

Plant–plant interactions scale up to produce vegetation spatial patterns: the influence of long- and short-term process

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Abstract. Vegetation spatial patterns emerge in response to feedback interactions between organisms and their environment, because of the redistribution of water and nutrients around the plant canopy or as a consequence of facilitation/competition interactions at the plant level, even in the absence of pre-existing substratum heterogeneities. It has been suggested that changes in vegetation spatial patterns are a signal of transition shift in ecosystems. Understanding the factors that lead to aggregated spatial patterns and control the transition to random distributions requires that environmental and species information is taken into account. In this study, we investigated the relative contributions of aridity (a long-term process), to which vegetation is adapted, and the area covered by bare soil (short-term process) to plant–plant associations and their contribution to aggregated spatial patterns. The study was conducted in a gradient of aridity ranging from that in subalpine grassland habitats in the Pyrenees and Sierra Nevada mountains to that in the semiarid steppes of Cabo de Gata and the middle Ebro Valley in Spain. We compared sites that differed in aridity and a geophysical feature (north- vs. south-facing slope). We observed that the relative contribution of aridity and bare soil to plant–plant facilitation and vegetation aggregation differed in subalpine and semiarid areas. Facilitation in subalpine habitats had a marked effect on aggregated spatial patterns, while aridity contributed to disruption of these patterns. Conversely, in semiarid habitats, the disruption of aggregated patterns was mainly promoted by an increase in bare soil area rather than in aridity. In semiarid habitats, the higher level of stress on south-facing slopes increased facilitation interactions relative to north-facing slopes, although this did not enhance the persistence of aggregated spatial patterns. We conclude that the use of aggregated spatial patterns as an indicator of ecosystem shift must distinguish and separately take account of long-term processes to which vegetation adapt, and short-term process.

Key words: aggregated patterns; aridity; diversity; facilitation; plant spatial association.

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INTRODUCTION

There is increasing interest in vegetation spatial patterns as an indicator of stress and a precursor of transition shifts in ecosystems

(Alados et al. 2003, 2004, Kéfi et al. 2007, Scheffer et al. 2009, Berdugo et al. 2017). The spatial patterns are the result of self-organization processes that develop during long periods of time (Bak et al. 1987, Dakos et al. 2008), and lead to stable

arrangements that are resilient to perturbation up to some threshold, beyond which the system moves to an alternative state (Scheffer et al. 2009). Systems are said to exhibit self-organization when patterns emerge from interactions among internal system components (Camazine et al. 2001). Self-organizing spatial patterns can integrate structural and functional aspects of the ecosystems at the same time (Okin et al. 2015). As spatial patterns develop as a result of interactions among various environmental components, the ecosystem undergoes change through time, giving rise to emergent patterns that provide feedback to the emergent trajectory (Berdugo et al. 2017).

Various mechanisms are responsible for the formation of self-organized spatial patterns in response to feedback processes; these are reviewed by Rietkerk and van de Koppel (2008). Some studies have emphasized abiotic processes, such as the redistribution of water and nutrients around the plant canopy (HilleRisLambers et al. 2001, Meron et al. 2004, Rietkerk et al. 2004, Meron 2011, Moreno-de las Heras et al. 2012, Okin et al. 2015), while others have focused on biotic processes, such as facilitative/competitive interactions among plants (Lefever and Lejeune 1997, Kéfi et al. 2007). Other biotic processes including seed dispersal also play important roles in pattern formation (Pueyo et al. 2008, Lefever et al. 2009, Saco and Moreno-de las Heras 2013). These processes operate at short to long temporal scales and small to large spatial scales. The direction and strength of plant interactions (short scale) influence vegetation spatial patterns at large scales, and can lead to niche development and differentiation over time, which can favor the coexistence of more species than would be expected based on a random spatial distribution (Kikvidze et al. 2005).

For sessile organisms including plants, positive interactions occur between nearby individuals, leading to spatial clustering and aggregation. Several studies have quantified the importance of these positive interactions in the formation of spatial patterns (Kikvidze et al. 2005, Mitchell et al. 2009, Maestre et al. 2010) and prevention of diversity loss (Hacker and Gaines 1997, Michalet et al. 2006, Le Bagousse-Pinguet et al. 2014), particularly in harsh environments (Cavieres et al. 2014), and have shown that they can trigger

positive feedbacks that lead to alternative stable states (Kéfi et al. 2016). Other studies have emphasized the importance of abiotic processes (including runoff and erosion) that are responsible for the redistribution of nutrients in the ecosystem (Turnbull et al. 2010*a*, Moreno-de las Heras et al. 2012, Okin et al. 2015), and have posited that these abiotic effects could be more important than plant–plant facilitation processes (Turnbull et al. 2010*b*).

To better understand the conditions under which vegetation spatial patterns develop, more empirical and theoretical research is needed on scaling up from interactions at the individual level to processes at community and ecosystem scales. Previous studies have investigated the importance of biotic interactions in driving ecological processes (Grime 1979, Huston 1979, Bertness and Callaway 1994), particularly changes in facilitative interactions in response to environmental stress (Callaway 2007, Brooker et al. 2008, Michalet et al. 2014). However, most of the empirical studies that have analyzing the mechanisms underlying the formation of vegetation patterns have been time limited; in real ecosystems, it is difficult to demonstrate pattern dynamics because self-organizing processes require long time periods for patterns to develop. Most research on plant–plant interactions has investigated pairs of species rather than interactions involving the entire plant community (for review, see Soliveres et al. 2015, but also see Saiz and Alados 2012). However, study of the net effect of all positive and negative interactions, rather than the interactions between pairs of species, is central to understanding vegetation dynamics. Our research focus is identifying the responses of the community to the types of environmental pressure associated with global warming, and to quantify the effects of positive and negative plant interactions on the diversity and structure of plant communities (Hacker and Gaines 1997).

The stress gradient hypothesis (SGH) posits that abiotic stress and disturbance increase the frequency, intensity, and effects of positive interactions (Bertness and Callaway 1994, Brooker and Callaghan 1998), although extremely stressful conditions can reduce positive interactions (Maestre et al. 2005, Michalet et al. 2006, Smit et al. 2007). Furthermore, the life histories of interacting species and the sources of stress can

influence the sign of that relationship (Michalet et al. 2006, Maestre et al. 2009, Malkinson and Tielbörger 2010); hence, the relationship is not always linear along an environmental stress gradient. Some have proposed a modified SGH that predicts an increase in the importance of positive plant–plant interactions up to moderate levels of stress (Holmgren and Scheffer 2010). In addition, unidentified stress factors that act concurrently, or differences in species-specific interactions, may have contributed to differences in the results among the various studies (Soliveres et al. 2015).

