Composition, Diversity, and Tree Structure of a Tropical Moist Forest in Gamboa, Colon, Panama

Libertas Academica
FREEDOM TO RESEARCH

José U. Jiménez, José Fábrega, Dafni Mora, Nathalia Tejedor and Marilyn Sánchez

Centro de Investigaciones Hidráulicas e Hidrotécnicas (CIHH) de la Universidad Tecnológica de Panamá (UTP), Panama City, Panama.

ABSTRACT: This study focuses on the floristic diversity of the forest trees found at Cerro Pelado Tropical Hydrology Observatory in Gamboa, Colon, Panama. Field work for the quantitative inventory was carried out in November 2012. Data were collected by assessing the status of the forest in terms of tree species diversity and structure from one-hectare plot divided into twenty-five 20 m × 20 m quadrats. All tree species were identified, and their diameters at breast height (dbh) were measured. A total of 384 individuals with (dbh ≥ 10 cm) were counted, corresponding to 28 families, 41 genera, and 43 species of which *Pera arborea*, *Oenocarpus mapora*, *Amaioua corymbosa*, *Vantanea depleta*, and *Matayba apetala* were the species with the highest ecological weight, achieving 57.99% of the importance value index. Results were compared with plots from other forests of the Panama Canal watershed in terms of diversity and number of species per area and number of individuals. It was found that the habitat studied has low diversity, with very few species in the study area, even though some of them were very abundant.

KEYWORDS: tropical moist forest, biodiversity, ecological weight, tree inventory, Panama

Introduction

Biodiversity includes various ecosystems and genetic differences within species, allowing the combination of multiple forms of life, and whose mutual interactions with the rest of the environment are the foundation for sustainable life on the planet.[1] Since the 1990s, biodiversity has been one of the most common topics discussed on local, regional, and global levels and in scientific and political writings.[2]

Important discussions about biodiversity include (i) its contribution to social and economic development, (ii) how to make sustainable use of it, (iii) biodiversity loss and its causes, (iv) instruments for conservation (in situ and ex situ), and (v) techniques for measuring and monitoring biodiversity.[3] This last topic is the interest of this study.

Panama is a developing country with relatively well-preserved natural resources and rich biodiversity, thus emphasizing the importance of integrating the processes of economic development with ecological sustainability.[4] The Panamanian National Strategy on Biodiversity recommends increasing knowledge and information on biodiversity, especially in terms of flora and fauna.[5] The forests of the Panama Canal watershed (PCW) have been scientifically studied for more than 100 years, and they are considered among the best studied tropical forests in the world.[6] Tropical moist forests (*sensu* Holdridge)[7] represent natural terrestrial communities

rich in plant species diversity, when measured by the number of tree species greater than 10 cm in diameter at breast height (dbh). It is possible to find more than 300 species per hectare in this type of forest,[8] and they are characterized by trees reaching between 25 and 35 m in height, with some emergent trees measuring up to more than 50 m in height. Other characteristics of these types of forest are the presence of buttresses on many species of trees, larger leaf sizes when compared with those of cold or higher areas, lianas of great size, and the surprising number of tree species growing together in close vicinity.[7] Currently, moist forest covers around 43% of the total land area of Panama.[9]

This exploratory/descriptive research was developed in a permanent sample plot (PSP) at the Cerro Pelado Tropical Hydrology Observatory. Our goal is to obtain a deeper knowledge of forest characteristics, as a baseline for the biological environment and its components. Therefore, this study makes an assessment of tree community characteristics, such as composition, diversity, and horizontal structure in a PSP of one hectare of forest in Cerro Pelado. The results achieved will establish causal relationships between environmental factors and groups of species or vegetation responses, which are essential for understanding the carbon and water cycles occurring at Cerro Pelado. This information is also necessary to better understand the water and carbon cycles occurring in this area.

