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GALÁN-DE-MERA, ANTONIO; SÁNCHEZ-VEGA, ISIDORO; LINARES-PEREA, ELIANA;  
CAMPOS, JOSÉ; MONTOYA, JUAN; VICENTE-ORELLANA, JOSÉ A.

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## A phytosociological analysis and synopsis of the dry woodlands and succulent vegetation of the Peruvian Andes

ANTONIO GALÁN-DE-MERA<sup>1</sup>, ISIDORO SÁNCHEZ-VEGA<sup>2</sup>, ELIANA LINARES-PÉREA<sup>3</sup>,  
JOSÉ CAMPOS<sup>4</sup>, JUAN MONTOYA<sup>2</sup> and JOSÉ A. VICENTE-ORELLANA<sup>1</sup>

<sup>1</sup>Laboratorio de Botánica, Universidad CEU San Pablo, Apartado 67, 28660 Boadilla del Monte, Madrid, España

<sup>2</sup>Laboratorio de Botánica, Universidad Privada Antonio Guillermo Urrelo (UPAGU), Jr. José Sabogal 913, Cajamarca, Perú

<sup>3</sup>Estudios Fitogeográficos del Perú, Sánchez Cerro 219, Manuel Prado, Paucarpata, Arequipa, Perú

<sup>4</sup>Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Apartado 140434, Lima, Perú

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### ABSTRACT

A phytosociological approach to dry forest and cactus communities on the occidental slopes of the Peruvian Andes is presented in base of 164 plots carried out following the Braun-Blanquet method. From them, 52 have been made recently, and the other 112 were taken from the literature. After a multivariate analysis, using a hierarchical clustering and a detrended correspondence analysis, the *Acacio-Prosopidetea* class (dry forest and cactus communities, developed on soils with some edaphic humidity or precipitations derived from El Niño Current), the *Opuntietea sphaericae* class (cactus communities of central and southern Peru, on few stabilized rocky or sandy soils) and the *Carico-Caesalpinietea* class (dry forests of the Peruvian coastal desert, influenced by the maritime humidity of the cold Humboldt Current), are differentiated. Within the *Acacio-Prosopidetea* class, two alliances are commented: the *Bursero-Prosopidion pallidae* (with two new associations *Loxopterygio huasanginis-Neoraimondietum arequipensis* and *Crotono ruiziani-Acacetum macracanthae*), and the new alliance *Baccharido-Jacarandion acutifoliae* (with the new associations *Armatocereo balsasensis-Cercidietum praecocis* and *Diplopterydo leiocarpae-Acacetum macracanthae*). For the *Opuntietea sphaericae* class, the association *Haageocereo versicoloris-Armatocereetum proceri* (*Espostoo-Neoraimondion*) is described on the basis of plots from hyperarid localities of central Peru. Finally, a typological classification of the studied plant communities is given.

**Key words:** *Acacio-Prosopidetea*, cactus communities, dry forests, *Opuntietea sphaericae*, Peru, Phytosociology.

### INTRODUCTION

Dry forests and cactus communities are widely extended in South America (Blanco et al. 2013). In Peru, they are concentrated on the western slopes of the Andean Cordillera, in the inter-Andean valleys,

and in the north of the country (Linares-Palomino et al. 2003). There, in the north, dry forests are further extended as a continuation of the Ecuadorian dry forests (Aguirre et al. 2006). These plant formations in Peru, with rainfall less than 500 mm/year, are linked to the uplift of the Andean Cordillera in the Paleocene, and the strengthening of the cold

Correspondence to: José Alfredo Vicente-Orellana  
E-mail: [avicore@ceu.es](mailto:avicore@ceu.es)

Humboldt Current in the Eocene (Livermore et al. 2005), evolving a hyperarid period in the Atacama Desert (Luebert and Gajardo 2005) which isolated some territories with a large number of endemic plants (Galán de Mera et al. 1997).

The floristic characterizations of Weberbauer (1945) and Ferreyra (1960, 1983), and recent studies on the dry deciduous forests of northern Peru, were analysed by comparing their structure and floristic relationships, with preference of a pool of woody species (Phillips and Miller 2002, Bridgewater et al. 2003, Linares-Palomino et al. 2003, Linares-Palomino 2004a, b, Linares-Palomino and Ponce Alvarez 2005). Regarding the cactus communities of Peru, some phytosociological data (Galán de Mera and Vicente Orellana 1996, Galán de Mera and Gómez Carrión 2001, Galán de Mera et al. 2002a, b, 2004, 2009, Galán de Mera and Linares Perea 2012, Montesinos et al. 2012) are known, as well as the plant systematic bibliography with geographical information (Rauh 1958, Ritter 1981, Hunt 2006).

The Peruvian endemic cactus occur also within northern dry forests around the Amotape-Huancabamba Zone (Weigend 2002), and the occidental Andean slopes and inter-Andean valleys, contributing to the original plant communities of this country. Thus, a new phytosociological contribution along the Peruvian Andes is reported in this paper, with the aim to understand better the beta-diversity of these dry plant communities throughout the syntaxonomical units.

## MATERIALS AND METHODS

### STUDY AREA

The studied area covers circa 1600 Km along the occidental slopes of the Peruvian Andes up to 3000 m asl, where vegetation changes from succulent vegetation to the Andean shrublands. We have taken data from the southern Peruvian border in the Tacna Department (approximate

latitude- 18°01'S-70°14'W) to North Peru in the Cajamarca Department (approximate latitude- 07°16'S-79°08'W). In the Cajamarca Department, the succulent vegetation around the Huancabamba Depression (06°03'S-79°04'W) and in the Marañón valley (between 06°35'S-78°06'W and 05°45'S-78°41'W) were also investigated as well the wide coast of the Arequipa Department in southern Peru (approximate latitude- 17°02'S-71°43'W).

The tropical climate in all the studied localities is arid (0-300 mm) to dry (300-500 mm), except for some sites of the northern, where annual precipitation can reach 900 mm. The annual average temperatures oscillate between 15°C to 25°C. For a bioclimatic diagnosis of Peruvian syntaxa, the bioclimatic model of Rivas-Martínez is followed (Rivas-Martínez and Rivas-Saenz 1996-2009), where data from meteorological stations between infra- and supratropical belts with hyperarid to dry precipitation range, have been considered. For its intervals and nomenclature see Table I.