It is important to differentiate between long-term processes (e.g., aridity), to which the vegetation is adapted, from short-term processes, such as an increase in bare soil (Grime 1979), although bare soil can also represent a direct response to aridity. Plants growing in semiarid habitats are habituated to long periods of water scarcity and show adaptive mechanisms (the “stress resistance syndrome”) to deal with drought (Grime 1979, Chapin et al. 1993). These communities are resilient to increased levels of aridity and are expected to be less sensitive to the direct impacts of global warming than predicted by models reported in other studies (Gunderson et al. 2010). Conversely, the increase in hydrological connectivity with increased bare soil triggers erosion process after rainfall events that results in the redistribution of water and nutrients (Moreno-de las Heras et al. 2012, Okin et al. 2015). These are short-term processes to which the plants need time to recover (Chapin et al. 1993); as the disturbance increases, the entry of opportunistic species reduces self-organized patterns because stochasticity increases during the colonization process (Soro et al. 1999). For example, a reduction in aggregated spatial patterns has been observed associated with grazing disturbance (Alados et al. 2003, 2004).

In this study, we investigated the contribution of regional long-term (aridity), local short-term abiotic (bare soil), and local biotic (facilitation) processes on vegetation spatial patterns. Bare soil cover controls the redistribution of water, sediments, and nutrients at local scale influencing the patches hydrological connectivity. Although there is much focus on determining the effect of aridity on facilitation and how biotic interactions affect vegetation pattern formation, this is the first study to quantitatively assess the relative

contributions of long- and short-term processes to vegetation spatial patterns, and to analyze the relationship of the patterns to facilitative interactions, with the exception of Berdugo et al. (2017). We conducted this observational study in an area in Spain having an aridity gradient ranging from semiarid steppes to subalpine habitat. We also compared north- and south-facing slopes in two environments (semiarid vs. subalpine); slope aspect has a strong effect in terms of incident solar radiation in the ecosystem, with south-facing slopes receiving more energy per unit area than north-facing slopes (Beniston 2006). Variation in solar energy and its effects on evapotranspiration control the soil moisture regimen (Zou et al. 2007, Bennie et al. 2008); this produces a gradient enabling study of plant tolerance to water deficits. In this study, the north- and south-facing slopes were used as proxies for climate warming, because average temperatures are higher on south-facing slopes than on north-facing slopes (Zhou et al. 2013). This difference has been used in previous studies to simulate the long-term effects of changes in climate (Escós et al. 2000, Alados et al. 2001, Sternberg and Shoshany 2001, Pueyo et al. 2007).

We hypothesized (H1) that the ratio of positive to negative associations in the plant community (a proxy for the importance of facilitation in the community) is positively correlated with aggregated vegetation spatial patterns, and that facilitation is one of the major mechanisms of pattern formation, favoring high diversity in the plant community.

The importance of facilitation on harsh environments, such as semiarid habitats (Pugnaire et al. 1996, Callaway 2007), and the positive relationship between facilitation and vegetation spatial patterns (Rietkerk and van de Koppel 2008) have led to assume, generally, that aridity and aggregated spatial patterns are positively related. However, we may expect that aggregated vegetation spatial patterns do not change with aridity in well-preserved semiarid ecosystems once they are established (long-term process), being rather the effect of bare soil cover (short-term process) that breaks the spatial structured patterns (H2).

The relative contributions of facilitation (the ratio of positive to negative plant–plant spatial associations) and bare soil area to pattern formation were investigated in two contrasting

environments (subalpine and semiarid habitats). If the modified SGH holds (Holmgren and Scheffer 2010), the importance of facilitation in aggregated vegetation patterns should decline in semiarid habitats, turning the vegetation pattern from aggregation to a random spatial distribution with increased bare soil areas. For subalpine habitat, it was hypothesized (H3) that the contribution of facilitative interactions to aggregated patterns will be limited by bare soil area and not resources availability.

We compared north- and south-facing slopes in semiarid and subalpine environments. On south-facing slopes, the stress caused by high temperatures and insolation reduces the water balance and exacerbates the effects of aridity on plant communities, which diminishes the ability of plants to improve the micro-environmental conditions for neighboring plants, and reduces the size of vegetation clusters. We hypothesized (H4) that in semiarid habitats, reduced aggregated vegetation patterns will characterize south-facing slopes, but the importance of facilitative interactions will be maintained, while in subalpine habitats,

increased competition on the more productive south-facing slopes will contribute to the breakdown of aggregated spatial patterns.

METHODS

Study sites

The study was conducted at 31 sites distributed along an aridity gradient in 14 locations ranging from subalpine grasslands (five locations) in high mountain areas (altitude ranging from 1800 to 2100 m) in the Pyrenees and Sierra Nevada (the Ordesa and Monte Perdido and the Sierra Nevada national parks) to semiarid steppes (nine locations) in the middle Ebro Valley in northeastern Spain and at Cabo de Gata in southeastern Spain (Fig. 1 and Appendix S1).

In the Ordesa National Park, the vegetation comprises dense pastures of *Bromion erecti* Koch and *Nardion strictae* Br.-Bl. typical of the alpine and subalpine belts of the Pyrenees, with caespitose dwarf *Echinopartum horridum* (Vahl) Rothm. partly colonizing south-facing slopes. Vegetation in the Sierra Nevada National Park

