008). Despite a number of studies on this topic, results vary greatly across the tropics, and it remains unclear how soil resources influence plant community composition in forests recovering from land use or other disturbance.

Although plant community diversity is generally greater at high precipitation and lower elevation, at any particular time, differences in physical environment can only weakly explain patterns of alpha-diversity within tropical forest communities (Laliberté *et al.* 2014; Laliberté *et al.* 2013). Therefore, to understand environmental–community relationships, we must first understand community composition in terms of beta-diversity, or compositional differences between forest areas. Globally, beta-diversity in tree species increases with increasing topographic variation (De Cáceres *et al.* 2012). It is equally useful to evaluate the how topographies influence community composition at more-localized scales within tropical forests. In a 20-ha permanent forest dynamics plot (FDP) in southwestern China, topography was shown to play a significant role in controlling distributions of a number of tree species, especially at early life-stages (e.g., saplings and immature trees; Lan *et al.* 2011). Other studies have documented the strong effects of topographic related habitat-filtering of juvenile trees, showing a trend of decreasing strength of filtering as trees mature (Kanagaraj *et al.* 2011; Punchi-Manage *et al.* 2013; Hu *et al.* 2012; Zemunik *et al.* 2016).

Here we examine the role of topography and soil resources in structuring a Neotropical plant community that was affected by land-use in the past of different intensities within a permanent 16-ha forest dynamics plot in Puerto Rico. In this study, however, we do not seek to differentiate the direct or indirect effects of land use on plant-community–soil interactions, but rather examine how the interactions change over time and with the recovery of the forest from the land use and the compound effect of two hurricane disturbances (Hurricane Hugo in 1989 and Hurricane Georges in 1998). Using multivariate redundancy analysis to partition the variability in plant community beta-diversity into spatial, edaphic, and topographic portions, we ask:

1. How well does variation in soil resources and topography explain patterns of plant diversity composition with respect to land-use legacies? We predicted soil resource and topographic variables would have less explanatory power in structuring plant communities with more intense land-use (i.e., weaker habitat association). The explanation could be that either the land-use has homogenized soil resource distributions, or plant species distributions have been affected by the effects of past land use. Alternatively, weak species-environment associations could reflect a compound effect of the two processes, resulting in a decoupling of the relationships between the abiotic environment and forest community composition.

2. To what degree do environmental–plant community relationships change over time, and in response to hurricane disturbances and with respect to land-use history? We expect the strength of plant community–environmental relationships to increase with time following hurricane disturbances as the effect of the hurricane damage diminishes and the plant community reflects the environment. We hypothesize environmental relationships to be

strongest in less-disturbed areas, because there was less of a decoupling effect associated with past low intensity land-use pressure in these areas.

## Materials and methods

### Site Description & Tree Census Methods

The Luquillo Forest Dynamics Plot (LFDP) [18°20' N, 62°49' W] is a permanent forest monitoring plot located in the montane wet forest of northeastern Puerto Rico. The forest type is described as *tabonuco* forest, named after a dominant species *Dacryodes excelsa* Vahl. (Wadsworth 1951). The forest canopy is uniform, lacking canopy emergents, in primary tabonuco forest with an average canopy height of about 30 m and with few trees exceeding 2 m diameter at breast height (dbh, diameter at 1.3 m above the ground surface; Brokaw *et al.* 2004). Topographic variability within the LFDP is large with elevation ranging between 333 and 428 masl. and slopes averaging 17%, but ranging from 3% to 60% (Thompson *et al.* 2002; Weaver 2000; Harris *et al.* 2012). Mean annual rainfall is 3685 mm (1975 to present) and temperature ranges from 20.5 to 22.8°C (Ramírez and Melendez-Colóm 2003; Thompson *et al.* 2004).

Soils in the LFDP are clay, comprised of deeply-weathered Oxisols and Ultisols developed in marine sedimentary lithology of volcanic origin. These soils orders are typical of lowland tropical forests worldwide, however soil fertility in the LFDP is higher than much of the continental lowland tropics (Beinroth 2010; Soil Survey Soil Staff 1995). The plot has been censused five times at approximately 5 year intervals between 1990 and 2011. Due to Puerto Rico being a medium-sized island located at a moderate distance from continental land-masses, species richness is relatively low when compared to other tropical forests, ranging from 43 to 54 species ha$^{-1}$ (Lawrence 1996). In the most recent (2011) tree census 123 species were recorded in the whole LFDP (Hogan 2015).

In the 16-ha (320 m × 500 m) LFDP, all free-standing wood stems ≥ 1 cm dbh are mapped, measured and identified to species. Tree measurement protocols follow those employed by the Center for Tropical Forestry Science (CTFS) and large forest dynamics plots across the globe (Condit 1998; Anderson-Teixeira *et al.* 2015). The LFDP was established in 1990, soon after Hurricane Hugo, which heavily damaged the forest (Zimmerman *et al.* 1994; Scatena and Larsen 1991). A second hurricane, Georges, passed over the forest in 1998, but caused much less damage. Land-use legacies resulting from settlement, coppicing, and charcoal production prior to the 20$^{th}$ century have emerged as a key driver of forest succession within the northern LFDP. The LFDP is made-up of three areas of secondary forest of differing past land-use intensity (all three areas ≤ 80% forest cover in 1936 aerial photographs; Foster *et al.* 1999), were combined to form one heterogeneous patch of secondary forest that we refer to as the high-land-use intensity area in the north of the plot (Thompson *et al.* 2002; Uriarte *et al.* 2009). This area was completely cut-over at some point prior to 1934 (Thompson *et al.* 2002). The southern third of the plot contains relatively well-conserved area of *tabonuco* forest, which harbored >80% canopy

cover in historical aerial photographs, and was only subjected to minor selective logging in the 1940's for tests of release thinning around individual tress (Frank Wadsworth, personal communication). Following major hurricanes in 1928 and 1932, it is believed that farming died out in the area and stopped entirely in 1934 when the forest service bought the land (Weaver 2012; Gerhart 1934), creating a land-use legacy gradient, of four distinct forest patches, that directly relates to forest successional stage across the plot (Fig. 1).

QUANTIFYING ENVIRONMENTAL VARIABLES WITHIN THE LFDP

Field soil collection took place in 2011. Soil samples were taken from 0-10 cm depth in the mineral soil across a 40-m grid within the LFDP following methodology in John *et al.* (2007), with additional samples taken at 2 m and 8 m in random directions from selected regular sample points to estimate local variability in soil chemistry. Soil pH was determined in both deionized water and 10 mM $CaCl_2$ in a 1:2 soil to solution ratio using a glass electrode. Concentrations of ammonium and nitrate were determined by extraction of fresh soils in the field in 2 M KCl, with detection by automated colorimetry on a Lachat Quikchem 8500 (Hach Ltd, Loveland, CO, USA). Plant-available phosphorus was estimated by extraction of air-dried and sieved (< 2 mm) samples by Bray-1 solution, with detection of phosphate by automated molybdate colorimetry. Exchangeable cations, including aluminum, calcium, iron, magnesium, manganese, and sodium, were extracted from air-dried soils in 0.1 M $BaCl_2$ (2 h, 1:30 soil to solution ratio), with detection by ICP – OES spectrometry on an Optima 7300 DV (Perkin Elmer Inc, Shelton, CT, USA; Hendershot *et al.* 2008). Total exchangeable bases (TEB) was calculated as the sum of calcium (Ca), potassium (K), magnesium (Mg), and sodium (Na); effective cation exchange capacity (ECEC) was calculated as the sum of aluminum (Al), Ca, iron (Fe), K, Mg, manganese (Mn), and Na; base saturation was calculated by (TEB ÷ ECEC) × 100. Values were kriged to obtain soil cation estimates at the 20 × 20-m scale.

Topographic variation within the LFDP is more variable than in most other permanent forest dynamics plots (Losos and Leigh, 2004). The CTFS method for measuring topographic variability in large FDPs is at the 20-meter, or quadrat, scale (Condit, 2012). Using previously surveyed elevations for quadrat corners within the LFDP (16 columns x 25 rows; see Thompson *et al.* 2002), finer-scale topographic variation was measured at the 5-m scale using clinometers to measure the elevation of 5 x 5 m grid points delineating the subplots and was used to calculate topographic variation. Elevation throughout the LFDP is shown in Fig 1, with the most-elevated areas toward the south-eastern plot boundary and the lowest elevations in the north-west corner.

