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ECOSYSTEMS

Phytosociological analysis of the mesophilic forest of the San Pedro volcano (Guatemala)

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Abstract: From a standpoint of phytosociological research, little is known about the phytocoenosis found on the volcanoes of Central America. This paper analyses the distribution of the vegetation on the volcano of San Pedro in terms of its species-richness, composition, structure and abundance, and the possible relationships between these components and the changes in elevation and orientation that occur there. We divided the study area into three altitudinal belts between 2,400 and 3,020 m a.s.l. where carried out 36 inventories, each one in an area of 0.1 ha. We then applied multivariate analysis to classify and order the data in the matrix obtained from the frequency of the sampled plants. Our results lead us to propose two mixed cloud-forest associations within the class *Alnetea acuminatae*. The first, *Saurauio oreophilae-Alnetum acuminatae ass. nova*, is found on the more humid western side, while the second, *Adianto andicolae-Quercetum peduncularis ass. nova*, appears in sunnier and less shady sites, mainly on the east face. As part of this latter association, we also identified the new subassociation *festucetosum amplissimae subass. nova*. These syntaxa are part of the alliance *Oreopanacion xalapensis all. nova*, which we have created to embrace the mesophytic montane forests dominated by broad-leaved species.

Key words: *Alnetea acuminatae*, cloud forest, Phytosociology, vegetation, volcanic mountain.

INTRODUCTION

Recent volcanic activity in Mesoamerica has given rise to highly abrupt terrain where pyroclastic materials have helped generate fertile soils. This fact, together with its position at a biogeographical crossroads, has favoured the establishment of great diversity in plant communities (Lauer et al. 2003). Besides the important effect that the mountainous terrain has on the region's climate, the influence of the Pacific and Atlantic (Caribbean and Gulf of Mexico) Oceans must be taken into account as the cause of a certain asymmetry in the rainfall records on the different faces of these mountains. There is a climatic difference between the slopes that drain into the Pacific in Mexico and Guatemala and those that drain into the Caribbean and Gulf of Mexico (Barthlott et al. 2005). The Mesoamerican Pacific slope is of great floristic, biogeographical and bioclimatic interest due to the great variation that is found there. Ranges in this territory lies between the subtropical high-pressure belt and the intertropical convergence zone; furthermore, it is exposed to the humid winds off the Pacific and possesses a great altitudinal and latitudinal range. All these factors cause a barrier and rain-shadow effect (Macías-Rodríguez et al. 2014, 2017). There is a dry season that lasts 2–6 months that has a significant effect on the vegetation (Rzedowski 2006). The vegetation types are related to the plant migration from cooler climates (Holarctic) towards the tropical zones of Central and South America (Stehli & Webb 1985). This phenomenon, along with the uplift of geologically young mountain ranges, has led to high levels of allopatric specification and great numbers of range-restricted endemic species (Gentry 1982a, b).

Monzón et al. (2000) have postulated the existence of a continuous corridor during the Pleistocene glacial periods between the volcanoes that form the volcanic chain that runs parallel to the Pacific coast in Guatemala. These mountains continue northwards as ridges that run along the Pacific coast in Mexico and, somewhat less clearly, along the coast of the Gulf of Mexico. For this reason, these authors have identified this volcanic chain as the most biogeographically diverse area of Guatemala, and the one with the greatest number of endemic species. Numerous studies of the flora and vegetation of the uplands of Guatemala have revealed a great richness and diversity of vascular plants (Véliz 1989, 1998, 2000, Viñals 1993, Islebe & Cleef 1994, Islebe et al. 1994, Spooner et al. 1998, Paiz Merino 2001, Véliz et al. 2001, 2006, Pineda 2004, Véliz & Vargas 2006, Quedensley & Bragg 2007, Martínez-Arévalo 2012).

The neotropical cloud forests are found between latitudes 23° N and 25° S at an altitude of 1,000–3,000 m a.s.l. (Webster 1995, Islebe & Véliz 2001, Rzedowski 2006, Jiménez-Barrios 2009), although these limits tend to be smaller in Mexico (Rzedowski 1996, 2006). They are characterised by vegetation that responds to the continual presence of clouds or mists in movement in which the associated atmospheric humidity – known as 'horizontal rain' – can be added to the actual rainfall of the area (Hamilton 2001).

These forests have been little studied in Guatemala despite their frequency and presence in a number of the country's administrative departments (San Marcos, Huehuetenango, Quetzaltenango, Sololá, Chimaltenango and Sacatepéquez). Most of these forests are located in the uplands of the Central Guatemalan Volcanic Belt (CGVB), also referred to as the Chortis Volcanic Front by Marshall (2007). This author describes these volcanoes as a range consisting of a group of aligned stratovolcanoes and calderas situated along a series of transversal faults. This chain in Guatemala is part of the larger Central American Volcanic Arc. The deforestation processes, together with the forecasts of rising average temperatures, project an unfavourable scenario for the conservation of these forests. According Villers & Trejo (1998), these temperate cloud forests will be the most affected by climate change, above all under a scenario in which temperatures rise by more than 2°C and rainfall falls by 10%.

Some studies of vegetation ecology have attempted to disentangle questions relating to the description of plant communities in the CGVB. Of note are the works by Véliz et al. (2001), Véliz et al. (2006) and Pardo et al. (2009), which provide floristics and statistics data that reveal the presence of certain plant communities. However, they fail to provide phytosociological inventories and do not ascribe the syntaxonomy of these plant communities according to the International Code of Phytosociological Nomenclature (ICPN, Theurillat et al. 2021).

Vegetation studies in the CGVB using the methodology of the Zürich-Montpellier phytosociological school (Braun-Blanquet 1979, Géhu & Rivas-Martínez 1981) are few and far between. It is worth highlighting the study of the volcanoes of Tajumulco, Tacaná and Acatenango by Islebe & Cleef (1994), who describe alpine zacatonal communities but without proper analysis due to the lack of inventories and diagnostic species. Subsequently, Islebe et al. (1995) described seven herbaceous and woody communities in these volcanoes and in the neighbouring Sierra de los Cuchumatanes. Their work concentrated on community composition, distribution and dynamics without entering into a floristic or syntaxonimical diagnosis of the proposed communities.

Phytosociological studies have been performed in the volcanic uplands of Mexico. It should be pointed out the studies of Velázquez & Cleef (1993), Almeida et al. (1994, 2004, 2007), Islebe & Velázquez (1994), Giménez de Azcárate et al. (1997, 2003, 2009), Giménez de Azcárate & Escamilla (1999), Velázquez et al. (2000), Medina (2016) and Medina et al. (2020). Most of these studies perform a geobotanical diagnosis of the studied communities, including bioclimatic, dynamic and catenal analyses.

The aim of this work is thus to use a phytosociological methodology to provide fresh data on the phytocoenosis of the tree species present on the volcano of San Pedro, and to compare the results of the analysis with those from neighbouring areas in the CGVB and other volcanoes. It aims to provide information on the composition, ecology and distribution of the upland forests that thrive in these habitats.

MATERIALS AND METHODS

Study area

The study area was the volcano of de San Pedro in the administrative department of Sololá (western Guatemala). This volcano is south-west of Lake Atitlán, whose surface area of 125.7 km^2 makes it the second largest lake in Guatemala. Around this lake are located the volcanoes of Atitlán and Tolimán, both of which peak at over 3,000 m a.s.l. They are part of the CGVB, which in all contains over 320 summits and runs parallel to the Pacific coast (Pardo 2007).

The volcano of San Pedro is covered by cloud forest from around 2,400 m a.s.l. to its summit at 3,020 m a.s.l. The study area covers around 378.23 ha; the coordinates of its summit are 14° 39’ 14.7’’N, 91° 15’ 29.76’’W. Below 2,400 m a.s.l. extends its piedmont, where most of the vegetation has been modified by anthropic and animal activity and so has been excluded from these analyses.

The volcano soils are deep, pale, and well-drained internally, and have formed on steep slopes. They have a horizontal layer (25–30 cm) whose texture is loose to loose-sandy, friable, and slightly acidic. The subsuperficial horizons are a metre deep and their texture is loose-clayey to loose-sandy, lightly acidic and with no quartz (Pardo 2007).

Human settlements and tourism around Lake Atitlán have affected the local ecosystems to greater or less degree. Islebe (1993) has noted that there are very few high mountain environments in Guatemala that are have not been modified in some way.

From a biogeographical standpoint and following Rivas-Martínez et al. (2011a), the study area lies within the Neotropical-Austroamerican Kingdom, Neotropical Subkingdom, Caribbean-Neogranadian Superregion, Caribbean-Mesoamerican Region, Chiapan-Honduran Province, Chiapaneco Sector, Guatemalan Subsector.

Bioclimatic diagnosis

The bioclimatic characterisation of the study area is based on data from three meteorological stations obtained from the period 2000–2019; belonging to the National Guatemalan Institute of Seismology, Volcanology, Meteorology and Hydrology (INSIVUMEH; https://insivumeh.gob.gt/): Santiago Atitlán (Sololá, Guatemala) at 1,605 m a.s.l., located at the base of the volcano of San Pedro, San Marcos (San Marcos, Guatemala) at 2,447 m a.s.l., and De Todos Santos Cuchumatán (Huehuetenango, Guatemala) at 2,706 m a.s.l.; the latter two stations, although outside the study area, are situated at similar elevations and have analogous climatic conditions with the study area. This information allowed to obtain the averages values for the thermal and ombric parameters of each station, which then served as references for calculating the bioclimatic indices and carrying out the appropriate territorial diagnosis (Rivas-Martínez et al. 2011b).

The bioclimatic diagrams have been made in R version 4.2.0 (R Core Team 2022) and the CLIMATOL version 3.1.2 package (Guijarro 2019) was used to make the figures.

Sampling the flora and vegetation

Data were collected using a systematic stratified sampling methodology. The stratification criterion was based on altitudinal variation (A = 2,800–3,020 m a.s.l., 18% total surface area; B = 2,600–2,800 m a.s.l., 31% total surface area; and C = 2,400–2,600 m a.s.l., 51% total surface area) and four cardinal orientations reflecting the observed climatic characteristics, identified in sampling numbering as NE(I), SE(II), SW(III) and NW (IV). The NW- and SW-facing slopes were more humid and less sunny due to convective airflow from the Pacific, whilst the NE- and SE-facing slopes are drier and sunnier. By combining the three altitudinal belts and the four aspects we created 12 sampling subareas in which three replicates were carried out. Sampling units were placed in representative rather homogeneous and well-conserved vegetation plots (Westhoff & van der Maarel 1978, Braun-Blanquet 1979), covering a surface of 0.1 ha (50 m long x 20 m wide); in this way all relevés were uniform.