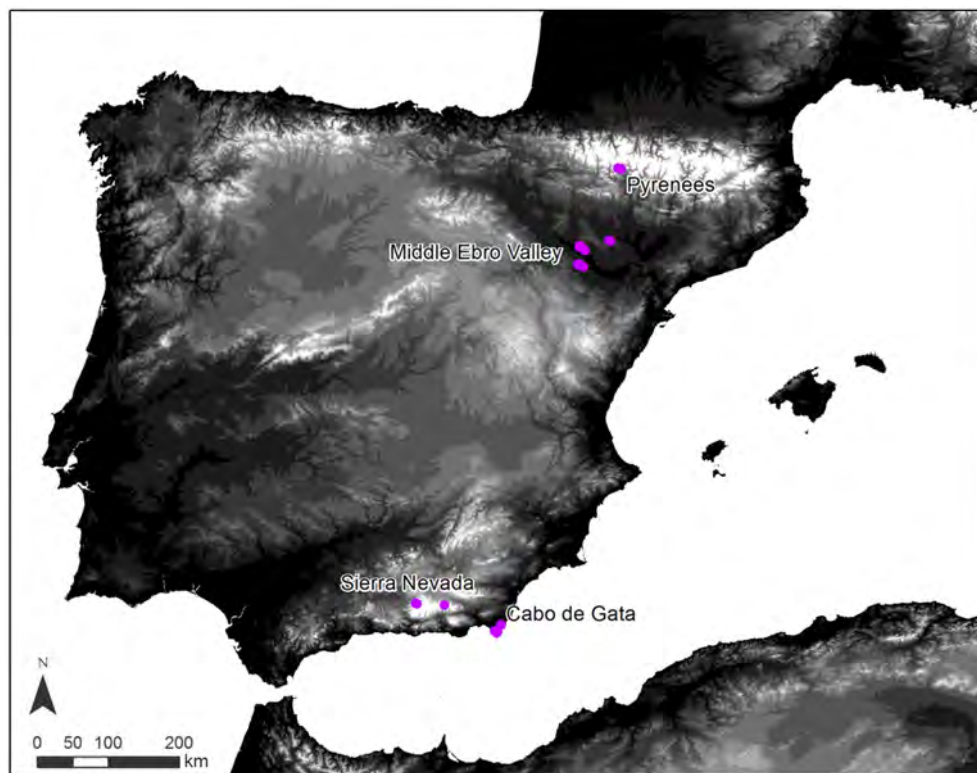


Fig. 1. Study area and the location of field sites.

sites comprises dwarf matorral dominated by cushion plants (e.g., *Erinacea anthyllis* Link, *Genista versicolor* Boiss, *Juniperus communis* L., and *Astragalus nevadensis* Boiss).

On the semiarid steppes in the middle Ebro Valley, the vegetation is dwarfland matorral dominated by *Rosmarinus officinalis* L., with gypsumophytes including *Helianthemum squamatum* (L.) on gypsum outcrops, and scrub including *Salsola vermiculata* L., *Artemisia herba-alba* Asso, and *Lygeum spartum* L. on the uncultivated silty soils in the base of the valleys; the altitude in this area ranges from 150 to 800 m a.s.l. The Cabo de Gata vegetation at 100 m a.s.l. is dwarf matorral comprising *Chamaerops humilis* L., *Periploca laevigata* Aiton, and *Stipa tenacissima* L.

Environmental data

Climate data at 1-km² resolution were obtained from Tomas-Burguera et al. (2016) for the period 1950–2015. Aridity was estimated as: $\text{Aridity} = 1 - P/Ev$, where P is precipitation and Ev is potential evapotranspiration (Delgado-Baquerizo et al. 2013). For this index, higher values indicate increasing drought conditions.

In a sample of the subalpine and semiarid habitats, we selected paired north–south sites separated from each other by at least 0.5–1 km. Soil moisture (%) was measured along a 500-m transect per site (20–30 samples) using a HH2 moisture meter (Delta-T Devices, Cambridge, England). Soil moisture was recorded simultaneously for paired slopes to avoid differences due to time from the last rainfall event, and proximity to rainfall events was avoided. Data were collected during the vegetation growth period at each location.

Soil samples were collected from the upper 15 cm of the soil along a 500-m transect per site (6–10 samples). The samples were dried in the laboratory and passed through a 2-mm sieve. The organic matter content (OM), total carbon (% total C), total nitrogen (% N), and the C/N relationship were quantified for each sample. After the soil samples were prepared, (% Total C) and (% N) were quantified in a Variomax Elementar elemental analyzer, using the Dumas procedure. The organic carbon content was quantified using dichromate (Heanes 1984). The OM content was calculated by multiplying the % organic carbon by the Van Bemmelen factor of 1.724 (Heanes 1984), which assumes that OM is 58% organic C.

Vegetation sampling and spatial patterns

At the peak of the vegetation growth period, the point–intercept method (Goodall 1952) was used to record the presence of individual plants at 20-cm intervals along 109 transects each of 500 m length (3–6 per site). Plant cover estimates based on this method had a precision that was similar to that of line interception, but required approximately 33% less sampling time (Floyd and Anderson 1987). Species diversity was estimated based on the Shannon index (Shannon 1948) $H' = -\sum_{i=1}^N p_i \ln p_i$, where p_i is the probability of the frequency of the i th species and N is the number of species. In this study, p_i was the probability that a given species (i) occurred on a given 500-m transect, and was determined as the number of occurrences of species i /the total number of points surveyed (2501).

We quantified vegetation aggregation patterns based on the presence/absence data collected along point intercept transects. Detrended fluctuation analysis (DFA; Peng et al. 1992) was used to quantify spatial sequences, later reviewed by several authors (Rutherford et al. 2004, Asher et al. 2009). The analytical protocol followed that of Peng et al. (1992, 1995), and its application to vegetation spatial data followed Alados et al. (2003). In the DFA, we extracted vegetation sequences comprising 2050 points at 20-cm intervals along a transect. The data were transformed to a binary sequence $[z(i)]$ in which the presence of the species or vegetation under examination was denoted as 1 and its absence (lag) was denoted as -1 . A random walk was generated from those binary sequences by integrating the sequence series $[y(s)]$ such that $y(s) = \sum_{i=1}^{s-1} z(i)$. The entire sequence was divided into non-overlapping boxes of length n , and a least-squares regression line was fitted to the data within each box $[y_n(s)]$. If $\hat{y}_n(s)$ is the regression estimate for $y_n(s)$ for each box size n , then the average fluctuation $[F(n)]$ of $y_n(s)$ about $\hat{y}_n(s)$ for each box size follows the modified root mean square equation

$$F(n) = \sqrt{\frac{1}{N} \sum_{i=1}^N (y_n(s) - \hat{y}_n(s))^2}$$

This procedure was repeated for each scale (box size), which were the nearest integers to 2^2 , $2^{2.5}$, 2^3 . . . , 2^9 . The resulting relationship fitted the power law $F(n) \sim n^\alpha$, where $\alpha = 0.5$ represents a

non-correlated random sequence (white noise) and $\alpha > 0.5$ represents a long-range correlation of the plant distribution sequence, which is said to have memory; this term means that what happens in one step depends on what occurred in previous consecutive steps over a long sequence. The parameter α (alpha-DFA hereafter) is equivalent to the Hurst exponent (Hausdorff et al. 1997), although it is a superior method for quantifying long-range autocorrelations (Hu et al. 2001). Theoretically, it is unaffected by the magnitude of fluctuations (in this case, total vegetation cover) and is only affected by the sequential ordering (distribution) of the fluctuations.