Topographic variables included slope, convexity, aspect, and terrain ruggedness. We incorporated a unique topographic variable, terrain ruggedness, which is a quantifiable measure of terrain heterogeneity. Slope was calculated using the CTFS method, where 4 planes are drawn through all possible, unique combinations of 3 quadrat corners at 5m-intervals within a 20m x 20m plot, and subsequently averaged (Condit 2012). Convexity was

calculated using the mean elevation of each quadrat relative to the mean of its eight orthogonal neighbors (Condit 2012). Aspect was decomposed into east-west and north-south orientations using sine and cosine, respectively (Lin *et al.* 2013). The terrain ruggedness index, quantified for at the 20m-scale, was implemented as defined by Riley (1999) and calculated in GRASS (Grass Development Team 2012) using the 5m scale topographic variation within the LFDP. We refer to environmental variables, hereafter, as the complete of set of the kriged soil nutrient estimates and topographic variables, excluding spatial variables.

BETA-DIVERSITY MAPS

To visually examine variation within the forest community across the LFDP, species-diversity maps were generated using floral gradient analysis (Thessler *et al.* 2005). Using Bray-Curtis dissimilarities, Nonmetric Multidimensional Scaling (NMS) ordinations for each census at the quadrat-scale (20 x 20 m) were constrained to three axes. Ordination axes scores, or their position in the 3-dimensional ordination space, were translated to hexadecimal color values for red, blue and green, respectively. The resulting maps display diversity differences in community composition chromatically (Baldeck *et al.* 2013). Quadrats with colors of similar shades between quadrats represent similar species composition, whereas colors of different shades show areas where tree species composition is more different. Within each census, redder shades were standardized within each census to show areas where compositional make-up was most similar. NMS and color standardization was done separately for each tree census, therefore, maps created using this method cannot be interpreted in relation to one another (i.e., across censuses).

REDUNDANCY ANALYSIS / VARIANCE PARTITIONING

We used canonical distance-based Redundancy Analysis (db-RDA; Legendre and Anderson, 1999), to examine the amount of variance explained by environmental differences related to soil resources, topography and space (Figure 3; Peres-Neto *et al.* 2006). Redundancy Analysis, an extension of Canonical Correspondence Analysis, is a method of multivariate linear predictive models for a combination of response variables (in our case, community composition) from a set of predictor variables (in our case, space, topographic and soil nutrient variables; Quinn and Keough 2002; McCune *et al.* 2002). We chose to use RDA to test how well environmental predictor variables, including space, could predict community composition as a direct test for plant community–environment relationships. Hellinger-transformed species abundance counts within quadrats made up the set of response variables (Dray *et al.* 2006; Legendre and Gallagher 2001).

Due to the auto-correlated nature of tree species distributions, space must be explicitly incorporated into the RDA (Legendre 1993). Principle Coordinates of Neighborhood Matrices (PCNM) is currently the most appropriate tool for this (Borcard and Legendre 2002; Dray *et al.* 2006), because it incorporates the spatial structure in species response data at the

most relevant species-environmental scale. PCNM decomposes the spatial structure present in the community data into distance-based Moran's Eigenvector Maps (db-MEM; Borcard *et al.* 2004; Borcard and Legendre 2002). The db-MEM comprised the set of all spatial variables. The PCNM was computed in the R statistical environment (ver. 3.1.1; R Development Core Team, 2014) with the "PCNM" package (Legendre *et al.* 2010).

We expanded the set of environmental variables to permit for non-linear relationships and increase model flexibility, by calculating second and third order polynomials of all variables, except for aspect, prior to their forward selection (Legendre *et al.* 2009). Forward selecting variables is one of the simplest data-driven model building approaches, where explanatory variables are added to a model separately and successively until no variables can be further added to improve model fit or flexibility. Prior to variance partitioning, explanatory variables were standardized and selected at the 95% confidence interval using forward selection in the "packfor" package (Dray *et al.* 2007; Blanchet *et al.* 2008). Three-way variance partitioning of response variables with respect to spatial, topographic and edaphic variables was carried out using the "vegan" package (Oksanen *et al.* 2008)

PERMUTATIONAL ANALYSIS OF VARIANCE & NONMETRIC MULTIDIMENSIONAL SCALING BI-PLOTS

Differences in of the community beta-diversity with respect to past land use were further explored by quantifying the magnitude of difference between quadrat-groups of varying land-use intensity across the LFDP (as determined by 1936 aerial photographs, Fig. 1) using Permutational Multivariate Analysis of Variance (PerMANOVA), and ordinating them using nonmetric multidimensional scaling (NMS). PerMANOVA was performed in the "vegan" R package using the community species counts from the most-recent (2011) tree census, and the a priori land-use classifications (Thompson *et al.* 2002). PerMANOVA p-values were Bonferroni-adjusted to correct for multiple comparisons. For the NMS, forward-selected explanatory variables from RDA models were overlain as environmental vectors on the ordination, using 0.100 as the coefficient of determination cut-off to allow for weak to moderate environmental variable relationships (McCune *et al.* 2002). Axis 1 in the ordination was rotated with respect to land-use intensity, and therefore can be directly interpreted as an explanatory axis for land use. Visually, this allows for the display of environmental–community relationships across the entire plot. NMS ordinations were completed in PC-ORD 6 (McCune *et al.* 2002; McCune and Mefford 2011).

## Results

BETA-DIVERSITY MAPS

Quadrats of similar species composition consistently grouped together for each census in relation to past land-use intensity. Quadrats in the northern portion of the LFDP, subject to more intense land use, was clearly similar in community composition, as were quadrats in the

southern portion where land use was less intense. A second area of high community compositional similarity was on the ridge at the western edge of plot (~ x=100 m, y=200 m), and compositional differences were captured along the elevation gradient from the upper left corner (northwest LFDP) to the bottom right corner of the maps (southeast LFDP; Fig. 2; see Appendix S1 of Supporting Information). Most notably, the dominant colors in the beta-diversity maps changed greatly for census 2 (1995). Redder shades (lowest compositional variability between quadrats) became more prominent in the high land-use intensity portion (north) of the plot in 1995 due to the widespread recruitment of understory pioneer species in the high-intensity past land use secondary forests following damage caused by Hurricane Hugo, and then switched back to less-red colors and more compositional variability, recorded in the 2000 census, as mortality in the understory occurs as the canopy recovers (Hogan, 2015).

REDUNDANCY ANALYSIS / VARIANCE PARTITIONING

Across the entire LFDP, over half of the variability in tree species community composition was related to spatial (db-MEM) and environmental variables (Fig. 3; see Appendix S2). Although environmental fractions (i.e., those related to either soil or topography) were explanatory to some degree, the portion of variability explained by spatial variables accounted for most of the variance explained by RDA models. Generally, there was a decreasing trend in explanatory power over time for all RDA models, both at the whole-plot level (Fig. 3) and with respect to past land-use intensity (i.e., north vs. south; Figs. 4 & 5). Additionally, RDA models had greater explanatory power in areas of more-intensive past land use (the northern part of the LFDP; see Figure S1 of Supporting Information). For the high land-use intensity part of the plot, environmental and spatial variables explained from 57 to 44 percent of community composition over time (Fig. 4). In contrast, the low land-use intensity area of *tabonuco* forest (i.e., the southern part of the LFDP) had weaker environmental–community relationships, with models explaining only 38 to 44 percent of variation in community composition (Fig. 5).

In all models spatial variables accounted for the majority of variation in community composition, explaining between 38 and 57 percent of the variability in community composition. For the entire LFDP, soil cation concentrations and topographic variables only explained 30-33 percent and 11 to 14 percent of variation, respectively (Fig. 3). The explanatory power of environmental fractions was similar in magnitude, but more variable for the high land-use intensity areas of the LFDP (Fig. 4). However, in forest areas with low levels of previous land-use, soil nutrients and topographic variation explained less of the difference in community composition than in the high land-use intensity areas, ranging between 23 and 27 percent and between 14 and 16 percent, respectively (Fig. 5).

PERMANOVA & NMS BI-PLOT

Community composition differed across the land-use gradient present in the LFDP, as shown in the beta-diversity maps (Fig. 2).  These differences have persisted over the twenty-one year study period, and were found to be statistically significant (PerMANOVA, $p < 0.01$) for both the high versus low land-use intensity comparison and also when comparing all four land-use intensities separately (Table 1; see Appendix S3).  In the NMS of the most recent tree census (Fig.6; 3-dimesional solution based on 125 iterations with a final stress of 14.89 using Bray-Curtis distance measure), a slight separation of the communities can be seen, with the high land-use intensity quadrats mainly clustering out more to the left hand side of axis 1 (land-use intensity), and with the lower land-use intensity quadrats tending toward the right side of the ordination.  Convex hulls, or a polygons containing all the sites within each land-use category, were overlain on the ordination to display a tendency for more compositional variability in forest community across the area of more intense past land-use in the LFDP. Axis 2 can be interpreted as a catena effect (convexivity) from high (ridge) to low (valley) going from bottom to top of the axis.  Base saturation of soil (BS) decreased along the catena (axis 2).  In 2011, all soil nutrient concentrations, and topographic convexity, were key in explaining differences in environmental–forest community relationships with respect to past land-use intensity, and were positively correlated with amount of canopy cover present in the 1936 historical aerial photographs (i.e., past land-use intensity).  For example, concentrations of exchangeable K, Na, Ca, Mg, Fe, and Mn were greater in less disturbed sites.  Total exchangeable bases (TEB) and effective cation exchange capacity (ECEC) were also greater in these areas.  Aluminum, soil bulk density, and soil pH were the main notable exceptions, which appeared on NMS bi-plots perpendicular to axis 1 (land-use), meaning that they had no noticeable relationships with past land-use intensity.  Similarly, topographic variables were neutrally or weakly negatively related to past land-use when examined across the entire LFDP (Fig. 6).