Methods

The PSP is located in Cerro Pelado, Gamboa, Colon Province, within the PCW, with Universal Transverse Mercator coordinates: 642,570E, 1,008,898N. It has an approximate elevation of 144 m above sea level (map in Appendix 1). PSP was originally established in May 2008, and it is divided into twenty-five 20 m × 20 m quadrats. Its location was chosen so that an automatic weather station tower aligns with the exact plot center, which is also the site of previous and current studies on soil characteristics, hydraulic balance, and carbon budget.

According to the Vegetation map of Panama based on the International Classification and Mapping Vegetation System of United Nations Educational, Scientific and Cultural Organization, this study site is a tropical semideciduous lowland forest.[9]

In this study, tree inventories were made following the standard methodology and materials of the Center for Tropical Forest Science (CTFS) of the Smithsonian Institution, as in the study by Condit.[10] Field data used in this work come from a tree census completed at PSP in November 2012 and include the following variables: tree number, individual's name (species), dbh using diameter tape, reference coordinates, and location defined by the individual quadrat number. Species identification was done by a botanist on the field with help from a CTFS team. Field registers entered double entry data into an electronic database to verify for errors, making corrections as needed. With the information collected, calculations for composition, horizontal structure, and diversity were made.

Composition. The 2012 inventory data were analyzed by employing spreadsheets, and a list of reported species was drawn including the scientific name, common name, and the family to which it belongs. Taxonomic names follow the Angiosperm Phylogenetic Group classification.[11] Measurement and identification were limited to woody plants with dbh $\geq$ 10 cm. Results were compared from a previous inventory made in this PSP in 2008.[12]

Diversity. The diversity of species and richness was calculated using both Chao1 and Chao2 estimators. Alpha diversity (α) was also estimated and rarefaction curves were developed by the accumulation of species-area and species-individual. The free software EstimateS (Statistical estimation of richness and shared species from samples) was used for all diversity calculations.[13]

Chao1 is an estimator based on abundance, and it is defined as[14]:

$$S_{est} = S_{obs} + F^2/2G \qquad (1)$$

where S_{est} is the number of species to calculate, S_{obs} is the observed number of species in a sample, F is the number of species represented by only one individual in the sample, and G is the number of species represented by exactly two individuals.

Chao2 is an estimator based on incidence and is expressed as[15]:

$$S_{est} = S_{obs} + (L^2/2M) \qquad (2)$$

where L is the number of species that occur only in one sample (*unique* species), and M is the number of species that occur in exactly two samples (*double* or *duplicate* species).

Alpha diversity using the Shannon–Wiener diversity index[2] (H) expressed by equation 3[16] was employed:

$$H = -\sum_{i=1}^{S} pi * \ln pi \qquad (3)$$

where pi is the proportion of the total sample corresponding to a species i. S is the number of different species or morphospecies in the sample.

Rarefaction curves of accumulation of species-area and species-individual are developed. Rarefaction curves of species-area were generated using 25 subplots where estimated species richness was calculated as S_{est} for different sizes of area to complete one hectare with a random selection of samples without replacement (where t is a sample unit, T is the set of sample units, and Yi is the observed species incidence frequency).

Sample-based interpolation model is given by the equation[17]:

$$\tilde{S}_{est}(t) = S_{obs} - \sum_{Yi>0}\left[\left(\frac{T-Yi}{t}\right)\Big/\left(\frac{T}{t}\right)\right] \qquad (4)$$

Species-area curves were generated placing the average number of species on the *y*- and the area on the *x*-axis. Species-individual curves were generated placing the average number of species on the *y*- and the average number of individuals on the *x*-axis.

The results of diversity were compared with a typical one-hectare plot from the plot of 50 hectares at Barro Colorado Island (BCI) and with those reported in nearby woods (Gamboa). The data plots come from Condit[10] and Hubbell et al.[18,19]

Horizontal structure. A graph representing the absolute frequency of numbers versus diameter class was made for evaluating the horizontal structure and the basal area in m²/ha (sum of the areas using cross-section of the stem obtained from diameter $\geq$10 cm). Equation 5 was employed to calculate the basal area:

$$A = \frac{\pi(d)^2}{40000} \qquad (5)$$

where A is the basal area in m² of the stem; d is the dbh in cm.

