Vascular plant family composition of the Eastern Cordillera of Colombia
Keizer, J.J.

Citation for published version (APA):

General rights
It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations
If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: http://uba.uva.nl/en/contact, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.
CHAPTER 7

SUMMARY and CONCLUSIONS

by
Jan Jacob KEIZER

Introduction

This thesis concerns the Neotropical montane vegetation of one of the three mountain chains of the northern Andes in Colombia, the Eastern Cordillera. Using two distinct data sets on quantitative vascular plant composition and a variety of statistical and multivariate methods, this work focuses on altitudinal vegetation diversity patterns, floristically-based vegetation types and vegetation-environment relationships. Whilst the current knowledge of tropical montane forests in particular still leaves much to be desired - especially since they are disappearing at an alarming rate - the significance of the present contributions resides first and foremost in that they involve broad elevational ranges (≥ 3000 m) on slopes contrasting strongly in rainfall regime. A further aspect that distinguishes this work from the bulk of tropical montane vegetation studies (in fact, vegetation studies in general), is the taxonomic resolution. Albeit the family rank is utilised here simply because too few taxa are identified to a lower taxonomic level, there is very little solid evidence against the suitability of the family rank for any of the purposes of this investigation.

The emphasis in this thesis lies on the vegetation relevé data of the so-called Sumapaz-transect, being used to address all three above-mentioned themes. With sampling intervals of generally 150 to 200 m, this altitudinal transect covers the opposite flanks of the Eastern Cordillera from footslope to their highest elevations at about 4° north latitude. The second, so-called HJM data set, on the other hand, is merely utilised here for the study of vegetation-environment relationships. The tree and shrub count data of the HJM set involve a rather unconventional and somewhat informal sampling method, and the accompanying environmental data are less exhaustive than in the case of the Sumapaz data set. A possible drawback of the HJM data set is its pronounced sampling imbalance with respect to elevation. The HJM set is, however, unique for tropical mountains in that it encompasses a very large number of forest stands (roughly 150). Also, the HJM data set with its six altitudinal transects deals with the Eastern Cordillera over considerably wider geographical extent than the Sumapaz data set (i.e. roughly from 4° to 7° north latitude).

A secondary research topic being addressed here is the climatic setting of the Sumapaz-transect.
Climate

The temperature and rainfall regime in the area of the Sumapaz-transect are investigated using stabilised soil temperature data gathered at 32 of the transect's 42 study sites, and temperature and rainfall data from 14 climate stations in the vicinity of the transect.

The altitudinal lapse rates of stabilised soil temperature - an estimate of mean annual air temperature - are 0.47 and 0.56 °C per 100 m, respectively, for the outer-andean, east slope and the inner-andean, west slope of the Eastern Cordillera. These values agree well with the ones reported for the other three ECOANDES-transect in the Colombian mountains. The same is true for the altitudinal lapse rate of annual mean air temperature on the west flank, being 0.66 °C per 100 m. With the data available, this lapse rate can not be assessed for the opposite slope. The air and soil temperature lapse rates for the west slope of the Eastern Cordillera are not significantly different. The higher air than soil temperature lapse rate is, however, a consistent phenomenon for the slopes of the ECOANDES-transects, and could involve a sampling effect.

The rainfall regimes of the two flanks of the Eastern Cordillera appear to differ in a number of respects. The most conspicuous of these differences is that the maximum annual rainfall is much higher, and occurs at a lower elevation on the outer-andean than on the inner-andean slope. Also, the annual rainfall distribution reveals an unimodal pattern in the case of the east slope, and - at least up to roughly 2000 m - a bimodal pattern in the case of the west slope. These and other results mostly fit in well with rainfall patterns previously reported for mountainous areas in the tropics and Colombia. Nonetheless, the lack of climate stations in the vicinity of the Sumapaz-transect, and their in general scanty rainfall data needs to be emphasised.