Alpha-DFA is related to another index commonly used to evaluate vegetation spatial patterns: the cumulative distribution function of patch size (White et al. 2008), which has recently been subject to criticism (Meloni et al. 2017). The scaling exponent of the frequency distribution is a measure of the fractal dimension (Hausdorff et al. 1997) and is inversely related to alpha-DFA (Appendix S2).

Facilitation vs. competition

Two species were said to co-occur if they were present at the same sampling point on a transect. Recurrent local co-occurrence patterns were assumed to reflect plant interactions, not merely plants that shared habitat requirements (Saiz and Alados 2012, Soliveres and Maestre 2014). We assumed that co-occurrence of two species more often than expected by chance indicated they benefited from the association (facilitation), and that interference was inferred when two species segregated from each other more often than expected (Tilman and Kareiva 1997, Tirado and Pugnaire 2005). To estimate the number of positive (K^+) and negative (K^-) associations on each transect, the probabilities of observed and expected pairs of species at the upper and lower limits of the 95% confidence interval of the Poisson distribution were compared (Saiz and Alados 2012). To control for the influence of species richness on association frequency, the numbers of positive (K^+) and negative (K^-) associations were divided by the number of species (S) on a transect ($Density^+ = K^+/S$). The ratio of positive to negative associations $(K^+ - K^-)/(K^+ + K^-)$ was calculated and used as a proxy of plant-plant facilitation; this ratio is a symmetrical estimate around zero that is widely

used in ecology (Armas et al. 2004). High values of this ratio (facilitation hereafter) reflect that the species are more prone to facilitate each other, whereas low values reflect a tendency for the species to interfere with each other.

Statistical analyses

To identify any significant effects of aridity on biotic interactions and self-organized vegetation spatial patterns (alpha-DFA), we used a linear mixed model (LMM) in which the aridity index was the explanatory variable, while facilitation, density of positive associations (D^+), density of negative (D^-) associations, number of links per species ($D = (K^+ + K^-)/S$), proportion of non-associative species (NAs: number of species with no significant associations to others), species diversity (Shannon index), and bare soil cover were the response variables. Sample site was included as a random factor.

We constructed structural equation models (SEMs) to determine the relative importance of aridity (long-term process) and bare soil cover (short-term process) on facilitation (the ratio of positive to negative plant-plant associations) and vegetation spatial pattern (alpha-DFA) as response variables, and their effects on diversity (Shannon diversity index: H'). The model was estimated using the lavaan package (Rosseel 2012) in R language. Structural equation model allows the testing of multivariate hypothesis in which some variables (e.g., facilitation) can simultaneously act as predictors and outcomes. We first built a general model of relationships in our system, and then, we constructed the best-fitting-specific model that corresponds to the conceptual model. The amount of variance explained (R^2) for each response was calculated, and the overall fit of non-saturated model (root mean square error of approximation) was assessed.

The influences of facilitation and bare soil cover on vegetation spatial patterns (alpha-DFA) were analyzed using a LMM, with location as the random effect factor. A LMM was also used to identify significant differences related to the slope aspect (north, south). Slope aspect was a fixed effect factor, while vegetation spatial patterns (alpha-DFA), biotic interactions (D , D^+ , D^- , facilitation, and NAs), and species diversity (H') were the dependent variables. Sample site was included as a random factor.

Choice of the best final model for each response variable was based on Akaike information criteria (Zuur et al. 2009). The statistical analyses were performed using R 3.2.2 (R Core Team 2014). We used the nlme R package (Pinheiro et al. 2014) for the LMM.

RESULTS

Influence of aridity on plant–plant facilitation and vegetation spatial patterns

Aridity was significantly ($F_{1,29} = 19.07$, $P < 0.001$) and negatively correlated (slope = -0.81 ± 0.18) with the density of positive (D^+) and negative (D^-) associations ($F_{1,29} = 44.99$, $P < 0.001$; slope = -0.81 ± 0.12). Aridity was positively correlated with facilitation (the ratio of positive to negative associations; slope = 0.14 ± 0.08), although the relationship was only marginally significant ($F_{1,29} = 3.03$, $P < 0.1$; Fig. 2).

The number of links per species (D) declined as the aridity index decreased ($F_{1,29} = 59.83$, $P < 0.001$), whereas the proportion of NAs increased with increasing aridity ($F_{1,29} = 48.77$, $P < 0.001$). Neither the Shannon diversity index ($F_{1,29} = 2.03$, n.s.) nor vegetation spatial patterns (alpha-DFA; $F_{1,29} = 0.71$, n.s.) were significantly correlated with the aridity index (Fig. 2). All the analyses involved LMMs, with the random intercept model providing the optimal model structure.

Influence of aridity on plant–plant facilitation and vegetation spatial patterns under semiarid and subalpine conditions

We investigated the importance of aridity (long-term process) and bare soil cover (short-term process) on facilitation and vegetation patterns by applying the SEM using facilitation and vegetation patterns as response variables and their effects on diversity (Shannon diversity index: H'). Because the ecosystem processes operating at semiarid and subalpine environments can be different, we analyzed separately the relative importance of aridity and bare soil cover on plant–plant facilitation and vegetation spatial patterns. The results of the SEM, showing the effects of aridity and bare soil cover on facilitation and vegetation patterns (as response variables) and their effects on diversity (Shannon diversity index, H'), are presented in Fig. 3. These show that in subalpine habitats (Fig. 3a), an increase in the

proportion of bare soil increased the aggregated vegetation patterns (the higher the proportion of bare soil, the higher the alpha-DFA). Parallel facilitation was also positively correlated with aggregated spatial patterns. In contrast, increasing aridity reduced aggregated spatial patterns and species diversity in subalpine habitats; as aridity increased, the vegetation spatial patterns became more randomly distributed. Diversity was not influenced by facilitation, aggregated vegetation patterns, or bare soil cover.