The importance value index (IVI) was also calculated for each species, using a matrix in Excel. The IVI is an indicator of the phytosociological importance of a species, within a

particular community.[20] The IVI was obtained from the sum of the relative values of the abundances, dominances, and frequencies, all divided by three.[21]

$$IVI = Ab\% + Fr\% + D\% \qquad (6)$$

where Ab%, Fr%, and D% are the relative abundance, frequency, and dominance, respectively. Ab% is defined as the proportion of individuals of each species in the total number of individuals in the sample.

$$Ab\% = (ni/N) \times 100 \qquad (7)$$

where ni is the number of individuals of the ith species. N is the total number of individuals in the sample.

Fr% is calculated as the percentage of the sum of the absolute frequencies of all species.

$$Fr\% = (Fi/Ft) \times 100 \qquad (8)$$

where Fi is the absolute frequency of the ith species, and Ft is the total frequencies in the sample.

Finally, D% is the proportion of space occupied by a species in the sum of all absolute spaces of evaluated species or the sum of basal area (m^2). It is expressed as a percentage.

$$D\% = (Ai/At) \times 100 \qquad (9)$$

where Ai is the basal area in m^2 for the ith species, and At is the total basal area in m^2 in the sample.

Results

Composition. The results showed 384 individuals (trees with dbh ≥ 10 cm), comprising 28 families, 41 genera, and 43 species. The better represented families were *Fabaceae* and *Lauraceae* with 7 and 4 species, respectively. Species are listed by their absolute abundance, in descending order and by their scientific name in alphabetical order in Appendix 2.

The census of 2012 includes three additional species that comply with the criteria of selection: *Astrocaryum standleyanum*, *Cinnamomum triplinerve*, and *Miconia poeppigii*.

The composition data from 2008 and originally published by Pinzón et al[12] were reviewed and corrected by four species, namely, *Henriettella fascicularis* (before *Henriettella tuberculosa*), *Matayba apetala* (before *Inga thibaudiana*), *Cordia bicolor* (before *Cordia panamensis*), and *Ormosia coccinea* (before *Guarea guidonia*).

Diversity.

Species richness. The sample plot of Cerro Pelado has a tree species richness of 43. This estimation was based on 25 subsamples of Cerro Pelado plot (CP) using the Chao1 and Chao2 estimators, as shown in Table 1.

Shannon–Wiener diversity index. Table 2 compares the results found in Cerro Pelado with other PSP sites of equal size for individuals with dbh ≥ 10 cm (Hubbell et al;[19] Pyke

Table 1. Estimate of richness.

ESTIMATOR	ESTIMATE RICHNESS	STANDARD DEVIATION
Chao1	64.3	± 4.49
Chao2	60.6	±11.77

et al)[22]. H increases with the number of species present in the sample, and the status of all species are equally abundant.[23]

Species accumulation curve. The average number of expected species (S), its standard deviation per area, and the number of individuals are shown in Figures 1 and 2, respectively.

The distance between CP and BCI plots is 16 km approximately, and there are only 15 shared species.

Horizontal structure.

Diameter distribution. Figure 3 shows the distribution of the number of individuals per diameter class. Tree diameters are arranged in seven diameter classes at intervals of 10 cm.

The diameter distribution shows a typical inverted J curve, common of tropical forests, accumulating numerous individuals in smaller diameter classes and very few individuals in higher diameter classes.

The sum of basal area was 18.396 m^2/ha in 2012, increasing from 16.175 m^2/ha in 2008.

Importance value index. The IVI is one of the most used indexes in the analysis of tropical forest ecosystems,[24] because it easily allows us to understand a species' share in the tree community.[25]

Figure 4 compares the analysis results of IVI for the species present in the plot. Species are represented by stacked column composed by the contribution of each individual index (abundance, frequency, and dominance).

The first 20 species of greatest ecological weight are sorted in descending manner according to the values of IVI, and the remaining species are placed in a single category called Remaining Species (23 in total).