TABLE I

**Bioclimatic belts and interval types of precipitation according to the bioclimatic model of Rivas-Martínez. It = 10 (T + m + M)[T: average annual temperature (in °C), m: average lowest temperature in the coldest month, M: average highest temperature in the coldest month], P: annual precipitation.**

Bioclimatic belts	It	Interval types of precipitation	
			P (mm)
Infratropical	> 610	Ultrahyperarid	< 5
Thermotropical	610-471	Hyperarid	5-30
Mesotropical	470-311	Arid	30-100
Supratropical	310-171	Semiarid	100-300
		Dry	300-500
		Subhumid	500-900

Except the sedimentary geologic materials linked to the rivers, the sea, and Aeolian deposits, the occidental slopes of the southern Peruvian Andes present a volcanic origin (Instituto de Geología y Minería 1975). From the Arequipa Department

to the South, the landscape is characterized by a sequence of volcanoes that reach approximately 6000 m asl (i.e. Ampato, Coropuna and Hualca Hualca). Central and northern Peru present specially metamorphic outcrops, as granites and diorites, as we can observe in the Huascarán (6768 m asl), and in the Huancabamba Depression (2145 m asl), the low zone of the tropical Andes, and where the central Andes and the northern Andes diverge between a landscape of dry forests. Dry forests and succulent plant communities of northern Peru are influenced by the rainfall originating from the warm maritime El Niño Current, while the cactus communities below 8°S indicate an arid climate originating from the rain shadow derived of the altitude of the Andes and the anticyclone situation produced by the cold maritime Humboldt Current.

#### STUDYING THE VEGETATION

A phytosociological study of northern dry forests and cactus communities of the occidental slopes of Peruvian Andes, including some localities of the coastal desert, is presented. It is based on 164 plots carried out following the Braun-Blanquet method (Braun-Blanquet 1979, Biondi 2011). Fifty-two of them have been made recently by the authors, and the rest have been taken from numerous references from other authors. A synthetic table was made up with all the plots (Table SII - Supplementary Material) using SORT 4.1 program (Ackermann and Durka 1997), where percentage intervals of species presence were transformed into symbols (< 10% = +, 11 to 20% = 1, 21 to 40% = 2, 41 to 60% = 3, 61 to 80% = 4, and > 81% = 5); their references are given in the Appendix I. Table SIII (Supplementary Material) shows the plots of the new associations and alliances; their localities are presented in the Appendix II.

In order to improve the manual classification of the columns of Table SII, a hierarchical clustering producing a dendrogram has been made, using

the similarity index (UPGMA) of Bray and Curtis (1957), which takes into account the abundance values of the plants of the plots. A detrended correspondence analysis (DCA) is provided in order to discuss how columns are grouped. This statistical analysis was performed by PAST 3.04 program (Hammer 2014).

To discuss the higher phytosociological units and their relationships with the vegetation neighboring Peru, some works from Ecuador (Aguirre et al. 2006, Weigend 2002, 2004), Colombia (Rangel et al. 1997, Ruiz et al. 2002) and Chile (Luebert and Gajardo 2005), have been consulted. As a result, some new associations and other phytosociological units are described.

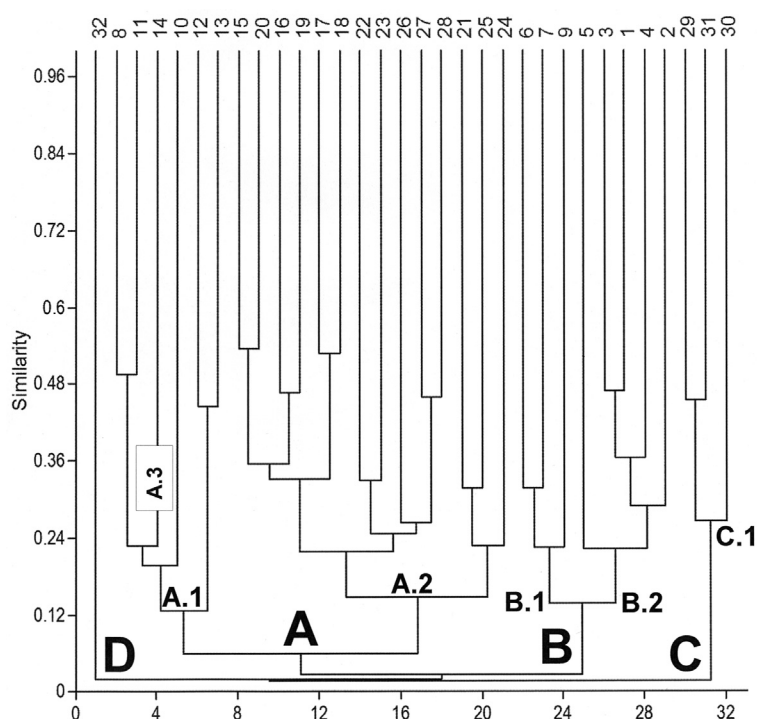
The nomenclature of taxa in the text and tables follows The Plant List (2013). For the nomenclature of syntaxonomical units, the International Code of Phytosociological Nomenclature is followed (Weber et al. 2000).

## RESULTS

#### STATISTICAL ANALYSIS

The dendrogram of Figure 1 and Table SII show the variability of dry forests and cactus communities in the Andean occidental slopes, the Marañón valley and some localities of the coastal desert. Four branches are clearly differentiated in the dendrogram: *Opuntietea* class (branch A, columns 8 to 24) -cactus communities of central and southern Peru-, *Acacio-Prosopidetea* class (branch B, columns 6 to 2) -dry forests and cactus communities of northern Peru-, and the desert forests of *Carico-Caesalpinietea* class (branch C, columns 29 to 31) (Galán de Mera and Vicente Orellana 1996, Galán de Mera et al. 2009). Column 32 (branch D) is the most separated from them, belonging to the *Echinopsio schoenii-Proustietea cuneifoliae* class (Montesinos et al. 2012).

The DCA of Figure 2 shows isolated plant groups (A-H) within each phytosociological

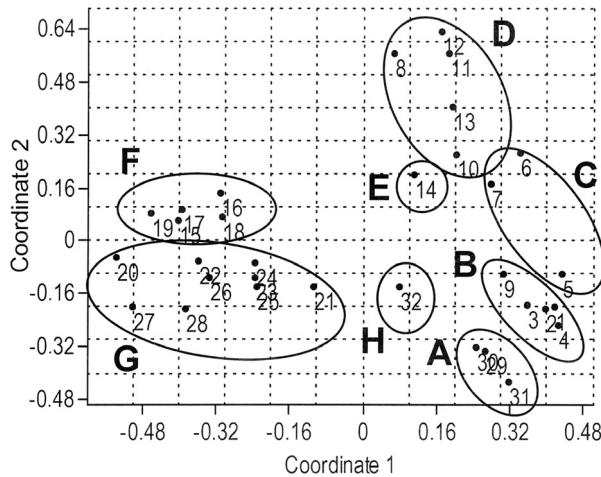


**Figure 1** - Dendrogram with the studied phytosociological classes and their alliances. (A) *Opuntietea sphaericae*: (A.1) *Espostoo-Neoraimondion*, (A.2) *Corryocaction brevistyli*, and (A.3) *Haageoceron procumbentis*. (B) *Acacio-Prosopidetea*: (B.1) *Bursero-Prosopidion pallidae* and (B.2) *Baccharido-Jacarandion acutifoliae*. (C) *Carico-Prosopidetea* with the *Gridelion glutinosae* alliance, (D) *Anredero diffusae-Diplostephietum meyenii* association (*Echinopsio-Proustietea* class). The reference numbers of the branches are indicated in the Appendix I.