In semiarid habitats (Fig. 3b), it was observed that as the proportion of bare soil increased, the aggregated spatial patterns decreased, and vegetation patterns became more randomly distributed. Neither facilitation nor aridity was correlated with aggregated spatial patterns. However, facilitation was correlated with the proportion of bare soil; there was more facilitation as the proportion of bare soil increased, and this favored greater plant diversity. Plant species diversity was negatively affected by increasing aridity and the proportion of bare soil; as aridity and bare soil increased, species diversity declined (Fig. 3b).

The influence of facilitation and bare soil cover on vegetation spatial patterns is shown in Fig. 4, separately for subalpine and semiarid conditions. The results of the LMM using the random intercept model as the optimal model structure revealed that in subalpine habitats, facilitation was significantly and positively correlated (slope = 0.12 ± 0.03) with aggregated spatial patterns ($F_{1,30} = 16.79$, $P < 0.001$). Similarly, bare soil cover positively influenced (slope = 0.004 ± 0.001) aggregated spatial patterns ($F_{1,30} = 4.47$, $P < 0.05$). In contrast, in semiarid habitat, facilitation was significant and negatively correlated (slope = -0.042 ± 0.01) with the aggregated spatial patterns ($F_{1,63} = 8.17$, $P < 0.01$), when the random intercept model was used as the optimal model structure. Bare soil cover was also negatively correlated (slope = -0.002 ± 0.001) with the aggregated spatial patterns when the random intercept model was used as the optimal model structure ($F_{1,63} = 7.83$, $P < 0.01$).

Influence of slope aspect on plant–plant associations and vegetation spatial patterns

The soil moisture content was significantly higher on north-facing than on south-facing slopes ($F_{1,374} = 81.72$, $P < 0.001$). The average

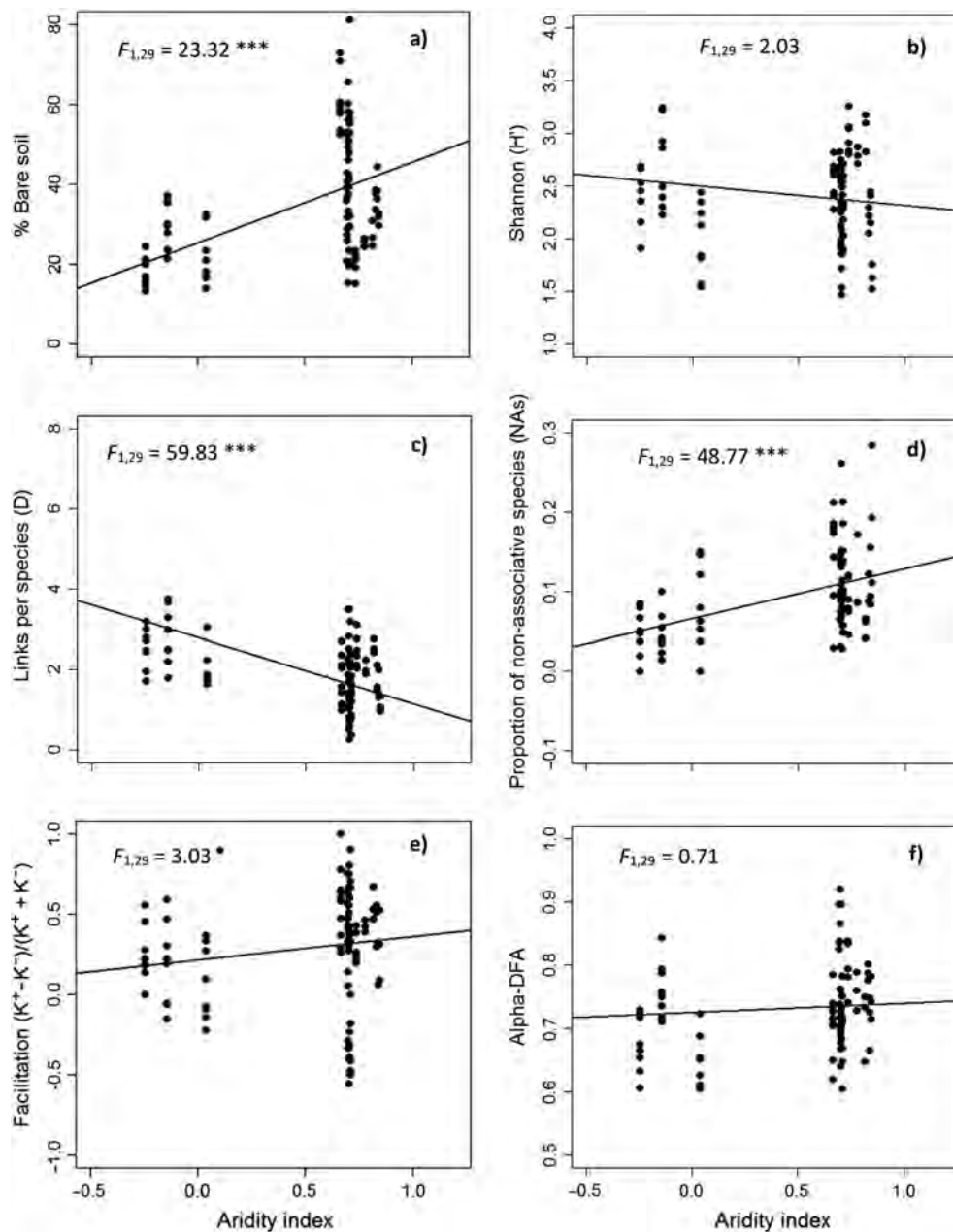


Fig. 2. Effects of aridity on (a) bare soil cover; (b) the Shannon diversity index; (c) the number of links per species (D); (d) the proportion of non-associative species (NAs); (e) facilitation, expressed as the ratio of positive to negative associations $(K^+ - K^-)/(K^+ + K^-)$; and (f) aggregated vegetation spatial patterns (alpha-detrended fluctuation analysis [DFA]). Parameters a–e were dependent variables, and the linear mixed model included sample site (31 sites) as a random factor. • $P < 0.1$, * $P < 0.5$, ** $P < 0.01$, *** $P < 0.001$.

values (\pm standard errors) are presented in Appendix S1.