Vascular plant family diversity

Vascular plant family diversity in the Eastern Cordillera of Colombia is investigated by means of direct, altitudinal gradient analysis. Using the vegetation relevé data of the Sumapaz-transect, altitudinal diversity patterns are studied separately for the Cordillera's east and west flank for differing noticeably in rainfall regime. Whilst both elevational gradients involve 21 relevés, that on the east slope is slightly longer than that on the west flank (550 - 4250 vs 470 - 4025 m). Alpha and beta diversity are measured as the number of families encountered in the individual sample plots ("overall family richness"), and beta turnover, respectively. Family richness is also assessed separately for three of Gentry's phytogeographical categories, their total richness revealing altitudinal patterns very similar to those of overall family richness. A variant of beta turnover ("local turnover") is used as measure of floristic change between neighboring relevés along the gradients. Altitudinal patterns in family richness and local turnover are tested for randomness by means of two non-parametric statistical tests.
On both mountain sides of the Eastern Cordillera, the altitudinal variation in overall family richness agrees poorly with the gradual impoverishment with increasing elevation generally found for woody plant species and families. Apart from a drop at the transition from andean forest to páramo, the overall richness patterns are rather distinct for the two slopes. This includes a clear peak as well as a non-random order of high and low values along the eastern but not the western gradient. The presence and altitude of this peak is in line with what was postulated by Gentry. That the peak is due to the combined occurrence of Amazon- and Andean-centered families, on the other hand, is not.

Separately, the three main phytogeographical categories of Amazon-centered, Andean-centered, and Laurasian families reveal mostly more straightforward richness-elevation relationships than that they do together. The high and low richness values of all three groups constitute non-random altitudinal series on the east as well as the west slope. Also on either mountain side, there is a strong tendency for the Amazon-centered, the Andean-centered, and the Laurasian family richness to be high at low, middle, and high elevations, respectively. Andean-centered richness is exceptional in that the precise location of its (predominantly) high values differs noticeably for at least the lower parts of the two gradients. The corresponding differences in Andean-centered family richness are exceptional as well. In general, the actual richness values of the three phytogeographical groups are remarkable similar at comparable elevations on the two slopes.

The opposite flanks of the Eastern Cordillera differ little with respect to beta turnover for vascular plant families. The values are also similar to those for the slopes covered by the ECOANDES-transects in Colombia's Central Cordillera and Sierra Nevada de Santa Marta. In the case of both mountain sides, the altitudinal variation in local turnover does not appear to support either the continuum, the community, or the ecotone model. The two altitudinal patterns also do not deviate significantly from randomness. Local turnover on the east slope is, nonetheless, significantly lower within the physiognomically-based altitudinal vegetation zones than at their transitions.

Vegetation types

The 42 vegetation relevés of the Sumapaz-transect, covering the east and west flank of the Colombian Eastern Cordillera from tropical lowland forests to (super-)páramo, are classified on the basis of their quantitative vascular plant family composition. Whilst - as mentioned before - the identification of the taxa prohibits the use of a higher taxonomic resolution in the present case, in the case of the relevé data of another ECOANDES-transect (TPN-transect, Colombian Central Cordillera) the family level was rejected for classification purposes as giving insufficiently informative results. TWINSPLAN is applied to two input data sets in view of its possible input-order Dependence. The TWINSPLAN-grouping of the families is refined by means of constrained block clustering.
In the present case, the taxonomic resolution of family is suitable for the classification of tropical montane phytocoenoses in that the results are meaningful both floristically and ecologically. Whilst the major divisions are largely altitude-related, differences between the two mountain sides prevail at the level of the recognised vegetation types. In general, these differences would appear to fit in with the role of rainfall regime. The differences occur as vegetation types that are restricted to a single slope, and as vegetation types that have distinct altitudinal distributions on the two slopes. The floristic relations between the relevé partitions are dominated by extensive and rather complex patterns of overlap, and especially the vegetation types involve few characteristic families. The quantitative phytogeographical composition of the vegetation types allows to distinguish three broad altitudinal belts on either of the mountain sides. In order of increasing elevation, these belts are characterised by the Amazon-centered, the Andean-centered, and the Unassigned families, respectively, being a main or the main cover component.

Also in a second respect, the family rank is useful for a floristically-based classification of the Sumapaz-relevés. The distinguished vegetation types agree rather well with the physiognomically-based altitudinal vegetation zones, in particular if the two flanks of Eastern Cordillera are considered separately.

