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Annual seasonality and diversity patterns of the plant community in a fog oasis ecosystem in the city of Lima

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Abstract: In the hyper-arid Peruvian-Chilean Desert, fog oasis ecosystems are formed in the hillslopes of the Andean foothills. Urban expansion and climate change are jeopardizing the conservation of these ecosystems with a high degree of endemic species. In the city of Lima, a fog oasis formation, Lomas de Quebrada Verde, has been under local conservation during 20 years; however, conservation has been empirical and without scientific support. The objectives of the present study were to: (i) describe a year-round spatio-temporal pattern of the plant diversity along the study area, and (ii) relate plant diversity and composition with environmental variables [altitude, slope, soil gravimetric moisture (θ_g) and soil organic matter (SOM)]. A marked seasonality was found in plant diversity, having two pronounced seasons, a dry of low diversity during March and May 2013 and January 2014, and a wet season of greater diversity that occurred between the July and November 2013 evaluations. Altitude, θ_g and SOM were positively correlated with canopy cover, but not with plant diversity indexes (Shannon-Weaver and species richness). Altitude, θ_g and SOM were found to have an effect on shaping the plant community composition. Herbaceous species were dominant in the low altitude and low SOM belt. Whereas woody species such as Croton alnifolius and Heliotropium arborescens were more abundant in the higher altitude belt, where SOM was greater and humidity was more persistent along the year.

Key words: Alpha diversity, Atocongo, environmental gradients, lomas, plant diversity, Quebrada Verde.

Introduction

The continuous Atacama and Peruvian Deserts are a consequence of the hyper-arid climatic condition shaped by the cool, south to north, Humboldt (Peruvian) Current, and the stable South Pacific High (Rundel et al. 1991). During the austral winter, however, thick stratocumulus clouds are formed in the sea and moved on-shore by advection, generating a humid zone in Andean foothills where fog oasis formations (lomas) are seasonally formed (Cereceda et al. 2008; Dillon et al. 2003). Lomas plant communities are mainly composed of herbaceous species, predominantly annual, tuberous, bulbous and rhizomatous species (Ferreyra 1953:

Weberbauer 1945). At higher altitudes, where the medium fog zone is located, woody and mesic species are also found (Péfaur 1982; Weberbauer 1945). Studies and observations of botanical composition across *lomas* formations highlight the importance of altitude in shaping the composition and structure of the plant community (Muenchow *et al.* 2013a,b; Rundel *et al.* 1991; Weberbauer 1945). In *lomas* ecosystem, water is the limiting factor, and altitude and other topographic features explain moisture distribution across the fog-zone (Cereceda *et al.* 2008; Latorre *et al.* 2011). Moisture follows a non-linear relation with altitude, increasing until the inversion layer (~1000 m asl), at which point begins a decrease of moisture with altitude (Latorre *et al.* 2011).

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Depending on the altitude belt, the *loma* plant community varies. Usually, a lower belt of cryptograms, followed by a belt dominated by herbaceous species, and in the medium and denser fog-zone a belt dominated by woody species is found (Rundel *et al.* 1991).

The plant community structure and composition in each *loma* formation is, however, highly site-specific (Dillon et al. 2003; Muenchow et al. 2013a,b; Rundel et al. 1991; Trinidad et al. 2012). These ecological formations are island-like ecosystems, isolated between each other by hyperarid desert areas depleted of plant life (Dillon et al. 2003). The island-like biogeographical condition confers lomas formations a high degree endemism. Around 40% of total lomas species are endemic, while in Central Peru about 20% species have this category (Manrique et al. 2014; Rundel et al. 1991). Of total lomas species, only around 7% are found simultaneously in Peruvian and Chilean fog oases, stressing the ecological singularity of each loma formation (Rundel et al. 1991). This ecological feature makes the need for conservation high for this ecosystem. Even more needed for Peruvian fog oases, if taking into consideration that Peruvian lomas tend to have greater diversity (847 spp., Dillon et al. 2011) than Chilean lomas (433 spp., Larrain 2007).