Slope orientation had a highly significant effect on facilitation in semiarid areas ($F_{1,26} = 16.96$,

$P < 0.001$). South-facing slopes were associated with higher levels of facilitation than north-facing slopes. Conversely, the density of negative associations (D^-) was significantly greater on

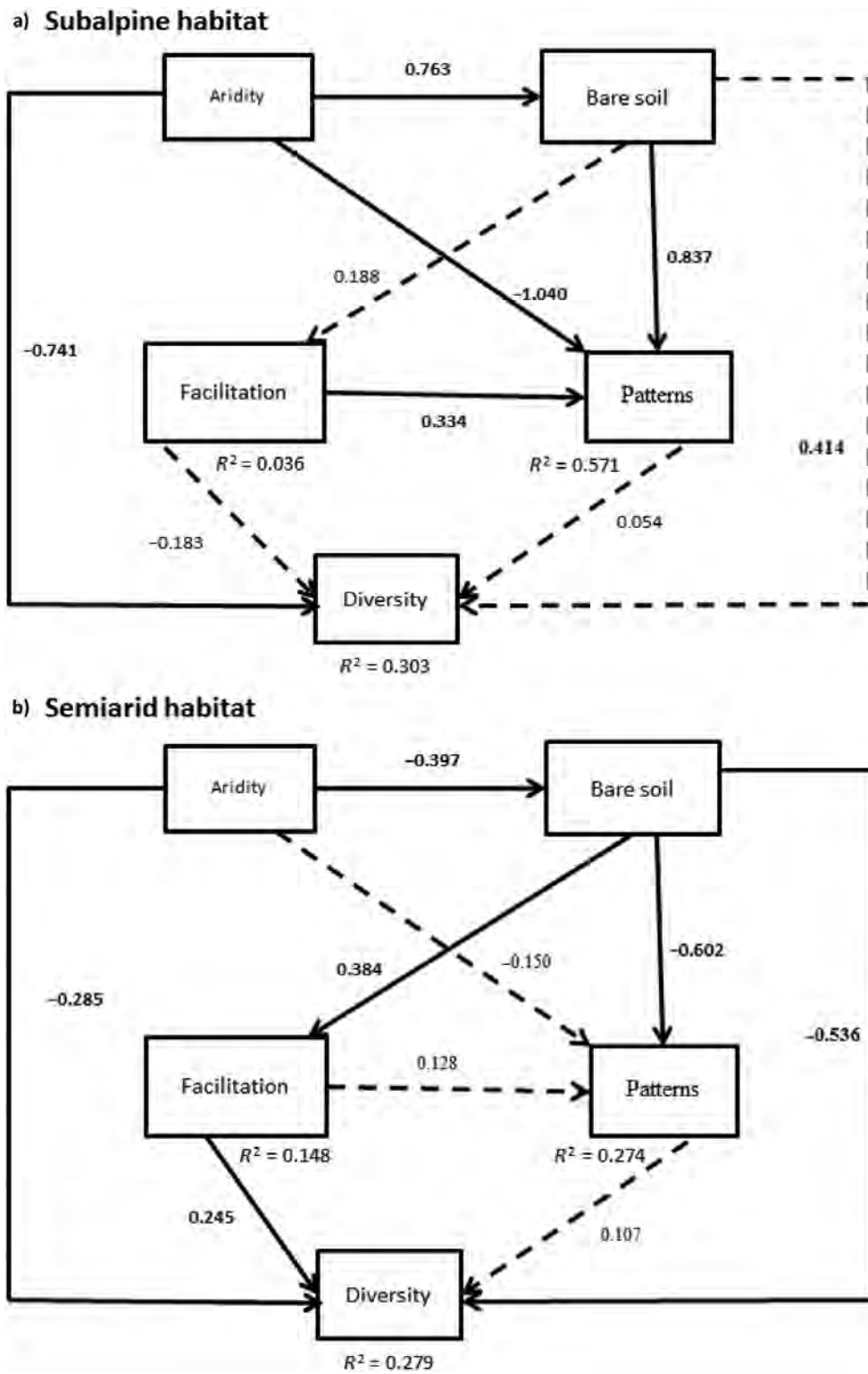


Fig. 3. Structural equation model for aridity and bare soil cover as predictors, and facilitation and aggregated spatial patterns (alpha-detrended fluctuation analysis) as response variables and their effects on diversity (Shannon diversity

(Fig. 3. Continued)

index: H'). Facilitation was quantified as the ratio of positive to negative associations $(K^+ - K^-)/(K^+ + K^-)$. Continuous lines indicate significant responses, and discontinuous lines indicated non-significant responses. Standardized path coefficients in boldface were significant at $P < 0.05$. (a) subalpine habitats ($n = 36$; $\chi^2 = 0.996$, $df = 1$, $P = 0.318$; root mean square error [RMSE] = 0.00); (b) semiarid steppes ($n = 73$; $\chi^2 = 2.76$, $df = 1$, $P = 0.097$; RMSE = 0.155).

north-facing slopes ($F_{1,26} = 9.81$, $P < 0.01$). The number of associations per species and the Shannon diversity index declined significantly in south-facing slopes ($F_{1,26} = 18.09$, $P < 0.001$; $F_{1,26} = 31.42$, $P < 0.001$, respectively), although the number of NAs did not change with slope orientation ($F_{1,26} = 0.32$, n.s.). South-facing

slopes showed less aggregation than north-facing slopes, but the difference was only marginally significant ($F_{1,26} = 3.84$, $P = 0.06$).

