

Changes in Semi-Arid Plant Species Associations along a Livestock Grazing Gradient

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Abstract

In semi-arid ecosystems, vegetation is heterogeneously distributed, with plant species often associating in patches. These associations between species are not constant, but depend on the particular response of each species to environmental factors. Here, we investigated how plant species associations change in response to livestock grazing in a semi-arid ecosystem, Cabo de Gata-Níjar Natural Park in South East Spain. We established linear point-intercept transects at four sites with different grazing intensity, and recorded all species at each point. We investigated plant associations by comparing the number of times that each pair of species occurred at the same spatial point (co-occurrences), with the expected number of times based on species abundances. We also assessed associations for each shrub and grass species by considering all their pairs of associations and for the whole plant community by considering all pairs of associations on each site. At all sites, the plant community had a negative pattern of association, with fewer co-occurrences than expected. Negative association in the plant community increased at maximum grazing intensity. Most species associated as expected, particularly grass species, and positive associations were most important at intermediate grazing intensities. No species changed its type of association along the grazing gradient. We conclude that in the present plant community, grazing-resistant species compete among themselves and segregate in space. Some shrub species act as refuges for grazing-sensitive species that benefit from being spatially associated with shrub species, particularly at intermediate grazing intensities where positive associations were highest. At high grazing intensity, these shrubs can no longer persist and positive associations decrease due to the disappearance of refuges. Spatial associations between plant species and their response to grazing help identify the factors that organize plant communities, and may contribute to improving management of semi-arid ecosystems.

Citation: Saiz H, Alados CL (2012) Changes in Semi-Arid Plant Species Associations along a Livestock Grazing Gradient. PLoS ONE 7(7): e40551. doi:10.1371/journal.pone.0040551

Editor: Kurt O. Reinhart, USDA-ARS, United States of America

Received: December 15, 2011; **Accepted:** June 8, 2012; **Published:** July 9, 2012

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Funding: The study was made possible by the financial support of CEBCE project Ref. CGL2008-0065 of the Spanish Ministry of Science and Innovation, and grant JAEPre from the National Research Council of Spain. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Plant species associations are a fundamental aspect of plant community ecology [1–3]. Analyses of plant species associations provide information about environmental heterogeneity, biotic interactions and patterns of seed dispersal [4–7]. This information is of particular interest in semi-arid plant communities where vegetation often occurs in patches. Usually, vegetation patches are composed of shrubs that can act as shelter against harsh environmental conditions. These shrubs are called ‘nurse plants’, for they appear to provide microhabitats that enhance survival for other plant species [2,8]. Theoretical models based on empirical studies suggest that these positive interactions between plant species are one of the main drivers for the formation of these patches [8–10].

Since the article by Callaway and colleagues [11], additional studies have proliferated showing the presence and importance of positive interactions in plant communities [6,7,10]. It has been suggested that positive interactions should be particularly common in communities developing under high stress conditions and in those exposed to high consumer pressure [2,11]. This theory has been referred to as the ‘Stress Gradient Hypothesis’ (SGH) and

can explain some of the patterns in plant species interactions occurring in stressed ecosystems (but see [12,13]). However, most studies have focused on a limited number of species within a community [14], and analyses at the community level have not provided unequivocal support for SGH [15–17]. Experiments at this scale are complicated because each species responds in a particular way to each stress, and, typically, those responses can change depending on the species’ ontogeny, habitat, and type of stress considered [17–19]. Usually, the response of a community is viewed as the net importance of positive and negative interactions in the community (*sensu*, the proportion of the total interactions in the community that are positive or negative [20]).

One alternative to studying interactions at the community level has been using spatial association between plant species as a surrogate for quantifying interactions [7,15,16]. This correlative approach assumes spatially associated species result from positive interactions, and species that are negatively associated are segregated by competitive interactions [7]. When interactions between species are weak, plant species will associate at random. Spatial association has been employed for studying plant species interactions in arid communities. For example, Verdú and Valiente-Banuet studied positive spatial associations between

shrubs and seedlings in the Sonoran Desert, and found that there was a relationship between positive interactions and co-evolutionary processes in that plant community [21].

Grazing is one of the most important biotic factors shaping plant communities. Biomass consumption by herbivores affects both plant species composition and community spatial structure [22–25]. In arid and semi-arid ecosystems, grazing reduces total plant cover, increases abundance of certain life forms such as annual plants, and changes the identity of dominant species [24,26]. Moreover, grazing may lead to increased positive interactions between plants as a result of associational defense; for example, some plant species protect themselves from herbivores by spatially associating with unpalatable plants [27–28]. Previous works testing SGH in ecosystems under grazing stress have found an increase in the importance of positive interactions at low grazing levels, but not at high grazing levels where negative interactions predominate [13,29]. Assessing the effects of grazing on plant interactions provides valuable information for ecosystem management (e.g. which species act as refuge for grazing-sensitive species; which species need a refuge to survive). Changes in community structure are central to detecting when an ecosystem is overgrazed [24].

In the present work, we analyze the spatial associations among all plant species in a semi-arid community occurring along a gradient of livestock grazing. We evaluate associations for each individual species, between all pairs of species, and in the whole plant community, and how these associations change due to grazing. We estimate all associations by comparing real spatial co-occurrences between plant species with expected co-occurrences due to species abundances. Specifically, we hypothesize that the whole plant community will become more positively associated at intermediate grazing intensities, and that associations of each plant species and between pairs of species will depend on species life forms. We distinguish among associations between shrubs (those species responsible for patch formation), between grasses, and between shrubs and grasses.

