



Tree families and physical structure across an elevational gradient in a Southern Andean Cloud forest in Ecuador

R. W. Myster

Department of Biology, Oklahoma State University, Oklahoma City, OK 73107, USA.

Abstract

Because the elevational gradient of the Andes is a fundamental correlate of the structure, function, and dynamics of its Cloud forest, I sampled tree species, families and physical structure across an 1100 m elevational gradient – at 100 m intervals from 1900 m to 2800 m – in an Andean Cloud forest close to Loja in Southern Ecuador. I found (1) the species *Clusia* sp., *Nectandra membrenacea* and *Miconia punctata*, and the families Clusiaceae, Lauraceae, Melastomataceae, and Rubiaceae, were most common with Annonaceae, Cyatheaceae, Hypericaceae, Malvaceae and Solanaceae least common and (2) skewed unimodal curves best fit the species and symmetric unimodal (Gaussian) curves best fit the families. I also found (1) total stem density increased with elevation (772/ha – 984/ha) but not monotonically with the smallest stem size always the most common and (2) linear curves best fit physical structure. I conclude that while both tree species and tree families were distributed individualistically across this Andean elevational gradient, with two families showing a peak at mid-elevations, stem density increased with elevation as stem size decreased which lead to several parameters (e.g., basal area, above-ground biomass) being unchanged while others (e.g., richness, diversity) were always low.

Keywords: Curve-fitting, Reserva Biologica San Francisco

Introduction

Research into how gradients structure ecosystems has a long history in ecology (1,2,3,4). For example, studies have shown that species are distributed randomly across gradients (1,2,5), gradients have various effects across latitudes, longitudes, and elevations (4), and gradients due to climate change have increasingly important impacts on ecosystems (6,7). Among gradients, spatial gradients across elevations have been perfect places to investigate this relationship they include abiotic drivers – for example, precipitation, humidity, and temperature – that have been shown to have fundamental effects on mountain ecosystems (Chapter 8).

Within the Neotropics, a large elevational gradient is created by the Andean mountains along the western edge of South America. These Andes consist of “cordilleras” (9) where at their eastern flank they drop down to Western Amazonia (10,11,12) and at their western flank to the Pacific ocean (13). Occurring on all the cordilleras between 1000 m and 3000 m at sea level (i.e., a.s.l) are Cloud forests (8,14). These Cloud forests both add to the biodiversity of the Neotropics (e.g., the Andes themselves have 16.4% of all the plant species in the world: 15) and significantly contribute to Neotropical hydrological and other biogeochemical cycles (16).

Therefore because of the importance of Andean cloud forests to the neotropics, and because of the importance of the elevational gradient in defining those Cloud forests, I take advantage of a well-defined Cloud forest and elevational gradient in the Andes of Ecuador to sample tree (including tree ferns) species, tree families and tree physical structure, and then use that data to test these six hypotheses dealing with plant taxa and ecosystem structure:

(1) Tree species and tree families are distributed along the Andean elevational spatial gradient individualistically (2,17,18) without any pattern of clumping,

(2) Some of these species and families have a mid-elevation peak along that gradient which may be due to the overlap of the distributions of the same tree species and tree families found at both higher and lower elevations (11),

(3) Many of the species and family gradient patterns can be fitted significantly to mathematical models (19,20) with a skewed unimodal pattern a plateau pattern most common (21,22,23),

(4) Tree physical structure is distributed along the Andean elevational spatial gradient individualistically (2,17,18) without any pattern of clumping,

(5) Many of these structural patterns can be fitted significantly to mathematical models (19,20) with a symmetric unimodal (Gaussian) pattern most common (21,22,23,24), and

(6) Structural patterns distributed across the Andean elevational gradient are similar to tree structural patterns found in other Cloud forests in the Neotropics (25,26,27).

Material and Methods

Study area

The study was conducted in the Reserva Biológica San Francisco (RBSF: 3° 58' 30" S, 79° 4' 25" W, 16,28) in Southern Ecuador. RBSF is in the Andean Cloud forest but not all of it is primary, some of that Cloud forest is secondary due to the past impacts on indigenous peoples (29,30). Soils include Dystrudepts, Haplosaprists, Petraquepts, and Epiaquents (31). Temperatures span 9° to 17° C and annual precipitation from 2200 to 5000 mm per year (31).

15 January 2024: Received | 10 February 2024: Revised | 07 March 2024: Accepted | 04 May 2024: Available Online

Citation: R. W. Myster (2024). Tree families and physical structure across an elevational gradient in a Southern Andean Cloud forest in Ecuador. *Journal of Plant Biota*. DOI: <https://doi.org/10.51470/JPB.2024.3.1.37>

R. W. Myster | mysterrwm1@gmail.com

Copyright: © 2024 by the authors. The license of *Journal of Plant Biota*. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).