In subalpine habitats, slope orientation did not significantly influence facilitation ($F_{1,30} = 0.31$, n.s.), density of negative associations ($F_{1,30} = 2.30$, $P = 0.1$), number of links per species

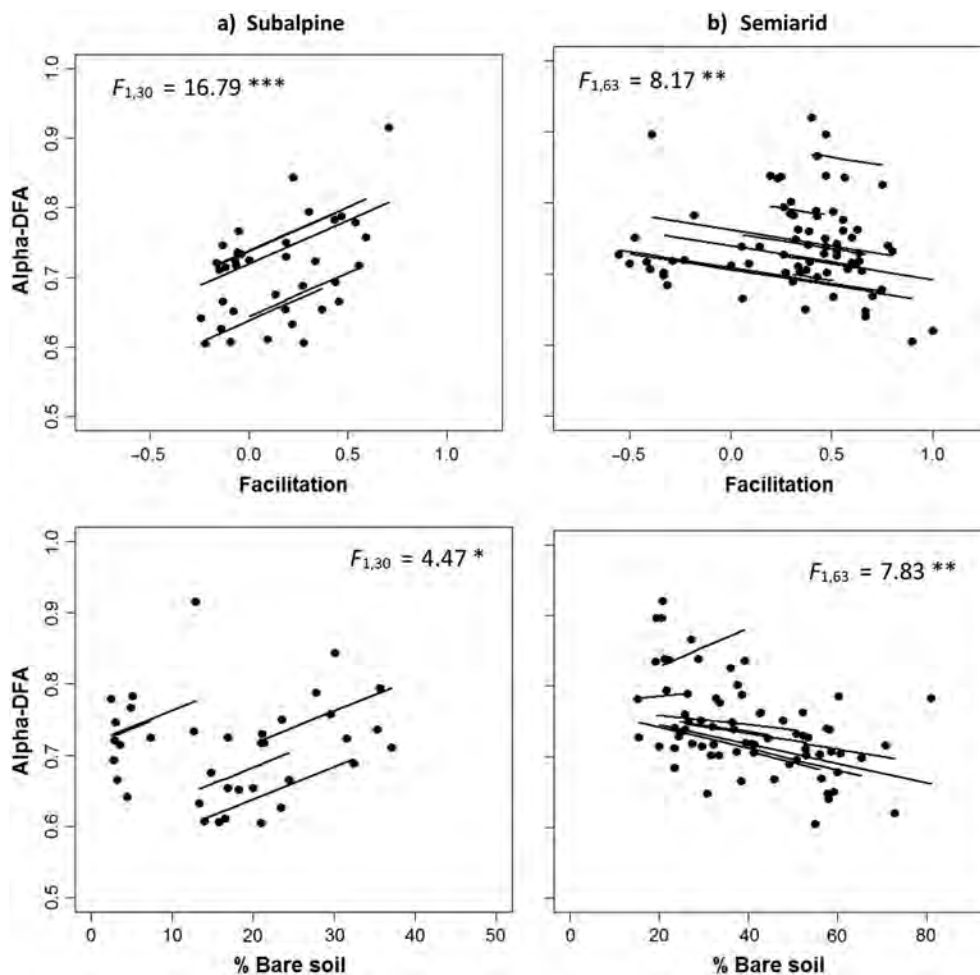


Fig. 4. Effects of facilitation, expressed as the ratio of positive to negative associations $(K^+ - K^-)/(K^+ + K^-)$, and bare soil cover on self-organized vegetation spatial patterns (alpha-detrended fluctuation analysis [DFA]), for subalpine habitats (a) and semiarid steppes (b) separately. The linear mixed model included location as a random factor. Five locations in subalpine habitats and nine locations in semiarid steppes were included in the analyses. • $P < 0.1$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

($F_{1,30} = 0.01$, n.s.), number of NAs ($F_{1,30} = 0.23$, n.s.), or the aggregated spatial patterns ($F_{1,30} = 0.32$, n.s.). The Shannon diversity index decreased significantly in south-facing slopes ($F_{1,30} = 14.32$, $P < 0.001$).

DISCUSSION

Aridity conditions in Spain ranging from those in subalpine mountain habitats to those in semiarid steppes were highly correlated with plant–plant positive and negative associations, and also highly correlated with the importance of plant–plant spatial associations. In particular, aridity was negatively correlated with the density of positive and negative associations and the number of links per species, and positively correlated with the proportion of NAs. Aridity was not correlated with vegetation spatial patterns as spatial patterns are the result of self-organizing processes that develop over long periods of time, and it may be expected that vegetation spatial patterns will not change with aridity in well-preserved ecosystems once they are established. The relative contributions of aridity and bare soil to plant–plant facilitation and vegetation aggregation differed in the subalpine and semiarid habitats. In subalpine habitats, aridity promoted the disruption of aggregated spatial patterns, whereas in semiarid habitats, an increase in the proportion of bare soil had a greater impact on the randomization of spatial patterns. When bare soil cover increases above critical threshold, the hydrological inter-patch connectivity triggers erosion process producing a drastic change in spatial arrangement of vegetation pattern (Moreno-de las Heras et al. 2012, Okin et al. 2015).

Vegetation patterns are a product of self-organizing processes (Rietkerk and van de Koppel 2008), with plant–plant interactions being an important driver because facilitative interactions between neighboring plants can lead to patch nucleation and coalescence (Yarranton and Morrison 1974, Kéfi et al. 2007, Cutler et al. 2008). Facilitative interactions drive spatial patterns because positive effects are strongest close to the facilitators, which leads to spatial clustering and patchiness (Haase 2001). In our study, a positive relationship was found between facilitation and vegetation patterns, supporting the hypothesis that facilitation is one of the major mechanisms

of pattern formation. This relationship in turn favors high diversity in the plant community, as we observed in this study and as has been reported elsewhere (Kikvidze et al. 2005, Alados et al. 2006, Pueyo et al. 2013).

Other studies have emphasized the importance of other processes (including runoff and erosion, which are responsible for the redistribution of nutrients; see Okin et al. [2015] for review) and suggested they are of greater importance than plant–plant facilitation mechanisms (Turnbull et al. 2010*a, b*). It has been reported that the range over which soil properties are correlated exceeds the range over which vegetation is auto-correlated (Turnbull et al. 2010*b*), which indicates that processes other than plant–plant interactions determine structural vegetation and soil patterns (Saco and Moreno-de las Heras 2013). Bare soil cover is commonly used as a surrogate for environmental stress and represents an integrated response of vegetation to the entire set of stress conditions (Maestre et al. 2009, López et al. 2016). Bare soil area was negatively related to OM content (Pearson's correlation coefficient = -0.69 , $P < 0.01$). It has been suggested that bare soil cover is a better predictor of ecosystem degradation than vegetation spatial patterns (Maestre and Escudero 2009). However, degradation and increased aridity are not the same, and it is expected that self-organized vegetation spatial patterns will not change with increasing aridity in well-preserved semiarid ecosystems, once they are established (long-term process) and a community adapted to the arid conditions has been selected; bare soil cover (short-term process) is more likely to break the spatial structured patterns triggering drastic changes once critical threshold is overtake (Moreno-de las Heras et al. 2012, Okin et al. 2015).