Materials and Methods

Study Area and Data Collection

The study was conducted in Cabo de Gata-Níjar Natural Park, which lies along the Mediterranean coast in Southeastern Spain (36° 46' N, 2° 09' W). The park occupies 37,570-ha park, with a maximum elevation of 493 m (El Fraile Peak). The climate is semi-arid Mediterranean (marked seasonality, drought in summer and most rainfall in spring and autumn. Average annual rainfall = 193.9 mm, Average annual temperature = 19.4 C [30]). Historically, the area has been used as an agro-pastoral system, with cereal cropping on floodplains and livestock (sheep and goat) grazing on slopes all the year. The plant community is characterized by *Chamaerops humilis* L., and other common species include *Rhamnus lycioides* L., *Pistacia lentiscus* L., *Periploca laevigata* Aiton, and *Stipa tenacissima* L. [31].

Vegetation data were collected from the Southern section of the park, a volcanic area where highly stony soils predominate [32]. All permits required to carry out the field studies were obtained from the Natural Park authorities. In that region, vegetation is characterized by open shrubland with shrubs organized in patches, which are embedded in a matrix of a large tussock grass, *S. tenacissima* L. *S. tenacissima* is a very strong competitor that colonizes the gaps within patches caused by livestock and aridity, and can exclude other species once it becomes the dominant species [10,33].

Within the area, four sites at different distances from El Romeral farm were selected. Movements of animals (sheep and goats) were monitored for one week per season with a GPS device. Effective stocking rate was calculated from the average stocking rate of the farm ($\text{ind}\cdot\text{ha}^{-1}$) multiplied by a correction factor based on the percentage of time each grazing site was used. Sites were ranked based on the amount of grazing pressure to which they had been exposed ($G1 = 0 \text{ ind}\cdot\text{ha}^{-1}$; $G2 = 0.27 \text{ ind}\cdot\text{ha}^{-1}$; $G3 = 0.46 \text{ ind}\cdot\text{ha}^{-1}$; and $G4 = 0.65 \text{ ind}\cdot\text{ha}^{-1}$). Grazing carrying capacity for this plant community is $0.39\text{--}0.57 \text{ ind}\cdot\text{ha}^{-1}$, so we considered G2 as low grazing intensity, G3 as intermediate grazing intensity and G4 as high grazing intensity [34]. In April, 2001, three 500-m-long linear transects were established at each site, and the Point-Intercept Method [35] was used to quantify vegetation. On each transect, the species occurring at each point were recorded every 20 cm. Presence and life form (shrub or grass) of all species were recorded and no distinction was made between the ontogenetic stages of individuals. All transects were run parallel to the slope, separated by 50 m and established at the same altitude, orientation and soil parent material.

Association Measurements

A plant-plant association matrix $A_{S\times S}$ was built for each site, based on the data pooled from the three transects. S is the number of species present at the site. In the matrix, a_{ij} is the number of times that species i and j co-occurred at the same sampling point (with $a_{ij} = a_{ji}$). The matrix was used to calculate the total number of co-occurrences for a given species i ($a_i = \sum_{j=1}^S a_{ij}$) and the total number of co-occurrences at a site ($A = \sum_{i=1}^S a_i/2$). The diagonal terms of the matrix were set to 0 because it was not possible to estimate the co-occurrence of a species with itself from the presence data.

To test the deviation from the expected patterns of plant species associations, an $E_{S\times S}$ matrix was calculated for each site. This matrix includes the expected number of co-occurrences between species based on their abundances. For each species i , its relative cover was calculated as $p_i = n_i/T$, where n_i is the number of points where species i occurred at each site, and T is the total number of points sampled (2501 sampling points * 3 transects = 7503). In that context, p_i is the probability of finding the species i at one randomly selected point at a site. Using those data for all of the plant species, a $P_{S\times S}$ matrix was computed, where $p_{ij} = p_i*p_j$. Therefore, p_{ij} is the probability of finding the species i and j at the same sampling point on the site. The expected co-occurrences matrix $E_{S\times S}$ was computed as $E_{S\times S} = P_{S\times S}*T$ (with $e_{ij} = p_{ij}*T$), and total expected co-occurrences for each species i ($e_i = \sum_{j=1}^S e_{ij}$) and each site ($E = \sum_{j=1}^S e_{ij}/2$) were calculated similarly as for a_i and A .

A Poisson distribution was employed to compare $A_{S\times S}$ and $E_{S\times S}$. The Poisson distribution is a statistical distribution widely used for analyzing count data. Furthermore, it has long been used in ecological analyses [36], particularly with vegetation data collected using the Point-Intercept Method (i.e. the number of contacts of a given species fits a Poisson distribution if individuals are distributed randomly and the probability of more than one contact for the same individual is negligible [35]). The Poisson distribution is characterized by one parameter, λ , which determines the mean and variance of the distribution. Thus, each value of A , a_i and a_{ij} was compared to a Poisson distribution fitted with its corresponding value, E , e_i and e_{ij} , as the λ parameter. To

determine whether observed co-occurrences (A , a_i and a_{ij}) differed significantly from the co-occurrences expected based on species abundances (E , e_i and e_{ij}), 95% confidence intervals were calculated for each distribution. The comparison between A and E is the general association pattern present in the plant community (plant community presents more, less or the expected total number of co-occurrences). The comparison between a_i and e_i is the general type of association of species i (species i presents more, less or the expected total co-occurrences with all other species), while the comparison between a_{ij} and e_{ij} is the particular association between species i and j (species i co-occurs more, less or as expected with species j). Plant species were believed to be positively associated when they co-occurred at a level greater than that expected by chance. Negative associations between plants were inferred when co-occurrences were less frequent than expected by chance. If actual co-occurrence values fell within the confidence interval, these values did not differ significantly from those expected because of species abundance and were considered a neutral association.