class: A- *Caesalpinia spinosa*, *Carica candicans*, *Croton alnifolius*, *Citharexylum flexuosum*, *Heliotropium arborescens*, *Randia rotundifolia*, *Senecio mollendoensis*, and *Stipa pachypus*; B- *Alternanthera porrigens*, *Armatocereus rauhii* subsp. *balsasensis*, *Baccharis oblongifolia*, *Cyathostegia weberbaueri*, *Dalea carthagenensis*, *Diplopterys leiocarpa*, *Dodonaea viscosa*, *Jacaranda acutifolia*, *Lantana camara*, *Matucana celendinensis*, *Melinis repens*, *Pappobolus acutifolia*, and *Puya mimia*; C- *Bursera graveolens*, *Capparicordis crotonoides*, *Loxopterygium huasango*, *Deuterocohnia longipetala*, and *Onoseris odorata*; D- *Espostoa melanostele*, *Mila nealeana*, *Orthopterygium huacui*, *Pluchea chingoyo*, and *Weberbauerocereus johnsonii*; E-

*Corryocactus brachypetalus*, *Eriocyce islayensis*, and *Haageocereus decumbens*; F and G- *Ambrosia artemisioides*, *Armatocereus riomajensis*, *Austrocylindropuntia subulata*, *Balbisia meyeniana*, *Browningia candelaris*, *Corryocactus aureus*, *C. brevistylus*, *Cylindropuntia tunicata*, *Euphorbia apurimacensis*, *Gochnatia arequipensis*, *Haageocereus platinospinus*, *Lantana scabiosiflora*, *Oreocereus hempelianus*, *Weberbauerocereus rauhii*, and *W. weberbaueri*; H- *Anredera diffusa*, *Bomarea ovata*, *Bowlesia sodiroana*, *Cumulopuntia corotilla*, *Cylindropuntia rosea*, *Diplostephium meyenii*, *Dunalia spinosa*, *Echinopsis schoenii*, *Fuertesimalva echinata*, *Heliotropium microstachyum*, *Jaegeria hirta*, *Lophopappus foliosus*, *Mirabilis expansa*,

*Mostacillastrum gracile*, *Mulguraea arequipensis*, *Mutisia acuminata*, *Neowerdermannia peruviana*, *Oxalis megalorrhiza*, *Philibertia solanoides*, *Proustia cuneifolia*, *Portulaca pilosa*, *Salvia oppositiflora*, *Senecio tovarii*, and *Viguiera lanceolata*. F is separated from G by the presence of *Neoraimondia arequipensis* in the plots.

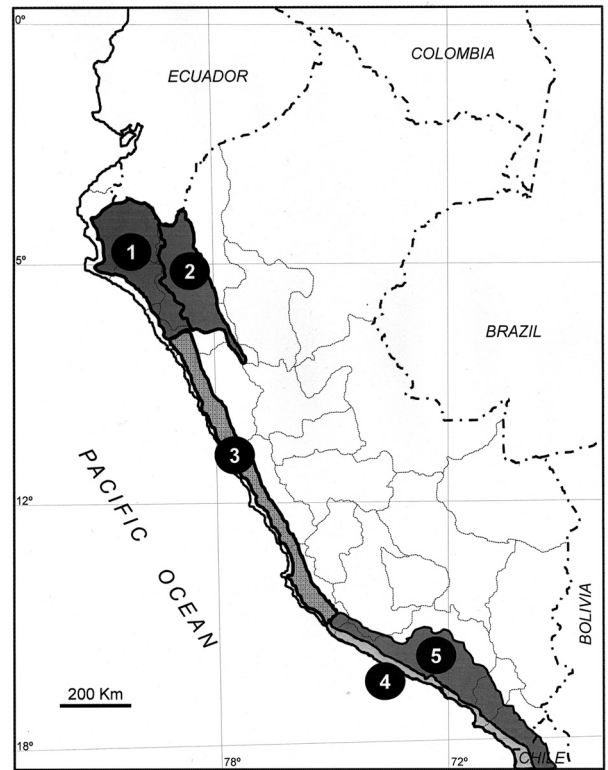


**Figure 2** - DCA with the alliances of the *Opuntietea sphaericae*, *Acacio-Prosopidetea*, and *Carico-Caesalpinietea* classes. (A) *Grindelion glutinosae*, (B) *Baccharido-Jacarandion acutifoliae*, (C) *Bursero-Prosopidion pallidae*, (D) *Espostoo-Neoraimondion*, (E) *Haageocerion procumbentis*, (F) thermotropical version of *Corryocaction brevistyli*, (G) mesotropical version of *Corryocaction brevistyli*, (H) *Anredero diffusae-Diplostephietum meyenii* association (*Echinopsio-Proustietea* class). The reference numbers are indicated in the Appendix I.

Figure 3 shows the distribution of *Acacio-Prosopidetea* and *Opuntietea* classes in Peru. The first class is distributed in the north, while the second is widely distributed in central and southern Peru.

ALLIANCES AND THEIR ASSOCIATIONS

The *Acacio-Prosopidetea* class encloses the dry forests and succulent plant communities of northern Peru, influenced by the rainfall originating from the warm El Niño Current, and also forests on riverside humid soils of the Western Andes, between 100 and 2500 m asl (Galán de Mera et al. 2009).



**Figure 3** - Distribution of the alliances of the *Acacio-Prosopidetea* class - (1) *Bursero-Prosopidion pallidae*, and (2) *Baccharido-Jacarandion acutifoliae*, and *Opuntietea sphaericae* class - (3) *Espostoo-Neoraimondion*, (4) *Haageocerion procumbentis*, and (5) *Corryocaction brevistyli* in Peru.

*Cryptocarpo-Prosopidetalia* shows two groups in the dendrogram (Fig. 1, branches 6 to 9, and 5 to 2) and also in the DCA (Fig. 2, groups B and C), which in Table SII are interpreted as the two phytosociological alliances, *Bursero-Prosopidion pallidae* (columns 6 to 5) and *Baccharido-Jacarandion acutifoliae* (columns 9 to 2).