In the last decades, however, urban expansion has considerably diminished *lomas* extension, being a constant threat for conservation purposes (Rundel et al. 1991; Trinidad et al. 2012). While climate change is reducing moisture availability, leading to a reduction of plant cover and vigor, and dieback of specific plant populations (Schulz et al. 2011). These menaces in an ecologically important desert ecosystem, calls for conservation practices to be in place along the Peruvian-Chilean coast. Especially in lomas formations nearby or within urban areas. Lomas de Quebrada Verde is a conservation area within the Atocongo lomas formation, located in the Lima southern and rural district of Pachacamac. This area has been under local conservation for ecotourism during the last 20 years. However, none scientific effort to understand the plant community structure and composition have been made in this conservation area. In the Peruvian Central region of Lima, there is none published study to our knowledge that analyzes the spatio-temporal dynamic of the plant community in a fog oasis ecosystems during a complete year cycle, or that assess how environmental gradients shape the plant community structure and composition. Taking into account the high specificity of each loma formation,

the objectives of the present study were to: (i) describe a year-round spatio-temporal pattern of alpha diversity along the study area, and (ii) relate plant diversity and composition with environmental variables [i.e., altitude, slope, soil gravimetric moisture (θ_g) and soil organic matter (SOM)]. A high seasonality of the plant diversity related to fog availability was hypothesized, and tested with a nonparametric Kruskal-Wallis test between sampling dates. While altitude was hypothesized to be the key environmental variable shaping plant diversity structure and composition due to availability. This hypothesis was tested with Spearman correlations between all measured environmental variables and diversity indexes, and a non-parametric MANOVA (NP-MANOVA) using the Bray-Curtis similarity index testing if measured environmental variables had an effect on species composition and structure of the plant community.

Materials and methods

Study Area

The present study was conducted at Lomas de Quebrada Verde, which is located in the southern district of Lima, Pachacamac, between latitudes 12°12'00"S 12°12'40"S and and longitudes 76°53'32"W and 76°52'40" W. Engel (1988) located this area as part of the broader fog oasis formation named "Lomas de Atocongo". Soils at Lomas de Atocongo are sandy-loam, with a granular structure and a smooth to slightly hard consistency (Torres 1981). Soil profile has two horizons: A and C; and SOM, N and pH have altitude gradients (Torres 1981). Soil moisture varies with fog seasonality, being maximum between August and October and minimum between February and April (Torres 1981). Soil moisture also varies spatially at Lomas de Atoncongo, being greater in the highlands (400-600 msnm) than in the lower parts (300 msnm) (Torres 1981). Climatically, during 2013, Peruvian coasts presented slight negative anomalies of sea surface temperature (SENAMHI 2013a,b, 2014). During July 2013, anomalies reached values of −2.5 °C in the coasts of the city of Lima (SENAMHI 2013a). However, a La Niña event did not occur during the year of study, being the year classified as neutral by the Peruvian National Service of Meteorology and Hydrology (SENAMHI 2013a,b, 2014). Average maximum and mini-mum daily temperatures recorded by Villa Maria del Triunfo meteorological station SENAMHI 76°55'12"W) were 26.8 and 19.8 °C

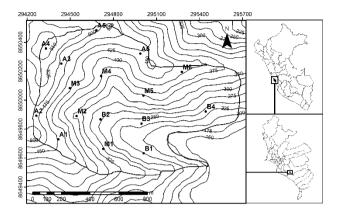


Fig. 1. Altitude contour map of the study area. Sampling stations are indicated. B – lower altitude belt sampling stations (150-299 m asl), M – medium altitude belt sampling station (300-449 m asl), A – higher altitude belt sampling stations (450-550 m asl).

during 2013 summer, and 16.5 and 13.2 °C during 2013 winter months, respectively. Total rainfall precipitation was 0.0 and 31.4 mm during 2013 summer and winter months, respectively.