Field sampling

In January 2019 my field assistants and I randomly chose an elevational gradient with a south-facing aspect in an Andean Cloud forest across from Rio San Francisco – RBSF – and set up one 50 m x 50 m (¼ ha) plot at 1900 m, 2000 m, 2100 m, 2200 m, 2300 m, 2400 m, 2500 m, 2600 m, 2700 m, and 2800 m. This plot size and shape have been used successfully to sample floristics and physical structure in this same Cloud forest at RBSF and at several of these same elevations (see Chapter 16). In each plot we sampled all trees (including tree ferns) at least 10 cm in diameter at breast height (dbh), measuring at the lowest point where the stem was cylindrical but above the buttresses if the tree was buttressed. We also identified the trees to family, to genus, and (if possible) to species, using (32) and (33) as taxonomic sources and also consulting the Missouri Botanical Garden website (www.mobot.org) where voucher samples are kept. No research permits were necessary because the sampling was non-destructive and did not include any removal of biomass.

Data analysis

The number of stems for each tree family and the number of stems for each common tree species (defined as those species having at least 5% of the total stems of their family) was first compiled in each sampling plot on the elevational gradient. Next for each plot, these structural parameters were computed (1) tree stem density, number of stems in each size class: $10 \leq 19$ cm dbh, $20 \leq 29$ cm dbh, $30 \leq 39$ cm dbh and ≥ 40 cm dbh, and the mean dbh for all stems combined, (2) family richness, genus richness and species richness, (3) Fishers' alpha (α) diversity (http://groundvegetationdb-web.com/ground_veg/home/diversity_index), (4) total basal area ($\sum \pi r^2$; r = dbh of an individual stem / 2), (5) above-ground biomass (ABG: [35]), and (6) canopy closure (sum of all tree crown areas in a plot divided by the area of that plot, where crown areas are estimated from regressions on dbh [36]).

The number of stems at each elevation for each common tree species, for each tree family, and for each structural parameter was then subjected to a curve-fitting analysis (19, 20, 37) using (1) a symmetric unimodal model (i.e., a standard normal Gaussian distribution: 38), (2) a skewed unimodal model, (3) a linear model and (4) a plateau model (21,22,23). Each model employed least-squares regression analysis after the appropriate transformation (38,39,40,41) where the stem data did not have an upper bound (42). The independent variable was elevation and the dependent variables were the number of stems in a species or a family, or a structural parameter (software @ www.MyCurveFit.com was used). Significant regressions are expressed in the results as (1) the Y-intercept of the best-fit regression line, (2) the slope of that line, (3) the amount of variation explained by that line (R^2), and (4) the p-value of the best-fit line.

Results

All 29 tree families had individualistic distributions, peaking at different elevations (e.g., the families Aquifoliaceae [at 2400 m] and Euphorbiaceae [at 2300 m] peaked at mid-elevation: Table 1). Melastomataceae (with 461 stems), Lauraceae (with 430), Clusiaceae (with 182), and Rubiaceae (with 180) were the most common. Solanaceae (with 1 stem), Malvaceae (with 3), Annonaceae (with 4), Cyatheaceae (with 4), and Hypericaceae (with 4) were the least common. Clusiaceae, Lauraceae, and Melastomataceae had stems in every plot.

Annonaceae, Hypericaceae, Malvaceae, Monimiaceae, Solanaceae, and Sapindaceae had stems in only one plot, where the plot at 2400 m was the only one with more than one (2) of those families. Ten of those families fit curves (mathematical models) significantly: a symmetric unimodal curve for Aquifoliaceae ($R^2 = 80\%$, $p = 0.03$), Clusiaceae ($R^2 = 78\%$, $p = 0.29$), Euphorbiaceae ($R^2 = 62\%$, $p = 0.05$), Primulaceae ($R^2 = 90\%$, $p = 0.01$) and Podocarpaceae ($R^2 = 82\%$, $p = 0.03$), a skewed unimodal curve for Lauraceae (left: $R^2 = 88\%$, $p = 0.02$) and Melastomataceae (left: $R^2 = 65\%$, $p = 0.05$), a linear curve for Myrtaceae (Y-intercept = 0.51, slope = 0.31, $R^2 = 75\%$, $p = 0.25$) and a plateau curve for Primulaceae ($R^2 = 85\%$, $p = 0.02$) and Rubiaceae ($R^2 = 70\%$, $p = 0.04$).