Figure 1 shows the location of the study territory and the points of the 36 samplings carried out.

The vegetation study was conducted using the phytosociological method (Braun-Blanquet 1979, Géhu & Rivas-Martínez 1981). For the syntaxonomical classification we followed the criteria of Galán de Mera (2005) and Galán de Mera et al. (2021). The nomenclature and description of the new syntaxonomical units are compliant with the International Code of Phytosociological Nomenclature (ICPN) (Theurillat et al. 2021).

To determine the flora, we used *Flora de Guatemala* (Standley & Steyermark 1946-1966, Standley & Williams 1961-1975, Gentry & Standley 1974), and for the taxonomic nomenclature we used the data base from the *World Flora Online* (WFO 2022) website (http://www.worldfloraonline.org/).

Statistical analyses

The statistical analyses were performed using the software *Ginkgo* (De Cáceres et al. 2007). An initial data matrix of 36 inventories x 109 species was employed, which was subjected to an exploratory data analysis using multivariate classification techniques to determine the initial number of general groups. The algorithm K-Means, an iterative technique used to group objects into K partitions or clusters (De Cáceres et al. 2010a), was applied to the matrix generated using Euclidean distance. The initial strategy chosen was *seed randomization* and the number of proposed routes was 120. The number of initial groups analysed was 2 (K=2) and the test were increased to K=6.

The value used to test for the ideal number of groups was the APS (Average Partition Silhouette) index, which indicates the ideal number of clusters (Rousseeuw 1987); the partition with the maximum APS value was retained. The APS indices with values near 1

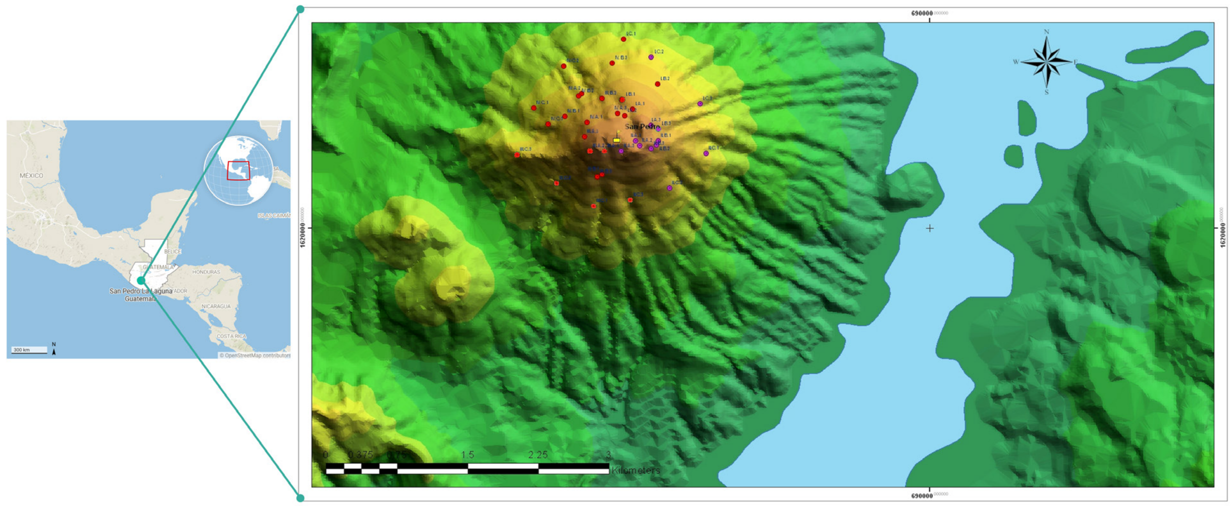

Figure 1. Location and georeferencing of the sampling carried out in the San Pedro volcano (San Pedro La Laguna, Guatemala). In red the samplings corresponding to the association *Saurauio oreophilae-Alnetum acuminatae ass. nova*. In violet the samples of association *Adianto andicolae-Quercetum peduncularis ass. nova*.

indicate greater security in the grouping; by contrast, negative values and values close to -1 indicate less reliable groupings.

Thus, we considered as a decisive factor in each of the K-Means analyses that the proposed groups – albeit having a general optimum value – had positive APS values that were far from 0 as in the opposite case the values would indicate that the group was not well defined (Rousseeuw 1987).

We also used the model Diagnostic Species Analysis from the program Ginkgo (De Cáceres et al. 2007) to study the characteristic taxa in the selected groups. This model is based on the determination used in the work by Chytrý et al. (2002), De Cáceres & Legendre (2009) and De Cáceres et al. (2010b). The significance level used was $p \leq 0.05$, with 999 permutations. Only those species with a minimum value of 0.5 in terms of their statistical power were selected.

Finally, we carried out classification (cluster, Ward's method) and ordination (Principal Component Analysis, PCA) analyses using the program Past v. 4.1 (Hammer et al. 2001, https://www.nhm.uio.no/english/research/resources/past/). In the graphical representation of this analysis of principal components, the biplots with the vectors of the floristic variables are observed in green. The length and angle with respect to the principal component axes are important. The more parallel a vector is to the axis of a component, the more it has contributed to the creation of that component. The greater the length of a vector related to a floristic variable, the better its information is represented in the graph.

RESULTS

Floristic species richness and abundance

We identified a total of 415 plant species inside and outside our phytosociological sampling areas, belonging to 102 botanical families. The most represented family was the *Asteraceae* (17.52%), followed by *Orchidaceae* (6.57%), *Poaceae* (4.62%), *Solanaceae* (3.65%), *Fabaceae* (3.16%) and *Lamiaceae* (2.68%). The *Asteraceae*, *Lamiaceae* and *Poaceae* species were most frequent in the sunniest ecological niches (NE- and SE-facing), whilst the *Solanaceae*, *Araliaceae*, *Piperaceae*, *Lauraceae*, *Myrsinaceae* and *Actinidiaceae* tended to be found in shady sites (NW- and SW-facing). A SE aspect had the greatest species richness in all three altitudinal bands due to the greater number of sunshine hours and the disturbance, which favour the presence of heliophile shrubs and herbaceous plants belonging to these families.

There a gradual increase in the number of taxa with greater elevation. The 2,800–3,020 m a.s.l. altitudinal band had more taxa than the others, followed by the 2,600–2,800 m a.s.l. band. This pattern coincides with elevations on the volcano's slopes that not only have the greatest amount of available habitat but also remain humid throughout the whole year.

Bioclimatic studies

All the stations are influenced by the Tropical Pluviseasonal bioclimate (Io ≥ 3.6; Iod2 ≤ 2.5) (Table I, Figure 2). The meteorological station at Santiago Atitlán is the station at the lowest altitude and is located in the upper Thermotropical thermotype with an upper Subhumid ombrotype. The San Marcos and Todos Santos Cuchumatán stations have an upper Mesotropical thermotype and an upper Humid ombrotype, even though the data they generate for Positive Temperature (Tp) are closer to the horizon of a lower Supratropical thermotype. Nevertheless, the values for their Thermicity Index (It) correspond with the thermotype assigned in Table I. These two stations are thus on the border between these two thermotypes.

Phytosociological studies

Figure 3 shows the values of the Silhouette Index once the successive exploratory K-means analyses had been applied to the different groups (from K=2 to K=6) in the initial data matrix (36 inventories x 109 species). The graph reveals how both indices tend to drop and the data indicate that the group K=2 is the best –– but without ruling out K=4, which had the second highest value. The APS values for each group proposed for K=2 are optimal (G-1=0.2792, G-2=0.4093).

Figure 4 depicts the classification analysis applied to the initial matrix (cophenetic correlation index: 0.8425) in which two groups of inventories appear. On the left (G-1), the inventories are characterized by the presence of *Alnus acuminata* Kunth, while on the right appear the 12 samples with in which *Quercus peduncularis* Née was abundant (G-2).

For G-1, the analysis recognizes diagnostic species such as *Saurauia oreophila* Hemls. (0.888; p-value<0.002), *Ardisia venosa* Mast. ex Donn.Sm. (0.836; p-value<0.003), *Meliosma idiopoda* S.F.Blake (0.816; p-value<0.002),

Table I. Summary of the bioclimatic data for the three meteorological stations studied. Abbreviations: Tp (Positive Temperature). Pp (Positive Rainfall). Io (Ombrothermal Index). Iod2 (Ombrothermal Index of the driest bimester of the driest trimester of the year). It (Thermicity Index).

Station	Altitude (m a.s.l.)	Tp	Pp	Io	Iod_2	It	Bioclime	Thermotype	Ombrotype
Santiago Atitlán (Sololá)	1,605	2,282.7	1,299	6	0.3	545	Tropical Pluviseasonal	upper Thermotropical	upper Subhumid
San Marcos	2,447	1,549	1,853	12	0.6	330	Tropical Pluviseasonal	upper Mesotropical	lower Humid
Todos Santos Cuchumatán	2,706	1,690.8	1,279	8	0.2	363	Tropical Pluviseasonal	upper Mesotropical	lower Humid

Oreopanax echinops (Cham. & Schltdl.) Decne. & Planch. (0.764; p-value<0.002) and *Oreopanax xalapensis* (Kunth) Decne. & Planch. (0.760; p-value<0.015), amongst others.