Plant Sampling

Sixteen sampling stations were located along the 102.7 ha of the study area (Fig. 1). The location of sampling stations was determined based on a stratified sampling by altitude, and readjusted in the field in case they were inaccessible. Plant sampling was performed six times with a twomonth interval between March 2013 and January 2014. At each sampling station, the sampling unit was a 25 m long transect located parallel to the level curve. Since fog oasis' plant species have an absence of identifiable boundaries per individual, canopy cover was used as an indicator of abundance (Matteucci & Colma 1982). In each transect, canopy cover was evaluated by the point transect method, using 50 points spaced by 50 cm. Canopy cover by species was found as suggested by Matteucci & Colma (1982):

$$X_i = (m_i / M_T) \times 100$$

Where X_i is the canopy cover of the i^{th} species, m_i the number of points in a given transect in which the i^{th} species was present, and M_T the total number of points per transect, which for the present study was always 50.

Taxonomic identification was made in the field by the authors, and those species that could not be identified were collected and treated for their subsequent identification based on the APG III (APG 2009) and the nomenclature validated according to the *Tropicos* database (2015).

Diversity and Canopy Cover Indexes

All plant indexes were estimated for each sampling station and sampling date. Total canopy cover was estimated as the percentage of soil covered by any plant species along the transect. Two diversity indexes were calculated. composition diversity, species richness (S) was used, while as a measure of structural diversity, the Shannon-Weaver index (H') was estimated in bits individual⁻¹ (Magurran 2004; Moreno 2001). Additionally, as an integration of year-long diversity, total canopy cover, S and H' were estimated using a matrix of the mean canopy cover from the six sampling dates. All indexes were calculated using canopy cover values from the point transect survey. Diversity indexes were calculated using PAST statistical software v.2.17 (Hammer et al. 2001).

Environmental Variables

During the first sampling, altitude and slope were measured for each sampling station using a GPS receiver and a clinometer, respectively. In every sampling station and sampling date, a soil sample between 15 and 20 cm depth was used to determine $\theta_{\rm g}$ and SOM. In order to determine $\theta_{\rm g}$, collected moist soil samples (W_m) were weighed in the field, oven-dried at 105 °C for 24 hours and weighed again (W_d). Finally, $\theta_{\rm g}$ was estimated as:

$$\theta_g = -\frac{W_m - W_d}{W_d}$$

Concentration of SOM was determined using 1 g of oven-dried soil by Walkley-Black wet combustion method in the Universidad Nacional Agraria La Molina Soils Lab (Walkley & Black 1934). In order to have a more robust SOM concentration value, the mean of the six soil samples for each sampling station was reported.

Data and Statistical Analysis

The normality of S and H' was tested using the Shapiro-Wilk test for each sampling date, having both variables a non-normal distribution. In order to test if seasonality had an impact on plant diversity, a Kruskal-Wallis one-way test was performed with the only factor being the sampling date. In order to have a spatial distribution of total

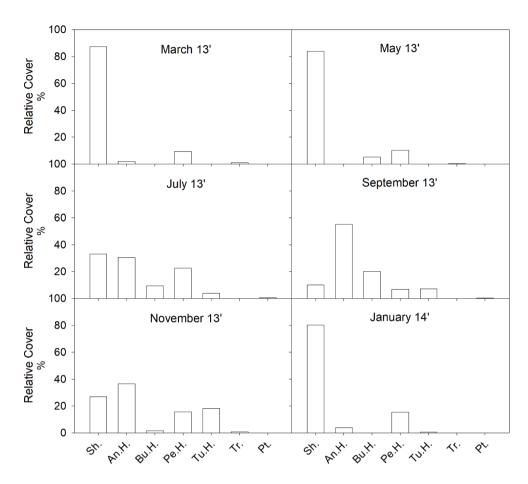


Fig. 2. Relative cover of sub-shrub and shrub (Sh.), annual herbaceous (An.H.), bulbous herbaceous (Bu.H.), perennial herbaceous (Pe.H.), tuberous herbaceous (Tu.H.), trees (Tr.) and pteridophytes (Pt.) during all sampling dates

canopy cover and H' across the study area, isoline maps were draw for each of the six sampling dates. Isolines were elaborated using the Kriging interpolation method in Surfer 10.7 software (Golden Software Inc., Golden, Colorado).