All of the most common tree species were in separate tree families – except for two species in Clusiaceae, three species in Lauraceae, three species in Melastomataceae, and two species in Rubiaceae – and also had individualistic distribution patterns with peaks at different elevations: (Anacardiaceae) *Tapirira cf guianensis* (2000 m), (Clusiaceae) *Clusia alata* (2200 m), (Clusiaceae) *Clusia doaoides* (2300 m), (Euphorbiaceae) *Alchornea lojaensis* (2300 m), (Lauraceae) *Nectandra membranacea* (2200 m), (Lauraceae) *Ocotea* sp. (2500 m), (Lauraceae) *Persea weberbourni* (2600 m), (Melastomataceae) *Graffearieda enarginata* (1900 m), (Melastomataceae) *Miconia punctata* (2700 m), (Melastomataceae) *Tibouchina lepidota* (2400 m), (Myrtaceae) *Myrcia* sp. nov. (2500 m), (Rubiaceae) *Palicourea uiloana* (2000 m) and (Rubiaceae) *Elaeagia cf. obovato* (1900 m). Four of those species fit curves (mathematical models) significantly: a symmetric unimodal curve for *Clusia alata* ($R^2 = 68\%$, $p = 0.04$) and skewed unimodal curves for *Nectandra membranacea* (left: $R^2 = 85\%$, $p = 0.03$), *Graffearieda enarginata* (left: $R^2 = 62\%$, $p = 0.05$) and *Miconia punctata* (right: $R^2 = 54\%$, $p = 0.05$).

stem density increased from 772/ha to 980/ha, but not monotonically because total tree stems per unit area decreased from 2100 m to 2200 m (Table 2). In every plot the smallest stem size was most common and the next smallest stem size had almost all of the remaining stems. All canopies were in the 60-70% closure range. Three structural patterns fit curves (mathematical models) significantly: linear curves for total stems (Y-intercept = 1.77, slope = 0.11, $R^2 = 85\%$, $p = 0.02$) and for % of the total stems $20 < 29$ cm dbh (Y-intercept = 22.54, slope = -1.81, $R^2 = 69\%$, $p = 0.04$), and a plateau curve for % of the total stems > 40 cm dbh ($R^2 = 73\%$, $p = 0.03$).

Discussion

Hypotheses 1, 2 and 3

There was support for the first hypothesis because species and families were distributed individually along the gradient (2) peaking at different elevations, similar to (17) and (18) and where species peaked at different times after abandonment from cultivation (a temporal gradient: 4), some support for the second hypothesis because three species and two families showed a mid-elevational peak at 2300 m or 2400 m, and some support for hypothesis three because four species out of 13, and 10 families out of 29, had significant curves with the symmetric unimodal most common.

There was a substantial number of plant families and a large variation in number of stems within the families. Plant families found across this elevational gradient were also commonly found (1) in primary cloud forests within RBSF (31), within the Andes (43,44,45), and the Neotropics (46), and (2) in secondary cloud forests within RBSF (16), within the Andes

(43,44,45,47,48) and the Neotropics (46). Curve-fitting algorithms found significant models for more than a third of the families half of those were symmetric unimodal (Gaussian) models (40). All of the most abundant families had significant models, which included both of the families that fit a skewed unimodal model. There were differences among the familial response curves across the elevational gradient (24). Linear monotonic familial responses were rare and most of the abundant species did not reach their peak abundance at mid-elevation (11). Distributions of species across this ACF elevational gradient were more continuous (which supports an ecocline perspective) than discrete (which would have supported an ecotone perspective: see discussion in [47]). Moreover, the number of families among sampling points did not increase with elevation (see Rapoport's rule: 49).

Common plant families sampled in this study were also common in the cloud forests in the Dominican Republic (Melastomataceae: 50), in Thailand (Lauraceae: 51), in India (Melastomataceae, Clusiaceae and Rubiaceae: 52), in Sri Lanka (Clusiaceae: 53) and Cameroon (Melastomataceae, Lauraceae, Clusiaceae and Rubiaceae: 54). Cloud forest studies outside the Neotropics that computed structural parameters using different tree sizes (starting at 5 cm dbh in Kenya:[55] and at 2 cm dbh in Hawaii:[56]) however, made comparisons with this study difficult.

As suggested in hypothesis two, several of the hump-shaped (symmetric unimodal) curves found in this study may be due to overlapping species distributions from the bottom and the top of the RBSF elevational gradient (the mid-domain effect:[61]), as was true for fern species richness along another elevational gradient (40). Also for ferns, this time in Costa Rica, species richness showed a symmetric unimodal curve with elevation (peaking at 1700 m:[62]). In Australia, Eucalypt species (*Eucalyptus* sp.) had skewed unimodal curves where the direction of the skew depended on the optimum temperature (21). Most of the curves for salt marshes vegetation were skewed unimodal (63) and for swamp forest vegetation unimodal curves were seen for species with low tolerance, but not seen for species that favored gradient extremes (23).