**Discussion**

To examine the direct effect of past land-use intensity in environmental niche structuring of plant communities, the variance partitioning results from the LFDP can be compared to those of five other larger FDP's; BCI in Panama, Huai Kha Kheng in Thailand, Korup in Cameroon, Pasoh in Malaysia, and Yasuni in Ecuador (Baldeck *et al.* 2013).  In these plots, both soil resources and topography explained about the same amount of variation in plant community composition (9–34 percent and 5–29 percent, respectively), and soil resources and topography together explained 13–39 percent of compositional variation (Baldeck *et al.* 2013).  In addition, these large FDP's ($\geq$ 50 ha each), which all largely lack previous well-documented land use, were divided in half to aid in comparison to smaller FDP's, such as the LFDP.  Differences between the north and south of the LFPD were greater than the other plots, especially following hurricane disturbances (i.e., census 1 in 1990 following Hurricane Hugo, and census 3 in 2000 following Hurricane Georges).  Difference between the total explanatory power of RDA models for five FDP halves in the Baldeck et al.

(2013) study averaged 0.04. Differences in RDA total model explanatory power for the northern and southern halves of the LFDP were 0.12, 0.08, 0.10, 0.04, and 0.06, for tree census 1 through 5 respectively, indicating that differences between plant communities in the LFDP tended to be greater than those in other large plots largely lacking the effects of past land use and hurricane damage.

The beta-diversity maps clearly showed the northern portion of the LFDP to be distinct in species composition. This area is the high land-use intensity portion of the plot, with three distinct areas of differing canopy cover, all less than 80 percent in the historical 1936 aerial photographs (Foster *et al.* 1999; Thompson *et al.* 2002). Historic land-use intensity varies across the three distinct areas, with some areas having been largely cut over, and others having been dominated by either agricultural practices or small subsistent human settlements (Thompson *et al.* 2002; Thompson *et al.* 2007). Land-use legacies are reflected in a structurally-younger forest where secondary forest species, with lower wood-density are more abundant (Thompson *et al.* 2002; Uriarte *et al.* 2009) and canopy structure allows more light through (Hogan 2015; Comita *et al.* 2010). These areas were more affected by hurricanes (Zimmerman *et al.* 1995; Uriarte *et al.* 2012; Canham *et al.* 2010) and have resulted in secondary forests that have faster dynamics driven by greater light availability in the understory after hurricane damage. The beta-diversity maps likely capture distance-restricted dispersal and recruitment within high intensity land-use areas, leading to greater similarity in community composition at census 2, with community differences increasing over time as shrub and pioneer species densities thin under a recovering canopy (Hogan 2015). These results are similar to responses measured in nearby USDA Forest Service plots, in terms of similarity of community composition along successional trajectories in time after hurricane disturbance (Heartsill Scalley *et al.* 2010).

RDA models decreased in explanatory power over time. Despite these changes, variance partitioning results were stable over time, when compared to changes in stem densities, stem-diameter size distributions (i.e., forest structure) or species diversity (i.e., compositional change) within the forest (Hogan 2015). The better explanatory power of RDA models in areas of more-intense past land use in the LFDP points to the large magnitude of change, and persisting effects of anthropogenic land use disturbance, within forest communities. This trend is well documented in vegetation succession of tropical forest systems (Chazdon 2003; Foster *et al.* 1998; Aide *et al.* 1995; Holz *et al.* 2009). Clear differences between RDA models for areas of high and low land-use intensity were observed. RDA models had greater explanatory power in areas more-intense past land-use history within the LFDP, most likely due to stronger successional responses to hurricane damage in these areas. In other words, areas more impacted by previous land use had greater plant community–environmental relationships, because they respond disproportionately to hurricanes, at least with respect to recruitment of understory pioneers (Hogan 2015). Such pioneer species often have considerably shorter lifespans than their primary forest counterpart species and, therefore, can more closely track successional changes related to spatial environmental variation (i.e., light availability; Uriarte *et al.* 2009; Uriarte *et al.* 2012),

providing an explanation for why RDA models had increased explanatory power in areas of more-intensive past land use.

Separation of quadrats within the LFDP with respect to past land use and as the forest recovers from Hurricane Hugo, which affected the forest in 1989, and to a much lesser degree Hurricane Georges which passed over the LFDP in 1998, can still be seen via community ordination. There is a greater clustering of quadrats, as community composition between areas of differing past land-use pressure converge in community composition, with the widespread recruitment of pioneers across the whole plot. In community ordinations for all five LFDP tree censuses, compositional differences attributed to land-use legacies peaked at census 3 in 2000, with land-use legacies explaining 58.6 percent of the plot-wise compositional variation. This trend is congruent with the pattern of the magnitude of land-use legacies within the LFDP, explored using statistical techniques that quantify the contribution of past land use to changes in community composition over time (Hogan 2015).

Environmental–community relationships within tropical forests are difficult to detect and are strongest in well-conserved areas that exhibit high levels of environmental heterogeneity (Paoli *et al.* 2006). In this study, we investigated the interactive effects of past land-use and hurricane disturbance in altering environmental relationships. The results supported our hypothesis that associations between plant community compositional and the environment would be stronger following hurricane damages to the forest (Introduction – Question 2). Despite this, environmental niche-partitioning (i.e., topographic and soil niche) was greatest in the areas of more-intense past land-use pressure, recorded in the census immediately following Hurricane Hugo, providing evidence that land-use alters abiotic and biotic variables within the forest. Alteration of the abiotic environment by land use selects for species suited for these conditions (e.g., secondary successional and pioneer species) to allow for competitive advantages for anthropogenically-associated species (e.g., species commonly associated with human settlement or other land-use activity). Such altered forest communities can persist for decades or longer following land-use abandonment, as shown via the lasting land-use legacies within the LFDP. Although, these findings are not new (Foster *et al.* 1998; Thompson *et al.* 2002), the possible explanatory mechanisms deserve further research.

We clearly were incorrect in expecting weaker plant community–environmental relationships in areas of higher past land-use pressure (Introduction – Question 1). Contrary to our expectation, environmental–plant community structuring was greater in areas of more-intense past land-use, probably due to decreased competition in these areas when compared to old-growth tabonuco forest. A similar study (Bachelot *et al.* 2016), found below-ground biotic factors (e.g., soil fungi and microbes) to be more important in affecting community composition in the high land-use areas of the LFDP, suggesting that land-use legacies not only alter soil fertility and structure, but also biotic communities within them, providing an insight into mechanisms for the lasting effects of land-use legacies on forest species composition via soils. This research is important because a widespread forest re-growth continues to take place in the tropics as land use patterns change (Mather 1992; Rudel *et al.* 2002; Meyfroidt and Lambin 2009; Chazdon 2014). Regenerating tropical forests may

resemble their old-growth counterparts in some metrics (e.g., structure), but it may take centuries or longer to recover old growth species composition and interactions (Lindenmayer *et al.* 2012; Wright 2005; Lugo and Helmer 2004; Chazdon 2003).

In complex tropical forests, identifying environmental drivers that organize plant communities is extremely difficult. Many signals tend to be weak and confounded with other factors, such as disturbance. Despite this, when comparing two areas of forest with differing previous land-use histories within the LFDP, environmental relationships were stronger in areas of more-intense past land-use pressure. These findings provide a mechanistic understanding of the possible role that abiotic conditions associated with land-use legacies play in altering the successional dynamics of recovering secondary tropical forests. That mechanism is through the direct anthropogenic-alteration of forest composition and structure via human land-use practices, likely providing competitive advantages to secondary forest, or oftentimes anthropogenically-selected species due to the more rapid turn-over and stronger spatial interactions present in second-growth tropical forests.