In order to measure the relation between all measured environmental variables (i.e., altitude, slope, SOM and θ_g) to each other, a correlation analysis using the Spearman correlation coefficient (r_s) was performed. The influence of environmental variables on the composition and structure of the plant community was estimated with a Spearman correlation analysis between all measured environmental variables and diversity indexes (i.e., S and H') and total canopy cover. Additionally, in order to test if botanical composition was influenced by environmental variables, a NP-MANOVA was performed. This analysis tests whether there are significant differences in a set of dependent variables due to the effect of an independent factor. The advantage of this analysis is that it can be

based on any measure of similarity, measures the effects and interactions of the chosen factors and generally allows for an additive distribution of variation for complex models (Anderson 2001). We performed a NP-MANOVA for each environmental variable and sampling date. An additional NP-MANOVA was run for each environmental variable using the mean of canopy cover values from the six sampling dates. Bray-Curtis similarity index, a quantitative similarity distance that excludes joint absences between sampling units, was used for all analyses (Anderson et al. 2011). Given that NP-**MANOVA** needs categorical variables independent factors, the data of altitude, slope, $\theta_{\rm g}$ and SOM were categorized in classes. In the case of altitude, it was categorized in three as: (i) 150 to 299 m asl, (ii) 300 to 449 m asl, and (iii) 450-550 m asl; slope as: (i) 10 to 19, (ii) 20 to 29, and (iii) 30 to 39°; and SOM as (i) 1.6–2.4%, (ii) 2.5–3.1%, (iii) 3.2– 3.8%. Since θ_g varies in each sampling date, it was categorized into three equidistant ranges according

Table 1. Environmental summary of each sampling station. SOM: soil organic matter, θ_g : soil gravimetric moisture.

| Sampling | Slope (°) | Altitude | SOM | $\theta_{\mathbf{g}}$ |
|------------|-----------|----------|-----|-----------------------|
| station | эторе () | (m) | (%) | (%) |
| B1 | 20 | 225 | 1.7 | 2.8 |
| B2 | 11 | 281 | 2.3 | 8.9 |
| B3 | 28 | 240 | 2.8 | 4.7 |
| B4 | 23 | 239 | 2.2 | 3.8 |
| M1 | 30 | 300 | 1.8 | 4.6 |
| M2 | 26 | 350 | 3.4 | 9.4 |
| M 3 | 27 | 436 | 2.6 | 7.1 |
| M4 | 26 | 375 | 3.0 | 6.7 |
| M5 | 19 | 345 | 1.9 | 4.3 |
| M6 | 18 | 405 | 2.5 | 5.8 |
| A1 | 27 | 453 | 2.5 | 7.5 |
| A2 | 18 | 475 | 3.8 | 7.6 |
| A3 | 36 | 493 | 2.6 | 6.4 |
| A4 | 36 | 570 | 3.5 | 5.3 |
| A5 | 31 | 509 | 3.6 | 4.8 |
| A6 | 22 | 446 | 2.4 | 5.8 |

to the results of each evaluation. All analyses were run in PAST v.2.17.

