

# Stress-gradient hypothesis and plant distribution along ecotonal gradients

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**Abstract** The stress-gradient hypothesis (SGH) predicts that, although facilitation and competition occur together, facilitative interactions will be more prevalent with increasing abiotic stress. In water-limited ecosystems, support for the SGH has been controversial. Because of the relevance of ecotones to local and regional diversity and the susceptibility to disturbance of the species inhabiting them, these systems represent interesting opportunities to test the SGH. Our aim was to determine whether the spatial pattern of species distribution along an arid ecotone is consistent with the SGH. Vegetation surveys were performed along topographical gradients found between several palaeochannels and bars where two communities dominated by *Chuquiraga avellanedae* and *Larrea divaricata* coexist. Daily precipitation and soil water potential at three depths were measured at a palaeochannel and a bar. Univariate and bivariate distribution patterns were investigated by second-order spatial analysis based on Ripley's *K* function in order to evaluate the possible existence of positive or negative interactions among plants. Soil water potential was higher at palaeochannels, indicating that a gradient of water stress exists between the palaeochannels and the bars. Whereas palaeochannels showed regularity among *C. avellanedae* individuals, bars showed aggregation among *L. divaricata* individuals and among both species. These results suggest a change in dominant interactions along the gradient from facilitative at the more xeric bars to more competitive at the relatively wetter palaeochannels in accordance with the stress-gradient hypothesis.

**Key words:** arid regions, environmental heterogeneity, geomorphology, species spatial pattern.

## INTRODUCTION

In recent decades, there has been controversy about the role of competition and facilitation in the structure of plant communities and their distribution in the landscape. The stress-gradient hypothesis (SGH) has been one of the approaches with which the study of interactions between plants and their relationship with the environment has been addressed. This hypothesis predicts that, although positive (i.e. facilitation) and negative interactions (i.e. competition) occur together, positive interactions will be more prevalent with increasing abiotic stress (Bertness & Callaway 1994). Support for the SGH has depended on the scale of analysis, the range of environmental gradient covered, the number of points evaluated within that gradient, the characteristics of the species involved and the response variable (Maestre *et al.* 2009; Malkinson & Tielbörger 2010; Zhang & Zhao 2015).

Although the SGH has been generally supported for water-limited ecosystems (Shumway 2000; Pugnaire & Luque 2001; Tewksbury & Lloyd 2001; Armas *et al.* 2011; Amat *et al.* 2015; Tirado *et al.*

2015), there have been some exceptions (Bertness & Ewanchuk 2002; López *et al.* 2013). Extremely high temperatures, overgrazing, as well as the low nutrient concentration (Amat *et al.* 2015) and, above all, water scarcity (Noy-Meir 1973; Fernández 2007) make arid environments sites of high stress. Since arid systems are threatened by desertification (Millennium Ecosystem Assessment 2005), a deep understanding of their functioning is of particular importance for a better implementation of environmental mitigation and restoration practices.

Arid ecotones represent special cases of arid environments because of the relative perception of the environment by species that are living close to their tolerance limits (Churkina & Svirzhev 1995). Thus, ecotones emerge as interesting opportunities to test the SGH. Such studies will also provide valuable information on ecological interactions with ecotones, which are important areas of local and regional diversity (Jordana *et al.* 2000).

Given that water is the most limiting resource in deserts (Noy-Meir 1973; Fernández 2007), any influence on its availability for plants will affect the vegetation that inhabits them. When considering ecotones, the geomorphology effects on vegetation are especially relevant (Gonçalves & Souza 2014) as

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species are constrained by environmental factors occupying small fragmented areas topoedaphically similar to their biome core (Neilson 1993; Buxbaum & Vanderbilt 2007; Reed *et al.* 2009). Low relief positions are moister and cooler than high relief positions, differences often accompanied by changes in physical and chemical soil attributes (Wysocki *et al.* 2011). The coexistence of different communities associated to topoedaphically diverse areas makes ecotones an appropriate place to evaluate the effects of variations in the environment on species distribution and their interrelationship.