In a more detailed analysis of group G-1, a data matrix was prepared using 24 relevés x 86 variables. These variables are related to 85 species and a new variable with data corresponding to the elevation of each inventory is incorporated. Then, a multivariate ordination analysis (PCA, percentage of variance accumulated by the first three axes of the 98.87%) was applied to this matrix, which revealed the existence of up to three subgroups of samples (Figure 5). This result was confirmed by applying to the group G-1 a K-means analysis for this data matrix, which gave K=3 as the maximum value for the APS (mean Silhouette=0.6877; A=0.6657, B=0.6838, C=0.7081). For subgrup A, the Altitude variable is quite significant. In fact, here we find the samplings carried out at higher altitudes in the volcano. The species that best characterize this group are *Meliosma idiopoda*, *Ardisia venosa*, *Salvia curtiflora* Epling, *Oreopanax echinops*, *Roldana heterogamma* H.Rob. & Brettell, *Arracacia donnell-smithii* J.H.Coult. & Rose, *Sibthorpia repens* (Mutis ex L.) Kuntze and *Senecio cobanensis* J.M. Coult.. For subgrup B, the floristic variables that best define this set of samples are *Buddleja nitida* Benth., *Quercus peduncularis*, *Chiranthodendron pentadactylon* Larreategui, *Fuchsia arborescens* Sims, *Verbesina apleura* S.F. Blake, *Cestrum pacayense* Francey and *Roldana gilgii* (Greenm.) H.Rob. & Brettell. Finally, subgrup C would be made up of six samplings and the species that stand out as characteristics of this group are *Euonymus enantiophyllus* (Donn. Sm.) Lundell, *Quercus crispifolia* Trel., *Oreopanax xalapensis* (Kunth) Decne. & Planch., *Quercus ocoteifolia* Liebm., *Neonelsonia acuminata* (Benth) J.M. Coult. &

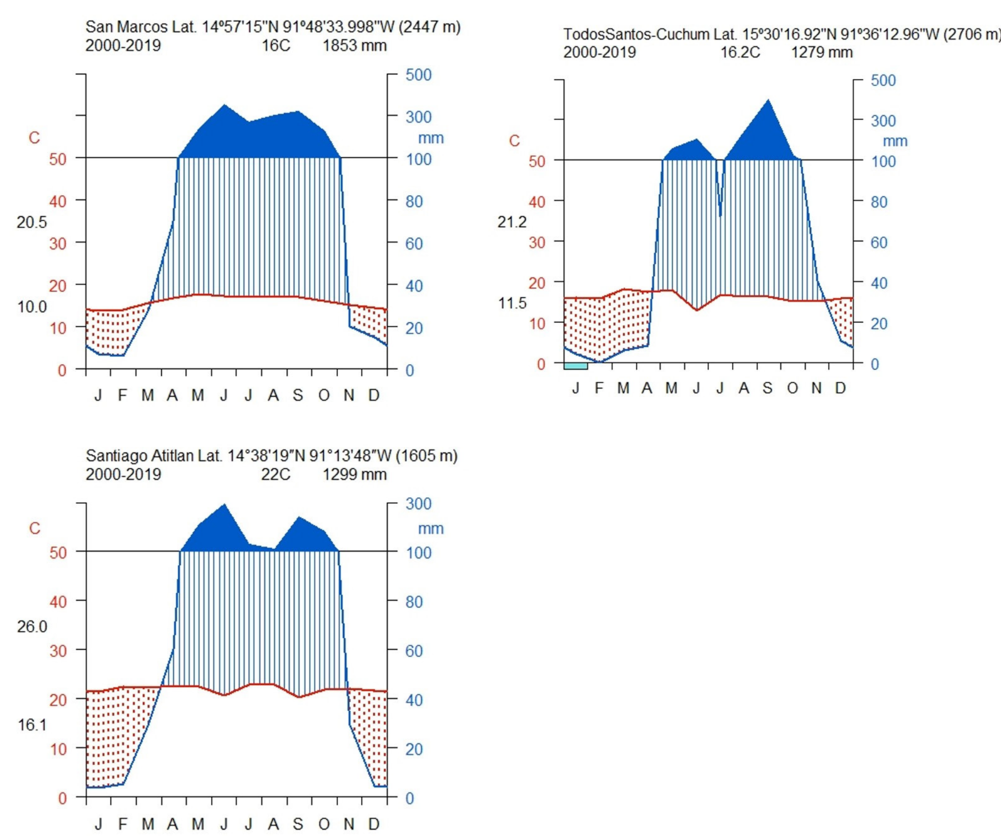

Figure 2. Ombrotermic diagram of the Santiago de Atitlán, San Marcos and Todos Santos Cuchumatanes meteorological stations studied (all in Guatemala) drawn using R and the packet CLIMATOL (v. 3.1.2) (Guijarro 2019).

Rose ex Drade and *Solanum appendiculatum* Dunal.

The results of the analyses of the diagnostic species reveal that for G-2 the dominant species is *Quercus peduncularis*, with a value of 0.994 (p-value<0.001); other characteristic species include *Adiantum andicola* Liebm. (0.888; p-value<0.001), *Festuca amplissima* Rupr. (0.816; p-value<0.001), *Galium mexicanum* Kunth (0.816; p-value<0.001), *Salvia laxiantha* Benth. (0.816; p-value<0.001), *Alnus acuminata* (0.808; p-value<0.013) and *Arbutus xalapensis* Kunth (0.764; p-value<0.002).

To conclude this section, Tables II and III together show the inventories corresponding to the groups G-1 and G-2, respectively. These tables show that the dominant species in both groups of inventories correlated with the results of the analysis of the diagnostic species mentioned above.

The new syntaxa

Four new syntaxa are described.

Saurauio oreophilae-Alnetum acuminatae ass. nov. (Table II, *holotypus* relevé IV.A.1)

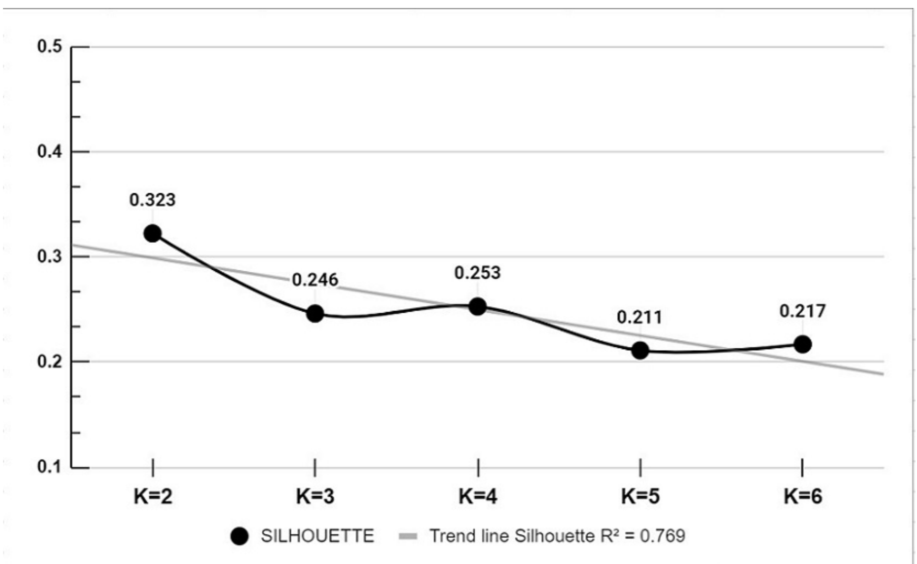

Figure 3. Silhouette Index values for the analysis of the 36 vegetation inventories.

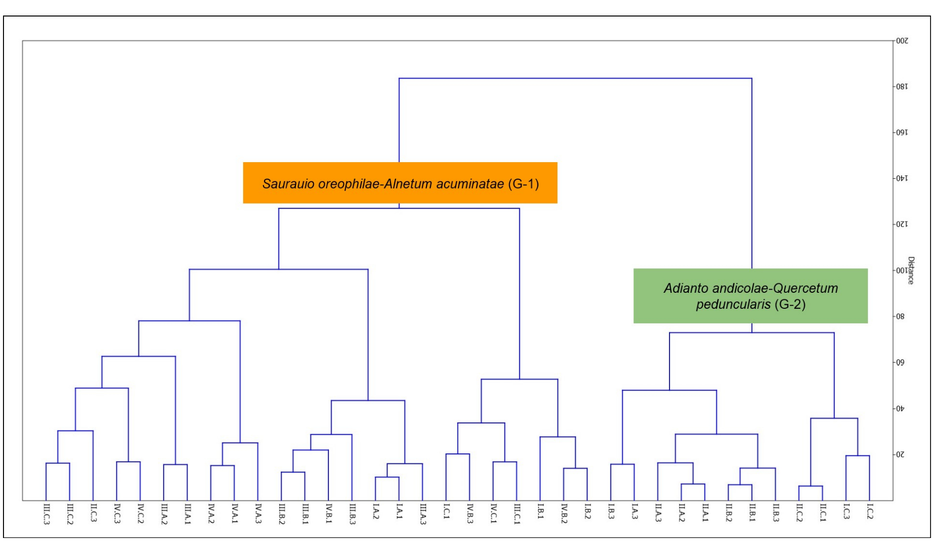

Figure 4. Cluster analysis of the initial data matrix.

We define this plant association as a cloud forest community, located between 2,400-3,020 m a.s.l., being possible that it is also present in higher altitude volcanoes. It has a clear preference for the more humid orientations of the volcano, with frequent mists and horizontal precipitation phenomena. It sits on volcanic soils and with slopes greater than 30%.

Characteristic or differential species: *Alnus acuminata*, *Saurauia oreophila*, endemic to Mexico and Guatemala, *Ardisia venosa*, *Meliosma idiopoda*, *Clethra mexicana*, *Cestrum pacayense*, *Oreopanax xalapensis* and *O. echinops*, the latter species classified as vulnerable (VU) and with distribution only in Mexico, Guatemala and Honduras (González-Espinosa et al. 2011). Lastly, they accompany a series of scandents and lianas such as *Maianthemum flexuosum* (Bertol.) LaFrankie, *Valeriana scandens* var. *candolleana* (Gardner) C.A. Mull., *Smilax moranensis* M. Martens & Galeotti and *Iresine calea* (Ibáñez) Standl.