*Bursero-Prosopidion pallidae* (Galán de Mera et al. 2002a) are the infratropical and thermotropical semiarid associations [Table SII: *Loxopterygio huasanginis-Neoraimondietum arequipensis* (column 6), *Cercidio praecocis-Prosopidetum pallidae* (column 7), and *Crotono ruiziani-Acacetum macracanthae* (column 5)], throughout the occidental slopes of the Andes between 100 and 2500 m (Fig. 3.1). The characteristic species of

the alliance are *Bougainvillea peruviana*, *Bursera graveolens*, *Capparicordis crotonoides*, *Cordia lutea*, *Croton lobatus*, *Deuterocohnia longipetala*, *Loxopterygium huasango*, *Onoseris odorata*, and *Prosopis pallida*, according to the altitudinal distribution indicated by Ceroni Stuva (2003). In a recent work (Galán de Mera et al. 2013), the subhumid forests of the *Annono cherimolae-Acacietaum macracanthae* association is mentioned between 2000-2500 m asl, but it is a very disturbed forest where we could not find plots of sufficient homogeneity.

*Baccharido oblongifoliae-Jacarandion acutifoliae* all. nova hoc loco (holotypus: *Diplopterydo leiocarpae-Acacietaum macracanthae* ass. nova; characteristic species: *Alternanthera porrigens*, *Anadenanthera colubrina* var. *cebil*, *Armatocereus rauhii* subsp. *balsasensis*, *Baccharis oblongifolia*, *Bauhinia glabra*, *Browningia altissima*, *Cedrela kuelapensis*, *Ceiba insignis*, *Celtis loxensis*, *Clusia pavonii*, *Cordia macrocephala*, *C. saccellia*, *Croton adipatus*, *C. thurifer*, *Cyathostegia weberbaueri*, *Dalea carthagenensis*, *Diplopterys leiocarpa*, *Dodonaea viscosa*, *Durantha triacantha*, *Ditassa endoleuca*, *Esenbeckia warszewiczii*, *Ferreyranthus verbascifolius*, *Flourensia cajabambensis*, *Geoffroea spinosa*, *Jacaranda acutifolia*, *Kageneckia lanceolata*, *Lantana camara*, *L. haughtii*, *Leucaena trichodes*, *Matucana celendinensis*, *Melinis repens*, *Melocactus bellavistensis*, *Mimosa incarum*, *M. pectinatipinna*, *Opuntia quitensis*, *Pappobolus acutifolia*, *P. hutchisonii*, *Pappophorum pappiferum*, *Pereskia horrida*, *Puya mima*, *Salvia loxensis*, *Salvia psilostachya*, *Senna galegifolia*, *Tecoma rosifolia*, and *Trixis subparadoxa*), is a new alliance represented by thermotropical dry-subhumid forests and succulent vegetation, with a canopy of 10-12 m, which extends between the Marañón Basin and the low altitudes in the surroundings of the Huancabamba Depression, between 1500-2500 m asl (Fig. 3.2) [Table SII: *Diplopterydo*

*leiocarpae-Acacietaum macracanthae* (columns 3 to 2); Table SIII, plots 28 to 43].

*Opuntietea sphaericae* class includes the cactus plant communities of central and southwestern Peru, and Chile, up 3000 m asl, on few stabilized rocky, or sandy soils (Fig. 3). Thus the concept of their distribution throughout South America has been amended, since the original description of Galán de Mera and Vicente Orellana (1996) that proposed a distribution throughout the Neotropics. Its *Oreocereus-Neoraimondietalia* order includes three alliances with a clear geographic distribution up to 3000 m asl: *Esposito melanostelis-Neoraimondion arequipensis* (Galán de Mera et al. 2002a, 2004), extended through the hyperarid and semiarid thermotropical belt of central Peru (Fig. 1, branches 8 to 13; Fig. 2, group D), between the parallel 8°S and Ica Department (Fig. 3.3) [characteristic species: *Armatocereus procerus*, *Esposito melanostele*, *Mila nealeana*, *Orthopterygium huaucui*, *Pluchea chingoyo*, *Weberbauerocereus johnsonii*; associations: Table SII. *Haageocereus limensis-Neoraimondietum arequipensis* (column 8 and 11), subassociation with *Pluchea chingoyo* (column 12), subassociation with *Puya ferruginea* (column 13), and *Haageocereus versicoloris-Armatocereetum proceri* (column 10)].

*Haageocerion decumbentis* (Ostolaza and Michles 1984, Galán de Mera et al. 2002b), represents the hyperarid cactus communities of the southern coastal desert up 250 m asl (Fig. 3.4) [characteristic species: *Corryocactus brachypetalus*, *Eriosyce islayensis*, and *Haageocereus decumbens*; associations: Table SII. *Neoporterio islayensis-Neoraimondietum arequipensis* (column 14)]. Although *Haageocerion decumbentis* is a southern alliance, in the dendrogram (Fig. 1, branch 14) and also in the DCA (Fig. 2, group E), it is close to the cactus communities of central Peru with *N. arequipensis*, due to its low diversity and the absence of *Corryocactus brevistylus*.

*Corryocactus brevistylus* grows between the arid and semiarid thermotropical and supratropical

belts, and indicates the *Corryocaction brevistyli* alliance from southern Peru (Fig. 1, branches 15 to 24; Fig. 2, groups F and G), between Ica and Tacna Regions (Galán de Mera and Vicente Orellana 1996, Galán de Mera et al. 2009, 2011), to northern Chile (Luebert and Gajardo 2005) (Fig. 3.5) [characteristic species: *Ambrosia artemisioides*, *Armatocereus riomajensis*, *Austrocylindropuntia subulata*, *Balbisia meyeniana*, *B. verticillata*, *Bougainvillea spinosa*, *Browningia candelaris*, *B. viridis*, *Cantua volcanica*, *Carica augusti*, *Corryocactus aureus*, *C. brevistylus*, *C. puquiensis*, *Cylindropuntia tunicata*, *Echinopsis schoenii*, *Euphorbia apurimacensis*, *Gochnatia arequipensis*, *Grindelia tehuelches*, *Haageocereus platinospinus*, *Jatropha macrantha*, *Lantana scabiosiflora*, *Larrea divaricata*, *Malesherbia ardens*, *Mulguraea arequipensis*, *Oreocereus hempelianus*, *O. tacnaensis*, *Weberbaueroceres rauhii*, *W. torataensis*, and *W. weberbaueri*; associations: Table SII. *Weberbauerocereo rauhii-Browningietum candelaris* (column 15), *Weberbauerocereo rauhii-Corryocactetum brevistyli* (column 20), *Weberbauerocereo weberbaueri-Browningietum candelaris* (column 16), *Weberbauerocereo rauhii-Browningietum candelaris* with *Larrea divaricata* subassociation (column 19), *Weberbauerocereo weberbaueri-Corryocactetum brevistyli* (column 22), *Neoraimondio arequipensis-Browningietum viridis* (column 17), *Armatocereo riomajensis-Neoraimondietum arequipensis* (column 18), *Weberbauerocereo torataensis-Corryocactetum brevistyli* (column 26), *Corryocactus aurei-Browningietum candelaris* (column 27), *Oreocereo tacnaensis-Corryocactetum brevistyli* (column 28), *Weberbauerocereo rauhii-Corryocactetum brevistyli* with *Croton ruizianus* subassociation (column 21), *Grindelio bergii-Corryocactetum puquiensis* (column 25), *Armatocereo riomajensis-Euphorbietum apurimacensis* (column 24), and *Balbisio weberbaueri-Ambrosietum artemisioidis* (column 23).