Two different approaches are commonly used to test the SGH. The first approach encompasses the manipulation of plant density to obtain direct evidence of competition/facilitation (e.g. Liancourt *et al.* 2013; Zhang & Zhao 2015). The second method is based on the study of the spatial distribution of individuals (e.g. Malkinson & Jeltsch 2007; Le Roux & McGeoch 2008; Ziffer-Berger *et al.* 2014). Both methods have advantages and disadvantages. Most ecologists agree that the evidence obtained from plant density manipulation is more direct and stronger than that obtained from plants' spatial pattern analysis. However, this method is field-intensive and the results of this kind of manipulation should become evident after several years, especially when long-lived perennial species are involved. In contrast, the study of the spatial distribution of individuals is less time consuming (i.e. all data can be collected at the same moment) and can integrate the dominant ecological processes that have prevailed throughout the life of individuals (Schöb *et al.* 2012). Nevertheless, aggregated or segregated spatial patterns could be due to other causes instead of facilitation and competition. The second approach was adopted in this research paper. Different features of plant spatial patterns can be recognized. First-order patterns reflect changes in plant density across a plot, while second-order patterns disclose the point patterns nested within the density variation (Perry *et al.* 2006). Commonly, first-order patterns are associated with environmental or resource gradients (Dickinson & Norton 2011), while second-order patterns could be a consequence of dispersal limitation, clonal growth and/or interactions among individuals (i.e. competition, facilitation), among other causes (Murphy & McCarthy 2012). Regular patterns have been considered as the result of strong competition for limited resources whereas clustered patterns are usually interpreted as evidence of facilitation. Both, first- and second-order patterns are related since changes in plant density along environmental gradients are commonly associated to changes in the nature and strength of plant interactions (Pugnaire & Luque 2001).

The purpose of this study was to determine whether the spatial pattern of species distribution along an arid ecotone is consistent with the SGH. We hypothesized that, according to the stress-gradient hypothesis, competition among plants would prevail at low relief positions, where water availability would be higher. Thus, facilitation among plants would prevail at high relief positions, where water stress would be more pronounced. Specifically, we expected segregated/regular distributions at palaeochannels but aggregated/clustered distributions at bars.

## METHODS

### Study area

Field work was carried out within the ecotonal area between the Monte and Patagonia Phytogeographic Regions in the northeast of the Chubut Province, in Argentina (W 65°05', S 42°55'). Climate is arid, temperate and windy. Mean annual temperature is 13.5°C and mean annual precipitation is 233.8 mm, with high interannual variation (series 1984–2013) (Laboratory of Climatology, CENPAT-CONICET, Puerto Madryn). Plant cover is distributed in the form of patches associated to soil mounds (Rostagno & del Valle 1988). Plant patches contain one or more shrubs and are dispersed in a matrix of bare soil (Bisigato & Bertiller 1997). Most patches are dominated by *Larrea divaricata* or *Chuquiraga avellanedae* but also contain several grasses, forbs and other less frequent shrub species. Landscape is defined by anastomosing systems of palaeochannels and bars that belong to an ancient alluvial fan of Upper Pleistocene age (Haller *et al.* 2005; González Díaz & Di Tommaso 2011) (Fig. 1). Two communities coexist in the area: the *L. divaricata* (Zygophyllaceae) community, typical of the Southern Monte (Bisigato & Bertiller 1997), and the *C. avellanedae* (Asteraceae) community, which is more characteristic of those areas related to the Patagonia Phytogeographic Region (Beeskow *et al.* 1995).