The distribution area of this association would be restricted to the Guatemalan subsector since we do not currently have data to reliably affirm that it is found in the Mexican volcanic chains. From the bioclimatic point of view, the association is optimal in the upper Mesotropical

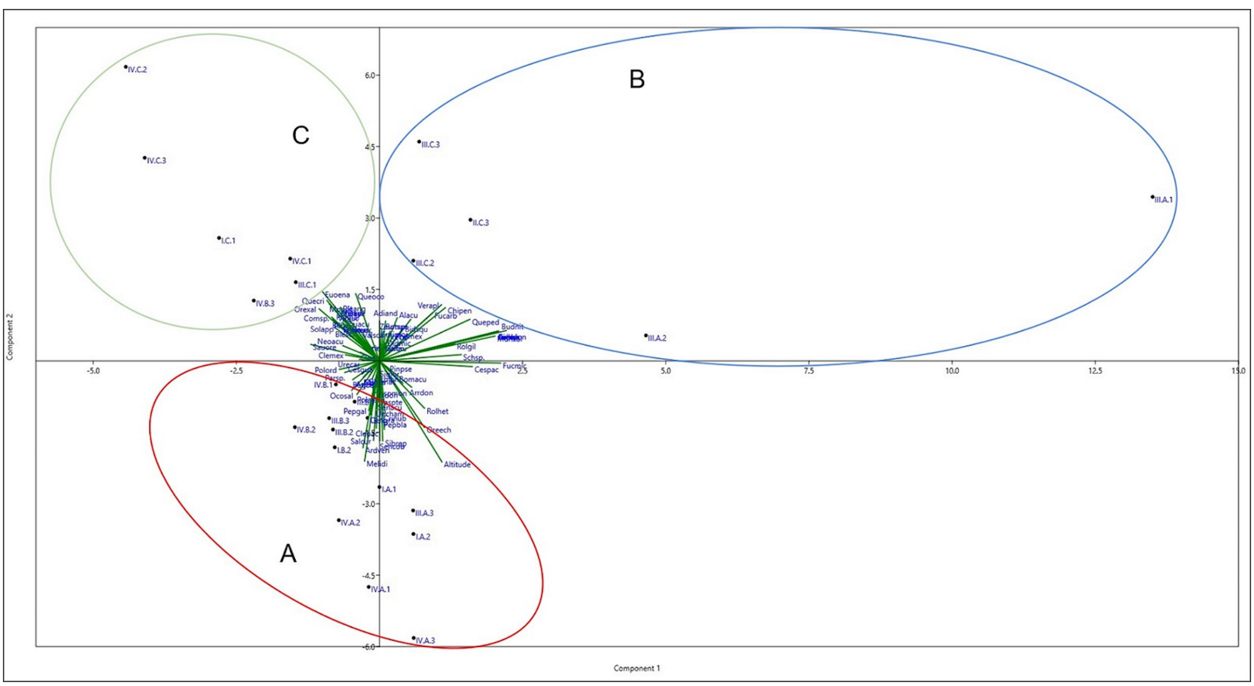

Figure 5. **Principal Component Analysis (PCA) of group G-1. Axis X (98.15% of the variance). Axis Y (0.41% of the variance). Abbreviations of the main taxa that appear in the graphic: *Adiantum andicola* Liebm. (Adiand), *Alnus acuminata* Kunth (Alaacu), *Ardisia venosa* Mast. ex Donn.Sm. (Ardven), *Arracacia donnell - smithii* J.H.Coult. & Rose (Arrdon), *Buddleja nitida* Benth. (Budnit), *Cestrum pacayense* Francey (Cespac), *Clethra mexicana* DC. (Clemex), *Euonymus enantiophyllus* (Donn. Sm.) Lundell (Euoena), *Fuchsia arborescens* Sims (Fucarb), *Fuchsia microphylla* Kunth (Fucmic), *Meliosma idiopoda* S.F.Blake (Melidi), *Neonelsonia acuminata* (Benth) J.M. Coult. & Rose ex Drade (Neoacu), *Ocotea salvinii* Mez (Ocosal), *Oreopanax echinops* (Cham. & Schltdl.) Decne. & Planch. (Oreech), *Oreopanax xalapensis* (Kunth) Decne. & Planch. (Orexal), *Parathesis* sp. (Parsp.), *Peperomia galioides* Kunth (Pepgal), *Polystichum ordinatum* (Kunze) Liebm. (Polord), *Quercus crispifolia* Trel. (Quecri), *Quercus peduncularis* Née (Queped), *Quercus ocoteifolia* Liebm. (Queoco), *Roldana gilgii* (Greenm.) H.Rob. & Brettell (Rolgil), *Roldana heterogama* H.Rob. & Brettell (Rolhet), *Salvia curtiflora* Epling (Salcur), *Saurauia oreophila* Hemsl. (Sauore), *Schistocarpha* sp. (Schsp.), *Senecio cobanensis* J.M. Coult. (Sencob), *Solanum appendiculatum* Dunal (Solapp), *Verbesina apleura* S.F. Blake (Verapl).**

thermotype, and can reach the lower Supratropical, under Humid and Hyperhumid ombrotypes.

Adianto andicolae-Quercetum peduncularis ass. nova (Table III, *holotypus* relevé II.A.3)

This association develops on volcanic soils and with slopes greater than 30%, and in places with altitudes above 2,400 m a.s.l., located on the most exposed, steep and sunny slopes of the mountain.

Characteristic or differential species: *Quercus peduncularis*, *Adiantum andicola*, *Alnus acuminata*, *Chiranthodendron pentadactylon*, and to a lesser extent *Fuchsia arborescens* and *F. microphylla* Kunth.

The biogeographical distribution of this association are the territories corresponding to the Guatemalan subsector. Bioclimatically it is restricted to lower Mesotropical and lower Supratropical termotypes under an upper Subhumid and lower Humid ombrotypes.

Adiantho andicolae-Quercetum peduncularis festucetosum amplissimae subass. nova (Table III, *holotypus* relevé II.A.1)

In the open and discontinuous areas of the mature forest, with rocky soils, a set of heliophyte species appear. They occur in the samples of the SE slope and above 2,800 m a.s.l. It can be considered as a transition to the more xeric plant formations.

Characteristic or differential species: *Festuca amplissima*, *Galium mexicanum*, *Salvia lasiantha* Benth. and *Brachypodium mexicanum* (Roem. & Schult.) Link.

The biogeographical distribution of this subassociation are the territories corresponding to the Guatemalan subsector. It is distributed by the lower Supratropical thermotype under a lower Humid ombrotype.

Oreopanacion xalapensis all. nova [*Holotypus*: *Saurauio oreophilae-Alnetum acuminatae ass. nov.*]

Both associations are proposed to be included in the class *Alnetea acuminatae* Galán de Mera 2005. Given the distribution area of these associations (Mexico – to be confirmed – and Guatemala).

The diagnostic species of this alliance are *Oreopanax xalapensis*, *O. echinops*, *Fuchsia arborescens*, *Meliosma idiopoda*, *Clethra mexicana*, *C. pachecoana* Standl. & Steyerm., *Verbesina apleura* and *Chiranthodendron pentadactylon*; and shrubs such as *Fuchsia microphylla* and *Roldana gilgii*. Most of them distributed exclusively in Mexico and Central America. From the bioclimatic point of view, the alliance is optimal in the lower Mesotropical thermotype, being able to reach the lower Supratropical, under the ombrotypes from Subhumid to Hyperhumid.

This alliance includes associations of cloud forest and mixed forest with a mixture of species of the genera *Pinus* spp., *Abies* spp., *Alnus* spp., *Quercus* spp., *Arbutus* spp., *Oreopanax* spp., *Clethra* spp., *Cleyera* spp., *Saurauia* spp., *Tilia* spp., *Carpinus* spp. *Ternstroemia* spp., *Liquidambar* spp., etc., along with scandent species and lianas typical of the territory. This alliance of alder forests distributed throughout Mexico and Central America are included in the order *Alnetalia acuminatae* Galán de Mera & Rosa in Galán de Mera, Rosa & Cáceres 2002.

Table II. ***Saurauio oreophilae-Alnetum acuminatae ass. nova.***

Group	A													B					C					
Relevé	**I.A.1**	**I.A.2**	**III.A.3**	**IV.A.1**	**IV.A.2**	**IV.A.3**	**I.B.1**	**I.B.2**	**III.B.1**	**III.B.2**	**III.B.3**	**IV.B.1**	**IV.B.2**	**III.A.1**	**III.A.2**	**III.C.2**	**III.C.3**	**II.C.3**	**IV.B.3**	**I.C.1**	**III.C.1**	**IV.C.1**	**IV.C.2**	**IV.C.3**
Altitude (Dm)	290	291	290	285	290	301	270	270	270	285	270	270	270	290	290	250	245	250	273	254	260	250	248	239
Cover (%)	98	96	98	100	98	100	100	97	90	89	93	100	99	98	100	96	93	96	99	99	99	100	93	95
Slope (%)	31	32	32	32	32	32	32	32	32	32	32	44	33	32	32	29	31	31	31	29	23	30	26	24
Orientation	NE	NE	SW	NW	NW	NW	NE	NE	SW	SW	SW	NW	NW	SW	SW	SW	SW	SE	NW	NE	SW	NW	NW	NW
Number of species	19	23	21	25	21	24	19	25	13	14	20	16	20	22	18	20	27	18	19	20	18	20	28	21
Characteristics of the association:																								
Alnus acuminata	2	2	1	2	1	1	+	+	1	+	1	+	+	1	1	+	2	1	1	1	+	1	+	1
Saurauia oreophila	2	1	1	2	1	1	+	2	2	2	1	2	1	+	+	+	1	2	2	1	2	2	2	2
Fuchsia arborescens	2	1	1	1	1	.	.	1	.	.	1	2	1	2	1	1	2	2	1	.	1	1	1	1
Meliosma idiopoda	2	2	2	2	2	2	1	2	2	2	1	1	2	.	.	1	1	.	1	.	.	.	.	.
Oreopanax echinops	2	2	2	1	1	2	1	1	2	+	1	2	.	+	1	.	.	.	1	.	.	.	.	.
Ardisia venosa	2	2	2	2	2	2	1	2	.	.	2	.	1	.	.	2	1	.	1	2	2	.	.	1
Polypodium alansmithii	.	1	.	1	.	.	2	2	2	2	2	2	2	.	.	.	1	.	.	.	.	.	1	.
Neonelsonia acuminata	.	.	.	.	.	.	3	2	.	.	.	.	2	.	.	.	.	1	2	2	3	3	.	.
Characteristics of *Quercus peduncularis* variant:																								
Quercus peduncularis	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	1	+	.	.	.	.	.	.
Schistocarpha sp.	.	.	1	.	2	.	.	.	.	.	.	.	.	2	2	.	1	1	.	.	.	.	.	.
Adiantum andicola	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	2	2	1	.	.	.	.	.	.
Zeugites munroanus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	.	.	.	2	.	.	.
Quercus crispifolia	.	.	.	.	2	1	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	1	2	2
Quercus ocoteifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.
Characteristics of *Prunus salasii* variant:																								
Prunus salasii	.	.	.	.	.	.	.	1	.	.	2	.	1	.	.	.	1	.	1	2	2	1	1	1
Billia hippocastanum	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	2	1	1	+	1	1
Piper martensianum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.
Characteristics of higher syntaxonomic units and transgressives:																								
Oreopanax xalapensis	+	+	1	2	2	1	.	1	.	.	1	.	2	.	.	2	1	.	1	1	2	2	2	2
Arracacia donnell-smithii	3	2	2	1	.	.	.	.	2	2	2	2	.	2	2	.	.	.	.	.	.	.	2	1
Ocotea salvinii	2	.		1		1		.		1		2		1		2		.		2		2		2
Chiranthodendron pentadactylon	.		1		.		1		.		.		.		.		2		.		.		.	
Parathesis sp.	.		.		.		1		.		.		.		1		.		2		2		.	
Polystichum ordinatum	2		1		.		.		2		.		.		.		.		.		.		.	
Clethra mexicana	1		2		1		.		+		.		.		.		2		.		.		1	
Begonia oaxacana	1	.	1	.	.	.	.	1	1	.	1	2	1	.	.	.	.	.	.	1	.	1	1	.
Cestrum pacayense	1	.	2	1	1	1	2	1	.	.	.	.	.	2	2	.	.	.	.	.	.	.	.	.
Tournefortia acutiflora	.	.	.	.	.	.	.	1	.	.	1	.	1	.	.	.	1	1	1	.	1	1	.	.
Goodyera striata	1	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.
Asplenium monanthes	.	1	2	1	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.
Fuchsia microphylla	.	1	1	.	.	1	.	.	.	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.
Viburnum jucundum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	2	.	1	.	1	1