To assess possible changes in community associations along the grazing gradient, the importance of positive/negative associations at each site was measured as the relative increase/decrease in total co-occurrences with respect to expectations ($R = (A - E)/E$). The positive association dominates the plant community if $R > 0$, whereas if $R < 0$, the negative association is more dominant. If $R \sim 0$, neither association dominates. Total co-occurrences (A and E) include all species in the plant community, but do not provide information about the number of species or pairs of species exhibiting each particular type of association. Therefore, we calculated the proportion of species and pairs of species that presented positive, negative and neutral associations. However, when species are uncommon it is not possible to detect a negative association because 0, the minimum observable value for a_i and a_{ij} , falls within the 95% confidence interval of the expected distribution. Therefore, we only considered species and pairs of species that were sufficiently abundant so that we could distinguish between positive, negative and neutral associations. For a_i , the proportions of species considered at each site were G1 = 70%, G2 = 69%, G3 = 57%, and G4 = 64%; and for a_{ij} the proportions of pairs of species considered were G1 = 3.3%, G2 = 4.1%, G3 = 3.3%, and G4 = 3%. Because it was possible to distinguish between neutral and positive associations among all species and pairs of species, we calculated the importance of positively associated species and pairs of species as the proportion of positive associations in relation to all possible associations (species, $R_s = s+/S$; and pairs of species, $R_{ss} = ss+/S(S - 1)$; where $s+$ is the number of species showing a positive association, and $ss+$ is the number of pairs of species that are positively associated with each other). As R_s and R_{ss} increase, more plant species represent a positive association, and more pairs of species are positively associated. R_s was calculated for both life forms and for all species, and R_{ss} was calculated for associations between species with the same life form, between different life forms and between all species. All analyses were performed using R (<http://www.R-project.org>). The variables and parameters used in the analyses are presented in table 1.

Results

Grazing modified the plant community in Cabo de Gata-Níjar Natural Park. Species richness was 70% greater at the ungrazed than grazed sites, particularly due to the large number of grass species, and biodiversity decreased as grazing became more intense (Table 2). The mean number of species recorded per point

Table 1. Variable and parameter codes employed in the study.

Code	Description
T	Total number of surveyed points
S	Number of species recorded
n_i	Abundance of species i
p_i	Relative abundance of species i
a_{ij}	Co-occurrences between species i and j
a_i	Total co-occurrences of species i
A	Total co-occurrences at the site
$A_{S \times S}$	Matrix with a_{ij} values
p_{ij}	Co-occurrence probability of species i and j
$P_{S \times S}$	Matrix with p_{ij} values
e_{ij}	Expected co-occurrences between species i and j
e_i	Expected total co-occurrences of species i
E	Expected total co-occurrences
$E_{S \times S}$	Matrix with e_{ij} values
$s+$	Species with positive associations*
$ss+$	Pairs of species with positive associations*
R	Deviation from total co-occurrences at the site
R_s	Proportion of species with positive associations at the site*
R_{ss}	Proportion of pairs of species with positive associations at the site*

Each value was calculated for each of four sampling sites within the study area. *When a_i and a_{ij} are higher than e_i and e_{ij} , and fall out of their confidence intervals.

doi:10.1371/journal.pone.0040551.t001

was largest at G1 and the number of points with no records (Bare soil) was largest at low and intermediate grazing values (G2 and G3). Mean number of co-occurrences per point decreased with grazing. Abundance (n_i) and co-occurrences (a_i) of each species for each grazing intensity are included as support information (Table S1).

At all four sampling sites, plant communities exhibited fewer total co-occurrences (A) than were expected by chance (E), which indicated that plants were more likely to be alone in this community, rather than in association (Fig. 1). Negative association was most important at the highest grazing intensity ($R_{G1} = -0.233$, $R_{G2} = -0.262$, $R_{G3} = -0.269$, $R_{G4} = -0.476$).

Regarding the general type of association of species (a_i), at all sampling sites there were species which associated positively,

Table 2. Characteristics of study sites in Cabo de Gata-Níjar Natural Park.

Site	Latitude	Longitude	BS	S	S/point	Ev	A/point
G1	36° 46' 6" N	2° 10' 37" W	2050	119 (24/95)	1.03	0.645	0.363
G2	36° 44' 45" N	2° 8' 45" W	2982	70 (22/48)	0.75	0.559	0.163
G3	36° 45' 24" N	2° 8' 12" W	2750	74 (26/48)	0.787	0.515	0.177
G4	36° 45' 5" N	2° 7' 52" W	2360	72 (18/56)	0.764	0.39	0.084

BS, Bare soil, number of points with no species; S, species richness (Shrub species/Grass species); S/point, mean number of species at each point; Ev, evenness (Shannon diversity/log(S)); A/point, mean number of co-occurrences per point (A/7503).