Columns 29-30 of Table SII represent the low diversity of the *Carico-Caesalpinietea* class (characteristic species: *Caesalpinia spinosa*, *Carica candicans*, *Citharexylum flexuosum*, *Croton alnifolius*, *Dicliptera tomentosa*, *Grindelia glutinosa*, *Heliotropium arborescens*, *Myrcianthes ferreyrae*, *Randia rotundifolia*, *Senecio mollendoensis*, and *Stipa pachypus*), grouping thermotropical forests of *Caesalpinia spinosa* on the coastal mountains of central Peru, shrubs of *Echinopsio chalaensis-Randietum armatae*, and forests of *Caesalpinio spinosae-Myrcianthetum ferreyrae* in southern Peru, with a dry rain interval (Galán de Mera et al. 2009). In the dendrogram (Fig. 1, branch C), and especially in the DCA (Fig. 2), *Carico-Caesalpinietea* (group A) is near *Bursero-Prosopidion pallidae* (group B) according to the presence of some plants in common, such as *Acacia macracantha*, *Caesalpinia spinosa*, *Croton ruizianus*, and *Trixis cacalioides*.

#### The new associations

- *Haageocereo versicoloris-Armatocereetum proceri* ass. nova hoc loco (Table SIII, plots 1-6, holotypus: plot 3; characteristic species: *Armatocereus procerus*, and *Haageocereus versicolor*).

Thermotropical hyperarid column cactus communities situated between 800-1000 m asl, on plutonic Tertiary rocks, where *Armatocereus procerus* and *Haageocereus versicolor* grow on slopes with an inclination between 50 and 60%. Unlike the *Haageocereo limensis-Neoraimondietum arequipensis*, this association is situated in localities where is submitted to a higher maritime influence.

- *Loxopterygio huasanginis-Neoraimondietum arequipensis* ass. nova hoc loco (Table SIII, plots 7-12, holotypus: plot 10; characteristic species: *Capparicordis crotonoides*, *Cnidocolus basiacanthus*, *Heliotropium ferreyrae*,



*Loxopterygium huasango*, and *Neoraimondia arequipensis*).

Infratropical arid-semiarid cactus community with *Neoraimondia arequipensis* and *Haageocereus versicolor*, enriched with small trees such as *Bursera graveolens*, *Cercidium praecox*, and *Loxopterygium huasango*, extending between 5°S and 8°S, with different inclinations up to 60%, from the surroundings of Sullana (Piura) to the North of Trujillo (La Libertad). The geological materials where it is placed are Cretaceous volcanic sedimentary soils, and Tertiary volcanic and plutonic rocks.

- *Crotono ruiziani-Acacieta macracanthae* ass. nova hoc loco (Table SIII, plots 13-15, holotypus: plot 14; characteristic species: *Croton ruizianus*, and *Verbesina* sp.).

Thermotropical dry forest where *Croton ruizianus* reaches its highest abundance on the occidental slopes of the Andes, between 1000 and 2000 m asl, accompanied by *Alternanthera halimifolia*, *Bursera graveolens*, *Ipomoea incarnata*, and *Ruellia floribunda*, and marking the difference with respect to the associations of the alliance *Baccharido-Jacarandion acutifoliae* occurring in the Marañón River system.

The plots of this association have been sampled in some localities to the South of the Cajamarca Department on Cretaceous volcanic sedimentary and Tertiary plutonic soils with heavy clay substrata.

- *Armatocereus balsasensis-Cercidietum praecocis* ass. nova hoc loco (Table SIII, plots 16-27, holotypus: plot 18; characteristic species: *Armatocereus rauhii* subsp. *balsasensis*, *Bougainvillea peruviana*, *Browningia altissima*, *Cordia saccellia*, *Croton adipatus*, *C. thurifer*, *Lantana haughtii*, *Melocactus bellavistensis*, *Mimosa incarum*, *M. pectinatipinna*, *Oxalis psoraleoides*, and *Pereskia horrida*).

Infratropical semiarid cactus community with *Armatocereus rauhii* subsp. *balsasensis* and *Brown-*

*ingia altissima* with shrubs and small trees such as *Bougainvillea peruviana*, *Cercidium praecox*, *Cordia saccellia*, or *Croton thurifer* that extends throughout the Huancabamba Depression and the Marañón Valley, with an inclination up to 60%. This association grows on volcanic sedimentary soils of the Jurassic and Cretaceous Ages, Tertiary volcanic and plutonic rocks, and also on recent sedimentary materials from the Marañón River.

- *Diplopterydo leiocarphae-Acacieta macracanthae* ass. nova hoc loco (Table SIII, plots 28-43, holotypus: plot 29; characteristic species: *Anadenanthera colubrina* var. *cebil*, *Cyathostegia weberbaueri*, *Diplopterys leiocarpa*, *Leucaena trichodes*, *Matucana celendinensis*, *Pappophorum pappipherum*, *Puya mima*, and *Tecoma rosifolia*).

Thermotropical dry forest characterized by elements with a concentrated distribution south of the Huancabamba Depression, between 1500 and 2500 m asl, where *Cedrela kuelapensis*, *Diplopterys leiocarpa*, *Flourensia cajabambensis*, *Matucana celendinensis*, *Pappobolus hutchisonii*, *Salvia psilostachya* and *Tecoma rosifolia* are endemic plants. This association grows on clay soils proceeding from Cretaceous volcanic sedimentary rocks with a maritime or continental origin.

The highest areas (2300-2500 m asl) of this association are enriched with *Flourensia cajabambensis*, *Ferreyranthus verbascifolius*, and *Salvia loxensis*, and can be described as *Diplopterydo leiocarphae-Acacieta macracanthae flourensietosum cajabambensis* subass. nova (Table SIII, plots 35-38, holotypus: plot 38; characteristic species: *Ferreyranthus verbascifolius*, *Flourensia cajabambensis*, and *Salvia loxensis*). On the other hand, the subassociation *Diplopterydo leiocarphae-Acacieta macracanthae clusietosum pavonii* subass. nova (Table SIII, plots 39-43, holotypus: plot 43; characteristic species: *Cedrela kuelapensis*, *Ceiba insignis*, *Celtis loxensis*, *Clusia pavonii*, *Esenbeckia warszewiczii*, *Pappobolus*

*hutchisonii*, *Peperomia glabella*, *Salvia cuspidata*, and *S. psilostachya*), is present in the lowest part of the Yangas Valley (1500-1800 m asl), with very frequent fogs.