Table II. Continuation.

Phanerophlebia macrosora	.	.	.	.	.	1	.	1	2	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.
Peperomia blanda var. *humilis*	.	1	1	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Peperomia galioides	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Sibthorpia repens	.	.	1	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Smilax moranensis	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	2	1	.	.	1	.	1	.
Clethra pachecoana	.	.	.	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Euonymus enantiophyllus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	2	1
Bomarea acutifolia	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Pinus pseudostrobus	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Monstera siltepecana	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2
Companions:																								
Solanum appendiculatum	.	1	1	1	1	1	1	1	.	.	1	.	.	.	1	.	1	1	1	2	.	2	1	2
Maianthemum flexuosum	1	.	2	2	2	1	.	1	.	.	1	.	.	.	1	2	2	.	1	1	1	.	1	1
Senecio cobanensis	1	1	.	2	.	1	.	1	1	.	1	.	1	.	.	1	.	1	.	.	.	.	.	.
Roldana heterogama	1	2	.	1	.	1	.	1	1	.	.	1	.	1	.	.	.	.	.	.	.	1	1	.
Salvia curtiflora	1	1	1	.	1	1	1	.	.	.	1	.	1	.	.	.	.	.	1	.	.	.	.	.
Centropogon grandidentatus	1	1	1	1	.	.	1	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Verbesina apleura	.	.	.	.	.	.	1	.	.	.	.	.	.	2	2	2	2	2	.	.	2	.	.	.
Cestrum guatemalense	.	1	.	.	.	.	.	.	.	.	1	2	1	.	.	.	.	.	.	.	.	1	.	1
Roldana gilgii	.	.	.	.	.	1	.	.	.	.	.	.	.	2	2	1	.	1	.	.	1	.	.	.
Urera caracasana	.	.	.	.	.	.	2	1	1	.	.	2	.	.	.	.	.	.	.	2	.	2	.	.
Valeriana scandens var. *candolleana*	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	1	2	.	.	.	.	.	1
Bidens squarrosa	.	.	.	.	.	.	1	.	.	.	.	1	.	.	1	.	2	.	.	.	.	.	.	.
Iresine calea	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	2	2	.	.	1	.	.	.
Commelina sp.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	2	.	.	.	2
Uncinia hamata	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Asplenium sp.	.	.	.	.	.	.	2	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Critoniadelphus nubigenus	.	1	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Clematis grossa	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
Monnina xalapensis	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.
Buddleja nitida	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.

Species present in a single inventory: I.A.1: *Schistocarpha longiligula* var. *seleri* 1. IV.A.1: *Senecio acutangulus* 1, *Passiflora pterocarpa* 1. IV.A.2: *Carex donnell-smithii* 2. I.B.1: *Sigesbeckia jorullensis* 1. III.A.1: *Archibaccharis corymbosa* 1, *Arenaria* sp. 1, *Cirsium subcoriaceum* 1, *Lopezia hirsuta* 1, *Lupinus montanus* 1, *Salvia lasiantha* 2. III.C.2: *Didymaea microphylla* 1, *Garrya laurifolia* 1. III.C.3: *Brachypodium mexicanum* II.C.3: *Phenax mexicanus* 1. I.C.1: *Blechnum schiedeanum* 1. IV.C.1: *Acalypha trachyloba* 1. IV.C.2: *Chamaedorea keeleriorum* 1, *Philadelphus myrtoides* 1, *Pleopeltis angusta* 1, *Malvaviscus arboreus* 1. IV.C.3: *Hydrocotyle mexicana* 1, *Peperomia quadrifolia* 1, *Solanum wendlandii* 1.

Coordinates: I.A.1: N 14° 39' 30.4'' W 91° 15' 54'' . I.A.2: N 14° 39' 28.2'' W 91° 15' 56.7''. III.A.3: N 14° 39' 21'' W 91° 16' 11''. IV.A.1: N 14° 39' 26'' W 91° 16' 10''. IV.A.2: N 14° 38' 36.24'' W 91° 15' 31.44''. IV.A.3: N 14° 39' 29.04'' W 91° 15' 59.22''. I.B.1: N 14° 39' 33.7'' W 91° 15' 57.4''. I.B.2: N 14° 39' 39'' W 91° 15' 45''. III.B.1: N 14° 39' 08'' W 91° 16' 05''. III.B.2: N 14° 39' 34.2'' W 91° 16' 4.68''. III.B.3: N 14° 39' 7.14'' W 91° 16' 6.54''. IV.B.1: N 14° 39' 28'' W 91° 16' 18''. IV.B.2: N 14° 39' 35'' W 91° 16' 13''. III.A.1: N 14° 39' 16'' W 91° 16' 04''. III.A.2: N 14° 39' 16'' W 91° 16' 09''. III.C.2: N 14° 39' 05'' W 91° 16' 21''. III.C.3: N 14° 39' 15'' W 91° 16' 35''. II.C.3: N 14° 38' 59'' W 91° 15' 55''. IV.B.3: N 14° 39' 46.38'' W 91° 16' 1.02''. I.C.1: N 14° 39' 54.5'' W 91° 15' 56.9''. III.C.1: N 14° 38' 57'' W 91° 16' 08''. IV.C.1: N 14° 39' 31'' W 91° 16' 29''. IV.C.2: N 14° 39' 45.5'' W 91° 16' 18.2''. IV.C.3: N 14° 39' 25.4'' W 91° 16' 23.8''.

Table III. ***Adianto andicolae-Quercetum peduncularis ass. nova.***

Relevé	I.A.3	II.A.1	II.A.2	II.A.3	I.B.3	II.B.1	II.B.2	II.B.3	I.C.2	I.C.3	II.C.1	II.C.2
Altitude (Dm)	295	295	295	290	284	283	284	284	247	250	250	250
Cover (%)	95	95	97	97	95	97	97	98	99	98	94	98
Slope (%)	32	32	32	32	32	32	32	32	35	32	32	32
Orientation	NE	SE	SE	SE	NE	SE	SE	SE	NE	NE	SE	SE
Number of species	21	15	21	21	24	13	14	16	19	13	14	16
Characteristics of the association:												
Quercus peduncularis	2	3	3	3	2	3	3	3	3	2	3	3
Adiantum andicola	1	2	1	1	1	1	.	1	2	2	2	2
Alnus acuminata	2	1	1	2	2	1	1	1	1	1	.	.
Chiranthodendron pentadactylon	.	.	.	.	1	1	1	2	1	1	.	.
Fuchsia arborescens	1	.	1	.	1	.	1	1	.	.	.	.
Fuchsia microphylla	.	.	1	.	.	1	1	1	.	.	.	1
Characteristics of the *festucetosum amplissimae subass. nova*:												
Festuca amplissima	2	2	2	2	2	2	2	2	.	.	.	.
Galium mexicanum	1	2	1	1	.	2	1	1	.	.	1	.
Salvia lasiantha	1	2	2	2	1	2	1	1	.	.	.	.
Characteristics of higher syntaxonomic units and transgressives:												
Arbutus xalapensis	1	1	+	2	1	+	1	1	+	+	+	1
Brachypodium mexicanum	1	.	1	.	1	2	2	1	.	1	2	2
Neonelsonia acuminata	1	.	.	.	1	2	2	2	1	.	2	2
Phanerophlebia macrosora	1	2	2	1	.	1	2	1	.	.	.	.
Maianthemum flexuosum	.	.	.	.	.	.	.	.	1	1	1	1
Roldana gilgii	.	.	.	.	.	.	.	.	1	1	.	1
Ceanothus caeruleus	1	.	.	.	.	1	.	.	1	.	.	.
Arracacia donnell - smithii	.	1	1	1	.	.	.	.	.	.	.	.
Zeugites munroanus	.	.	1	.	.	.	.	.	2	2	.	.
Quercus ocoteifolia	.	.	.	.	.	.	.	.	.	2	2	2
Oreopanax xalapensis	.	.	.	.	1	.	.	.	.	.	1	.
Pinus pseudostrobus	.	.	.	.	1	.	.	.	1	.	.	.
Viburnum hartwegii	.	.	.	.	.	.	.	.	.	.	1	1

Table III. Continuation.