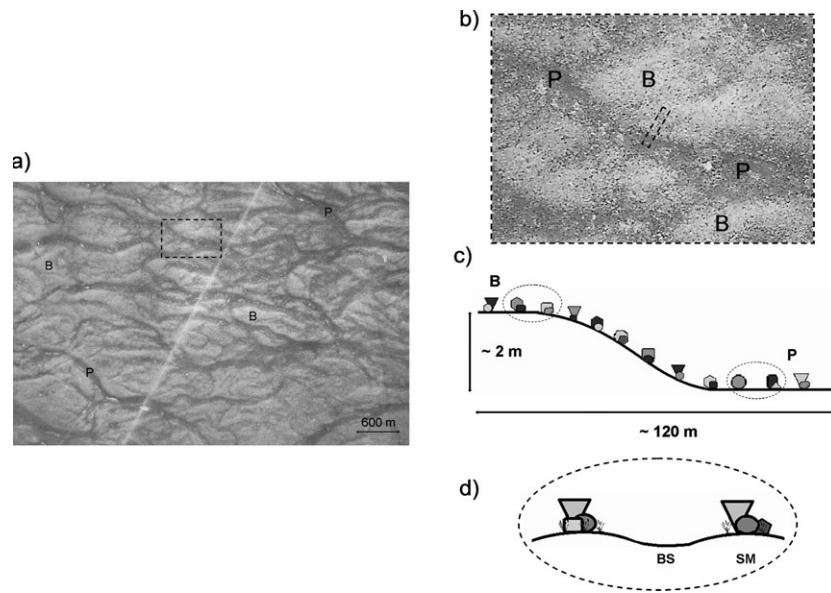
### Field sampling

#### *Precipitation and soil water potential*

Daily precipitation and soil water potential at 5, 20 and 50 cm depth were measured at a palaeochannel and a bar with two Davis Vantage Pro weather stations. These variables were measured from October 2012 to June 2017. Daily precipitation records were averaged to show a unique precipitation series since both weather stations were 1.4 km apart and differences between them were negligible.

#### *Species spatial pattern*

To determine the relationship between topography (i.e. water stress) and the distribution of dominant species (i.e.



**Fig. 1.** (a) Aerial photograph of the study site showing the anastomosing systems of palaeochannels (P) and bars (B), (b) example of the position of plots (rectangle), (c) schematic diagram of terrain unevenness between landforms (bar-palaeochannel), (d) microrelief representation showing both microsites (BS, bare soil areas; SM, soil mounds). The rectangle in (a) indicates the area shown in (b).

*L. divaricata* and *C. avellanadae*) in the landscape, we selected four locations where both communities coexist. In each location, a 10-m width plot was set. Plot length varied among locations; it was defined by the distance between the centre of a palaeochannel and the top of the closest bar, ranging between 100 and 160 m (Fig. 1b,c). The coordinates (i.e.  $x$ ,  $y$ ) and the soil level ( $z$ ) at each individual centre of these species were recorded in each plot with a Pentax V-227 total station. This theodolite electronically measures the distance, as well as the vertical and horizontal angles, between the total station and any points to be surveyed. In our case, the distance between the total station and the surveyed points was always lower than 100 m, keeping a precision of  $\pm 3.6$  mm.

## Data analysis

### First-order patterns

In order to test if species distribution differed along the plots a Monte Carlo test based on random labelling was performed. Each plot was systematically gridded (grid cell size =  $0.5 \times 0.5$  m) and 99 density ratio values as  $\rho_s(x) = \lambda_{Ld}/\lambda_{Ca}$  (where  $\lambda_{Ld}$  represents *L. divaricata* density and  $\lambda_{Ca}$  the same value for *C. avellanadae*) were calculated for each cell and contrasted to the observed values. Contour lines for  $P = 0.025$  and  $P = 0.975$  were extracted and superimposed to  $P$ -value maps using ‘maptools’ package (Bivand & Lewin-Koh 2013), obtaining areas where density of *L. divaricata* was significantly higher or lower respect to *C. avellanadae*.