## DISCUSSION

Within the *Opuntietea* class, southern Peru presents a high beta-diversity in terms of associations (Whittaker 1972), stimulated by the important influence of the cold Humboldt Current, coupled with the western rain shadow caused by the elevation of the Peru-Bolivia Altiplano (~ 4500 m asl) (Galán de Mera et al. 2012). According to the investigations of Schwarzer et al. (2010), the diversity of this territory is also a consequence of successive volcanic events. An example of this high diversity is that the *Corryocaction brevistyli* alliance is represented in the DCA (Fig. 2) by the separated groups F and G, where F shows the thermotropical associations with *Neoraimondia arequipensis*, and G are the meso- and supratropical ones. However, in the *Espostoo-Neoraimondion* alliance, only the thermotropical associations are found.

The *Anredero diffusae-Diplostephietum meyenii* association (Table SII, column 32) described by Montesinos et al. (2012) in Moquegua is isolated, both in the dendrogram (Fig. 1, branch 32) and in the DCA (Fig. 2, group H). It involves plants of *Oreocereo-Neoraimondietalia* order (*Austrocylindropuntia subulata*, *Echinopsis schoenii*, *Ephedra americana*, *Gochnatia arequipensis*, *Mulguraea arequipensis*, and *Oreocereus leucotrichus*). However, the presence of *Dunalia spinosa*, *Mutisia acuminata*, *Philibertia solanoides*, *Proustia cuneifolia*, *Salvia oppositiflora*, and *Viguiera lanceolata* shows a mixture of *Opuntietea sphaericae* and *Baccharidetea latifoliae* communities (see Galán de Mera et al. 2011).

Peruvian dry forest communities are floristically and ecologically linked to those of the Caribbean Region and the north of southern America. Borhidi (1991) described the *Cercidio-Prosopidetea* class

in Cuba, where *Cercidium praecox*, *Prosopis juliflora* (also reported for Peru), and different species of *Capparis* and *Melocactus*, are present. In Colombia, forests and cactus communities with *Browningia*, *Capparis*, *Melocactus*, *Pereskia*, and *Prosopis juliflora* can also be found (Ruiz et al. 2002, Fernández Alonso 2006, Rangel 2012). To the South, *Acacia macracantha*, *Annona cherimola*, *Espostoa lanata*, *Loxopterygium huasango*, *Prosopis pallida*, *Schinus molle*, and others are present in Ecuador (Aguirre and Delgado 2001, Aguirre et al. 2006), belonging to the *Acacio-Prosopidetea* class (Galán de Mera et al. 2002a). However, on the western slopes of the Peruvian Andes and the coastal desert, dry forest and cactus communities with climate dependence, show some plants which support the originality of this type of vegetation with respect to those of Ecuador (*Croton ruizianus*, *Encelia canescens*, *Krameria lappacea*, *Lycianthes lycioides*, *Melocactus peruvianus*, *Neoraimondia arequipensis*, *Trixis cacalioides*, and *Waltheria ovata*). A particular phytogeographical element is *Neoraimondia arequipensis*, an endemic plant of Peru, which is distributed from Tacna to La Brea in Piura (Svenson 1946, Ostolaza 2011), within the Amotape-Huancabamba Zone (Weigend 2002). *Acacio-Prosopidetea*, with *Cryptocarpo-Prosopidetalia* order (Galán de Mera et al. 2002a), encloses the dry forests that stretch to the occidental slopes of the Andes in Piura to 8°S, in the surroundings of Trujillo, and coincide with the southern part of the Amotape-Huancabamba Zone (Weigend 2002).

*Armatocereo balsasensis-Cercidietum praecocis* (Table SII, column 9; Table SIII, plots 16 to 27), represented in the dendrogram as a separated association from those of *Bursero-Prosopidion pallidae*, really belongs to the *Baccharido-Jacaranthion acutifoliae* alliance (see Fig. 2, group B), because it is an oriental association distributed through the Marañón Valley and the Huancabamba Depression. Among its floristic components, several occidental plants, such as *Bursera graveolens*,

*Loxopterygium huasango*, *Capparis crotonoides*, and specially *Neoraimondia arequipensis* are absent. In the same way, *Crotonoruiziani-Acacietum macracanthae* (Table SII, column 5), includes occidental plants such as *Bursera graveolens*, *Croton ruizianus*, or *Deuterocohnia longipetala*, belonging to the *Bursero-Prosopidion pallidae* alliance (Fig. 2, group C). Both alliances are also present in Ecuador (Aguirre et al. 2006), even a large number of plants, such as *Cedrela kuelapensis*, *Cyathostegia weberbaueri*, *Deuterocohnia longipetala*, *Diplopterys leiocarpa*, *Flourensia cajabambensis*, *Matucana celendinensis*, *Neoraimondia arequipensis*, *Onoseris odorata*, *Pappobolus acutifolia*, *P. hutchinsonii*, *Puya mimia*, *Salvia psilostachya*, and *Tecoma rosifolia*, are missing from this territory (Jørgensen and León-Yáñez 1999), which characterize the associations within this alliance.

In general, dry forests can be found on deep soils along the Peruvian territory. These forests are replaced by succulent plant communities on rocky or sandy slopes ( $\pm 60\%$ ), or few stabilized soils. Independently of geomorphological aspects, the *Acacio-Prosopidetea* class extends from the 8°S parallel through northern Peru (Fig. 3), linked to the influence of the warm El Niño Current (50-900 mm/year). Even so, in the center and south of Peru it is also placed on soils with edaphic humidity which were suitable for crops from ancient times, but without cactus (Beresford-Jones 2009). Below the 8°S parallel, this class is substituted by several associations of the *Opuntietea sphaericae* class, which tolerate higher aridity (5-100 mm/year) and are influenced by the cold Humboldt Current. The forests and bushes of the *Carico-Caesalpinietea* class are marginal, being located in those places of the coastal desert with higher humidity (300-500 mm/year).

### CONCLUSIONS

The hierarchical classification of dry forest and succulent plant communities studied, resulted in

the following syntaxonomical scheme of the *Opuntietea*, *Acacio-Prosopidetea* and *Carico-Caesalpinietea* classes in Peru. This scheme includes the proposal of two new alliances, five associations and two subassociations.