Results

Description of the Plant Diversity and Composition

Throughout the six evaluations, 67 different species were reported, of which 45 were identified up to species level, 7 to be consulted (cf.), 14 at the genus level, and species of the Poaceae family were not identified at a more specific level. Species from different families were recorded, Asteraceae (11), Boraginaceae (8), and Solanaceae (5) the most representative genus. According to León et al. (2006) guide, 6 of the recorded species (~13%) were endemic (Ismene amancaes, Ophryosporus pubescens, Philoglossa peruviana, Nicotiana Nolana humifusa paniculata, and Begoniaoctopetala). Of the 67 reported species, 29 were annual herbaceous, 9 tuberous herbaceous, 3 bulbous herbaceous, 10 perennial herbaceous, 13 shrubs or sub-shrubs, 2 leguminous trees and 1 pteridophyte. Of the shrub and sub-shrub species, the most abundant were Croton alnifolius, Ophryosporus peruvianus and Ophryosporus floribundus. Of the annual herbaceous, Veronica persica,

Astrephia chaerophylloides, Parietaria debilis and Sicvos baderoa. While the tuberous and bulbous herba-ceous plants were represented mainly by Solanum montanum and Clinanthus coccineus, respectively. Lomanthus sp. and Dyschoriste sp. were the most abundant perennial herbaceous species. Adiantum sp. was the only recorded pteridophyte species, and Acacia macracantha and Caesalpinia spinosa the only two tree species recorded during all samplings. During the dry season (March and May 2013, and January 2014 sampling dates), shrub and sub-bush species dominated the plant community, whereas during the beginning (July 2013) and end (November 2013) of the wet season there was a co-dominance between herbaceous, shrub and sub-shrub (Fig. 2). During the climax of the wet season (September 2013) dominance was of annual herbaceous plants (Fig. 2). The dominance of shrub and sub-shrub species during the dry season coincided with the greater canopy cover recorded during these months in the higher altitudes and in the gully where transect M2 was located (Fig. 3).

The two alpha diversity indexes had the same dynamics throughout the evaluated year (Fig. 4). For both variables, the Mann-Whitney test grouped three significantly different diversity seasons: (i) a lowest diversity season during March and May of 2013 and January of 2014, (ii) intermediate diversity season during July and November 2013, and (iii) high diversity season during September 2013 sampling date (Fig. 4). However, temporal diversity patterns differed depending on the location of the sampled transects. As with canopy cover (Fig. 3), during the dry season (March-May 13 and January 14), the diversity was greater in intermediate and high altitude areas (Fig. 5). However, in the evaluation when diversity was greatest (September 2013, Fig. 4), the most diverse transects were located in the lower zone (transects B1 and B3) (Fig. 5).

Environmental Variables and its Relation with the Plant Diversity

Average terrain slope was 25° , the maximum recorded slope was 36° , and the minimum, 11° (Table 1). Altitude ranged from 225 to 570 m asl; while mean SOM and θ_g ranged from 1.7 to 3.8% and from 2.8 to 9.4%, respectively (Table 1). Following a temporal dynamic similar to that described for the plant community diversity, θ_g had its lowest mean values during March and May of 2013 and January of 2014 (2.5 \pm 0.2%); while during July and November of 2013, θ_g was $7.9 \pm 0.6\%$ and

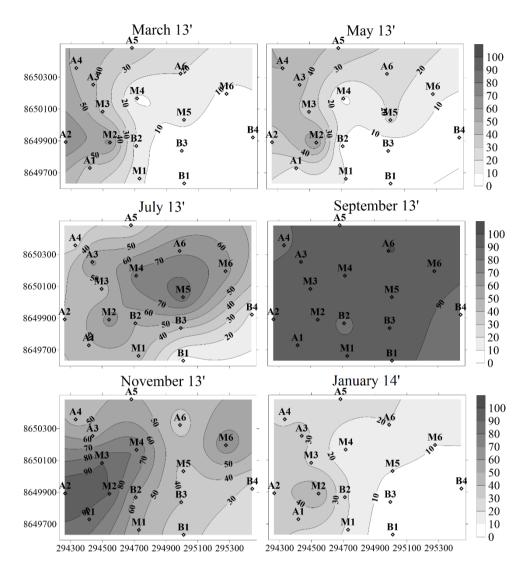


Fig. 3. Total canopy cover isoline map.