Pera arborea (19.27%) was the species with the highest IVI followed by *Oenocarpus mapora* (11.83%), *Amaioua corymbosa* (10.47%), *Vantanea depleta* (8.30%), and *M. apetala*

Table 2. Shannon–Wiener diversity index.

PSP	N	S_{obs}	H	TYPE OF SECONDARY SUCCESSION
CP	**384**	**43**	**2.74**	**Intermediate**
Gamboa[b]	568	60	2.99	Intermediate
Gamboa[b]	590	60	2.74	Intermediate
Gamboa[b]	508	75	3.37	Advanced
Gamboa[b]	405	78	3.76	Advanced
BC[a]	438	89	3.86	Advanced

Notes: [a]Hubbell et al;[19] [b]Pyke et al.[22]
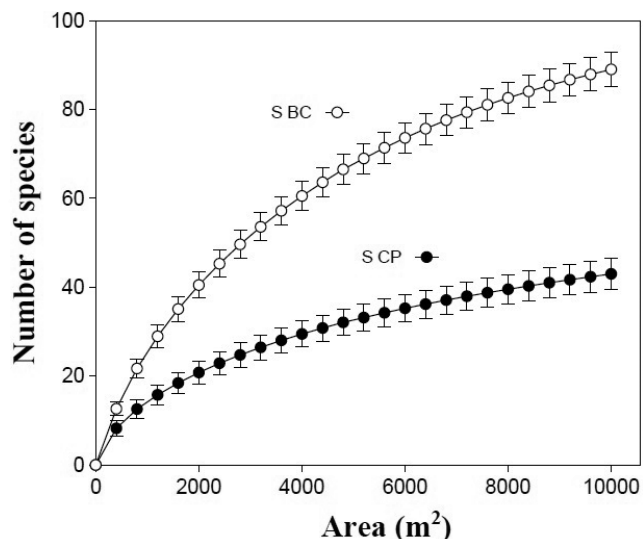
Figure 1. Species-area accumulation curve for CP and a typical one-hectare plot from BCI.

Figure 3. Distribution of the number of individuals per diameter class for CP.

(8.11%). *P. arborea* was also the leading species in terms of individual indexes, with values for abundance, frequency, and dominance of 19.79%, 11.65%, and 26.73%, respectively.

Discussion

The census of 2012 showed the occurrence of trees like *Virola sebifera* and *Alseis blackiana*, and palms like *O. mapora* and *Astrocaryum standleyanum* for the CP. These four species are reported among the 10 most frequently occurring species within the tropical lowland moist forest of the PCW.[22]

As already mentioned, *P. arborea* was the species with the highest values for IVI and for individual indexes also. In its Latin designation, *Pera* means sack or bag, referring to the bag-shaped involucres hosting the flowers.[26]

These results seem to agree with those reported in the study by Pinzón et al,[12] who also presented that *P. arborea*
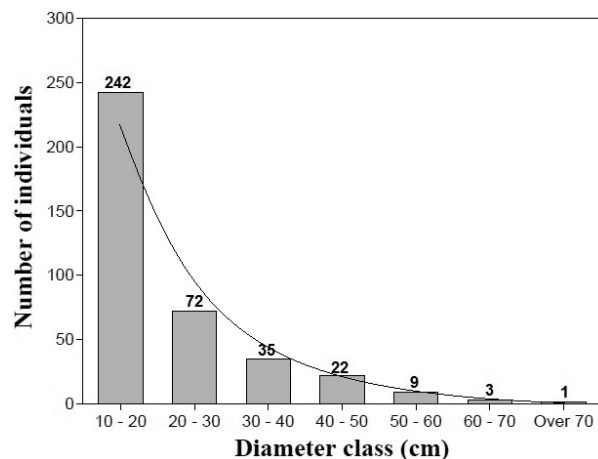
(incorrectly identified as arborius pear in that article) was the most abundant species in terms of absolute values.