doi:10.1371/journal.pone.0040551.t002

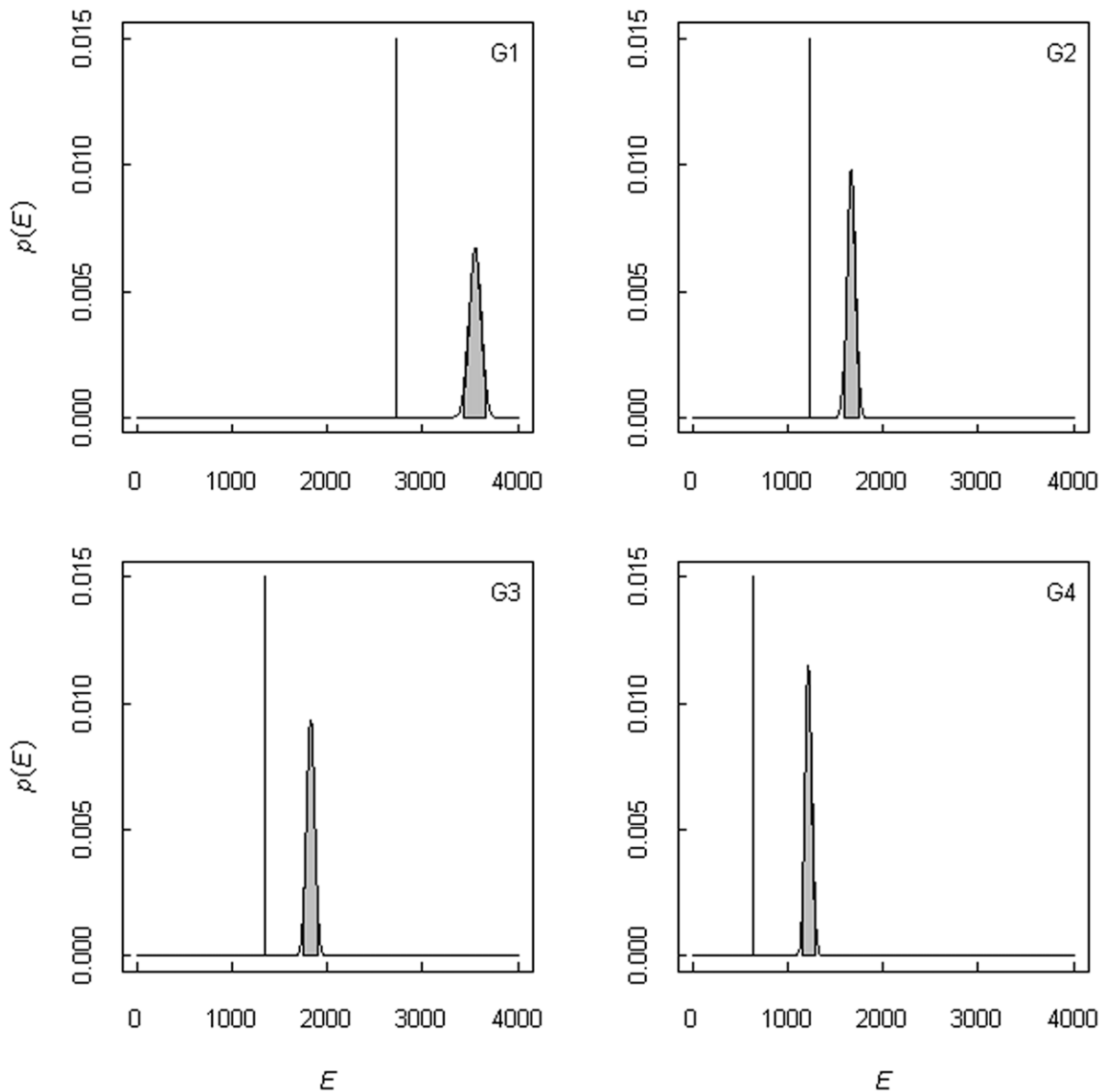


Figure 1. Distribution of expected total co-occurrences for the entire plant community in Cabo de Gata-Níjar. E , plant community total co-occurrences; $p(E)$, probability distribution of expected total co-occurrences $p(N/E) = (1/N!) \cdot e^{-A} \cdot A^N$, where N is the number of surveyed points (7503). G1 to G4 are the sampling sites and are sorted by grazing intensity (G1 = 0 ind·ha⁻¹; G2 = 0.27 ind·ha⁻¹; G3 = 0.46 ind·ha⁻¹; and G4 = 0.65 ind·ha⁻¹). Vertical lines represent A . Because the observed values are smaller and fall outside the 95% confidence interval (grey area), the community is considered to be dominated by negative associations.
doi:10.1371/journal.pone.0040551.g001

neutrally or negatively, but species that associated neutrally were the most common. Besides neutrally associated species, those negatively associated were more frequent than positively associated ones (Fig. 2a). No species presented a shift in its type of association along the grazing gradient (i.e. no species exhibited both a positive and a negative type of association along the gradient, Table 3). Negatively associated shrubs were common, particularly at the non-grazed site (Fig. 2b), while negatively associated grasses increased at sites with highest grazing (Fig. 2c). For associations between pairs of species (a_{ij}), all three types of association were also detected. Neutral associations were the most common, and negative associations were more common than positive ones (Fig. 3a). Negative associations between shrubs were highest in areas with low and intermediate grazing intensities

(Fig. 3b), whereas negative associations between grasses and between shrubs and grasses were highest at high grazing intensity (Fig. 3c–d). Individually, each species could associate positively with some species, and neutrally or negatively with the rest.