**Data Accessibility**

Tree census data for the Luquillo Forest Dynamics Plot are available for download through the Smithsonian Tropical Research Institute ForestGEO (formerly The Center for Tropical Forest Studies) data portal: http://ctfs.si.edu/Public/plotdataaccess/index.php.

## References

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.

Anderson-Teixeira, K. J., Davies, S. J., Bennett, A. C., Gonzalez-Akre, E. B., Muller-Landau, H. C., Joseph Wright, S., Abu Salim, K., Almeyda Zambrano, A. M., Alonso, A. & Baltzer, J. L. (2015) CTFS-ForestGEO: a worldwide network monitoring forests in an era of global change. *Global Change Biology,* **21,** 528-549.

Bachelot, B., Uriarte, M., Zimmerman, J. K., Thompson, J., Leff, J. W., Asiaii, A., Koshner, J. & McGuire, K. (2016) Long-lasting effects of land use history on soil fungal communities in second-growth tropical rain forests. *Ecological Applications*.

Baldeck, C. A., Harms, K. E., Yavitt, J. B., John, R., Turner, B. L., Valencia, R., Navarrete, H., Davies, S. J., Chuyong, G. B., Kenfack, D., Thomas, D. W., Madawala, S., Gunatilleke, N., Gunatilleke, S., Bunyavejchewin, S., Kiratiprayoon, S., Yaacob, A., Supardi, M. N. & Dalling, J. W. (2013) Soil resources and topography shape local tree community structure in tropical forests. *Proceedings of the Royal Society B: Biological Sciences,* **280,** 20122532.

Beinroth, F. H. (2010) Updated taxonomic classification of the soils of Puerto Rico, 2002. University of Puerto Rico-Mayaguez, Agricultural Research Station, Rio Piedras, PR.

Blanchet, F. G., Legendre, P. & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology,* **89,** 2623-2632.

Booth, T. H., Nix, H. A., Hutchinson, M. F. & Jovanic, T. (1988) Niche analysis and tree species introduction. *Forest Ecology and Management,* **23,** 47-59.

Borcard, D. & Legendre, P. (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecological Modelling,* **153,** 51-68.

Borcard, D., Legendre, P., Avois-Jacquet, C. & Tuomisto, H. (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology,* **85,** 1826-1832.

Brokaw, N. & Busing, R. T. (2000) Niche versus chance and tree diversity in forest gaps. *Trends in Ecology & Evolution,* **15,** 183-188.

Brokaw, N., Fraver, S., Grear, J., Thompson, J., Zimmerman, J., Waide, R., Everham III, E., Hubbell, S. & Foster, R. (2004) Disturbance and canopy structure in two tropical forests. *Tropical Forest Diversity and Dynamism*, 177-194.

Canham, C. D., Finzi, A. C., Pacala, S. W. & Burbank, D. H. (1994) Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research,* **24,** 337-349.

Canham, C. D., Thompson, J., Zimmerman, J. K. & Uriarte, M. (2010) Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica,* **42,** 87-94.

Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E. & Tilman, D. (1997) Biotic control over the functioning of ecosystems. *Science,* **277,** 500-504.

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. (2014) *Second growth: The promise of tropical forest regeneration in an age of deforestation.* University of Chicago Press, Chicago, Illinois USA.

Cleveland, C. C., Townsend, A. R., Taylor, P., Alvarez-Clare, S., Bustamante, M., Chuyong, G., Dobrowski, S. Z., Grierson, P., Harms, K. E. & Houlton, B. Z. (2011) Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. *Ecology Letters,* **14,** 939-947.

Comita, L. S., Thompson, J., Uriarte, M., Jonckheere, I., Canham, C. D. & Zimmerman, J. K. (2010) Interactive effects of land use history and natural disturbance on seedling dynamics in a subtropical forest. *Ecological Applications,* **20,** 1270-1284.

Condit, R. (1998) *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots.* Springer.

Condit, R. (2012) CTFS R Pacakge. Center for Tropical Forest Science http://ctfs.si.edu/Public/CTFSRPackage/.

Cram, S., Sommer, I., Fernández, P., Galicia, L., Ríos, C. & Barois, I. (2015) Soil natural capital modification through landuse and cover change in a tropical forest landscape: implications for management. *Journal of Tropical Forest Science,* **27,** 189-201.

Davies, S. J., Palmiotto, P. A., Ashton, P. S., Lee, H. S. & Lafrankie, J. V. (1998) Comparative ecology of 11 sympatric species of Macaranga in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology,* **86,** 662-673.

De Cáceres, M., Legendre, P., Valencia, R., Cao, M., Chang, L. W., Chuyong, G., Condit, R., Hao, Z., Hsieh, C. F. & Hubbell, S. (2012) The variation of tree beta diversity across a global network of forest plots. *Global Ecology and Biogeography,* **21,** 1191-1202.

Ding, Y., Zang, R., Liu, S., He, F. & Letcher, S. G. (2012) Recovery of woody plant diversity in tropical rain forests in southern China after logging and shifting cultivation. *Biological Conservation,* **145,** 225-233.

Dray, S., Legendre, P. & Blanchet, F. (2007) Packfor: forward selection with permutation, R package version 0.0–7.

Dray, S., Legendre, P. & Peres-Neto, P. R. (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). E*cological Modelling,* **196,** 483-493.

Duan, W. J., Ren, H., Fu, S. L., Guo, Q. F. & Wang, J. (2008) Pathways and determinants of early spontaneous vegetation succession in degraded lowland of South China. *Journal of Integrative Plant Biology,* **50,** 147-156.

Ellis, R. & Pennington, P. (1992) Factors affecting the growth of Eucalyptus delegatensis seedlings in inhibitory forest and grassland soils. *Plant and Soil,* **145,** 93-105.

Foster, D., Fluet, M. & Boose, E. (1999) Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications,* **9,** 555-572.

Foster, D. R., Motzkin, G. & Slater, B. (1998) Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. *Ecosystems,* **1,** 96-119.

Gerhart, G. (1934) Tract 11. *Land acquisition supplementary report, Luquillo purchase unit. Caribbean National Forest. USDA Forest Service. Open file report. International Institute of Tropical Forestry, Catalina Service Station, Palmer, Puerto Rico.*

Grass Development Team (2012) Geographic Resource Analysis Support Team (GRASS GIS) Software. Open Source Geospatial Foundation, U.S. Army Construction Research Laboratory.

Harms, K. E., Wright, S. J., Calderón, O., Hernández, A. & Herre, E. A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature,* **404,** 493-495.

Harris, N. L., Lugo, A. E., Brown, S. & Heartsill Scalley, T. (2012) Luquillo experimental forest: research history and opportunities. (ed U.S.D.A.), pp. 152. Washington DC.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T. & Reich, P. B. (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science,* **348,** 336-340.

Heartsill Scalley, T., Scatena, F. N., Lugo, A. E., Moya, S. & Estrada Ruiz, C. R. (2010) Changes in Structure, Composition, and Nutrients During 15 Yr of Hurricane-Induced Succession in a Subtropical Wet Forest in Puerto Rico. *Biotropica,* **42,** 455-463.

Hendershot, W. H., Lalande, H. & Duquette, M. (2008) Ion exchange and exchangeable cations. *Soil Sampling and Methods of Analysis* (eds M. R. Carter & E. Gregorich), pp. 173-178. Canadian Society of Soil Science and CRC Press, Boca Raton, FL, USA.

Hogan, J. A. (2015) *Revisiting the Relative Roles of Land-Use and the Environment in Subtropical Wet Forest: 21-years of Dynamics from the Luquillo Forest Dynamics Plot, Puerto Rico. MSc Thesis*. University of Pierto Rio, Rio Piedras (Puerto Rico).

Holdridge, L. R., Grenke, W., Hatheway, W. H., Liang, T. & Tosi Junior, J. A. (1971) *Forest environments in tropical life zones: a pilot study.* Oxford Pergamon Press, New York, NY.

Holz, S., Placci, G. & Quintana, R. D. (2009) Effects of history of use on secondary forest regeneration in the Upper Parana Atlantic Forest (Misiones, Argentina). *Forest Ecology and Management,* **258,** 1629-1642.

Hu, Y.-H., Lan, G.-Y., Sha, L.-Q., Cao, M., Tang, Y. & Xu, D.-P. (2012) Strong neutral spatial effects shape tree species distributions across life stages at multiple scales. *PloS one,* **7,** e38247.

Hubbell, S. P. (2001) *The unified neutral theory of biodiversity and biogeography.* Princeton University Press.

Hutchinson, G. (1957) Concluding remarks: Cold Spring Harbor Symposia on Quantitative Biology. *Quantative Biology,* **22,** 415-427.

Hutchinson, G. E. (1978) *An introduction to population ecology.* Yale Univeristy Press, New Haven, CT.