#### SYNTAXONOMICAL SCHEME

*OPUNTIETEA SPHAERICAE* Galán de Mera and Vicente Orellana 1996

+ *Oreocereo leucotrichi-Neoraimondietalia arequipensis* Galán de Mera and Vicente Orellana 1996

\* *Espostoo melanostelis-Neoraimondion arequipensis* Galán de Mera and Rosa in Galán de Mera, Rosa and Cáceres 2002

*Haageocereo limensis-Neoraimondietum arequipensis* Galán de Mera and Rosa in Galán de Mera, Rosa and Cáceres 2002 (*neoraimondietosum arequipensis*, *pluchetosum chingoyonis* Galán de Mera, Baldeón, Beltrán, Benavente and Gómez 2004, *puyetosum ferrugineae* Galán de Mera, Baldeón, Beltrán, Benavente and Gómez 2004)

*Haageocereo versicoloris-Armatocereetum proceri* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente ass. nova hoc loco

\* *Haageocerion procumbentis* Galán de Mera, Cáceres and González 2002

*Neoporterio islayensis-Neoraimondietum arequipensis* Galán de Mera, Cáceres and González 2002

\* *Corryocaction brevistyli* Galán de Mera and Vicente Orellana 1996

*Armatocereo riomajensis-Euphorbietum apurimacensis* Galán de Mera, Linares, Campos and Vicente Orellana 2009

*Armatocereo riomajensis-Neoraimondietum arequipensis* Galán de Mera, Linares, Campos, Trujillo, Villasante and Vicente Orellana 2011  
*Balbisia weberbaueri-Ambrosietum artemisoidis* Galán de Mera, Linares, Campos, Trujillo, Villasante and Vicente Orellana 2011

- Corryocactus aurei-Browningietum candelaris* Galán de Mera and Vicente Orellana 1996
- Grindelio bergii-Corryocactetum puquiensis* Galán de Mera and Gómez Carrión 2001
- Neoraimondio arequipensis-Browningietum viridis* Galán de Mera, Linares, Campos, Trujillo, Villasante and Vicente Orellana 2011
- Oreocereo tacnaensis-Corryocactetum brevistyli* Galán de Mera and Vicente Orellana 1996
- Weberbauerocereo rauhii-Browningietum candelaris* Galán de Mera, Linares, Campos and Vicente Orellana 2009 (*browningietum candelaris*, *larreetosum divaricatae* Galán de Mera, Linares, Campos, Trujillo, Villasante and Vicente Orellana 2011)
- Weberbauerocereo rauhii-Corryocactetum brevistyli* Galán de Mera, Linares, Campos and Vicente Orellana 2009 (*corryocactetum brevistyli*, *crotonetosum ruizani* Galán de Mera, Linares, Campos and Vicente Orellana 2009)
- Weberbauerocereo torataensis-Corryocactetum brevistyli* Galán de Mera, Linares, Campos and Vicente Orellana 2009
- Weberbauerocereo weberbaueri-Browningietum candelaris* Galán de Mera and Linares Perea 2012
- Weberbauerocereo weberbaueri-Corryocactetum brevistyli* Galán de Mera and Gómez Carrión 2001
- ACACIO MACRACANTHAE-PROSOPIDETEA PALLIDAE** Galán de Mera 1999
- + *Cryptocarpo pyriformis-Prosopidetalia pallidae* Galán de Mera and Cáceres in Galán de Mera, Rosa and Cáceres 2002
- \* *Bursero graevolentis-Prosopidion pallidae* Galán de Mera and Cáceres in Galán de Mera, Rosa and Cáceres 2002
- Cercidio praecocis-Prosopidetum pallidae* Galán de Mera and Cáceres in Galán de Mera, Rosa and Cáceres 2002
- Crotono ruiziani-Acacietum macracanthae* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente ass. nova hoc loco
- Loxopterygio huasanginis-Neoraimondietum arequipensis* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente ass. nova hoc loco
- \* *Baccharido oblongifoliae-Jacarandion acutifoliae* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente all. nova hoc loco
- Armatocereo balsasensis-Cercidietum praecocis* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente ass. nova hoc loco
- Diplopterydo leiocarpae-Acacietum macracanthae* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente ass. nova hoc loco (*acacietosum macracanthae*, *flourensietosum cajabambensis* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente subass. nova hoc loco, *clusietosum pavonii* Galán de Mera, Sánchez Vega, Linares, Campos, Montoya and Vicente subass. nova hoc loco)
- CARICO CANDICANTIS-CAESALPINIETEA SPINOSAE** Galán de Mera, Linares, Campos and Vicente Orellana 2009
- + *Citharexlo flexuosi-Crotonetalia alnifolii* Galán de Mera, Linares, Campos and Vicente Orellana 2009
- \* *Grindelion glutinosae* Galán de Mera, Linares, Campos and Vicente Orellana 2009
- Caesalpinio spinosae-Myrcianthetum ferreyrae* Galán de Mera, Linares, Campos and Vicente Orellana 2009
- Caesalpinia spinosa* plant community
- Echinopsio chalaensis-Randietum armatae* Galán de Mera, Linares, Campos and Vicente Orellana 2009

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### RESUMO

Um método fitossociológico alternativo para a avaliação de comunidades de cactos e da floresta seca das encostas ocidentais dos Andes Peruanos é apresentado com base em 164 parcelas seguindo o método de Braun-Blanquet. Destes, 52 parcelas foram obtidas recentemente, enquanto que 112 foram observadas na literatura. Após o uso de análise multivariada dos dados, seguido da aplicação de clusterização hierárquica e de uma análise de correspondência destendenciada, a classe *Acacio-Prosopidetea* (presente na floresta seca e na comunidade de cactos, crescendo em solos com alguma umidade edáfica ou precipitações derivadas do Fenômeno El Niño), a classe *Opuntietea sphaericae* (comunidade de cactus do Peru Central e do Sul, presente em rochas estáveis ou em solos arenosos) e a classe *Carico-Caesalpinietea* (florestas secas do deserto costal do Peru, influenciado pela umidade marítima e pela corrente fria de Humboldt) mostraram-se diferenciadas. Dentro da classe *Acacio-Prosopidetea*, duas alianças são discutidas no trabalho: a aliança *Bursero-Prosopidion pallidae* (com duas novas associações *Loxopterygio huasanginis-Neoraimondietum arequipensis* e *Crotono ruiziani-Acacietaum macracanthae*), bem como a nova aliança *Baccharido-Jacarandion acutifoliae* (com as novas associações *Armatocereo balsasensis-Cercidietum praecocis* e *Diplopterydo leiocarpae-Acacietaum macracanthae*). Para a classe *Opuntietea sphaericae*, a associação *Haageocereo versicoloris-Armatocereetaum proceri* (*Espostoo-Neoraimondion*) é descrita com base nas parcelas de localidades hiperáridas do Peru Central. Finalmente, uma classificação tipológica das comunidades de plantas estudadas é mostrada.

**Palavras-chave:** *Acacio-Prosopidetea*, comunidades de cactus, florestas secas, *Opuntietea sphaericae*, Peru, fitossociologia.