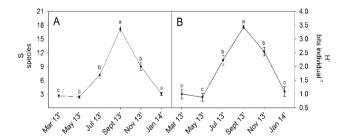


Fig. 4. Temporal pattern of species richness (S) and Shannon-Weaver diversity index (H'). Different letters indicate statistical significance (P < 0.05, Kruskal-Wallis one-way test).

during September, the evaluation of greatest humidity, was 12.8 \pm 0.6%. In sampling stations associated with gully B2, M2 and A2, θ_g tended to

be greater (Table 1). Greater SOM was related to the same gully, as well as to the higher altitudes (Table 1). Correlation analyses showed that SOM correlated positively with θ_g and altitude (Table 2). Average θ_g , SOM and altitude were highly correlated with total canopy cover (Table 3), while plant diversity did not correlate with any environmental variable (Table 3).

Altitude significantly influenced the botanical composition (Table 4). In all evaluations, except for July 2013, the composition of the lower belt (150–299 m asl) differed from the highest one (450–550 m asl); while the middle altitude belt (300–449 m asl) differed from the high or low altitude area depending on the evaluation (Table 4). Both SOM and $\theta_{\rm g}$ conditioned the composition of the plant community mainly in the dry season and at the transition with

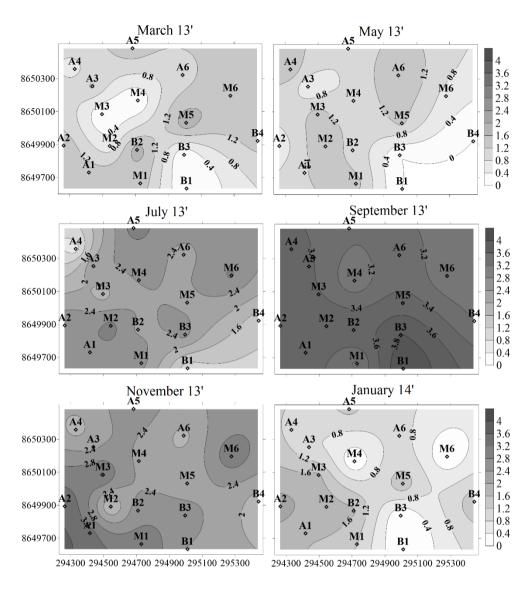


Fig. 5. Shannon-Weaver diversity index isoline map.

the wet season (Table 4). Slope did not have a significant relation with the composition of the plant community based on our results (data not shown).

Discussion

Botanical considerations of the Lomas de Quebrada Verde

Lomas formations are segregated in three different groups based on floristic similarities; being the *lomas* within and surrounding the city of Lima are part of the northern Peruvian group (Manrique *et al.* 2014). Manrique *et al.* (2014) found that in this group of *lomas* formations around ~22% of species are endemic. In the present study we found a lower percentage (13%). The database we used to deter-

mine the endemic status of plant species (León et al. 2006) excludes a series of lomas species that have been traditionally reported as endemic from Peru (e.g., Clinanthus coccineus, Ophryosporus floribundus, Croton alnifolius and Caesalpinia spinosa), and that could have been overestimating the endemic characteristic of lomas formations. Thus, explaining the difference between our findings and the values that have been reported in the past (Manrique et al. 2014; Trinidad et al. 2012). Rundel et al. (1991) estimated that Atocongo lomas formation had a plant richness of ~80 spp., while Trinidad et al. (2012) reported 112 spp. in Lomas de Villa María del Triunfo, another sector of the Atocongo formation. The lower diversity found in the present study might be partially explained by: (i) a

Table 2. Spearman correlation (r_s) between soil gravimetric moisture (θ g), soil organic matter (SOM), slope and altitude. * $P \le 0.05$, ** $P \le 0.01$.