Comparing our result with the results from other forests of the PCW, we found that a square plot of one hectare in the PCW can hold 421 trees and 79 species on an average.[22] Our main reference plot of 50 hectares on BCI, for example, can hold on an average of 425 trees and 91 species.[27]

Also, other one-hectare plots in the Gamboa area have reported values for observed species, between 60 and 78,[22] which confirms the tendency of Cerro Pelado to lesser richness when compared with other control plots.

A comparison between CP and BCI plots shows that 90% of the reported species in each one-hectare plot was reached after covering 75% of the one-hectare plot. In terms of individuals, these values translate in at least 292 individuals for PSP CP and 325 individuals for PSP BCI to reach 90% of the total number of species in each plot.
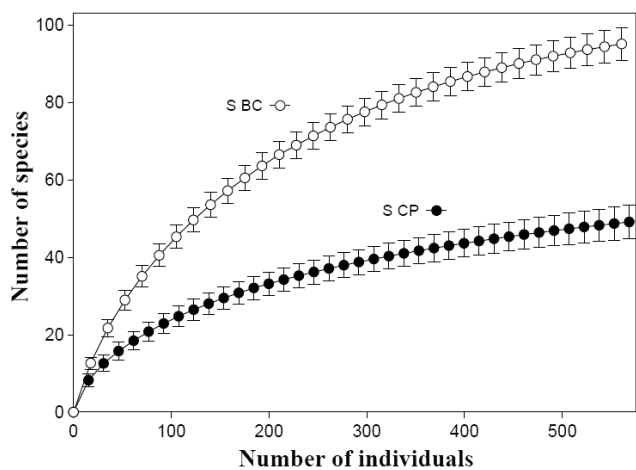

Figure 2. Species-individual accumulation curve for CP and a typical one-hectare plot from BCI.
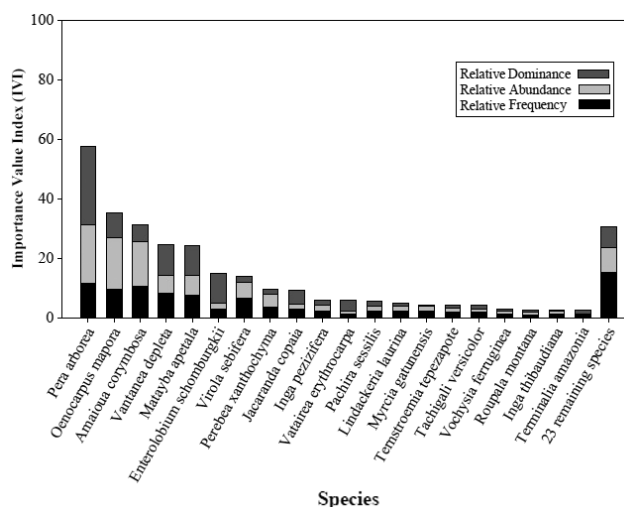

Figure 4. Variation of the IVI for the tree species on one-hectare plot of tropical moist forest at Cerro Pelado.

The inverted J shaped curve pattern is evident when looking at the individuals' number per diameter class distribution, where the largest number of stems belongs to the smaller diameter class. Therefore, when the diameter stem size increases, the number of stems decreases exponentially. The trend to get an inverted J dbh density distribution is characteristic of tropical forests in general, which should have a greater number of young individuals to ensure the replacement of trees with larger diameters.[24] This pattern is an indicator of healthy recruitment in the forest.[28] It was observed that over 80% of individuals belong to the smaller diameter class (10–30 cm dbh), resulting in only one individual with over 70 cm in stem diameter at the PSP CP.