Jansen, P. A., Visser, M. D., Wright, S.J., Rutten, G. & Muller-Landau, H. C. (2014) Negative density dependence of seed dispersal and seedling recruitment in a Neotropical palm. *Ecology Letters,* **17,** 1111-1120.

Janzen, D. H. (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist,* **104,** 501-528.

John, R., Dalling, J. W., Harms, K. E., Yavitt, J. B., Stallard, R. F., Mirabello, M., Hubbell, S. P., Valencia, R., Navarrete, H. & Vallejo, M. (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences,* **104,** 864-869.

Kanagaraj, R., Wiegand, T., Comita, L. S. & Huth, A. (2011) Tropical tree species assemblages in topographical habitats change in time and with life stage. *Journal of Ecology,* **99,** 1441-1452.

Laliberté, E., Grace, J. B., Huston, M. A., Lambers, H., Teste, F. P., Turner, B. L. & Wardle, D. A. (2013) How does pedogenesis drive plant diversity? *Trends in ecology & evolution,* **28,** 331-340.

Laliberté, E., Zemunik, G. & Turner, B. L. (2014) Environmental filtering explains variation in plant diversity along resource gradients. *Science,* **345,** 1602-1605.

Lan, G., Hu, Y., Cao, M. & Zhu, H. (2011) Topography related spatial distribution of dominant tree species in a tropical seasonal rain forest in China. *Forest Ecology and Management,* **262,** 1507-1513.

Lawrence, W. T. J. (1996) Plants: The food base. *The food web of a tropical rain forest* (eds D. P. Reagan & R. B. Waide), pp. 17-51. University of Chicago Press, Chicago, IL.

Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology,* **74,** 1659-1673.

Legendre, P. & Anderson, M. J. (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs,* **69,** 1-24.

Legendre, P., Borcard, D., Blanchet, G. & Dray, S. (2010) PCNM: PCNM spatial eigenfunction and principal coordinate analyses. R package version 2.1/r82.

Legendre, P. & Fortin, M. J. (1989) Spatial pattern and ecological analysis. *Vegetatio,* **80,** 107-138.

Legendre, P. & Gallagher, E. D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia,* **129,** 271-280.

Legendre, P., Mi, X., Ren, H., Ma, K., Yu, M., Sun, I.-F. & He, F. (2009) Partitioning beta diversity in a subtropical broad-leaved forest of China. *Ecology,* **90,** 663-674.

Lin, G., Stralberg, D., Gong, G., Huang, Z., Ye, W. & Wu, L. (2013) Separating the effects of environment and space on tree species distribution: from population to community. *PloS One,* **8,** e56171.

Lindenmayer, D. B., Laurance, W. F. & Franklin, J. F. (2012) Global decline in large old trees. *Science,* **338,** 1305-1306.

Losos, E. C. & Leigh, E. G. (2004) *Tropical forest diversity and dynamism: Findings from a large-scale plot network.* University of Chicago Press, Chicago, Illinois USA.

Lugo, A. E. & Helmer, E. (2004) Emerging forests on abandoned land: Puerto Rico's new forests. *Forest Ecology and Management,* **190,** 145-161.

Martins, K. G., Marques, M. C. M., dos Santos, E. & Marques, R. (2015) Effects of soil conditions on the diversity of tropical forests across a successional gradient. *Forest Ecology and Management*.

Mather, A. S. (1992) The forest transition. *Area,* **24,** 367-379.

McCune, B., Grace, J. B. & Urban, D. L. (2002) *Analysis of ecological communities.* MjM Software Design Gleneden Beach, OR.

McCune, B. & Mefford, M. J. (2011) *PC-ORD 6: multivariate analysis of ecological data.* MjM Software Design, Gleneden Beach, OR  USA.

Meyfroidt, P. & Lambin, E. F. (2009) Forest transition in Vietnam and displacement of deforestation abroad. *Proceedings of the National Academy of Sciences,* **106,** 16139-16144.

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G., Solymos, P., Stevens, M. & Wagner, H. (2008) The vegan package version 2.2-1. *http://CRAN.R-project.org/package=vegan.*

Pacala, S. W. & Rees, M. (1998) Models suggesting field experiments to test two hypotheses explaining successional diversity. *The American Naturalist,* **152,** 729-737.

Paoli, G. D., Curran, L. M. & Zak, D. R. (2006) Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology,* **94,** 157-170.

Peres-Neto, P. R., Legendre, P., Dray, S. & Borcard, D. (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology,* **87,** 2614-2625.

Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Savitri Gunatilleke, C., Nimal Gunatilleke, I., Wiegand, K. & Huth, A. (2013) Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. *Journal of Ecology,* **101,** 149-160.

Quinn, G. P. & Keough, M. J. (2002) *Experimental design and data analysis for biologists.* Cambridge University Press, United Kingdom.

R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramírez, A. & Melendez-Colóm, E. (2003) Meteorological summary for El Verde Field
Station: 1975–2003. (ed I.T.E.S. U.P.R.). San Juan, PR.

Ricklefs, R. E. (1977) Environmental heterogeneity and plant species diversity: a hypothesis.
*American Naturalist,* **111,** 376-381.

Riley, S. J. (1999) A Terrain Ruggedness Index That Quantifies Topographic Heterogeneity.
*Intermountain Journal of Sciences,* **5,** 23-27.

Rudel, T. K., Bates, D. & Machinguiashi, R. (2002) A tropical forest transition? Agricultural
change, out-migration, and secondary forests in the Ecuadorian Amazon. *Annals of
the Association of American Geographers,* **92,** 87-102.

Scatena, F. & Larsen, M. (1991) Physical aspects of hurricane Hugo in Puerto Rico.
*Biotropica,* **23,** 317-323.

Soil Survey Soil Staff (1995) Order I soil survey of the Luquillo Long-Term Ecological
Research grid, Puerto Rico. USDA, Natural Resources Conservation Services,
Lincoln, Nebraska.

Sousa, W. P. (1984) The role of disturbance in natural communities. *Annual Review of
Ecology and Systematics,* **15,** 353-391.

Tateno, M. & Chapin III, F. (1997) The logic of carbon and nitrogen interactions in terrestrial
ecosystems. *American Naturalist,* **149,** 723-744.

Terborgh, J. (1992) *Diversity and the tropical rain forest.* Scientific American Library, New
York.

Thessler, S., Ruokolainen, K., Tuomisto, H. & Tomppo, E. (2005) Mapping gradual landscape-scale floristic changes in Amazonian primary rain forests by combining ordination and remote sensing. *Global Ecology and Biogeography,* **14,** 315-325.

Thompson, J., Brokaw, N., Zimmerman, J. K., Waide, R., Everham III, E. M. & Schaefer, D. A. (2004) Luquillo Forest Dynamics Plot, Puerto Rico. *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale plot newtwork* (eds E. C. Losos & E. G. Leigh), pp. 540-550. Chicago University Presss, Chicago.

Thompson, J., Brokaw, N., Zimmerman, J. K., Waide, R. B., Everham III, E. M., Lodge, D. J., Taylor, C. M., García-Montiel, D. & Fluet, M. (2002) Land use history, environment, and tree composition in a tropical forest. *Ecological Applications,* **12,** 1344-1363.

Thompson, J., Lugo, A. E. & Thomlinson, J. (2007) Land use history, hurricane disturbance, and the fate of introduced species in a subtropical wet forest in Puerto Rico. *Plant Ecology,* **192,** 289-301.

Tylianakis, J. M., Rand, T. A., Kahmen, A., Klein, A.-M., Buchmann, N., Perner, J. & Tscharntke, T. (2008) Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biol,* **6,** e122.

Uriarte, M., Canham, C. D., Thompson, J., Zimmerman, J. K., Murphy, L., Sabat, A. M., Fetcher, N. & Haines, B. L. (2009) Natural disturbance and human land use as determinants of tropical forest dynamics: results from a forest simulator. *Ecological Monographs,* **79,** 423-443.

Uriarte, M., Clark, J. S., Zimmerman, J. K., Comita, L. S., Forero-Montaña, J. & Thompson, J. (2012) Multidimensional trade-offs in species responses to disturbance: implications for diversity in a subtropical forest. *Ecology,* **93,** 191-205.

Wadsworth, F. (1951) Ordenación forestal en las montañas de Luquillo. Forest management in the Luquillo mountains. *Caribbean Forester (Puerto Rico),* **12,** 115-132.

Weaver, P. L. (2000) Environmental gradients affect forest structure in Puerto Rico s luquillo mountains. *Interciencia,* **25,** 254-259.

Weaver, P. L. (2012) The Luquillo mountains: forest resources and their history. *General Technical Report-International Institute of Tropical Forestry, USDA Forest Service.*

White, P. S. (1979) Pattern, process, and natural disturbance in vegetation. *The Botanical Review,* **45,** 229-299.