| | COM | CI | A14.14 1 |
|---------------------|--------|--------|----------|
| - | SOM | Slope | Altitude |
| θ g Mar 13' | 0.09 | -0.54* | 0.00 |
| θ g May 13' | 0.48 | -0.24 | 0.36 |
| θg Jul 13' | 0.29 | -0.27 | 0.25 |
| θ g Sept 13' | 0.26 | 0.33 | 0.09 |
| θ g Nov 13' | 0.54* | -0.10 | 0.53* |
| θ g Jan 14' | 0.27 | 0.08 | 0.14 |
| θ g Mean | 0.51* | -0.15 | 0.39 |
| Slope | 0.35 | - | - |
| Altitude | 0.69** | 0.43 | - |

Table 3. Spearman correlation (r_s) between average soil gravimetric moisture (θ g) soil organic matter (SOM), slope and altitude with total canopy cover (CC), Shannon-Weaver index (H') and species richness (S). ** $P \le 0.01$.

| | CC | H' | S |
|---------------------|--------|-------|-------|
| SOM | 0.71** | -0.18 | 0.23 |
| $\theta \mathbf{g}$ | 0.73** | -0.02 | 0.37 |
| Altitude | 0.76** | -0.29 | -0.15 |
| Slope | 0.26 | -0.28 | -0.34 |

survey approach destined to sample the spatiotemporal pattern of the plant community and not a species exhaustive survey, (ii) an underestimation in our results due to the lack of identification of Poaceae species, (iii) a probable lower diversity in Lomas de Quebrada Verde than Lomas de Villa María del Triunfo.

A marked seasonality was found in the plant community, which is consistent with seasonality of fog formations along the Peruvian-Chilean coast (Fig. 4; Cereceda et al. 2008). A winter dominance of opportunistic herbaceous that take advantage of winter water pulses was found across the study area, but was more evident in the lower belt. This was evidenced by a great increase of plant cover and diversity in lower areas during the wet season, whereas during the dry season it was near zero due to the scarce presence of perennial species (Figs. 3, 5). Moreover, during the dry season, the relative cover of the plant community was dominated by the scarce sub-shrub and shrub species; while during the wet season it was dominated by the herbaceous species, considerably increasing the diversity during this season of the year (Figs. 2, 4).

Environmental Gradient Structures Plant Community

The altitude gradient modified the plant community composition (Table 4). In the higher areas, there was a greater canopy cover from shrub species such as Croton alnifolius, Heliotropium arborescens, and some annual herbaceous, such as Veronica persica and Parietaria debilis. On the other hand, Ismene amancaes, a bulbous herbaceous, was inversely correlated with altitude (Spearman's $\rho = -0.54$, P = 0.03), being present exclusively in the lower zone (220-250 m asl). The conservation status of Ismene amancaes important due to its high cultural and touristic value, and for being endemic from the department of Lima (León et al. 2006). Our results are consistent with that of Muenchow et al. (2013a), which found that altitude alone explained 96% of the plant composition in a study in Cerro Campana fog oasis. Several studies in *lomas* formations relate altitude with the amount of condensed fog, which increases continuously until reaching the altitude of inversion (~1000 m asl in Central Peruvian coast) at which point moisture availability decreases (Cereceda et al. 2008; Latorre et al. 2011; Muenchow et al. 2013a,b; Péfaur 1982; Trinidad et al. 2012). This humidity gradient explains the Peruvian *lomas* altitude profile described by Rundel (1991), where there is a lower belt of cryptograms, followed by an herbaceous species belt, and in the medium and denser fog-zone the plant community is dominated by woody species (Rundel et al. 1991). In most of these studies, the most diverse belt was the medium fog-zone where moisture availability was greater (Muenchow et al. 2013a,b; Péfaur 1982). In our study, diversity followed that pattern during the dry season. During the wet season, however, we had a greater diversity in the lower area (stations B1 and B3) (Fig. 5). A possible explanation for the greater diversity in the B1-B3 area might be the influence of livestock grazing, which has been related to an increase on plant diversity (Galán de Mera et al. 2011).