Mature forests have the capacity to keep a stable structure based on a dynamic balance between mortality, recruitment, and plant growth. Based on this fact, the average value of basal area of 28.5 m^2/ha of the mature forest of BCI (oldest forest) was used as a reference.[29,30]

The sum of basal area in 2008 was 16.175 m^2/ha, and it increased to 18.396 m^2/ha in 2012. Compared with the reference value of 28.5 m^2/ha, it shows that the successional community type is younger and still growing and has not yet attained its potential maximum level of maturity. The sum of basal area is used as an index of the stage of development of a forest.[31]

In addition, compiled data suggest that the secondary forest at CP is currently in an intermediate stage of succession, where trees have not yet reached 100 cm dbh. Moreover, the basal area is still far from reaching the average basal area shown by our reference site on Barro Colorado. We discuss the studies conducted by Leigh, which examine the differences between the young and mature forests on the BCI site and relate to a quantity of very large trees with dbh $\geq$ 100 cm.[29] The young forest has fewer large trees compared with a mature forest in this area, highlighting the absence or presence of up to 3 trees with dbh $\geq$ 100 cm per hectare for young forest and the existence of 3–10 trees with dbh $\geq$ 100 cm per hectare in old forests.[30]

Foster and Browkaw estimated that the young forest on BCI is about 100 years old, and the majority of the old forest has had few disturbances over the past 300–400 years.[32] Foster and Browkaw used local history to help establish an approximate age of the old and new forests on BCI.[32] The categories they used to establish the age were well defined and explained in their article. Pyke et al, in turn, used three age categories to analyze the forests in the PCW, which includes the island of Barro Colorado: young (secondary forest), secondary (mature secondary), or old growth (primary forest).[22] These age categories are established by the size of the larger trees, yet Pyke et al do not clearly explain or reference their criteria.

In both cases, the criteria to determine the stage of succession of the community and whether it was a old or a new forest, was based on the forest structure, specifically the size (height and diameter) and quantity of the large trees in a given area, a method which has not been proven to accurately calculate the age of a tropical forest. Problems in collecting data in a mature forest arise when sample plots are located in areas that have suffered recent large light-gap disturbances and have a regenerative growth pioneer species.

Now, when discussing the structural and functional complexity achieved by the biological community, we prefer to use the terms "intermediate forest" and "advanced forest"; since the terminology, "young" or "old" forest is commonly associated with age. This means specifically the time of a forest without significant intervention and comparing it with another, which is subjective and does not facilitate an easy comparison between sites. For example, a 200-year-old forest may be considered "old forest" when compared with a 100-year-old forest, but it would be a "young forest" when compared with a 400-year-old one.

Ecological weight comparisons of each species within the ecosystem were possible by utilizing the IVI index.[25,33] IVI results are based on the tree community with dbh $\geq$ 10 cm and the sampling of 25 subplots of 400 m^2 at the CP plot. The first five species, such as *P. arborea*, *O. mapora*, *A. corymbosa*, *V. depleta*, and *M. apetala*, showed the highest ecological weight with an IVI value of 57.99%, becoming more evident when compared with the group of Remaining Species, which together showed a ecological weight of 10.23%. *P. arborea*, the most common tree species in the CP, has not been reported on BCI.[34]

Our results characterize the tree community as slightly diverse, in a typical stage of intermediate secondary succession, with few species of trees, some of these being very abundant. *P. arborea* is the most abundant, more frequent, and most dominant species in this habitat (plot). It is expected for future census results to evaluate the succession rates of this and future plots in Cerro Pelado with known rates achieved in other experimental plots at the PCW. This evaluation will give an idea of the effect of hydroclimate changes in the development of tropical moist forests.

Conclusion

The forest in Cerro Pelado is a secondary forest, product of a natural regeneration process of more than 90 years without significant intervention. The study found that the successional community on CP is less diverse than other forests in the PCW. The tree diversity at CP plot is below the average diversity of similar one-hectare reference plots reported in forests at BCI and the PCW. These results can be explained by the fact that compared with BCI forest, Cerro Pelado is not only a younger forest in terms of age, but a forest in an intermediate stage of succession in terms of its structural and functional complexity.

Therefore, when compared with our reference forest (mature forest/advanced forest) in BCI, the CP has a moderate basal area per hectare and continues to grow. These results show that the tree community with dbh $\geq$ 10 cm in Cerro Pelado (represented by the CP) is less diverse, because it has

very few species by area or individuals observed, even though some of these species are abundant.