For tree pollen collected in Peru *Alchornea* sp. and families Urticaceae (Moraceae), Bignoniaceae and Cecropiaceae dominated below 1000 m, *Acalypha* sp., *Alchornea* sp. and Cecropiaceae, Rubiaceae and Urticaceae (Moraceae) between 1000 m and 1600 m, *Hedyosmum* sp., *Alnus* sp. and Poaceae and Combretaceae (Melastomataceae) between 1600 m and 2000 m, *Alnus* sp. between 2000 m and 2700 m, and above 2700 m, *Polylepis* sp., and Asteraceae, Poaceae and Myrsine (64). In the Bolivian Andes richness of epiphytes peaked at 1500 m and then declined with elevation, with ridges having lower richness than slope forests and usually hump-shaped curves (65). But effects of the elevational gradient may be less than effects of forest edge and topographical heterogeneity (66).

Hypotheses 4, 5 and 6

There was some support for hypothesis four because some structural parameters were individualistic, some support for hypothesis five, because there were significant curves but unimodal patterns were not most common, and mixed support for hypothesis six because Cloud forest structural parameters in this plot compared well to another sampling in Ecuador and also to sampling in Venezuela but not as well to samplings in Costa Rica or Puerto Rico. Most other studies did not have the data to confirm the result of similarities of basal area and AGB with

elevational changes ([67] did not show this). When compared to other Neotropical Cloud forests, total stems in this RBSF Cloud forest were similar (25,26,27,44,67) but the basal area was less. This gradient had a higher density at 1400 m in Ecuador (44) but similar in Venezuela (27), with larger stems at 1400 m both in Ecuador (44), and in Costa Rica (25,26). Species richness and basal area was similar to Ecuador (44) but not to Costa Rica (25,26) or Puerto Rico (67).

The most general result for physical structure was that as stem density increased with elevation, stem size decreased which lead to similarities in basal area, AGB and canopy closure among the sampled points across the gradient. Two of the three significant curves were linear which may relate to the linear variation of temperature and precipitation along this gradient (16). In addition, many of the changes in physical structure along this elevational gradient reflect known trends of a decrease in primary productivity, height of canopy and emergent trees, and number of strata as elevation increases (44,45). There was not an increase in stems of all sizes with elevation in this study and diversity showed little variation, compared to elsewhere in Ecuador Cloud forests (44). There were mid-elevation peaks in Puerto Rican montane forest for basal area, above-ground biomass, canopy height, and mean species richness, and an increase in the proportion of native and endemic species with elevation (68). Finally across most of the tropical latitudinal gradient richness patterns are symmetrically hump-shaped, but at the edges of the Andes (18° N and 18° S latitude) there are differences (69).

Conclusion

I conclude for the three floristic hypotheses (1) tree floristic patterns along the Andean elevational gradient were individualistic with no families clumping in distribution with other families, (2) Aquifoliaceae and Euphorbiaceae did show a mid-elevation crest in abundance (i.e., a symmetric unimodal/Gaussian pattern) and (3) many of the familial patterns were fitted to common mathematical models with all models present and a symmetric unimodal pattern most common.

I conclude for the three structural hypotheses (1) several structural patterns (i.e. basal area, AGB, richness, diversity) along this gradient were not individualistic, (2) several patterns were fitted to common mathematical models with a linear curve most common and (3) patterns compared well to several other Neotropical Cloud forests. While stem density increased with elevation, the size of stems decreased making several parameters (e.g., basal area, above-ground biomass) similar regardless of elevation. Across the gradient richness and diversity were consistently low and the study Cloud forest had a more closed canopy than Amazon forests.

This study constructed and analyzed response patterns, and then could only compare those patterns against hypotheses about pattern. This study does set-up, however, future studies that could investigate mechanisms causing the shapes of these and other response curves. Those mechanisms could include (1) competition and physiological tolerance (57), (2) geometric constraints on habitat for unimodal response curves, and (3) resource availability and temperature relationships within the elevational gradient for linear response curves (see discussion in 58). In particular, for the Andes higher relief and steeper rainfall gradients as well as more human disturbance and climate change on the eastern flank of the Andes compared to the western flank, might help explain future response curves if

they show a loss of plant families and a reduction of structure over time (11,59,60). I suggest that many of these mechanisms relate to the plant-plant replacement process (8,71) by influencing (assuming a low degree of seed rain limitation:[72]) seed (i.e., predation, pathogens, germination) and seedling (i.e., herbivory, pathogens, competition) processes (i.e., the regeneration niche [73]). And so an important research area in the future should be how insects, birds, mammals (all potential predators), and fungi (a potential pathogen) taxa vary and function along Andean elevational gradients (see chapters in [8]).