The importance of species with positive association (R_s) was highest at low grazing levels for both life forms and for all species (Fig. 4a). The importance of positive associations between all pairs of species (R_{ss}) remained nearly constant, but they decreased at the site with the highest level of grazing (Fig. 4b). The importance of positive associations between shrubs was highest at low grazing intensities, whereas between grasses and between shrubs and grasses it was highest at the non-grazed site.

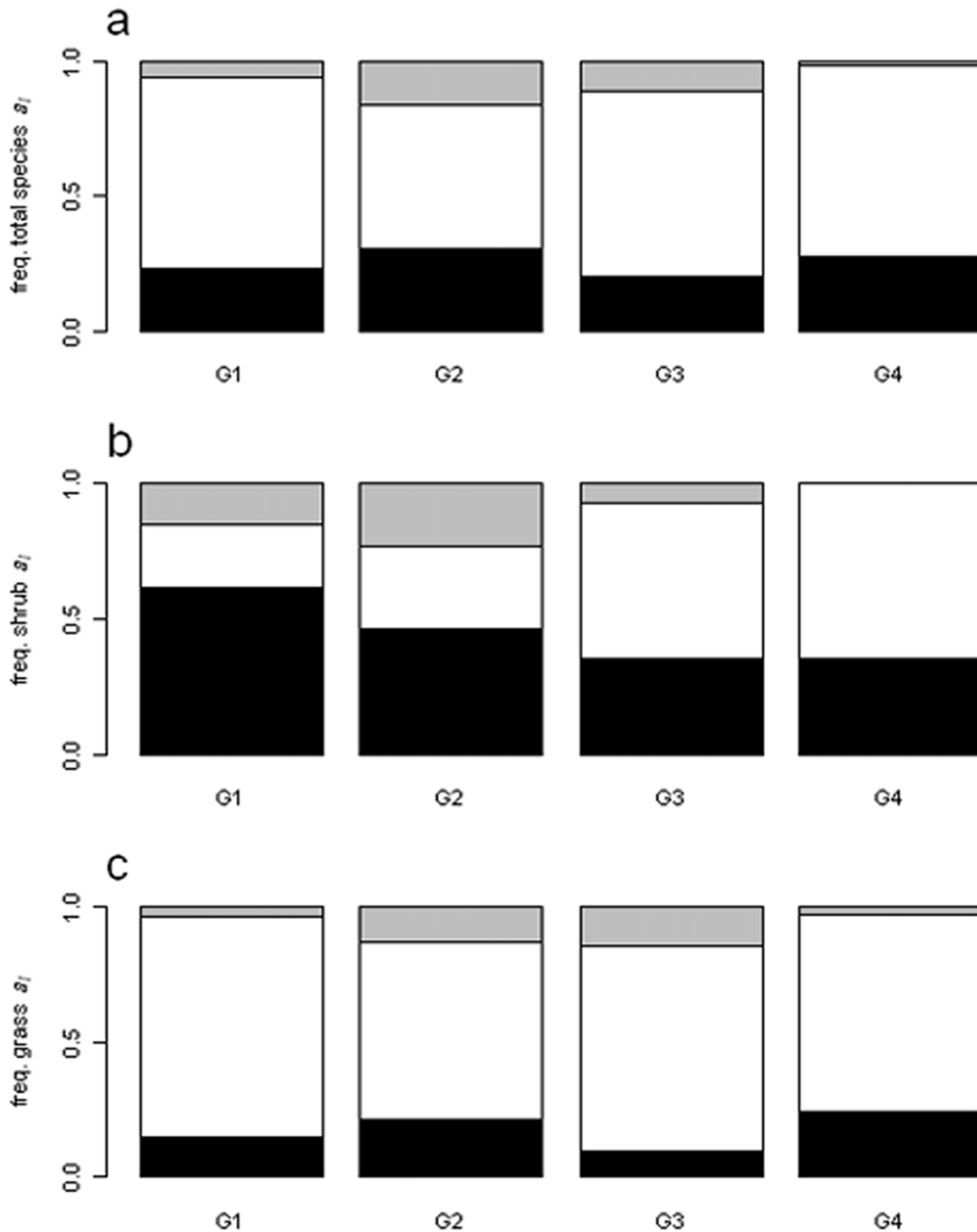


Figure 2. Relative number of species for each type of association. a, proportion of species with each type of association; b, proportion of shrubs with each type of association; c, proportion of grasses with each type of association; G1 to G4 are the sampling sites. Associations are classified as negative (black area), neutral (white area) or positive (grey area) depending on the relationship between a_i value and the expected distribution. Only species that could allow distinguishing negative from neutral associations were employed.
 doi:10.1371/journal.pone.0040551.g002

Discussion

In Cabo de Gata-Níjar Natural Park, plant community responded to grazing intensity. Grazing reduced community

biodiversity, and increased bare soil except at the site with highest grazing intensity (Table 2). Grazers preferentially feed on palatable species, favoring the persistence of non-palatable species [24]. This selective removal modifies the abundance of

Table 3. Plant species association type along a grazing gradient in Cabo de Gata-Níjar.