Companions:												
Pteridium aquilinum	1	.	1	1	.	.	.	1	1	.	.	.
Arenaria sp.	1	.	1	1	.	.	1	.	.	.	.	.
Stevia lucida var. *oaxacana*	1	1	1	.	1	.	.	.	.	.	.	.
Lupinus montanus	.	1	1	1	1	.	.	.	.	.	.	.
Calea integrifolia	1	.	.	.	.	.	1	2	.	.	.	.
Geranium andicola	1	1	.	1	.	.	.	.	.	.	.	.
Archibaccharis corymbosa	.	1	1	1	.	.	.	.	.	.	.	.
Senecio cobanensis	.	.	1	.	.	.	.	.	1	1	.	.
Roldana acutangula	.	.	.	.	.	.	.	1	.	.	1	1
Roldana barba-johannis	.	.	.	1	2	.	.	.	.	.	.	.
Lopezia hirsuta	2	.	.	2	.	.	.	.	.	.	.	.
Buddleja nitida	1	.	.	.	1	.	.	.	.	.	.	.
Pseudognaphalium liebmannii	.	.	.	.	1	.	.	.	.	.	1	.
Euphorbia orizabae	.	.	.	.	.	.	.	.	.	.	1	1

Species present in a single inventory: I.A.3: *Trisetum* sp. 2, *Salmea scandens* 1. II.A.1: *Dahlia australis* 1, *Chimaphila maculata* 2. II.A.2: *Roldana heterogama* 1, Vulpia bromoides 2. II.A.3: *Bromus carinatus* 1, *Dahlia coccinea* 1, *Salvia cinnabarina* 1, *Schistocarpha longiligula var. seleri* 1. I.B.3: Clethra *pachecoana* 1, *Ocotea salvinii* 1, *Monnina xalapensis* 1, *Parathesis* sp. 1, *Tournefortia acutiflora* 1, *Saurauia oreophila* 1. I.C.2: *Clethra mexicana* 1, *Quercus crispifolia* 2, *Bidens squarrosa* 1, *Lasiacis divaricata* 1, *Iresine calea* 1. I.C.3: *Polypodium alansmithii* 1, *Smilax moranensis* 1. II.C.1: *Commelina* sp. 1. II.C.2: *Asplenium monanthes* 1, *Coaxana purpurea* 1, *Peperomia galioides* 1, *Garrya laurifolia* 1.
Coordinates: I.A.3: N 14° 39' 24.84'' W 91° 15' 47.34''. II.A.1: N 14° 39' 19.4'' W 91° 15' 52.9''. II.A.2: N 14° 39' 17.8'' W 91° 15' 51.5''. II.A.3: N 14° 39'' 16'' W 91° 15' 58''. I.B.3: N 14° 39' 23.4'' W 91° 15' 44.8''. II.B.1: N 14° 39' 19.4'' W 91° 15' 44.9''. II.B.2: N 14° 39' 18'' W 91° 15' 45.5''. II.B.3: N 14° 39' 16.6'' W 91° 15' 47.4''. I.C.2: N 14° 39' 48.3'' W 91° 15' 47.1''. I.C.3: N 14° 39' 32'' W 91° 15' 30''. II.C.1: N 14° 39' 15'' W 91° 15' 28''. II.C.2: N 14° 39' 03'' W 91° 15' 41''.

DISCUSSION

Alnus acuminata (Andean alder) is a species that Table II (G-1) shows is present consistently in the inventories of this group. It is found in Mexico and other parts of Central America, Colombia, Venezuela, Ecuador, Peru, Bolivia and as far south as Argentina. It is one of the most characteristic species of the cloud forests, although it is found in other types of ecosystems. It frequently appears in oak and pine-oak forests that are sufficiently humid above 1,000 m a.s.l. (González-Espinosa et al. 2011). This species gives its name to the phytosociological plant class *Alnetea acuminatae* Galán de Mera 2005, which embraces the ombrophilous uplands tropical forests where this alder, along with other trees (*Fagaceae*, *Lauraceae*, *Clethraceae*, *Theaceae*, etc.) and many climbers and epiphytes, is the dominant species.

A revision of the literature and similar phytocoenosis described from Sierra de los Cuchumatanes (Guatemala) shows that Islebe et al. (1995) described an alder-pine community from elevations over 3,000 m a.s.l. They named it a 'mixed disturbed forest' and it is dominated by *Pinus hartwegii* Lindl., *Alnus jorullensis* Kunth (=*Alnus firmifolia*), *Alnus acuminata* subsp.

arguta (Schltdl.) Furlow (=*Alnus arguta*) and *Alnus acuminata* (=*A. ferruginea*), along with an abundance of the endemic *Agave hurteri* Trel. These authors indicate that this community is a successional stage of the *Abies guatemalensis* Rehder fir forests, and consists of an association that substitutes the mixed pine-alder forest dominated by *Pinus hartwegii* and *Agave hurteri*, found at greater elevations (upper Supratropical).

In Sierra de Angangueo (states of Michoacán and Mexico) at an altitudinal range of 2,500–3,100 m a.s.l., Giménez de Azcárate et al. (2003) describe a 'mixed forest' community disturbed by human action that is dominated by *Pinus pseudostrobus* Lindl., accompanied by *Quercus laurina* Bonpl., *Abies religiosa* (Kunth) Schltdl. & Cham., *Alnus acuminata* subsp. *arguta* and *Clethra mexicana* DC. These authors describe it as a pre-climax community that substitutes the climax "oyamel" mixed forest (*Cleyero integrifoliae-Abietetum religiosae* G. Azcárate & Ramírez 2004). This last one is a mesophyllous and thermophylous association, located in the lower Supratropical and Humid bioclimatic belt. Its composition includes differential species like *Pinus pseudostrobus*, *Clethra mexicana* DC., *Quercus laurina*, *Cleyera integrifolia* (Benth.) Choisy, *Smilax morannensis* M. Martens & Galleotti, *Cornus disciflora* Moc. & Sessé ex DC., *Simplocos prionophylla* Hemsl. etc. All of them are absent in the association that replaces it in altitude (*Sibthorpio repentis-Abietetum religiosae* G. Azcárate & Ramírez 2004), and dominated exclusively in the tree layer by *Abies religiosa* (Giménez de Azcárate & Ramírez 2004). An analogous situation has been described by Ern (1976) for the volcanoes in the Puebla Valley, and by Rzedowski et al. (1977) and Rzedowski & Calderón de Rzedowski (2005) for the Sierra Nevada (both in central Mexico). Depending on the interpretation, this mixed forest formation consists of serial heliophilous coniferous forests ("oyamel" fir), with other trees, shrubs and grassland that are more or less resistant to disturbance. These authors differentiate a thermophile variant (variant with *Alnus acuminata* subsp. *arguta*), found most commonly on shady east-facing slopes and gullies, where the species finds the edaphic humidity that it requires.

Catalán-Heverástico et al. (2003) did not perform any phytosociological studies but do provide a list of tree species for the mountains of Guerrero (Mexico) that includes *Abies guatemalensis*, *Quercus salicifolia* Née, *Oreopanax xalapensis*, *Ocotea chiapensis* (Lundell) Standl. & Steyerm., *Persea americana* Mill., *Meliosma dentata* (Liebm.) Urb., *Clethra mexicana*, *Alnus acuminata* and *Chiranthodendron pentadactylon* Larreategui, amongst other species characteristic of the upland mesophile cloud forests. Their study was performed at 2,500–2,800 m a.s.l. and reveals a floristic composition with similarities to the one we describe here. Velázquez et al. (2021) in an exercise on the integration of geographic, physiognomic and geobotanical attributes of the plant formations of Michoacán (Mexico) and their relationship at the syntaxonomic level with the units defined in the state, recognize the the class *Alnetea acuminatae* Galán de Mera 2005. This is proposed by temporarily assigning of lower rank syntaxa, pending validation, included in the provisional order *Alnetalia acuminate-jorullensae* (Takaki et al. 2019) and included in the Cloud Forest concept. The absence of types for the syntaxonomic units, as well as reference inventories, prevent their analysis and relationship with those here defined.

Likewise, Medina et al. (2020) describes a number of coniferous forest communities from the volcano Tancitaro, Michoacán (Mexico), including the new subassociation *quercetosum* *laurinae* within the association *Sibthorpio repentis-Abietetum religiosae* G. Azcárate & Ramírez 2003, found in the lower Supratropical horizon with a Humid ombrotype, at 2,600–3,000 m a.s.l. This subassociation is based on the presence of *Quercus laurina, Geranium seemannii* Peyr.*, Galium mexicanum, Pinus pseudostrobus* and *Alnus jorullensis*. These authors consider that this subassociation represents a catenal transition from the pine-oak forests in the Mesotropical stage to the "oyamel" forests belonging to the typical association. Further north in the Sierra Madre Occidental, Giménez de Azcárate et al. (2013) have identified the presence of upland mesophile forests (mixed sub-evergreen macro-forests) in the shady gullies on steep slopes at around 2,000 m a.s.l., coinciding basically with the humid Mesotropical stage. The most representative species here include *Alnus acuminata*, *Carpinus caroliniana* Walter, *Cleyera integrifolia* (Benth.) Choisy, *Clethra* spp., *Cornus disciflora*, *Garrya laurifolia* Benth., *Ilex quercetorum* I.M.Johnst., *Magnolia pacifica* subsp. *tarahumara* A. Vázquez, *Oreopanax xalapensis, Ostrya virginiana* (Mill.) K.Koch, *Persea liebmannii* Mez, *Tilia americana* L., in addition to different species of *Pinus* spp. and *Quercus* spp. (*Pinus herrerae* Martínez, *P. maximinoi* H.E.Moore, *P. oocarpa* Schiede, *Quercus candicans* Née, *Q. castanea* Née, *Q. diversifolia* Née, *Q. obtusata* Bonpl., *Q. splendens* Née and *Q. subspathulata* Trel.). With greater elevation and proximity to the Supratropical thermotype, the more thermophile species tend to disappear and others such as *Clethra rosei* Britton, *Pinus ayacahuite* Ehrenb. ex Schltdl., *P. douglasiana* Martínez, *P. pseudostrobus* and *Abies durangensis* Martínez, appear, and the formations assume an appearance that is more reminiscent of the pine-oak forests.