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### SUPPLEMENTARY MATERIAL

**TABLE SII - Synthetic table made up with all the plots studied.**

**TABLE SIII - Table with the new associations described and their higher units.**

### APPENDICES

APPENDIX I: REFERENCES OF COMMUNITY NUMBERS OF THE TABLE SII

1. *Diplopterydo leiocarpae-Acacietaum macracanthae* (authors, Table SIII, plots 28-31).
2. *Diplopterydo leiocarpae-Acacietaum macracanthae clusietosum pavonii* (authors, Table SIII, plots 39-43).
3. *Diplopterydo leiocarpae-Acacietaum macracanthae* (authors, Table SIII, plots 32-34).
4. *Diplopterydo leiocarpae-Acacietaum macracanthae flourensietosum cajabambensis* (authors, Table SIII, plots 35-38).
5. *Crotono ruiziani-Acacietaum macracanthae* (authors, Table SIII, plots 13-15).
6. *Loxopterygio huasanginis-Neoraimondietum arequipensis* (authors, Table SIII, plots 7-12).
7. *Cercidio praecocis-Prosopidietum pallidae* (Galán de Mera et al. 2002b, tab. 2, plots 1-9).
8. *Haageocereo limensis-Neoraimondietum arequipensis* (Galán de Mera et al. 2002a, tab. 3, plots 1-8).
9. *Armatocereo balsasensis-Cercidietum praecocis* (authors, Table SIII, plots 16-27).
10. *Haageocereo versicoloris-Armatocereetaum proceri* (authors, Table SIII, plots 1-6).
11. *Haageocereo limensis-Neoraimondietum arequipensis* (Galán de Mera et al. 2004, tab. 6, plots 1-4).
12. *Haageocereo limensis-Neoraimondietum arequipensis pluchetosum chingoyonis* (Galán de Mera et al. 2004, tab. 6, plot 5).
13. *Haageocereo limensis-Neoraimondietum arequipensis puyetosum ferrugineae* (Galán de Mera et al. 2004, tab. 6, plots 6 and 7).
14. *Neopterterio islayensis-Neoraimondietum arequipensis* (Galán de Mera et al. 2002a, tab. 1, plots 1-6).
15. *Weberbauerocereo rauhii-Browningietum candelaris* (Galán de Mera et al. 2009, tab. 11, plots 1-5).
16. *Weberbauerocereo weberbaueri-Browningietum candelaris* (Galán de Mera and Linares Perea 2012, tab. 17, plot 8 and 9).
17. *Neoraimondio arequipensis-Browningietum viridis* (Galán de Mera et al. 2011, tab. 2, plots 1-9).
18. *Armatocereo riomajensis-Neoraimondietum arequipensis* (Galán de Mera et al. 2011, tab. 2, plots 10 and 11).
19. *Weberbauerocereo rauhii-Browningietum candelaris larretosum divaricatae* (Galán de Mera et al. 2011, tab. 2, plots 12 and 13).
20. *Weberbauerocereo rauhii-Corryocactetaum brevistyli* (Galán de Mera et al. 2009, tab. 12, plots 1-5).
21. *Weberbauerocereo rauhii-Corryocactetaum brevistyli crotonetosum ruiziani* (Galán de Mera et al. 2009, tab. 12, plots 6 and 7).
22. *Weberbauerocereo weberbaueri-Corryocactetaum brevistyli* (Galán de Mera and Gómez Carrión 2001, tab. 2, plots 1-7).
23. *Balbisio weberbaueri-Ambrosietum artemisioidis* (Galán de Mera et al. 2011, tab. 4, plots 1-4).
24. *Armatocereo riomajensis-Euphorbietum apurimacensis* (Galán de Mera et al. 2009, tab. 13, plots 1-7).
25. *Grindelio bergii-Corryocactetaum puquiensis* (Galán de Mera and Gómez Carrión 2001, tab. 3, plots 1-4).
26. *Weberbauerocereo torataensis-Corryocactetaum brevistyli* (Galán de Mera et al. 2009, tab. 12, plots 8 and 9).
27. *Corryocacto aurei-Browningietum candelaris* (Galán de Mera and Vicente Orellana 1996, tab. 2, plots 1-8).
28. *Oreocereo tacnaensis-Corryocactetaum brevistyli* (Galán de Mera and

Vicente Orellana 1996, tab. 2, plots 9 and 10). 29. *Echinopsio chalaensis-Randietum armatae* (Galán de Mera et al. 2009, tab. 3, plots 1-4). 30. *Caesalpinia spinosa* plant community (Galán de Mera et al. 2009, tab. 3, plots 5-7). 31. *Caesalpinio spinosae-Myrcianthetum ferreyrae* (Galán de Mera et al. 2009, tab. 4, plots 1-9). 32. *Anredero diffusae-Diplostephietum meyenii* (Montesinos et al. 2012, tab. 4, plots 30-41).

APPENDIX II: LOCALITIES OF THE PLOTS OF THE TABLE  
SIII

1-6- Ancash, Chamana (1- 18L 0218561-8866860, 2- 18L 0218561-8866860, 3- 18L 0218276-8866442, 4- 18L 0218276-8866442, 5- 18L 0216710-8862156, 6- 18L 0216710-8862156), 7-12- Cajamarca, Tembladera (7- 17M 0705813-9198832, 8- 17M 0705813-9198832, 9- 17M 0712341-9197226, 10- 17M 0712341-9197226, 11- 17M 0719716-9205886, 12- 17M 0719716-9205886), 13-15- Cajamarca, Magdalena (13- 17M 0755789-9198704, 14- 17M 0755789-9198704,

15- 17M 0755789-9198704), 16-21- Cajamarca, Corral Quemado (16- 17M 0755321-9363707, 17- 17M 0755351-9363723, 18- 17M 0755411-9362946, 19- 17M 0755321-9362300, 20- 17M 0755423-9363054, 21- 17M 0755371-9361692), 22-26- Cajamarca, Chamaya (22- 17M 0755333-9361688, 23- 17M 0755333-9361688, 24- 17M 0751915-9359574), 25- 17M 0751915-9359574, 26- 17M 0751857-9358444), 27- Cajamarca, entre Chamaya y Jaén (17M 0748509-9354658), 28-30- Cajamarca, Puente Crisnejas (28- 17M 0817143-9171706), 29- 17M 0817515-9171654, 30- 17M 0817526-9171594), 31-38- Cajamarca, San Marcos (31- 17M 0818838-9176016, 32- 17M 0819841-9177512, 33- 17M 0819841-9177512, 34- 17M 0819663-9177160, 35- 17M 0817822-9178416, 36- 17M 0817822-9178416, 37- 17M 0810269-9190694, 38- 17M 0810269-9190694), 39-43- Cajamarca, río de las Yangas (39- 17M 0811865-9250066, 40- 17M 0812175-9249430, 41- 17M 0811894-9249428, 42- 17M 0812082-9248978, 43- 17M 0812879-9247668).