Life form	Species	G1	G2	G3	G4
Shrubs	<i>Anthyllis cytisoides</i> L.	0	+	0	0
	<i>Ballota hirsuta</i> Benth	0	+	0	0
	<i>Chamaerops humilis</i> * L.	–	–	–	–
	<i>Dianthus charidemi</i> Pau.	0	0	+	0
	<i>Genista ramosissima</i> * (Desf.) Poir.	–	–	–	0
	<i>Genista spartoides</i> Spach	–	0	0	0
	<i>Genista umbellata</i> * Poiret	0	0	–	0
	<i>Launaea lanifera</i> * Pau.	–	–	–	–
	<i>Lavandula multifida</i> * L.	0	0	–	0
	<i>Lycium intricatum</i> Boiss	0	0	0	–
	<i>Periploca laevigata</i> * Aiton.	–	–	0	0
	<i>Phagnalon saxatile</i> L.	0	+	0	0
	<i>Phlomis lychnitis</i> L.	–	0	0	0
	<i>Phlomis purpurea</i> * L.	+	0	0	0
	<i>Salsola genistoides</i> * Juss. ex Poiret	–	–	0	–
	<i>Teucrium charidemi</i> * Sandw.	+	0	0	0
	<i>Thymus hyemalis</i> * Lange	–	–	–	–
Grasses	<i>Asparagus albus</i> L.	0	+	+	0
	<i>Asphodelus</i> sp. L.	–	0	0	0
	<i>Asphodelus tenuifolius</i> * Cav.	0	0	0	–
	<i>Avena sterilis</i> sp. L.	0	–	0	0
	<i>Brachypodium distachyon</i> * L.	0	0	0	–
	<i>Brachypodium retussum</i> * (Pers.) Beauv	0	+	+	+
	<i>Euphorbia segetalis</i> L.	0	+	+	0
	<i>Hippocrepis ciliata</i> Willd.	–	0	0	0
	<i>Leontodon longirostris</i> (Finch and Sell) Talavera.	0	–	0	0
	<i>Lygeum spartium</i> * L.	–	0	0	0
	<i>Medicago truncatula</i> Gaertner	0	0	0	–
	<i>Melica minuta</i> * L.	0	+	0	0
	<i>Plantago afra</i> L.	0	–	0	–
	<i>Plantago albican</i> L.	0	–	0	0
	<i>Plantago amplexicaulis</i> Cav.	0	0	0	–
	<i>Plantago bellardi</i> * Ail.	–	0	–	–
	<i>Reichardia picroides</i> (L.) Roth	+	0	0	0
	<i>Sonchus tenerrimus</i> L.	+	0	0	0
	<i>Stipa capensis</i> Thunb	–	0	0	0
	<i>Stipa tenacissima</i> * L.	–	–	–	–
<i>Viola arborescens</i> L.	0	–	0	0	

G1-4, study sampling sites; +, $a_i > e_i$; –, $a_i < e_i$ (a_i must fall outside the 95% confidence interval of e_i).

*. species that had $p_i > 0.01$. Only those species that differed significantly from expectation on at least one site were included in the table.

doi:10.1371/journal.pone.0040551.t003

plant species, with some species becoming dominant while others disappear from the community [26]. The effect of grazing was particularly remarkable for grasses, which lost half their species. When grazing became very intense, the plant community was dominated by one very abundant species (*S. tenacissima*). These changes in species composition and abun-

dance also modified the associations between species in the plant community.

Regarding the general association pattern in the community, there were fewer co-occurrences than expected by chance. At all sites, irrespective of grazing intensity, plants showed a tendency to segregate rather than associate. Thus, it seemed that negative associations dominated the community, particularly at maximum grazing intensity. In recent works in the Spanish Mediterranean region, positive interactions between plant species have been presented as a main determinant of the plant community [37]. Here the predominant interaction across all grazing intensities was negative. Furthermore, associations among abundant species were predominantly negative. Grasses such as *S. tenacissima*, and shrubs like *Launaea lanifera* and *Thymus hyemalis* generally associated negatively with other species independently of grazing level. These species are common in degraded habitats and, through competitive exclusion (*S. tenacissima* [33]) or allelopathy (*T. hyemalis* [38]), they usually occur alone in the area rather than in association. In this area, abundant plant species are adapted to the harsh semi-arid environment and grazing, and they compete with other well-adapted species for space and other resources [39]. On the other hand, some abundant species benefit from the association with other plant species. For example, the grass *Brachypodium retussum* preferentially develops under the canopy of other species [33] and the shrub *Phlomis purpurea* presents low-density branching, which allows it to enter vegetation patches [40]. Although some plant taxa exhibited positive associational patterns, neutral and negative associational patterns were most common across all species in the communities.

Large shrubs such as *Chamaerops humilis*, *Genista ramosissima* and *Periploca laevigata* are responsible for the development of vegetation patches in the area [31]. Often, in semi-arid environments, these shrub species act as ‘nurse plants’ because they facilitate establishment and development of species under their canopy [21,41,42]. In our study, several positive associations between shrubs or between shrubs and grasses reflect this nursery effect. However, negative associations between these shrubs and the competitive abundant species overcame the positive association that shrubs established with other species. There are some examples of the facilitative effect of grasses on the establishment of other species in semi-arid ecosystems [43], but in our case most of the positive associations included at least one shrub, suggesting the role shrubs have as ‘nurse plants’ in the community.

In order to analyze associations of species and pairs of species, we considered only those species abundant enough to allow distinguishing negative from neutral associations. Typically, in plant community studies uncommon species are excluded from the analyses because they do not provide robust results [7,44]. In our case, despite the low likelihood of detecting negative associations in uncommon species, we found many positive associations between these species. Others have suggested that rare species are more likely to be facilitated than abundant ones [44]. Our results also suggest that rare species are likely to be associated with other species in semi-arid plant communities.