These mixed forests of *Pinus* spp., *Abies* spp., *Alnus* spp., *Quercus* spp. and *Arbutus* spp. are found throughout the volcanic mountain chains in Mexico and Guatemala, at similar elevations and in analogous ecological conditions. They represent particular dynamic, catenal and transitional situations between the *Abies* spp. forests and the mixed *Pinus* spp. and *Quercus* spp. forests.

Based on our statistical results that reveal the existence of at least two groups of inventories with different floristic and ecological compositions, we hereby propose two new phytosociological associations to be included in the class *Alnetea acuminatae* Galán de Mera 2005.

We describe the association *Saurauio oreophilae-Alnetum acuminatae ass. nova* (Table II, *typus* relevé IV.A.1) as an upland cloud forest found at 2,400–3,020 m a.s.l., that may also be present on volcanoes at greater altitudes. It has a clear preference for humid and slopes (over 30°) of the volcano, where mists and 'horizontal rain' are frequent. The characteristic species are *Alnus acuminata*, which is accompanied by trees and shrubs of 5–25 meters in height such as *Saurauia oreophila*, endemic to Mexico and Guatemala, *Ardisia venosa*, *Meliosma idiopoda*, *Clethra mexicana*, *Cestrum pacayense* Francey, *Oreopanax xalapensis* and *O. echinops*, the latter species classified as Vulnerable (VU) and found only in Mexico, Guatemala and Honduras (González-Espinosa et al. 2011). Finally, it is accompanied by a series of climbers and lianas including *Maianthemum flexuosum* (Bertol.) LaFrankie, *Valeriana scandens* var. *candolleana* (Gardner) C.A. Mull., *Smilax moranensis* M. Martens & Galeotti and *Iresine calea* (Ibáñez) Standl.

This association is found only in the Guatemalan subsector as, for the time being, we have no data that conclusively prove that it is found on the Mexican volcanic chains. From a bioclimatic standpoint, the optimum of this association is the upper Mesotropical thermotype, although it will reach the lower Supratropical horizon in Humid and Hyperhumid ombrotypes.

In Table II, which shows the main group of the 13 inventories (subgrup A, Fig. 5), two other subgroups of inventories are apparent. The first consists of five inventories (Fig. 5, subgroup B) enriched by *Quercus peduncularis*, *Quercus crispifolia*, *Adiantum andicola* Liebm. and *Zeugites munroanus* Hemsl. The presence of *Quercus* species suggest that it is a transition to the formations dominated by *Q. peduncularis*. We thus believe that it is an ecological variant that indicates the transition to oak-dominated formations that do not require such high levels of humidity.

In the other subgroup of inventories (subgrup C, Fig. 5) *Prunus salasii* Standl and *Billia hippocastanum* Peyr are frequent. They are found above all in shady gullies below 2,730 m a.s.l., subject to erosion with deep organic soils on north-west facing slopes. The shady humid conditions encourage a proliferation of terrestrial orchids such as *Goodyera striata* Rchb. f.

Prunus salasii and *Billia hippocastanum* are two trees that reach 15–25 m height and are founded in mature undisturbed cloud forests (González-Espinosa et al. 2011) in Mexico and Central America (Roskov et al. 2019) on volcanoes at low-to-mid elevations (1,500–2,700 m a.s.l.) (Kappelle & Uffelen 2006). Both species are abundant in the depressions in the volcano – known as *rejoyas* – caused by landslips that create large clearings in the forests. This situation, along with the constantly high humidity levels, ensure that this cohort of species appears at elevations of 2,400–2,700 m a.s.l. Thus, we propose the existence of this variant of the association *Saurauio-Alnetum acuminatae* on disturbed soils, which is found on the lower slopes of the volcanoes where most landslides occur. Their frequency and the natural fall of trees, together with the shady nature of these sites, favour the presence of subnitrophile species of disturbed soils such as *Arracacia donnell-smithii* J.H.Coult. & Rose, *Maianthemum flexuosum* (Bertol.) LaFrankie, *Roldana heterogama* H.Rob. & Brettell, *Neonelsonia acuminata*, *Begonia oaxacana* A.DC., *Solanum appendiculatum* and *Polypodium alansmithii* R.C. Morán.

The inventories in Table III (G-2, Fig. 4) correspond to mixed forests of trees up to 25 m in height dominated by *Quercus peduncularis*, *Arbutus xalapensis*, *Alnus acuminata* and *Adiantum andicola*. This latter taxon has been recognised by other authors as characteristic of the mixed oak forests of Mexico (Rodríguez-Romero et al. 2008). This phytocoenosis is clearly dominated by *Quercus peduncularis*, *Arbutus xalapensis* and, to a lesser extent, by *Alnus acuminata*. In some inventories appear *Quercus crispifolia* and *Quercus ocoteifolia*. (Table III).

Quercus peduncularis thrives at 900–3,000 m a.s.l. in Honduras, Guatemala, Nicaragua, Belize and Mexico (Sierra Madre Oriental). In Mexico its distribution has been severely limited by anthropic activity (CONABIO 2020). Normally, it is found in mixed pine-oak forests but does not form part of the montane mesophile cloud forests (González-Espinosa et al. 2011); *Quercus ocoteifolia* is, nevertheless, characteristic of these cloud forest ecosystems.

For Chiapas uplands (Mexico), González-Espinosa et al. (1991) describe for a mature stage of pine-oak forests with the presence of *Pinus oocarpa*, *Prunus serotina* Ehrh., *Quercus laurina* Bonpl., *Q. crassifolia* Bonpl., *Q. rugosa* Née, *Myrsine juergensenii* (Mez) Ricketson & Pipoly, *Oreopanax xalapensis* and *Alnus acuminata*. It's climatic conditions of that study are similar to those found in the lower parts of the volcano of

San Pedro. In a later work (González-Espinosa et al. 2006) they influence the different composition between the pine-oak forests discussed and the tropical cloud forest formations, which are even more biodiverse in terms of the plant species, containing essentially various *Quercus* species plus 1–3 pine species and dozens of other broad-leaved trees.

Giménez de Azcárate et al. (2003) provide a table with 17 samples from mixed pine-oak forests in which the dominant species are *Pinus pseudostrobus*, *Quercus laurina* and, to a lesser extent, *Abies religiosa*, *Alnus* spp., *Arbutus* spp., *Salix paradoxa* Kunth, *Quercus rugosa*, *Clethra mexicana* and *Ternstroemia lineata* DC., amongst others. Of note in this community is the proliferation of the typical shrubs found in preforestry environments with open canopies due to timber extraction. This community is found at 2,500–3,070 m a.s.l. in the upper Mesotropical and lower Supratropical horizons with upper Subhumid-lower Humid horizons. From a dynamic viewpoint, this community replaces in disturbed areas the mesophytic mixed fir formations belonging to the association *Cleyero integrifoliae-Abietetum religiosae* Giménez de Azcárate & Ramírez 2003. This is a similar case to that mentioned for the same altitudinal band in Valle de México (Rzedowski et al. 1977, Velázquez & Cleef 1993) and in Sierra de los Cuchumatanes (Islebe & Velázquez 1994).

Finally, Medina (2016) in a phytosociological study of the west of Michoacán (Mexico) proposed provisionally two associations that are very similar to those we detected in Guatemala. Firstly, the association *Querco laurinae-Pinetum moztezumae* Medina 2016 is described as a mixed coniferous and broad-leaved association of sub-evergreen species that occupies slopes of average gradient, west-facing, at 2,600–2,800 m a.s.l., which contact catenally with the alder formations of *Sibthorpio-Abietetum religiosae quercetosum laurinae*. This phytocoenosis thrives between the upper Mesotropical-lower Supratropical stages, both of which possess a upper Subhumid-Humid ombrotype. Secondly, the association *Clethro mexicanae-Pinetum pseudostrobi* Medina 2016 is defined as a mixed polyspecific forest, with broad-leaved and coniferous species, dominated by trees of up to 20–40 m in height, with species such as *Pinus pseudostrobus*, *Clethra mexicana*, *Quercus laurina*, *Q. candicans*, *Oreopanax xalapensis*, *Tilia americana* var. *mexicana* (Schltdl.) Hardin and *Carpinus caroliniana*. This latter association is found in gullies deep and steep valleys at 1,900-2,550 m a.s.l. in the Humid Mesotropical stage on the south face of the volcano de Tancítaro. There is a coincidence of species between these two phytocoenosis and our community; nevertheless, in our inventories *Quercus peduncularis* and *Arbutus xalapensis* clearly dominate, and there is a residual presence of *P. pseudostrobus*.

The reiterated presence of these mixed formations in the mountains of Mexico and Guatemala at 2,000–3,300 m a.s.l., linked to the Meso- and Supratropical thermotypes, reveals subtle but important biogeografical, bioclimatic, edaphic and geomorphological differences that enable us to differentiate phytocoenosis, each with particular floristic assemblages. The *Quercus*, *Pinus* and *Alnus* species, along with the other trees commonly found in these environments (e.g. *Clethra* spp., *Cleyera* spp., *Saurauia* spp., *Tilia* spp., *Carpinus* spp. *Ternstroemia* spp. and *Liquidambar* spp.) are important indicators of the environmental conditions and of the extent – to a greater or lesser degree – that human action has had an impact on these forest in recent times.

The phytocoenosis that we studied are found basically at lower elevations than those similarly studied in Mexico, where the climax communities above the timberline are dominated by *Abies* spp. and *Pinus* spp. forests, or by mixed forests of these species and others. The plant communities of the volcano of Sant Pedro in Guatemala is situated at a lower elevation that on the Mexican volcanoes, with the consequence that certain climax forest such as fir (*Abies* spp.) and pine (*Pinus* spp.) founded in the upper Supratropical and lower Orotropical horizons, are absent (Velázquez 1994, Islebe & Velázquez 1994, Velázquez & Islebe 1995, Islebe et al. 1995, Giménez de Azcárate et al. 2003, Medina et al. 2020). With the lower temperatures at greater elevations, these climax forest formations tend to lose the polyspecific characteristic that distinguishes the mixed upland forest that are studying here.

We propose *Adianto andicolae-Quercetum peduncularis ass. nova* (Table III, *typus* relevé II.A.3) as a new association of mixed forest that develops on volcanic soils with slopes around 30% at elevations over 2,400 m a.s.l. It is present in the lower Mesotropical-lower Supratropical thermotype and upper Subhumid-lower Humid ombrotype, above all on steep, sunny exposed slopes. The characteristic or differential species of this association are: *Quercus peduncularis*, *Adiantum andicola*, *Alnus acuminata*, *Chiranthodendron pentadactylon*, *Fuchsia arborescens* and *F. microphylla*. The biogeographical distribution of this association are the territories corresponding to the Guatemalan subsector.