The input of organic matter into the soil is directly or indirectly of plant origin (Stockmann *et al.* 2013). Thus, the greater concentration of SOM in stations with consistently greater canopy cover along the dry and wet season was expected (Table 3). The greater concentration of SOM results in greater infiltration rates and water retention capacity (Saxton & Rawls 2006), which are used by vegetation for greater growth and development. This is especially important in arid ecosystems, where water

Table 4. Statistical significance of the Bray-Curtis dissimilarity between groupings of transects based on their altitude, soil gravimetric moisture (θ g) and soil organic matter (M.O.) based on NP-MANOVA. Different letters represent statistical differences ($P \le 0.05$).

| | Altitude | | | | $\theta \mathbf{g}$ | | | SOM | | |
|----------|----------|--------|------|-----|---------------------|------|-----|--------|------|--|
| • | Low | Medium | High | Low | Medium | High | Low | Medium | High | |
| Mar 13' | a | ab | b | a | a | a | a | ab | b | |
| May 13' | a | b | b | a | b | ab | a | ab | b | |
| Jul 13' | a | a | a | a | ab | b | a | a | a | |
| Sept 13' | a | b | b | a | a | a | a | a | a | |
| Nov 13' | a | a | b | a | a | a | a | b | b | |
| Jan 14' | a | a | b | a | a | a | a | a | a | |
| \sum | a | b | b | a | b | ab | a | ab | b | |

is usually the limiting factor for plant development. Altitude was positively correlated with canopy cover due to the dominance of sub-shrub and shrub species in the upper area. The greater canopy cover and vertical structure of shrub species in the upper zone contribute to increase θ_g through the interception of fog and root system's hydraulic redistribution (Holdridge 1967; Muñoz et al. 2008). This is consistent with Muenchow et al. (2013a) study, which found a greater concentration of SOM in the zone of shrub dominance. Both variables, SOM and $\theta_{\rm g}$, are highly related to moisture availability - the limiting variable in hyper-arid ecosystems. Consistently with this idea, our results showed that both variables had an impact on the composition of the plant community (Table 4). Species that their canopy cover positively correlated (Spearman's r > 0.55, P < 0.05) with SOM were: Cristaria sp., Dyschoriste sp., Heliotropium arborescens, Adiantum sp., and Silene gallica. While canopy cover of Alternanthera halimifolia, Acmellaoleracea, Galinsoga cf. caligensis and Ophryosporus pubescens were negatively correlated with SOM. In the case of ofSolanumcanopy cover montanum, Fuertesimalva peruviana and Trixis cacalioides had a negative correlation with this variable, whilst Ophryosporus peruvianus and Calceolaria pinnata were positively correlated.

The understanding of the environmental factors shaping the plant community is useful for restoration and/or reforestation purposes. In Lomas de Quebrada Verde, restoration is currently being practiced with tree species; however, the use of shrub or sub-shrub species, which are already adapted to the current conditions of the ecosystem, could be more efficient. In addition, in order to assure a greater establishment rate of reforested

individuals, reforestation should begin in the medium altitude areas and in gullies, where plant cover, SOM and θ_g tends to be greater along the year.

Conclusion

This study gave more insights about the spatiotemporal pattern of the *lomas* plant community, and the environmental gradients that shape it. We confirmed and provided a quantitative diversity measure to the seasonality of the plant diversity. During the dry season, there was a dominance of sub-shrub and shrub species, while during the wet season the dominance was of the annual herbaceous species. We found a greater plant diversity in the lower belt of the study area, probably boosted by livestock grazing activity increasing species richness. An environmental gradient of altitude, SOM and θ_g was found to shape the composition of the plant community. Greater canopy cover in higher altitudes due to the dominance of woody species increased the input of water into the system (fog condensation and root hydraulic redistribution), and thus the photosynthetic activity and input of organic matter into the soil. However, none environmental variable had an effect on plant alpha diversity indexes (H' and S).

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