In our study, the proportion of positive species associations increased at low and intermediate grazing intensities (G2–3) and was lowest at the highest intensity (G4). This result has been reported in other studies dealing with changes in the interactions between plant species along grazing gradients, but to our knowledge this is the first time that this result is evaluated at community level [13,26,29]. As grazing increases, associations between plant species become more frequent, particularly those associations with shrub species that act as refuges against grazers. However, once a particular threshold is reached, grazing intensity

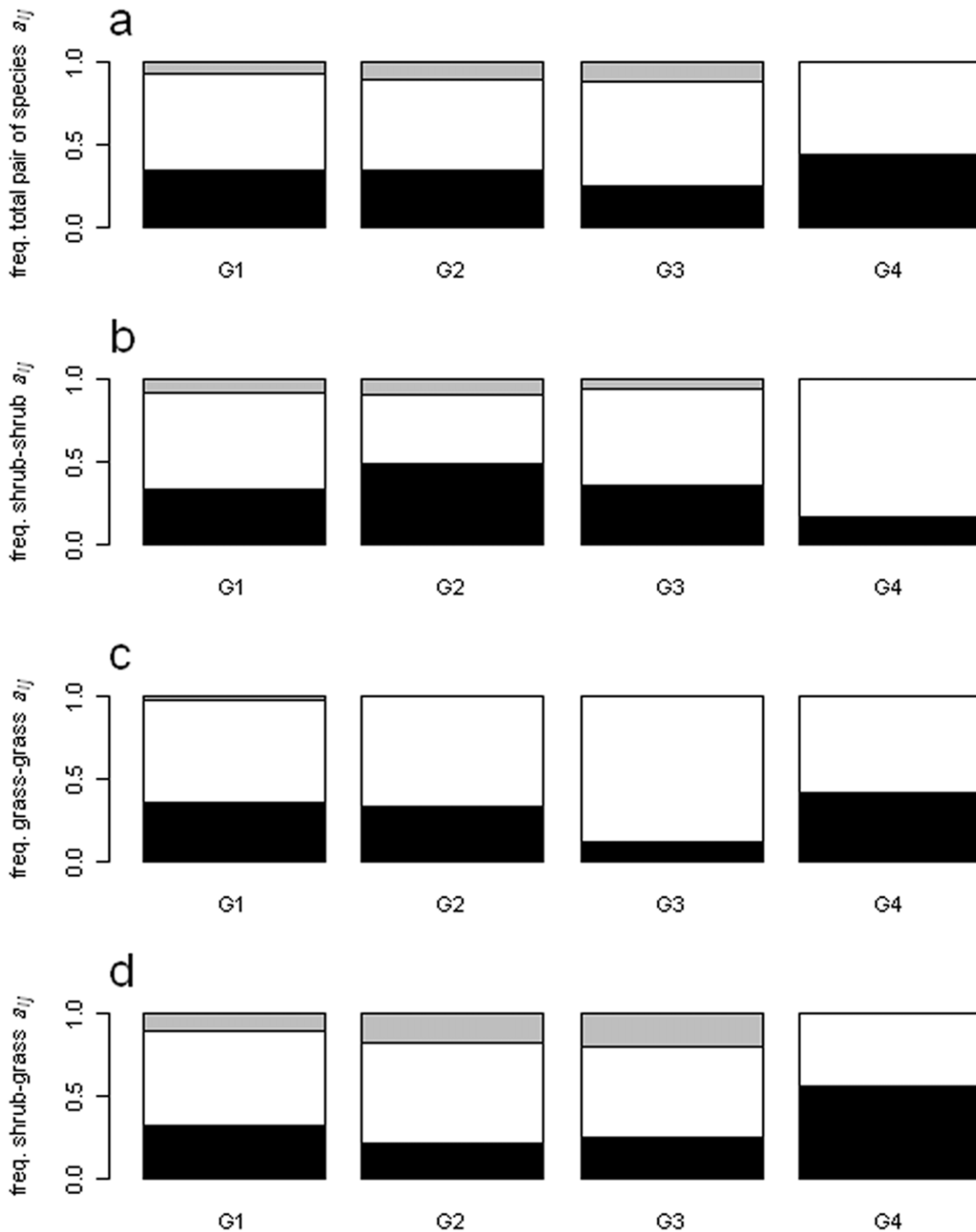


Figure 3. Relative number of pairs of species for each type of association. a, proportion of pairs of species with each type of association; b, proportion of types of association between pairs of shrubs; c, proportion of types of association between pairs of grasses; d, proportion of types of association between pairs of shrubs and grasses. G1 to G4 are the sampling sites. Associations are classified as negative (black area), neutral (white area) or positive (grey area) depending on the relation between a_{ij} value and the expected distribution. Only pairs of species that could allow distinguishing negative associations were employed.

doi:10.1371/journal.pone.0040551.g003

is such that facilitative species cannot provide protection and positive associations decrease [29]. Interestingly, the particular type of association of each species remained consistent across the

grazing gradient. One possible explanation is that each species exhibits a predominant associative type in the community, regardless of grazing intensity (i.e., competitive species never