### Second-order patterns

Spatial distribution patterns were evaluated by Ripley’s K function, recommended for point pattern data (Dale 1999). This function is defined, so that  $\lambda K(r)$  equals the expected number of points anticipated within a distance  $r$  in a complete random spatial pattern (CSR) with  $\lambda$  density. Positive deviations between the empirical and theoretical K curves may suggest clustering or spatial aggregation while negative deviations from expected under CSR suggest spatial regularity or segregated patterns. Univariate (nearest-neighbour distances among individuals of the same species) and bivariate (nearest-neighbour distances of an individual of one species around individuals of the other species) distribution of dominant species (i.e. *L. divaricata* and *C. avellanadae*) were evaluated with ‘spatstat’ package (Baddeley & Turner 2005). For this analysis, plots were split in 20-m long subplots. K values were evaluated at radius until 2.5 m in order to avoid border effects. Empirical K functions were compared with 95% envelopes (null models) generated from 39 simulations in order to test significant deviations from CSR. In the case of bivariate patterns, we made use of the null model of independence which assumes that the two patterns were produced by two independent processes (Wiegand & Moloney 2004).

## RESULTS

### Precipitation and soil water potential

Annual precipitation varied between 133.3 and 299.2 mm (2013 and 2015, respectively). There were

only six events of daily precipitation >20 mm. The temporal dynamics of soil water potential strongly differed between landforms (Fig. 2). In general, soil water potential in the palaeochannel showed more frequent potential increases in all layers and remained moist longer than in the bar. In particular, deep soil at the palaeochannel (50 cm depth) remained moist during the whole period, whereas infiltrating water hardly ever reached this soil layer at the bar. These results confirm the existence of a gradient of water availability between bars and palaeochannels.

### First-order patterns

All plots presented several small patches of high *L. divaricata* density with respect to *C. avellanadae* on bars (left side of the plots on Fig. 3), while few big patches of low *L. divaricata* density with respect to *C. avellanadae* were located on palaeochannels (right side of the plots on Fig. 3). In fact, *L. divaricata* was mostly absent from palaeochannels (Fig. 3).

### Second-order patterns

Concerning univariate patterns, *C. avellanadae* individuals were regularly distributed at palaeochannels, mostly at scales between 0.5 and 2 m. However, this species was randomly distributed at bars. Only at plot II *C. avellanadae* maintained a regular pattern at bars. Conversely, *L. divaricata* showed a clustered pattern at bars at scales between 0.5 and 2.5 m (Fig. 4).

A positive association between both species (i.e. aggregation) was observed at bars at different scales and a negative one (i.e. segregation) at high scales at plot centres (i.e. between 40 and 80 m). Palaeochannels showed no deviation from CSR (Fig. 5).