Wilson, S. (2000) Heterogeneity, diversity and scale in plant communities. *Hutchings, MJ, John, EA, and Stewart, A. JA (eds.), The Ecological Consequences of Environmental Heterogeneity. Oxford: Blackwell Science***,** 53-69.

Wright, J. S. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia,* **130,** 1-14.

Wright, S. J. (2005) Tropical forests in a changing environment. *Trends in Ecology & Evolution,* **20,** 553-560.

Wright, S. J., Kitajima, K., Kraft, N. J., Reich, P. B., Wright, I. J., Bunker, D. E., Condit, R., Dalling, J. W., Davies, S. J. & Díaz, S. (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology,* **91,** 3664-3674.

Zemunik, G., Turner, B. L., Lambers, H. & Laliberté, E. (2016) Increasing plant species diversity and extreme species turnover accompany declining soil fertility along a long-term chronosequence in a biodiversity hotspot. *Journal of Ecology,* **104**, 792-805.

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., Everham III, E. M., Waide, R. B., Lodge, D. J., Taylor, C. M. & Brokaw, N. V. (1994) Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology,* **82,** 911-922.

Zimmerman, J. K., Willig, M. R., Walker, L. R. & Silver, W. L. (1996) Introduction: disturbance and Caribbean ecosystems. *Biotropica,* **28,** 414-423.

Zimmermann, B., Papritz, A. & Elsenbeer, H. (2010) Asymmetric response to disturbance and recovery: Changes of soil permeability under forest–pasture–forest transitions. *Geoderma,* **159,** 209-215.