Finally the floristics and the physical structure data sampled here in the primary Andean Cloud forest (and elsewhere in the primary Andean Cloud forest: author, unpub. data) creates an important baseline data set which can be used in future comparative studies of primary, but also secondary Andean Cloud forests as they recover from disturbances across their elevational gradients (e.g., tree-fall, landslides, conversion to agriculture and pasture after slash-and-burn, roads and urban development). Long-term sampling of both primary and secondary Cloud forest in the Andes (see chapters in [8]) also contributes to this research objective.

Funding: This work was self-supported.

Acknowledgements: I thank Jessica Paccha and Edgar Dario Ramon Castillo for their help in the field and Pedro Paladines for logistic assistance at the RBSF field station. I also thank D. Strong, D. Bonte, K. Gross, J. Powers, H. Asbjornsen, D. Williams, V. Novotny, T. Whitfeld and D. Gibson for commenting on a past draft of the manuscript. Please visit my webpage (www.researchgate.net/profile/Randall_Myster) for more details about this and similar research.

Table 1. Number of stems sampled at each elevation (m), divided into plant families.

Family	1900	2000	2100	2200	2300	2400	2500	2600	2700	2800
Alzateaceae	0	0	14	4	0	1	11	9	0	9
Anacardiaceae	0	22	7	8	14	3	19	7	0	0
Annonaceae	0	0	0	0	4	0	0	0	0	0
Aquifoliaceae	0	0	8	11	8	19	9	0	11	1
Araliaceae	0	16	0	0	5	1	0	9	15	
Arecaceae	0	0	12	5	9	6	12	0	0	0
Clethraceae	0	0	0	0	0	3	9	0	0	0
Chloranthaceae	0	0	4	0	0	1	0	0	0	0
Clusiaceae	10	10	12	28	21	19	19	19	22	22
Connoriaceae	0	0	4	0	0	4	0	14	0	0
Cyatheaceae	0	0	3	0	0	1	0	0	0	0
Euphorbiaceae	0	4	5	14	19	7	15	13	9	13
Fabaceae	4	0	0	0	0	0	0	4	9	11
Hypericaceae	0	0	4	0	0	0	0	0	0	0
Lauraceae	28	50	49	43	47	36	47	48	39	43
Malvaceae	0	0	0	0	0	3	0	0	0	0
Melastomataceae	74	34	28	40	29	70	44	21	67	54
Moraceae	16	0	0	0	0	0	15	19	27	
Monimiaceae	0	0	0	0	0	0	0	5	0	0
Myrtaceae	0	14	13	18	13	19	25	8	0	0
Phyllanthaceae	0	0	6	0	0	5	0	17	0	0
Podocarpaceae	0	0	4	4	10	10	3	7	0	9
Primulaceae	0	0	27	7	4	8	5	0	0	0
Proteaceae	0	0	0	0	0	0	0	4	7	18
Rosaceae	0	2	0	8	0	0	0	1	0	0
Rubiaceae	44	43	5	11	20	0	2	12	28	17
Sapindaceae	16	0	0	0	0	0	0	19	11	7
Solanaceae	1	0	0	0	0	0	0	0	0	0

Table 2. Physical structural parameters sampled at each elevation (m) per ¼ ha. Plots were sampled for all trees at least 10 cm dbh.

Family	1900	2000	2100	2200	2300	2400	2500	2600	2700	2800
Total number of stems	193	195	205	201	204	214	221	223	231	246
% stems 10 ≤ 19 cm dbh	79	88	79	83	83	89	89	81	88	100
% stems 20 ≤ 29 cm dbh	19	8	18	17	15	11	11	18	11	0
% stems 30 ≤ 39 cm dbh	0	2	2	0	2	0	0	1	1	0
% stems > 40 cm dbh	2	2	1	0	0	0	0	0	0	0
mean stem dbh (cm)	15.3	14.1	17.1	17.1	16.7	18.5	15.9	14.9	14.5	13.3
family richness	8	9	17	13	11	19	14	17	11	14
genus richness	13	14	22	17	15	21	18	20	14	14
species richness	16	15	22	18	15	23	18	23	15	17
fishers α diversity	4.14	3.78	6.24	4.78	3.73	6.53	4.63	6.43	3.58	4.14
basal area (m ² /25ha)	3.5	4.2	4.4	3.9	3.6	4.2	4.3	3.8	4.0	4.1
above-ground biomass (Mg/25ha)	55.4	52.3	56.6	51.3	59.7	52.2	60.3	55.6	52.7	58.8
% canopy closure	67.7	62.7	60.8	71.3	70.4	69.9	65.3	63.8	68.7	61.6