## DISCUSSION

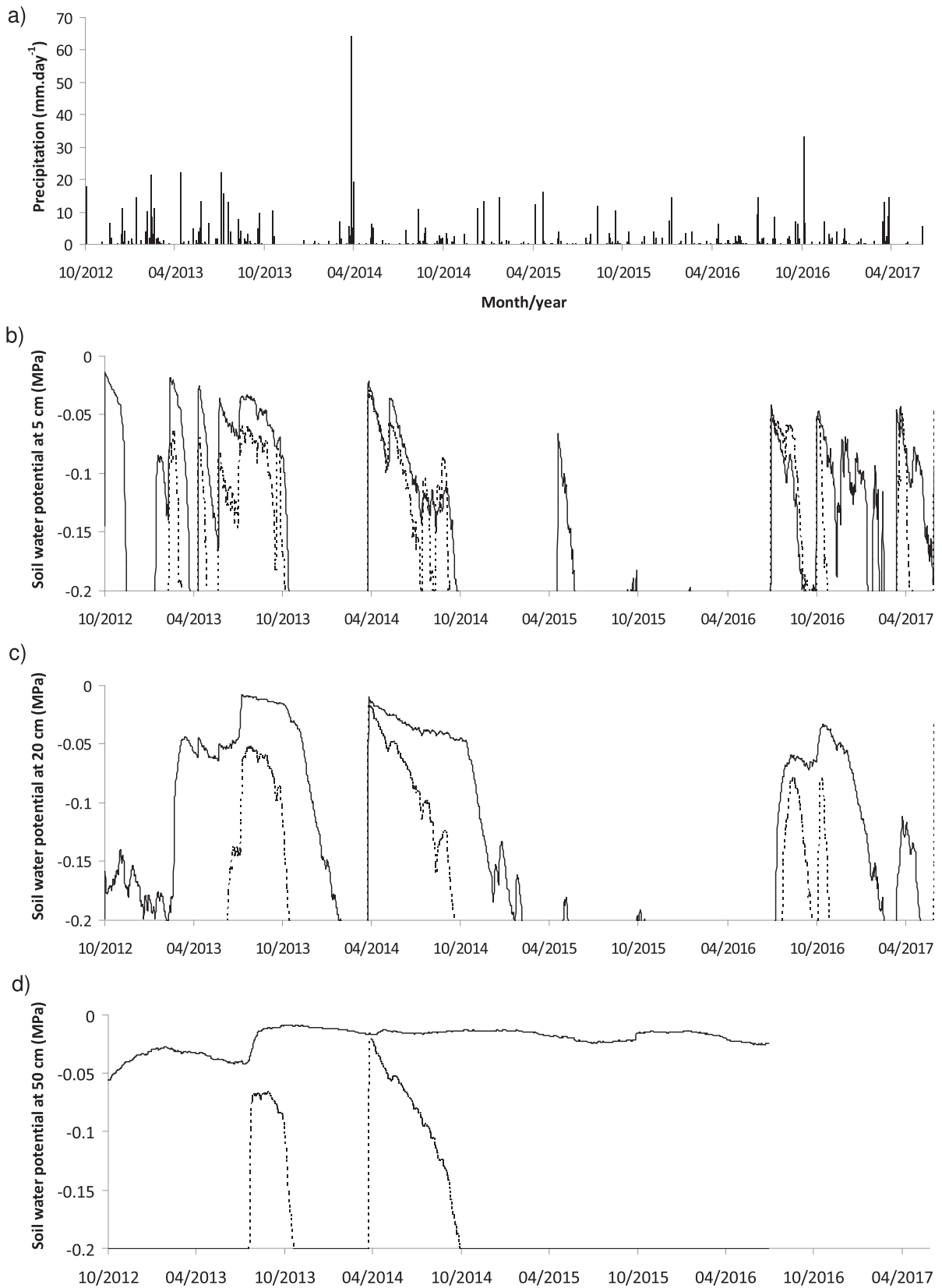
Our results are consistent with spatial patterns predicted by the stress-gradient hypothesis such that aggregated patterns detected at drier bars (Figs 4 and 5) suggest facilitation between species and among individuals of *L. divaricata*, while segregated patterns at less xeric palaeochannels (Fig. 4) would be evidence of intraspecific competition among individuals of *C. avellanadae*. In addition, we found some evidence of interspecific segregation between species at plot centres (i.e. subplots 40–60 and 60–80) which could be reflecting rapid environmental change. We did not find evidence of interspecific segregation at palaeochannels. However, the low frequency of

*L. divaricata* at palaeochannels limits the inferences that can be drawn about interspecific interactions in that landform. Although *L. divaricata* could be excluded from this landform by environmental factors, we note that strong asymmetric competition can exclude weaker competitors (Yu & Wilson 2001).