**Figures**

**Fig. 1.** Historical land-use demarcations within the LFDP (Thompson *et al.* 2002), based on the amount of forest canopy in 1936 aerial photographs (Foster *et al.* 1999). Percent forest cover in 1936, in order from lightest to darkest: 0-20%, 20-50%, 50-80% & 80-100%. The low land-use intensity area is shown in the darkest shade, and the three lightest shaded areas, together, make up the high land-use intensity portion of the plot.
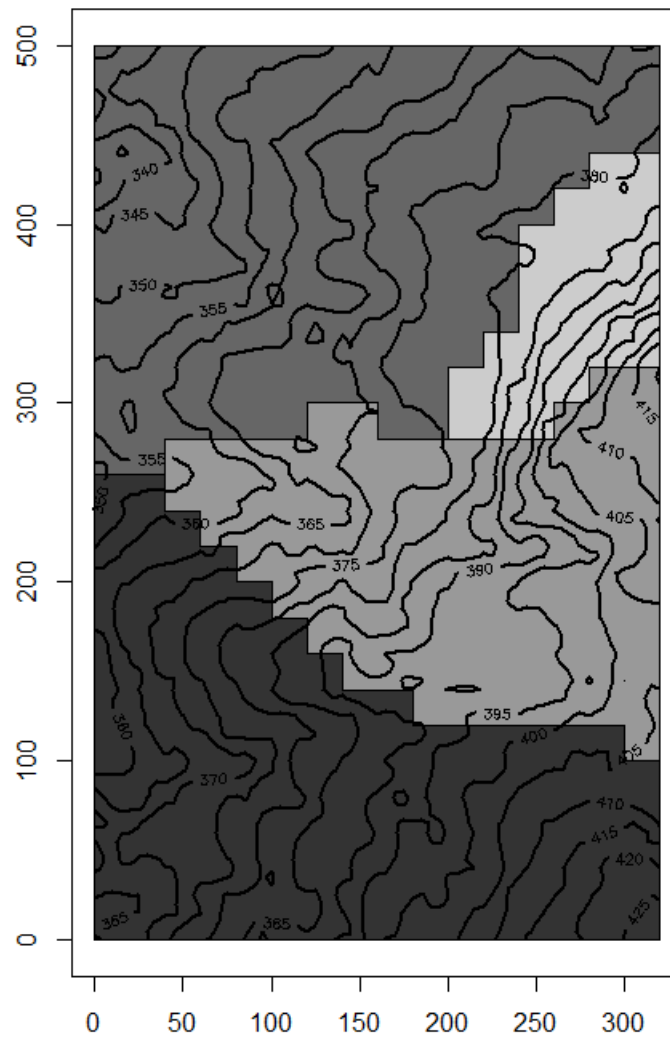
**Fig 2.** Beta-Diversity maps for the LFDP, created using floral gradient analysis (Thessler *et al.* 2005) for each of the five tree censuses. Color represents the degree of compositional similarity (raw interpretation of Bray-Curtis dissimilarities) of tree species community composition between 20-meter quadrats; quadrats of similar color represent communities with similar species composition. Redder shades were standardized to areas of greatest community compositional similarity for that census. Notably, maps cannot be compared across censuses as the method compares compositional similarity between 20-meter quadrats for each census separately. Red vertical lines show the hurricanes occurrences (Hugo in September 1989 and Georges in September 1998).
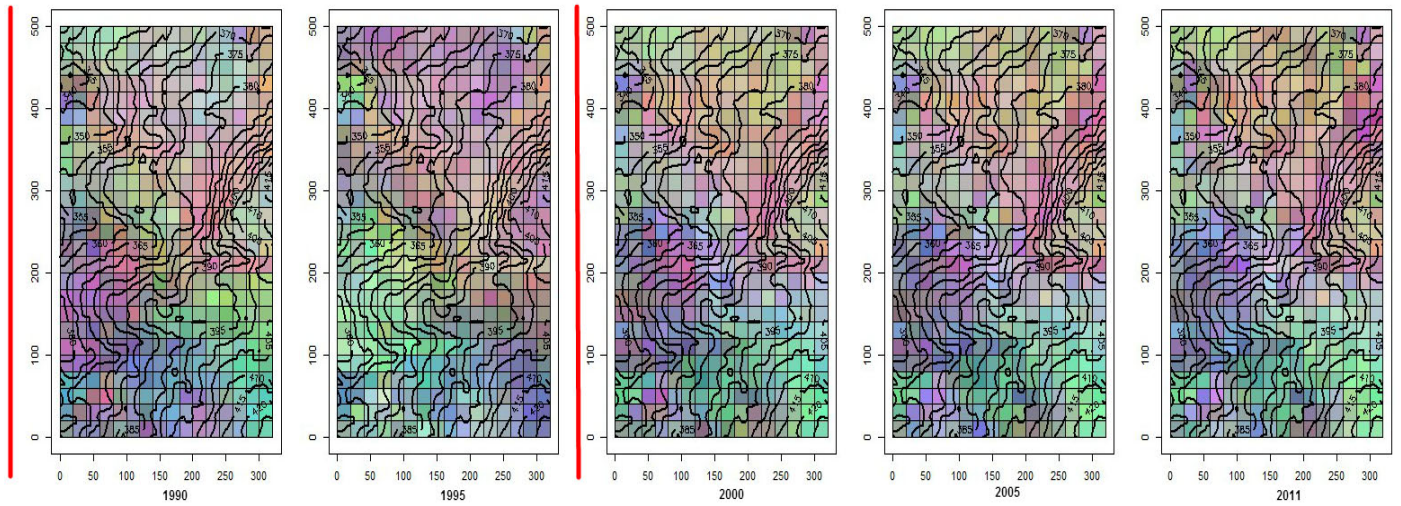
**Fig. 3.** Variance partitioning diagram (upper-left panel) and results for the entire LFDP by tree census. Census 1 (top-middle panel) took place from 1990 to 1992, and subsequent censuses occurred at approximately 5-year intervals with census 5 (lower-right panel) occuring in 2011. Numerical values represent the percent of variance explained by distance-based RDA models for their respective fractions. Spatial Variables (Principle Coordinate of Neighborhood Matrix (Dray *et al.* 2006)) are presented in red, edaphic variables in green, and topographic variables in blue. Fraction a = the pure spatial component (space | environment). Fractions b + d = the proportion explained by soil after accounting for topography (soil | topography). Fractions c + f = the proportion explained by topography after accounting for soil (topography | soil). Fractions e + g = the topographically structured soil component (soil & topography). Fractions d + f + g = the spatially structured environmental component (space & environment). Fractions a + d + f + g = the proportion of variation explained by spatial variables (PCNM) alone (space). Fractions b + d + e + g = the proportion explained by only soil nutrients. Fractions c + e + f + g = the proportion explained by topographic variables solely. Fractions b + c + d + e + f + g = the proportion explained by the environmental variables (soil resources & topography). Total explanatory power of db-RDA models = the percentage of variability explained by all spatial and environmental variables combined (a + b + c + d + e + f + g, or 100 − residuals (h)).
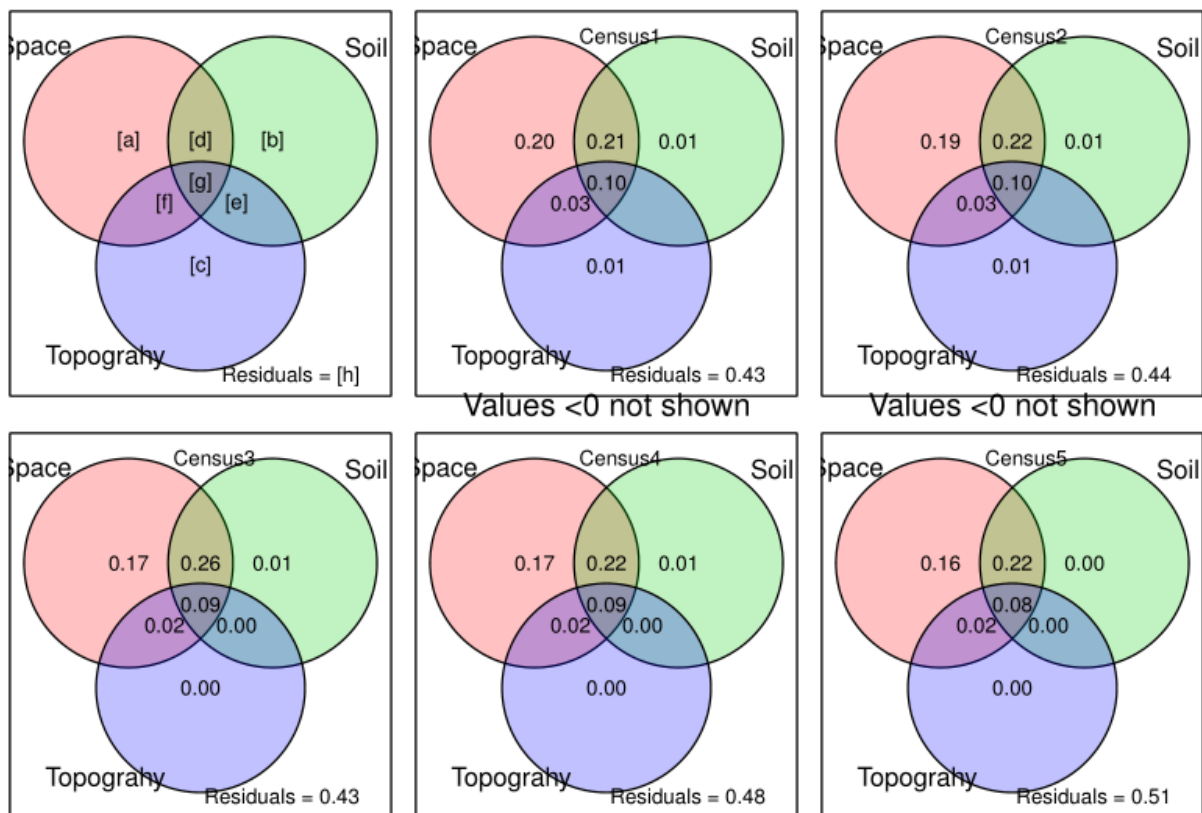
**Fig. 4.** Variance partitioning diagram (upper left panel) and results for the higher land-use intensity portion (northern) LFDP by tree census. Numerical values represent the percent of variance explained by distance-based RDA models for their respective fractions. Figure panels and their partitioned fractions are identically labeled with respect to Fig. 3a.
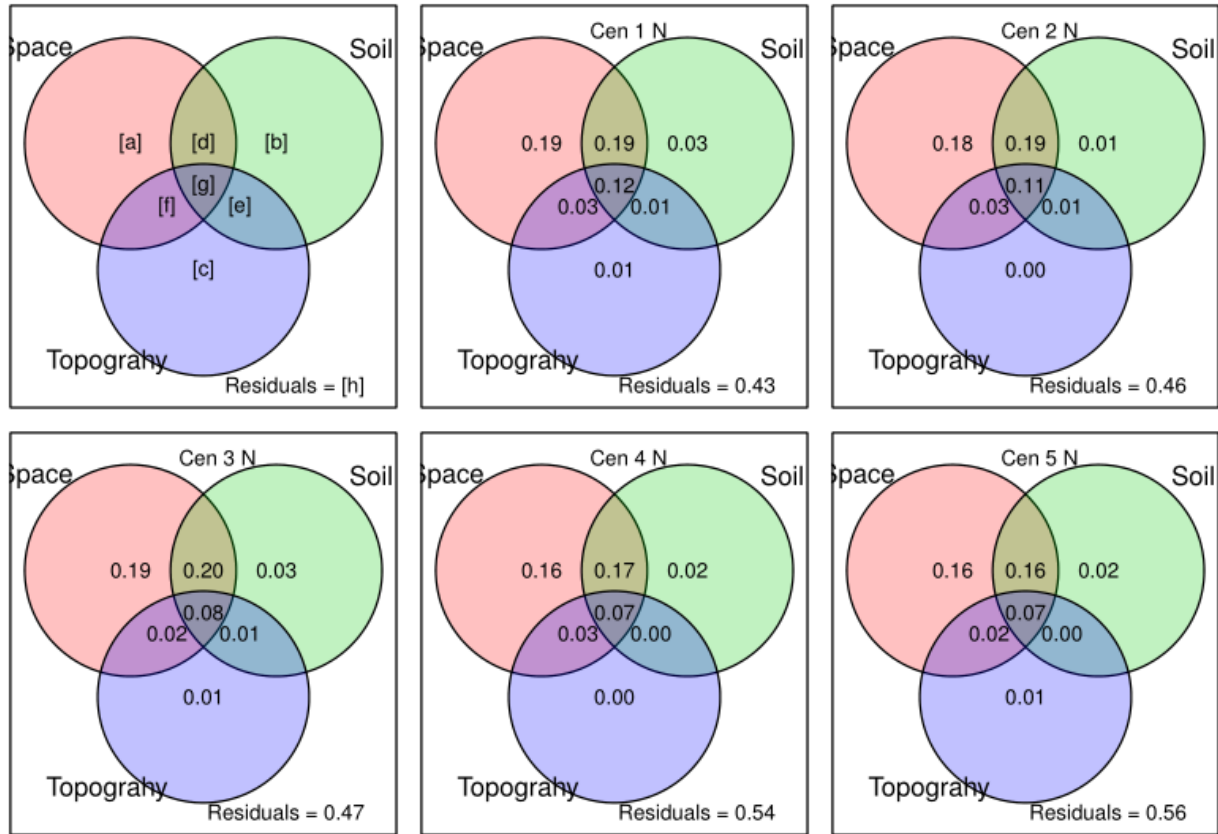
**Fig. 5.** Variance partitioning diagram (upper left panel) and results for the low land-use intensity portion (southern) LFDP by tree census. Numerical values represent the percent of variance explained by distance-based RDA models for their respective fractions. Figure panels and their partitioned fractions are identically labeled with respect to Fig. 3a.
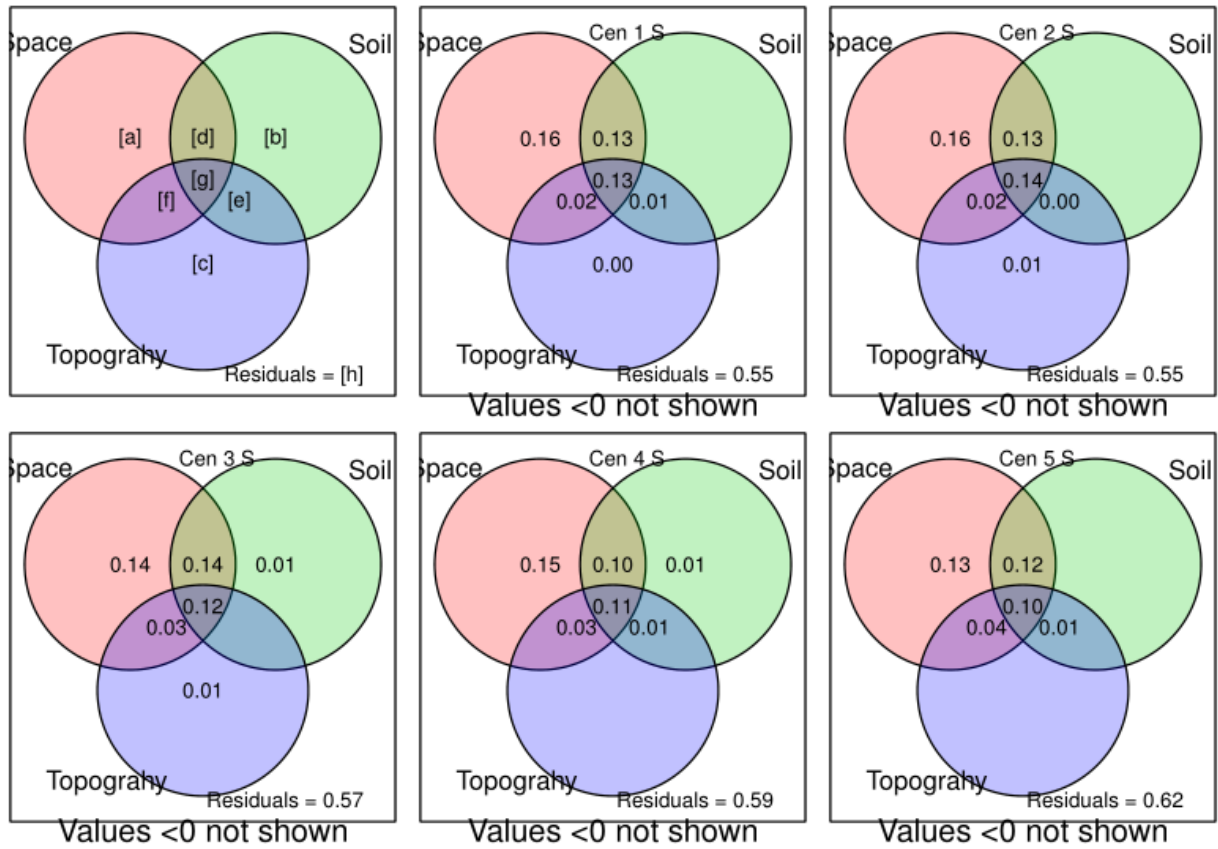
Table 1: Results for Permutational Multivariate Analysis of Variance (PerMANOVA) for Bray-Curtis Dissimilarities for the 2011 (census 5) tree community within the LFDP in relation to the land-use intensity (i.e., the amount of canopy cover in 1936 aerial photographs). DF = degrees of freedom, SS = sum of squares, Pseudo-F = F value by permutation. Bold face indicates statistical significance ($P < 0.05$); P-values are based on 999 permutations (i.e. the lowest possible P-value is 0.001).