Biogeographically, belongs the Guatemala subsector; the presence of *Quercus peduncularis* in other Central American countries and Mexico suggest that this association or similar ones are also present in this subsector.

It is important to add that a number of samples were enriched by the presence of *Festuca amplissima*, *Galium mexicanum*, *Salvia lasiantha* Benth. and *Brachypodium mexicanum*. All these species except the last one were detected from above 2,800 m a.s.l. as far as the summits. As mentioned in the previous section, the ascendency here of these species is due to the ‘rain-shadow’ effect, together with the more open canopy and increase in sunshine hours. These grasses tend to dry out in summer (November–May), which leads to a proliferation of wildfires and increases the impact of erosion and landslips in winter (the rainy season). In certain areas the soil is completely covered by these grasses and various layers of dry material, whose presence – together with low scrub dominated by *Salvia lasiantha* – slows down the development of a well-structured mature forest. In these conditions – i.e. an open and discontinuous forest canopy – heliophile plants thrive and so on this side of the volcano wildfires are commonplace. Due to its suberification, the oak *Quercus peduncularis* resists relatively well the extreme temperatures provoked by such fires, whose frequency mean that soils are exposed to rain and severe run-off, and landslips occur that have led to the loss of up to two metres of soil in some places of the volcano.

In the forests of *Sibthorpio repentis-Abietetum religiosae* (Giménez de Azcárate & Ramírez 2004) and *Polysticho speciosissimae-Abietetum religiosae* (Medina et al. 2020) appear scattered *B. mexicanum*, *F. amplissima* and various *Salvia* spp., being more abundant in their shrub forest fringes.

These species were present regularly in our inventories, above all on the south-east-facing slopes and at the highest elevations above 2,800 m a.s.l. We thus believe that this represents a subassociation within the association *Adianto andicolae-Quercetum peduncularis* that occurs in higher, rockier and treeless sectors, and where *Brachypodium mexicanum*, *Festuca amplissima* and *Salvia lasiantha* are common (*festucetosum amplissimae subass. nova*, relevé *typus*: II.A.1,

Table III). This latter species is regarded by Rivera-Hernández et al. (2019) as being typical of semi-arid thorny woodland and so is an indication of a transition towards other, more xeric plant formations.

In terms of the syntaxonomy of these two associations, it is clear that they correspond to phytocoenosis of cloud or mixed forests found in very humid mesophile environments, which leads us to link them with the class *Alnetea acuminatae* Galán de Mera 2005. This unit embraces the alder forests dominated by *Alnus acuminata* and other climbers and lianas (Galán de Mera & Vicente Orellana 2006).

Nevertheless, our inventories contain species restricted to the cloud forests of Mexico and Central America and so at a syntaxonomical level we cannot include this association in the syntaxa created originally for Colombia, Peru, Bolivia or Argentina.

In Colombia the communities belonging to *Alnetea acuminatae* Galán de Mera 2005 are described from around Lago de Tota (Boyacá), a locality at above 3,025 m a.s.l., where the characteristic species include *Viburnum tinoides* L.f., *Oreopanax incisus* (Willd. ex Schult.) Decne. & Planch., *Solanum elaeagnifolium* Cav., *Weinmannia microphylla* Kunth, *Hesperomeles heterophylla* Hook., *Clusia multiflora* Kunth, *Verbesina elegans* Kunth, *Morella parvifolia* (Benth.) Parra-Os., *Passiflora mixta* L.f., *Bomarea multiflora* (L.f.) Mirb. and *Clethra fimbriata* Kunth., amongst others (Rangel-Churio & Aguirre 1986). This study contains no syntaxonomical ascription.

The characteristic species of the Andean alder formations include *Berberis lutea* Ruiz & Pav., *Dioscorea stenopetala* Hauman, *Fuchsia denticulata* Ruiz & Pav., *Morella pubescens* (Humb. & Bonpl. ex Willd.) Wilbur, *Passiflora mollissima* (Kunth) L.H.Bailey, *P. trifoliata* Cav., *Rubus urticifolius* Poir. and *Brachypodium mexicanum* (Galán de Mera et al. 2002, Galán de Mera & Vicente Orellana 2006). The alliance *Myrico pubescentis-Alnion acuminatae* Galán de Mera, Rosa & Cáceres 2002 includes the alder formations of central sector of the Andean Cordillera (Peru and Bolivia).

For the southern Bolivia and northern Argentina communities belonging to the alliance *Pruno tucumanensis-Alnion acuminatae* Galán de Mera 2005 have been described, with the characteristic species including *Myrsine laetevirens* (Mez) Arechav., *Clinopodium gilliesii* (Benth.) Kuntze, *Kaunia lasiophthalma* (Griseb.) R.M.King & H.Rob., *Boehmeria caudata* Sw., *Podocarpus parlatorei* Pilg., *Polystichum montevidense* (Spreng.) Rosenst., *Sambucus peruviana* Kunth, *Prunus tucumanensis* Lillo, *Crinodendron tucumanum* Lillo and *Duranta serratifolia* (Griseb.) Kuntze, amongst others.

The *Cyatheo herzogii-Alnion acuminatae* Galán, Campos, Linares Montoya Torres & Vicente 2020 alliance includes Andean alder vegetation from the thermotropical montane forest in soils rich in clay and hydromorphism (Galán de Mera et al. 2020) with dominance of plant species *Acanthus ilicifolius* L., *Asplenium auriculatum* Sw., *Aulonemia longiaristata* L.G. Clark & Londoño, *Cyathea herzogii* Rosenst., *Cyathea lechleri* Mett., *Geonoma orbignyana* Mart., *Hedyosmum sprucei* Solms, *Hypolepis parallelogramma* (Kunze) C. Presl, *Hypolepis obtusata* (C. Presl) Kuhn, *Inga acuminata* Benth., *Miconia aff asperrima* Triana, *Miconia aggregata*, *Saccoloma inaequale* (Kunze) Mett., and *Serpocaulon fraxinifolium*.

Finally, the *Escallonio pendulae-Alnion acuminatae* Galán, Campos, Linares Montoya Torres & Vicente 2020 alliance lincludes the riparian forests and peat bogs of northern Peru. The main characteristic species are *Bia alienata* Didr., *Escallonia pendula* (Ruiz & Pav.) Pers., *Ladenbergia oblongifolia* (Humb. ex Mutis)

L.Andersson, *Pentacalia reflexa* (Kunth) Cuatrec., *Thelypteris pennata* (Poir.) C.V. Morton, and *Styloceras laurifolium* (Willd.) Kunth.

The new associations that we describe here, restricted to Mexico (to be confirmed) and Guatemala, are included in a new phytosociological alliance *Oreopanacion xalapensis all. nova* [*Holotypus: Saurauio oreophilae-Alnetum acuminatae*], which embraces cloud and mixed forest associations with species from genera such as *Pinus* spp., *Abies* spp., *Alnus* spp., *Quercus* spp., *Arbutus* spp., *Oreopanax* spp., *Clethra* spp., *Cleyera* spp., *Saurauia* spp., *Tilia* spp., *Carpinus* spp. *Ternstroemia* spp., and *Liquidambar* spp., along with the typical climbers and lianas from this region.

The order *Alnetalia acuminatae* Galán de Mera & Rosa in Galán de Mera, Rosa & Cáceres 2002 was created to cover the alder formations of the Supratropical belt in an area stretching from Venezuela to Argentina (Andean region) (Galán de Mera et al. 2002). In the hope that future studies in Mexico and Central America will gather more information on the phytocoenosis with these characteristics, we maintain the new alliance in this order, although we propose that the range of this order and of this phytosociological class be extended.

CONCLUSIONS

This study has highlighted the variation of mixed cloud forest communities at mid- and high elevations on Mexican and Guatemalan all of which gathering an ecological identities, such as altitude and orientation. Nevertheless, these phytocoenosis are not identical as there are differences in their floristic composition and elevation ranges, which are determined by their biogeographical locations and their ombroclimatic context, which is much more humid in the mountains of Chiapas sector than in those in the province of Neovolcánica (central Mexico).

Our studies must be complemented in future with other phytosociological work that will allow us to appreciate the full extent of the forest associations presents in this biogeographical complex, as well as their successional dynamics. This knowledge is essential if we are to manage these forests correctly, above all in terms of the extraction of resources and the reforestation with appropriate tree species.

These forests are, moreover, subject to continuous anthropic activity, mainly in areas of easy access and gentler slopes. Uncontrolled cutting and clearing to create agricultural land are the main negative impacts that are currently affecting these ecosystems, although we should not forget that climate change may also seriously modify its distribution and composition. Finally point out, these formations harbour many plant and animal species of great importance, of which it is worth highlighting the resplendent quetzal (*Pharomachrus mocinno mocinno*), endemic to Central America, and the horned guan (*Oreophasis derbianus*), both species that are currently classified as Endangered (IUCN Red List of Threatened Species 2020, https://www.iucnredlist.org/). Indeed, the forests analysed form part of the diet of the horned guan and are its main habitat. Thus, it is urgent that conservation plans that will manage the exploitation of these forests' natural resources be drawn up and put in place.

Syntaxonomical scheme

Class *Alnetea acuminatae* Galán de Mera 2005
+ Order *Alnetalia acuminatae* Galán de Mera & Rosa in Galán de Mera, Rosa & Cáceres 2002

- Alliance *Oreopanacion xalapensis all. nov.* [*Holoyypus: Saurauio oreophilae-Alnetum acuminatae*, *typus ass.*: rel. IV.A.1, Table II]
- *Saurauio oreophilae-Alnetum acuminatae ass. nov.* (*Holotypus*: rel. IV.A.1, Table II)
- *Quercus peduncularis* variant
- *Prunus salasii* variant
- *Adianto andicolae-Quercetum peduncularis ass. nova* (*Holotypus*: rel. II.A.3, Table III)
- *festucetosum amplissimae subass. nov.* (rel. I.A.3 to II.B.3. *Holotypus*: inv. II.A.1, Table III)

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