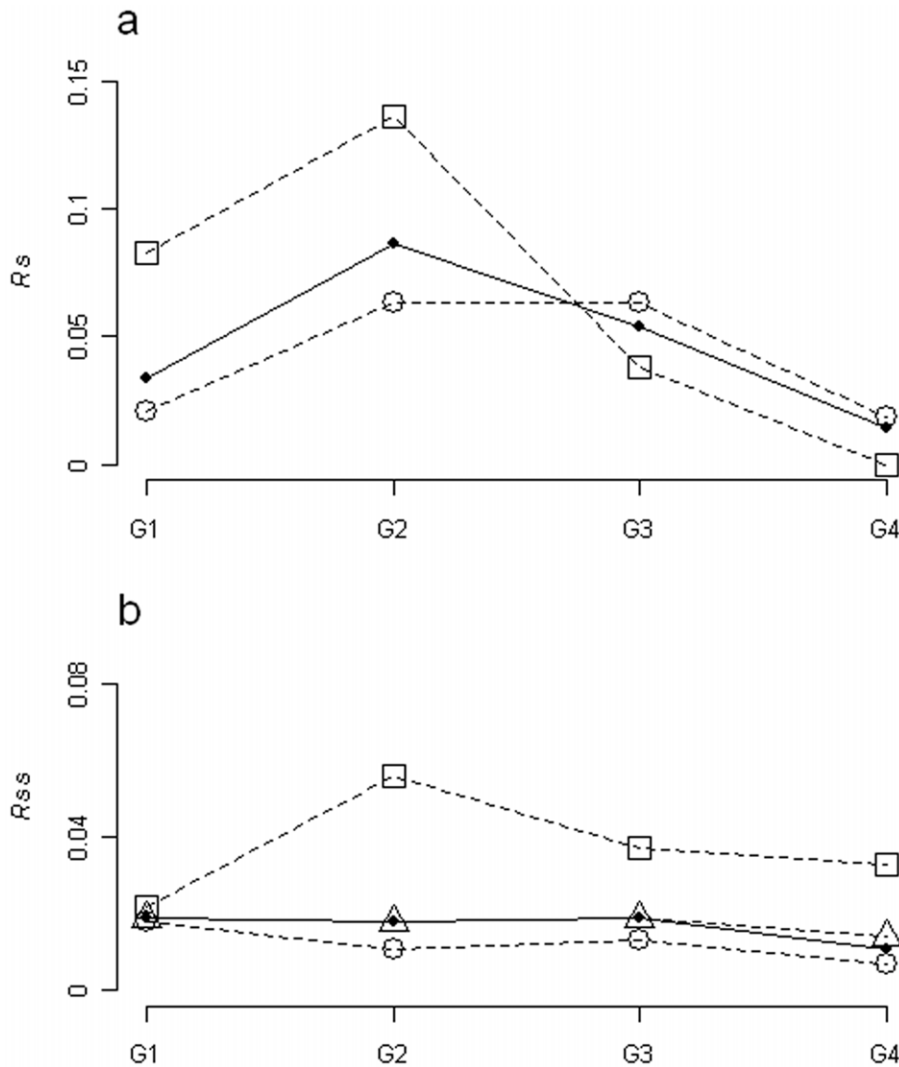


Figure 4. Importance of positive associations along grazing gradient. a, R_s , importance of positively associated species for each life form. b, R_{ss} , positively associated pairs of species importance for each life form. G1 to G4 are the sampling sites. In a, importance of positive associations for species is evaluated for shrubs (open circles), grasses (open squares) and all species (black circles). In b, importance of positive associations for pairs of species is evaluated for shrub-shrub (open circles), grass-grass (open squares), shrub-grass (open triangles) and for all associations of pairs of species (black circles).
doi:10.1371/journal.pone.0040551.g004

become associative [25]). Others have documented associational changes across different stages of plant ontogeny [19], but here the observed associations reflect the general type of association of the species in the area.

Spatial associations between species have been presented as an indirect measure of species interactions, but this approach has limitations. The spatial association of species is the net result of biotic interactions, seed dispersal and environmental heterogeneity [45]. The present study has additional limitations. For example, inter-specific associations are not measured, all individuals of each species are considered ecologically identical (e.g. different life stages may interact differently [19,46]) and other effects of interactions are ignored (e.g. changes in species biomass [14]). Nevertheless, our results are consistent with those reported by works about SGH including a limited number of species [13,27]. Identifying the processes that drive the organization of natural communities under grazing and the role that each species plays in said organization provides valuable information about which

species maintain the structure of grazed ecosystems. This information is central to detect overgrazing events in grazed ecosystems [24].

In conclusion, most species were not associated with other species and the most common association among plants in this semi-arid plant community was negative, especially associations with dominant species. This suggests that either neutral processes and/or competitive interactions are structuring these plant communities. The associational patterns of most species did not vary with grazing intensity; however, there was a tendency for positive associations among species to become less frequent at high levels of grazing. Positive associations among plants appeared to be most important at low and intermediate grazing intensities. Identifying non-neutral species associations provide information about the processes and species driving the organization of natural communities and helps further the development of conservation and restoration plans.

Supporting Information

Table S1 Life form, abundance (n_i), co-occurrences (a_i) and association type (ass) of plant species in Cabo de Gata-Níjar Natural Park along grazing gradient. Association values are presented for species that could distinguish between neutral and negative associations. (XLSX)

Acknowledgments

We specially thank the authorities of Cabo de Gata-Níjar Natural Park for their collaboration in the development of the study. We thank Bruce

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MacWhirter and Nelly Horak for critically reading on the manuscript, and Jaime Iranzo, Yamir Moreno, Stefano Allesina's lab and colleagues from the Pyrenean Institute of Ecology for their helpful suggestions on the manuscript.

Author Contributions

Conceived and designed the experiments: CLA. Performed the experiments: HS CLA. Analyzed the data: HS. Contributed reagents/materials/analysis tools: HS CLA. Wrote the paper: HS CLA.