Indeed, the relative influence of plant facilitation and resource distribution (bare soil cover) on vegetation spatial patterns is mediated by environmental conditions (Callaway 2007, Brooker et al. 2008, Butterfield et al. 2010, Michalet et al. 2014). Understanding the mechanisms of pattern formation along aridity gradients will improve detection of the major processes that result in emergent patterns. To assess the importance of plant–plant facilitation, runoff, and erosion on pattern formation, we analyzed changes in vegetation spatial patterns and plant

facilitation in response to changes in aridity and bare soil cover in contrasting subalpine and semiarid habitats.

In subalpine habitats, increasing aridity promoted the disruption of aggregated spatial patterns, whereas in semiarid habitats, an increase in bare soil area was more important than changing aridity in the decline of vegetation aggregation, with vegetation becoming more randomly distributed as the bare soil area increased. As bare soil overcome a critical threshold, the increases in hydrological connectivity will increase runoff and erosion (Moreno-de las Heras et al. 2012, Okin et al. 2015), and the free-scale vegetation spatial patterns are disrupted (Moreno-de las Heras et al. 2011). Other studies have shown that under severe abiotic stress (Maestre and Cortina 2004) or high herbivore pressure (Alados et al. 2003, Smit et al. 2007), the advantage of clustering disappears, and spatial vegetation patterns and species distributions become more random (Alados et al. 2004).

Facilitation contributed markedly to aggregated spatial patterns in subalpine habitats, but was not important in semiarid habitats. Several studies in alpine environments have reported that facilitation contributed markedly to pattern formation (Callaway et al. 2002, Cavieres et al. 2002, Michalet et al. 2014), including in environments where cushion plants facilitate nutrient availability (Yang et al. 2010, Anthelme et al. 2012). For example, in the Sierra Nevada National Park, the cushion chamaephyte *Arenaria tetraquetra* is a facilitator under conditions of high stress at the highest elevations, but not at low elevations (Schöb et al. 2013).

Overall, positive plant–plant interactions play an important role under harsh environmental conditions (e.g., drylands and alpine environments; Callaway 2007, Brooker et al. 2008, Soliveres and Maestre 2014), as suggested by the SGH (Bertness and Callaway 1994). Positive plant–plant interactions ameliorate the environment for plant growth by improving micro-environmental conditions (Callaway 2007, Holmgren et al. 2012), increasing resource availability (Pugnaire et al. 1996, Armas et al. 2008), and providing protection from predation (Milchunas and Noy-Meir 2002, Smit et al. 2005). In harsh environments, facilitation reduces the extremes of conditions to which the facilitated plants are exposed

(Bruno et al. 2003). This increases the realized niche of species (Hacker and Gaines 1997) and results in increased ecosystem performance, diversity, and richness (Cavieres and Badano 2009). However, when the environmental conditions become extremely severe, the positive effects of facilitation are diminished, and diversity can be reduced (Michalet et al. 2006). The importance of facilitation varies depending on the species-specific response, ontogeny, and environmental stress (Butterfield et al. 2010). A review of 208 sites in alpine (71) and dryland (137) areas varying in environmental conditions (Soliveres and Maestre 2014) indicated that positive interactions were more important in alpine (37%) than in dryland (29%) environments and that facilitation was weakly negatively correlated with aridity. As expected, in our study, the importance of facilitation for vegetation patterns declined in semiarid habitats, whereas bare soil cover led to a change in vegetation from aggregated spatial patterns to a more random spatial distribution. Nevertheless, facilitation is still of critical importance on semiarid landscapes. However, in subalpine habitats, an increase in bare soil area has been reported to favor aggregated spatial patterns (Alados et al. 2007), as it increases the colonization of grasslands by cushion plants (Komac et al. 2011a, b). In addition, an increase in bare soil areas creates gaps in the thick layer of subalpine perennial grasses and provides an opportunity for colonization by species dispersed by seed (Pakeman and Field 2005).

Comparisons between north- and south-facing slopes in a Mediterranean ecosystem, where significant periods of desiccation can occur during summer, facilitated assessment of the likely effect of climate warming along the studied aridity gradient, based on the assumption of increasing temperatures and reduced moisture conditions under climate change (IPCC 2007). South-facing slopes have higher insolation and desiccation than north-facing slopes (Isard 1986), which results in a reduced water balance on these slopes under similar conditions of precipitation and runoff. In particular, droughts in Mediterranean regions cause soil desiccation and reduce availability of nutrient for plants (Mooney et al. 1965, Reverter et al. 2010); this is exacerbated on south-facing slopes, where temperatures are highest. The soil moisture content was significantly higher on

north-facing than on south-facing slopes. Thus, as productivity increases on north-facing slopes (Kikvidze et al. 2011), plant negative associations increase (Callaway et al. 2002, Michalet et al. 2014).

In this study, we observed that the high temperatures and insolation on south-facing slopes reduced water availability for vegetation, which reduced the plant canopy. The average vegetation patch size was smaller on south-facing than on north-facing slopes (Appendix S3), such that the relative importance of facilitation decreased as stress increased, as the effectiveness of micro-environmental amelioration decreased. Our finding that under semiarid conditions there was greater stress on south-facing than on north-facing slopes supports the SGH, with increased facilitation occurring under the higher stress conditions, although the increased facilitation did not ensure the persistence of aggregated spatial patterns. Thus, consistent with the modified SGH (Holmgren and Scheffer 2010), we observed that the importance of positive plant–plant interactions on vegetation aggregation declined in semiarid habitats, leading to the vegetation organization pattern changing from aggregation to random spatial distribution and increased bare soil area; however, this did not occur in subalpine habitats.

CONCLUSION

We conclude that the use of aggregated spatial patterns as early warning signals must separate long-term processes to which vegetation adapts, from short-term process, given that once community is adapted to the arid conditions, vegetation spatial patterns remain. However, vegetation does not have enough time to adapt to bare soil enhancement coming from hydrological connectivity and consequently runoff and erosion, resulting in the destruction of vegetation spatial patterns and the increase in randomness. As aridity increases, the relative contribution of facilitation to pattern formation declines, whereas the contribution of bare soil that results in the disruption of aggregated patterns increases.

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