References

1. Holdridge, L.R. (1967). Life zone ecology. Tropical Science Center. San Jose, Costa Rica.
2. Whittaker, R.H. (1975). Communities and ecosystems. New York:Macmillan.
3. McDonnell, M. J. and Pickett, S. T. A. (1990). Ecosystem Structure and Function along Urban-Rural Gradients: An Unexploited Opportunity for Ecology. *Ecology* 71:1232-1237.
4. Myster, R. W. (2023). Introduction. Pp 1-27 in Neotropical gradients and their analysis. Myster R.W. (ed). Springer-Verlag, Berlin.
5. Willig, M. R. and S. J. Presley. (2018). Latitudinal gradients of Biodiversity; Theory and Empirical patterns. Pp 13-19 in The encyclopedia of the Anthropocene, volume 3. DellaSala, D. A. and M. I. Goldstein. (eds). Oxford: Elsevier.
6. Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., and Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Nat. Acad. Sci.* 105:6668-6672.
7. Chen, I.C., Shiu, H.J., Benedick, S., Holloway, J.D., Cheye, V.K., and Barlow, H. S. (2009). Elevation increases in moth assemblages over 42 years on a tropical mountain. *Proc. Nat. Acad. Sci.* 106:1479-1483.
8. Myster, R.W. (2020). The Andean cloud forest. Springer-Verlag, Berlin.
9. Oncken, O., Chong, G., Franz, G., Giese, P., Götze, H., Ramos, V.A., Strecker, M.R. and Wigger, P. (2006). The Andes: Active Subduction Orogeny. *Frontiers in Earth Sciences*. Springer-Verlag, Berlin.
10. Fisher, J. B., Malhi, Y., Torres, I. C., Metcalfe, D. B., van de Weg, M., Meir, P., Silva-Espejo, J. E. and Huasco, W. H. (2013). Nutrient limitation in rainforests and cloud forests along a 3,000-m elevation gradient in the Peruvian Andes. *Oecologia* 172:889-902.

11. Cardelús, C.L., Colwell, R.K., and Watkins, J. E. (2006). Vascular Epiphyte Distribution Patterns: explaining the Mid-Elevation Richness Peak. *J. Ecol.* 94:144-156.
12. Myster, R.W. (2016). Forest structure, function and dynamics in Western Amazonia. Wiley -Blackwell, Oxford, UK.
13. Rehak, K., Bookhagen, B., Strecker, M. R., and Echtler, H. P. (2010). The topographic imprint of a transient climate episode: the western Andean flank between 15.5° and 41.5°S. *Earth surface processes and landforms* 35:1516-1534.
14. Minga, D., Cordero, P., Donoso-Correa, M., Montesinos, K., Jimenez, M., Antaki, B and Sarmiento, F. (2019). The Uchucay microrefugium: an interandean forest relict with an important arboreal richness in Southern Ecuador. *Pirineos* 174:1-16
15. Bruijnzeel, L.A., Scatena, F.N., and Hamilton, L. S. (2010). Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge University, UK.
16. Beck, E., Bendix, J., Kottke, I., Makeschin, F., and Mosandl, R. (2008). Gradients in a Tropical mountain ecosystem of Ecuador. Springer-Verlag, Berlin.
17. Pickett, S. T. A. (1982). Population patterns through twenty years of oldfield succession. *Vegetatio* 49:45-59.
18. Myster, R. W. and Pickett, S. T. A. (1988). Individualistic patterns of annuals and biennials in early successional oldfields. *Vegetatio* 78:53-60.
19. Wilson, J.B. (1991). Methods for fitting dominance/diversity curves. *J. Veg. Sci.* 2:35-46.
20. Guest, R.G. (2013). Numerical methods of curve fitting. Cambridge University press. Cambridge University, UK.
21. Austin, M.P., Nicholls, A.O., Doherty, M.D., and Meyers, J.A. (1994). Determining species response functions to an environmental gradient by means of a β -function. *J. Veg. Sci.* 5:215-228.