More than half of the total ecological weight is found in only five species. At the top of them, *P. arborea* appears as the most abundant, frequent, and dominant species.

Further studies on species composition, diversity, and forest structural attributes in Cerro Pelado are necessary. Also, increasing the number of plots will contribute to a higher significance in results.

Acknowledgments

Author Contributions

Conceived and designed the experiments: JUJ and JF. Analyzed the data: JUJ, DM, NT, and MS. Wrote the first draft of the manuscript: JUJ. Contributed to the writing of the manuscript: JUJ, JF, DM, NT, and MS. Agreed with manuscript results and conclusions: JUJ, JF, DM, NT, and MS. Jointly developed the structure and arguments for the paper: JUJ, JF, and DM. Made critical revisions and approved the final version: JF. All the authors reviewed and approved the final manuscript.

Supplementary Materials

Appendix 1. Location of the PSP in Cerro Pelado, Gamboa, Colon. The image was taken from Google Earth. Image Date: January 31, 2013.

Appendix 2. The common names in Spanish to Panama. Abun. is absolute abundance of species; BA (m^2) is the sum of basal area by species; IVI is IVI of species.

REFERENCES

1. Convenio sobre la diversidad biológica. *The United Nations Conference on Environment and Development*. Rio de Janeiro, Brazil: 1992:34. Available at: http://www.cinu.org.mx. Accessed January 9, 2015.
2. Magurran A. *Measuring Biological Diversity*. UK: Blackwell; 2004.
3. Butler T, Boontawee B. *Measuring and Monitoring in Tropical and Temperate Forest*. Bonger, ID: Center for International Forestry Research (CIFOR); 1995.
4. Urza A. *Sustainable Development and Biological Diversity: A Case Study of Deforestation in Panama*. Panama: VDM Publishing; 2008.
5. Madrigal P, Solís V. *Diagnóstico sobre el Ordenamiento Jurídico e Institucional de la Biodiversidad en Panamá*. San José, Costa Rica: Unión Internacional para la Conservación de la Naturaleza (UICN); 2000.
6. Perez RA. *Árboles de los Bosques del Canal de Panamá*. Panamá: Boski, S.A.; 2008.
7. Holdridge LR. *Ecología basada en Zonas de Vida*. San José, Costa Rica: Instituto Interamericano de Cooperación para la Agricultura (IICA); 1978.
8. Gentry A. Tree species richness of upper Amazonian forest. *Proc Natl Acad Sci U S A*. 1988;85(1):156–159.
9. Autoridad Nacional del Ambiente (ANAM). *Atlas Ambiental de la República de Panamá*. Panamá: Novo Art, S.A; 2010.
10. Condit R. *Tropical Forest Census Plots*. Germany: Springer-Verlag; 1998. doi:10.1007/978-3-662-03664-8.
11. Stevens P. *Angiosperm Phylogeny Website. Version 13*. 2013. Available at: mobot.org/MOBOT/research/APweb/. Accessed January 15, 2015.
12. Pinzón R, Fábrega J, Vega D, et al. Estimates of biomass and fixed carbon at a rainforest in Panama. *Air Soil Water Res*. 2012;5:79–89. doi: 10.4137/ASWR.S9528.
13. Collwell R. *Estimate S: Statistical Estimation of Species Richness and Shared Species from Samples*. 2013. Available at: purl.oclc.org/estimates. Accessed January 9, 2015.
14. Chao A. Nonparametric estimation of the number of classes in a population. *Scand J Stat*. 1984;11:256–270.
15. Colwell RK, Coddington JA. Estimating terrestrial biodiversity through extrapolation. *Philos Trans R Soc Lond B Biol Sci*. 1994;345(1311):101–118. doi: 10.1098/rstb.1994.0091.