Vegetation-environment relationships

The relationships of quantitative vascular plant family composition with environment are assessed for the tropical montane forests of the Eastern Cordillera using the Sumapaz and HJM data sets. For reasons mentioned above, the two data sets are investigated separately. In the case of the 31 Sumapaz forest relevés, the relationships concern three separate structural categories, i.e. the overstorey, the understorey, and the epiphytes and lianas. In the case of the HJM set, they concern the trees and shrubs over the entire altitudinal study range (525 - 3725 m) as well as its upper part (2250 - 3500 m). The basic approach to data analysis comprises the combined use of indirect and direct ordination (DCA and CCA). For the three structural categories of the Sumapaz relevés, the DCA and CCA relevé ordinations are compared numerically by means of Procrustes analysis, and their mutual similarities are summarised using PCO. In the case of the HJM data set - covering a much larger geographic area than the Sumapaz data set - CCA is applied following the method of Borcard et al. in order to determine, aside the environmental component of the floristic variation, its spatial component. Apart from to the entire HJM data set, DCA and CCA are applied to five subsets that - created through stratified resampling - cover the full altitudinal study range. This is done in order to assess the robustness of both methods with respect to a pronounced skewness in the altitudinal distribution of all 146 study sites.

From the eight environmental variables included in the Sumapaz data set - among which several physico-chemical characteristics of the top soil - stabilised soil temperature can account clearly best, and to a remarkably similar extent for the floristic variation in the three structural categories.
Also the relevé ordinations along the first, temperature-defined CCA-axis themselves reveal the good agreement generally found for the floristic patterns of different vegetation layers over long environmental gradients. That stabilised soil temperature could well be the prevailing ecological factor in general, can be inferred from a comparison with the results of DCA. This applies to both the over- and understorey as well as to the epiphytes and lianas. For as far as the other environmental variables of this study are concerned, the three categories differ most notably in relation to pH and C. Their more pronounced role in the case of the understorey is in line with the earlier suggested marginality of this habitat due to light and nutrient limitations. For all three structural categories, there presumably exist one or more environmental scalars that - except for stabilised soil temperature - are more important than the present variables and their linear combinations. In particular variables related to rainfall regime are likely to have been "overlooked". As was stated earlier, and is common for tropical mountains, rainfall data are limited for the area surrounding the Sumapaz-transect.

For as far as the entire HJM data set is concerned, altitude is clearly better associated with the variation in tree and shrub composition than the other two environmental variables, i.e. slope type (inner- versus outer-Andean) and slope angle. While its role is undoubtedly an indirect one, altitude can even be regarded as the predominant ecological factor in general. Both conclusions equally apply in the case of the five resampled subsets, i.e. with the altitudinal sampling imbalance largely removed. Also in terms of the actual values of the relevant summary statistics, and of the overall similarity of the site and the family arrangements along the altitude-defined ordination axis, the sampling imbalance appears to have a minor impact on the results of both DCA and CCA. The weighted average altitudes of selected families, on the other hand, reveal simultaneously a close overall agreement and systematic as well as substantial individual differences between the entire data set and the subsets. While some of these differences can easily be understood as being due to the sampling balance, the present approach is not entirely satisfactory in that the impact of the sampling balance can at least to some extent be confounded with the effect of sample size reported for DCA.

In the case of the upper part of the altitudinal study range of the HJM data set, the floristic variation can also be better explained by altitude than by slope type and angle. The limited importance of the X and Y geographical coordinates is a further point in common with the results for the entire data set. A major difference is that some hypothetical environmental scalar is better associated with the floristic composition than altitude.

**Taxonomic rank of family**

To conclude, the taxonomic rank of family is suitable to study the altitudinal diversity patterns, typology and environmental relationships of the vascular vegetation of the Eastern Cordillera of Colombia. In general, the results obtained either fit in well with studies using higher
taxonomic resolutions, or are - if not directly interpretable - at least sufficiently simple to be interesting in the context of the present, still rather limited knowledge of the ecology and evolution of (Neo-)tropical mountains. Even if only for the sake of presenting first results more speedily or for the sake of facilitating data analysis, the use of a higher taxonomic level than the standard rank of species would seem worthwhile considering.