22. Oksanen, J., and Minchin, P. R. (2002). Continuum theory revisited: what shape are species responses along ecological gradients? *Ecol. Model.* 157:119-129.
23. Rydgren, K., Okland, R.H., and Okland, T. (2003). Species response curves along environmental gradients: a case study from SE Norwegian swamp forests. *J. Veg. Sci.* 14:869-880.
24. Austin, M.P., and Gaywood, M. (1994). Current problems of environmental gradients and species response curves in relation to continuum theory. *J. Veg. Sci.* 5:473-482.
25. Heaney, A., and Proctor, J. (1990). Preliminary studies on forest structure and floristics on Volcan Barva Costa Rica. *J. Trop. Ecol.* 6:307-320.
26. Nadkarni N, M., Matelson, T.J., and Haber, W. A. (1995). Structural characteristics and floristic composition of a Neotropical Cloud Forest, Monteverde, Costa Rica. *J. Trop. Ecol.* 4:481-495.
27. Schwarzkopf, T., Riha, S.J., Fahey, T.J., and Degloria, S. (2011). Are cloud forest tree structure and environment related in the Venezuelan Andes? *Austral Ecol.* 36:280-289.
28. Bussmann, R. W. (2001). The montane forests of Reserva Biologica San Francisco. *Die Erde*, 132:9-25.
29. Loughlin, N. J. D. (2017). Changing human impact on the montane forests of the eastern Andean flank, Ecuador. Ph.D thesis, the Open University.
30. McMichael, C.N.H., Witteveen, N. H., Scholz, S., Zwier, M., Prins, M. A., Loughheed, B. C., Mothes, P. and Gosling, W. D. (2021). 30,000 years of landscape and vegetation dynamics in a mid-elevation Andean valley. *Quaternary Science Reviews* 258:106866.
31. Bussmann, R.W. (2003). The vegetation of Reserva Biológica San Francisco, Zamora-Chinchipec, Southern Ecuador – a phytosociological synthesis. *Lyonia* 12:71-177.
32. Martinez, C.E.C. (2005). Manual de Botanica: Sistemática, Etnobotánica y Métodos de Estudio en el Ecuador. Ditorial Universitatia, Quito, Ecuador.
33. Liede-Schumann, S. and Breckle S. W. (2008) Provisional checklist of flora and fauna of the San Francisco Valley and its surroundings. *Ecotropical Monographs* 4
34. Fisher, R.A., Corbet, A.S., and Williams, C. B. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Ani. Eco.* 12:42-58.
35. Chave, J., Rejou-Mechain, M., Burquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C. Duque, A., Eid, T., Fearnside, P.M., Goodman, R. C., Henry, M., Martinez-Yrizar, A., Mugasha, W.A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A., Nogueira, E. M., Ortiz-Malavassi, E., Pelissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G., and Vieilledent, G. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20:3177-3190.
36. Buchholz, T., Tennigkeit, T., and Weinreich, A. (2004). *Maesopsis eminii* – a challenging timber tree species in Uganda – a production model for commercial forestry and smallholders. Proceedings of the international union of forestry research organizations on the economics and management of high productivity plantations, Lugo, Spain.
37. Myster, R.W. (2010). Testing dominance-diversity hypotheses using data from abandoned plantations and pastures in Puerto Rico and Ecuador. *J. Trop. Ecol.* 26:247-250.
38. Hwang, J., and Blitzstein, J. K. (2014). Introduction to Probability. Chapman & Hall Publishers.