16. Shannon C, Wiener W. *The Mathematical Theory of Communication*. Urbana: University of Illinois Press; 1963.
17. Colwell RK, Chao A, Gotelli NJ, et al. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J Plant Ecol*. 2012;5(1):3–21. doi: 10.1093/jpe/rtr044.
18. Hubbell S, Condit R, Foster R. *Barro Colorado Forest Census Plot Data 2010*. 2014. Available at: https://ctfs.arnarb.harvard.edu/webatlas/datasets/bci. Accessed August 15, 2014.
19. Hubbell S, Foster R, O'Brien S. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*. 1999;(80). Avaialable at: http://www.sciencemag.org/content/283/5401/554.short
20. Lozada Dávila JR. Consideraciones metodológicas sobre los estudios de comunidades forestales. *Rev For Venez*. 2010;54(1):77–88.
21. Curtis J, McIntosh R. The interrelations of certain analytic and synthetic phytosociological characters. *Ecol Soc Am*. 1950;31(3):434–455. doi: 10.2307/1931497.
22. Pyke CR, Condit R, Aguilar S, Lao S. Floristic composition across a climatic gradient in a neotropical lowland forest. *J Veg Sci*. 2001;12(4):553–566. doi: 10.2307/3237007.
23. Moreno CE. Métodos para medir la biodiversidad. *M T Manuales y Tesis Soc Entomológica Aragon*. 2001;1:84.
24. Lamprecht H. *Silvicultura en los Trópicos: los Ecosistemas Forestales en los Bosques Tropicales y sus Especies Arbóreas—Posibilidades y Métodos para un Aprovechamiento Sostenido*. Deutsche Gesellschaft fur Technische Zusammenarbeit (GTZ) GmbH; 1990.
25. BOLFOR, Mostacedo B, Fredericksen TS. *Manual de Métodos Básicos de Muestreo y Análisis en Ecología Vegetal*. Santa Cruz, Bolivia: Editorial El País; 2000.
26. Cardiel Sanz JM. Una nueva especie de Pera (Euphorbiaceae) de Colombia. *Caldasia*. 1991;16(78):311–315.
27. Condit R, Hubbell S, La Frankie J, et al. *Relaciones especie-área y especie-individuo en árboles tropicales: una comparación de tres parcelas de 50 hectáreas*. In: Ecología y Evolución en los Trópicos. Leigh E, Allen E, Jackson J, Santos-Granero F, eds. Panamá: Novo Art, S.A; 2006:448–464.
28. Sahu S, Dhal N, Mohanty R. Tree species diversity, distribution and population structure in a tropical dry deciduous forest of Malyagiri hill ranges, Eastern Ghats, India. *Trop Ecol*. 2012;53(2):163–168.
29. Leigh EGJ. Introducción: ¿por qué hay tantos tipos de árboles tropicales? In: Leigh EGJ, Rand AS, Windsor DM, eds. *Ecología de un Bosque Tropical*. Bogotá, Colombia: Editorial Presencia LTDA; 1992:75–99.
30. Leigh EG. *Tropical Forest Ecology: A View from Barro Colorado Island*. New York, US: Oxford University; 1999.
31. CATIE (Centro Agronómico Tropical de Investigación y Enseñanza). *Silvicultura de Bosques Latifoliados Húmedos con énfasis en América Central*. In: Serie Técnica—Manual Técnico N° 46. Louman B, Quirós D, Nilsson M, eds. Turrialba, Costa Rica:CATIE; 2001.
32. Foster R, Browkaw N. Estructura e historia de la vegetación de la isla de Barro Colorado. In: Leigh EGJ, Rand AS, Windsor DM, eds. *Ecología de un Bosque Tropical*. Bogotá, Colombia: Editorial Presencia LTDA; 1992:113–127.
33. Cruz Melo OA, Ríos Vargas R. *Evaluación Ecológica y Silvicultural de Ecosistemas Boscosos*. Ibagué, Colombia: Universidad del Tolima; 2003.
34. Smithsonian Tropical Research Institute. *Barro Colorado Island Species List*. 2015. Available at: http://www.ctfs.si.edu/site/Barro+Colorado+Island/species/?page=5. Accessed January 20 2015.