| Land Use Intensity Comparison (percentage canopy cover in 1936) | DF | SS | Pseudo-F | $R^2$ | P-value | Bonferroni-adjusted P-value |
|---|---|---|---|---|---|---|
| 80-100% vs. 50-80% | 1 | 8.916 | 64.887 | 0.194 | **0.001** | **0.006** |
| 80-100% vs. 20-50% | 1 | 6.289 | 45.782 | 0.167 | **0.001** | **0.006** |
| 80-100% vs. 0-20% | 1 | 4.536 | 35.099 | 0.182 | **0.001** | **0.006** |
| 50-80% vs. 20-50% | 1 | 2.195 | 15.502 | 0.061 | **0.001** | **0.006** |
| 50-80% vs. 0-20% | 1 | 1.643 | 12.108 | 0.067 | **0.001** | **0.006** |
| 20-50% vs. 0-20% | 1 | 0.929 | 6.877 | 0.052 | **0.001** | **0.006** |
| < 80 % vs. ≥ 80 % | 1 | 10.367 | 71.687 | 0.152 | **0.001** | **0.001** |

**Fig. 6.** Nonmetric Multidimensional Scaling (NMS) ordination of tree communities of the LFDP for the most recent tree census (2011). Black circles indicate low intensity land-use quadrats (80-100 % forest cover in 1936), while grey triangles show quadrats in the high intensity land use portion of the LFDP. A three dimensional solution was achieved with an average plot stress was 14.89 after 125 iterations; axes 1 and 2 are shown. Overlain vectors for forward-selected explanatory environmental variables (either topographic or edaphic) from RDA models with an $r^2$ value $\geq 0.100$ are shown. The length of the vector is proportional to the strength of the environmental–community relationship for that variable. Axis 1 was oriented with respect to land-use strength from high intensity to low intensity going from left to right.
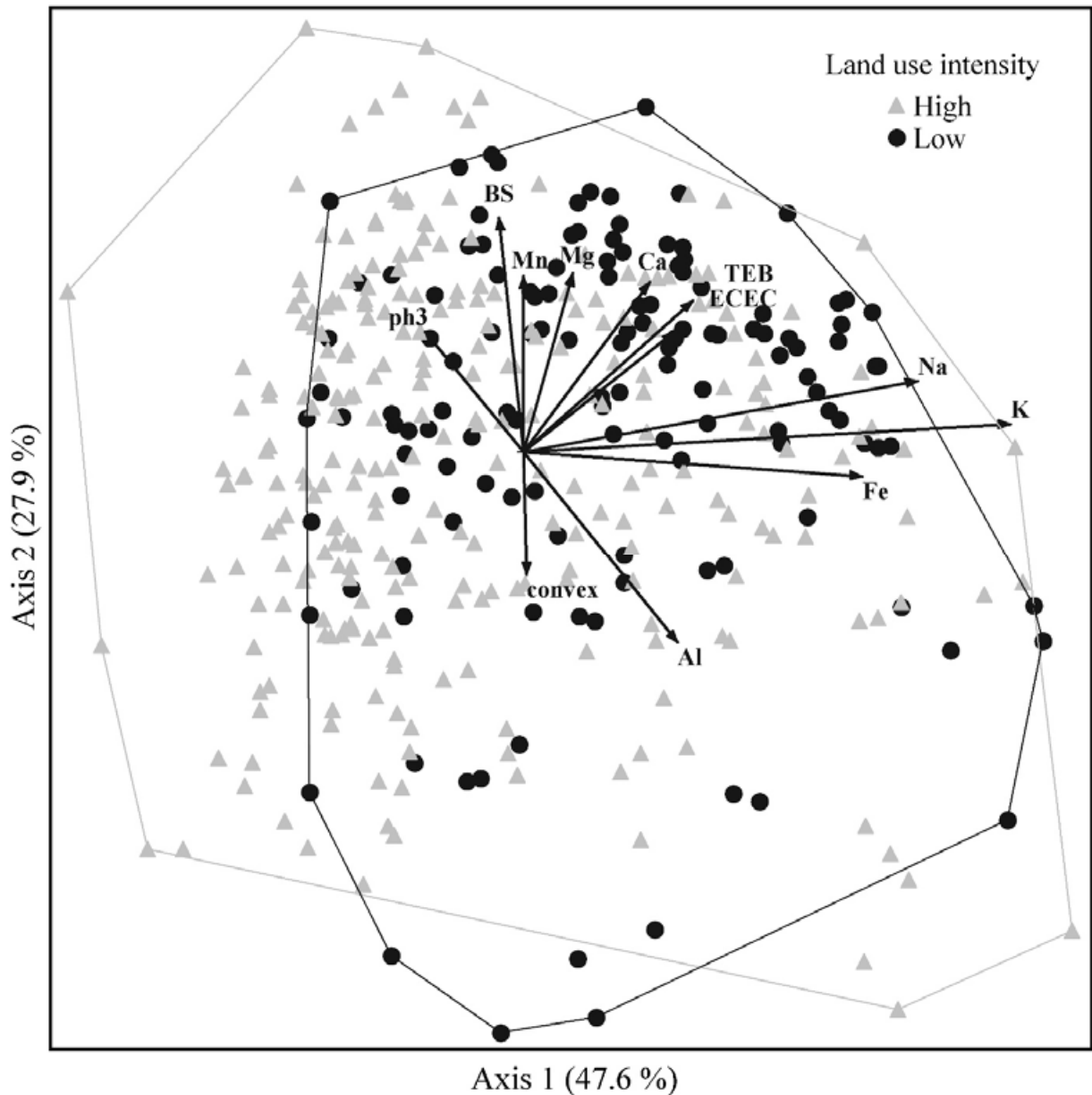
**Supporting Information**

**Figure S1:** Variance Partitioning Barplots: Results from distance-based Redundancy Analysis (db-RDA) models shown in barplot form for the entire (a), the high land-use intensity area (b), and the low land-use intensity area if the Luquillo Forest Dynamics Plot (LFDP). Bar Fractions correspond to the variance portioning diagram shown in Figures 3-5.

**Appendix S1: Beta_Diversity.pdf:** Literate Statistical Document outlining the exploration of beta-diversity variability within the LFDP.

**Appendix S2: Var_par.pdf:** Literate Statistical Document showing the transformation of response variables, forward selection of predictor variables, and db-RDA.

**Appendix S3: LFDP_PERMANOVA.pdf:** Literate Statistical Document containing the PerMANOVA results shown in Table 1.