39. SAS (1985). User's guide: statistics, Ver. 5. SAS Institute Inc.
40. Marini, L., Bona, E., Kunin, W.E., and Gaston, K. J. (2010). Exploring anthropogenic and natural processes shaping fern species richness along elevational gradients. *J. Biogeog.* 37:1-7.
41. Condit, R., Engelbrechta, B. M. J., Pinob, D., Péreza, R. and Turnera, B.L. (2013). Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc. Nat. Acad. Sci.* 110:5064-5068.
42. Huisman, J., Olf, H. and Fresco, L. F. H. (1993). A hierarchical set of models for species response analysis. *J Veg Sci.* 4:37-46.
43. Myster, R.W. (2014). Primary vs. secondary forests in the Neotropics: two case studies after agriculture. Pp 1-42 in *Forest Ecosystems: biodiversity, management and conservation.* Schwartx, R (ed) Nova publishers, NY.
44. Myster, R.W. (2017a). Gradient (elevation) vs. disturbance (agriculture) effects on primary cloud forest in Ecuador: floristics and physical structure. *New Zealand J. For. Sci.* 47:1-7.
45. Myster, R.W. (2018a). Gradient (elevation) vs. disturbance (agriculture) effects on primary cloud forest in Ecuador: seed predation, seed pathogens and germination. *New Zealand J. For. Sci.* 48:4
46. Myster, R. W. (1993). Spatial heterogeneity of seed rain, seed pool and vegetative cover on two Monteverde landslides, Costa Rica. *Brenesia* 39-40:137-145.
47. Myster, R.W. (2012a). Ecotones between forest and grassland. Springer-Verlag, Berlin.
48. Myster, R.W. (2012b). Long-term data from fields recovering after sugarcane, banana and pasture cultivation in Ecuador. *Dataset papers in Ecology*, 468973, doi: 10.7167/2013/46873.
49. Sanders, N.J. (2002). Elevational Gradients in ant Species Richness: Area, Geometry, and Rapoport's Rule. *Ecography* 25:25-32.
50. udd, W.S., Skean, J.D. and Beaman, R. (1988). *Miconia zanonii* (Melastomataceae: Miconieae), a new species from Hispaniola. *Brittonia* 40:208-213.
51. Sri-Ngernyuang, K., Mamoru, K., Mizuno, T., Noguchi, H., Teejuntuk, S., Sungpalee, C., Hara, M., Yamakura, T., Sahunalu, P., Dhanmanonda, P., and Bunyavejchewin, S. (2003). Habitat differentiation of Lauraceae species in a tropical lower montane forest in northern Thailand. *Ecological Research* 18:1-14.
52. Malia, S., and Borges, R. M. (2003). Phenolics, fibre, alkaloids, saponins, and cyanogenic glycosides in a seasonal cloud forest in India. *Biochem. System. Ecol.* 31:1221-246.
53. Werner, W.L. (2012). Biogeography and Ecology of the Upper Montane Rain Forest of Sri Lanka (Ceylon). Pp 343-352 in *Tropical Montane Cloud Forests.* (Hamilton, L. S., Juvik, J. O., and Scatena, F. N. eds). Springer-Verlag, Berlin.
54. Cheek, M. 2009. *Mussaenda epiphytica* sp. nov. (Rubiaceae), an epiphytic shrub from cloud forest of the Bakossi Mts, western Cameroon. *Nordic J. Bot.* 27:456-459.
55. Omoro, L.M.A., Pellikka, P.K.E., and Rogers, P.C. (2010). Tree species diversity, richness, and similarity between exotic and indigenous forests in the cloud forests of Eastern Arc Mountains, Taita Hills, Kenya. *J. For. Res.* 21:255-264.
56. Santiago, L.S., Goldstein, G., Meinzer, F.C., Fownes, J.H., and D. Mueller-Dombois. (2000). Transpiration and forest structure in relation to soil waterlogging in a Hawaiian montane cloud forest. *Tree Physiology* 20:673-681.
57. Okland, R.H. (1992). Studies in SE Fennoscandian mires: relevance to ecological theory. *J. Veg. Sci.* 3:279-284.
58. Fiedler, K., and Beck, E. (2008). Investigating gradients in Ecosystem analysis. Pp 49-55 in Beck, E., Bendix, J., Kottke, I., Makeschin, F. and Mosandl, R. (eds) *Gradients in a Tropical mountain ecosystem of Ecuador.* Springer-Verlag, Berlin.
59. Bush, M.B. (2002). Distributional change and conservation on the Andean flank: a paleoecological perspective. *Global Ecol. Biogeo.* 11:463-473.
60. Gasparini, N.M., and Whipple, K. X. (2014). Diagnosing climatic and tectonic controls on topography: Eastern flank of the northern Bolivian Andes. *Lithosphere* 6:230-250.
61. Zapata, F.A., Gaston, K.J., and S. L. Chown. (2005). The Mid-Domain Effect Revisited. *Am. Nat.* 166:E144 -E148.
62. Kluge, J., Kessler, M., and Dunn, R. R. (2006). What drives elevational patterns of diversity? A test of geometric constraints, climate and species pool effects for pteridophytes on an Elevational gradient in Costa Rica. *Global Ecol. Biogeog.* 15:358-371.
63. Suchrow, S., and Jensen, K. (2010). Plant species responses to an elevational gradient in German north-sea salt marshes. *Wetlands* 30:735-746.
64. Weng, C., Bush, M.B., and Silman, M.R. (2004). An analysis of modern pollen rain on an elevational gradient in southern Peru. *J. Trop. Ecol.* 20:113-124.
65. Kromer, T., Kessler, M., Gradstein, S.R., and Acebey, A. (2005). Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *J. Biogeog.* 32:1799-1809.
66. Lippok, D., Beck, S.G., Renison, D., Hensen, I., Apaza, A.E., and Schleunig, M. (2014). Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest. *J. Veg. Sci.* 25:724-733.

67. Weaver, P.L., Medina, E., Pool, D., Dugger, K., Gonzales-Liboy, J., and Cuevas, E. (1986). Ecological observations in the dwarf cloud forest of the Luquillo Mountains in Puerto Rico. *Biotropica* 18:79-85.
68. Gould, W.A., González, G., and Carrero-Rivera, G. (2006). Structure and composition of vegetation along an elevational gradient in Puerto Rico. *J. Veg. Sci.* 17:653-664.
69. Salazar, L., Homeier, J., Kessler, M., Abrahamczyk, S., Lehnert, M., Kromer, T., and Kluge, J. (2015). Diversity patterns of ferns along elevational gradients in Andean tropical forests. *Plant Ecol. Drivers* 8:13-24.
70. Myster, R.W. (2012c). Plants replacing plants: the future of community modeling and research. *Bot. Rev.* 78:2-9.
71. Myster, R.W. (2018b). The nine classes of plant-plant replacement. *Ideas in Ecol. Evol.* 11:29-34.
72. Myster, R.W. (2017b). Does the seed rain limit recruitment, regeneration and plant community dynamics? *Ideas in Ecol. Evol.* 10:1-12.
73. Grubb, P. J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52:107-145.