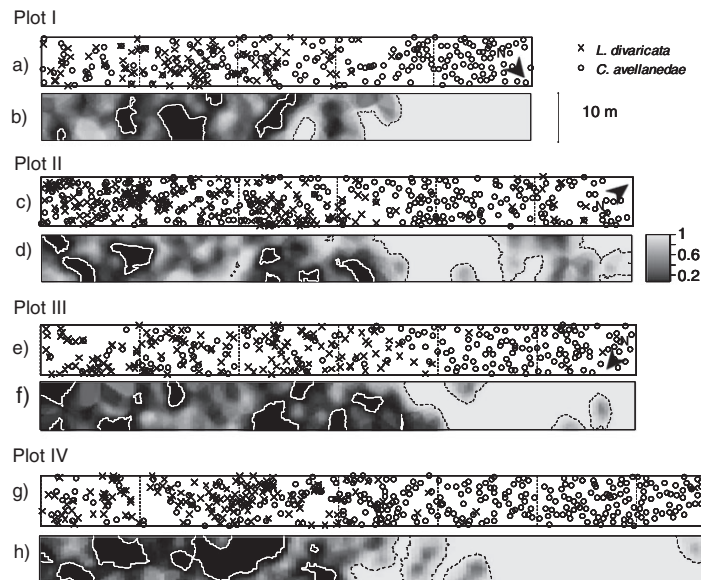
The lower availability of water in the bars compared to the palaeochannels is consistent with those expected due to a lower infiltration of rain water caused by both the high flow of water downslope, and as a consequence of the enhanced evaporative demand in more exposed areas (Moeslund *et al.* 2013). Differences in water availability along the bar/palaeochannel gradient can be related to species requirements. *Larrea* species characterize the Monte Desert of Argentina, which is warmer and generally drier than the extra-Andean Patagonia (Labraga & Villalba 2009). In this sense, at the study site *L. divaricata* is near the limit of its regional distribution, thus its competitive ability could be diminished, prevailing facilitative effects. Conversely, environmental conditions at palaeochannels better resemble the optimal niche of *C. avellanadae* (Correa 1988), such that this species is more competitive in that landform than in bars.

Thus, an improvement in soil water balance is a possible driver of positive interactions at bars. This mechanism is frequent in arid and semiarid ecosystems (Aguar & Sala 1999; Tirado *et al.* 2015) and involves decreased soil evaporation (Aguar & Sala 1994), reduced vapour pressure difference between air and leaves (Maestre *et al.* 2003), attenuated thermal stress, insolation (Malkinson & Tielbörger 2010) and runoff water (Amat *et al.* 2015), increased infiltration (Pugnaire *et al.* 2004; Cecchi *et al.* 2006) and reduced soil bulk density (Wood *et al.* 1987). However, these effects would be very different qualitatively in the two species studied because of the characteristics of their canopy. Whereas *L. divaricata* exhibits inverted cone-shaped crowns with open canopies, *C. avellanadae* shrubs are hemispherical with closed canopies. Other authors have reported canopy structure as determinant of the balance between competitive and facilitative effects (Zhang & Zhao 2015). In fact, a previous study has proven the existence of stem flow in *L. divaricata* and a concomitant increase in soil infiltration (Cecchi *et al.* 2006). Conversely, the closed canopy of *C. avellanadae* (Campanella & Bertiller 2008) could deprive plants growing beneath it from light and promote the segregated pattern observed in the palaeochannels. Away from the bar, where water stress is less pronounced and growth of established plants would be faster, segregation could also be caused by competition for nutrients.

Interactions between plants of both the same and different species may change along their life cycle



**Fig. 2.** Daily precipitation (a) and soil water potential at 5 (b), 20 (c) and 50 (d) cm. of depth at a bar (dashed line) and a palaeochannel (solid line).



**Fig. 3.** Positions of *Larrea divaricata* (x) and *Chuquiraga avellaneda* (O) individuals at each plot (a, c, e and g), and *P*-value surfaces from Monte Carlo test for species density ratio at each plot (b, d, f and h). Areas of high ( $P < 0.025$ ) and low ( $P > 0.975$ ) *L. divaricata* density with respect to *C. avellaneda* are delimited by solid white lines and dashed black lines, respectively. Vertical dashed lines in (a), (c), (e) and (g) indicate subplots. Bars are on the left side and palaeochannels on the right side.

(Haase *et al.* 1996; Bruno *et al.* 2003; Reisman-Berman 2007; Schöb *et al.* 2012). Consequently, current aggregated patterns at bars may not correspond with recent positive interactions between adults and instead reflect the patterns that result from differential germination caused by entrapment of seeds (among other resources) at mounds, which is so frequently seen at arid and semiarid environments (Guo *et al.* 1998). Competition for soil water could also change as the plants grow and change the depth and intensity at which they exploit the resource (Doussan *et al.* 2003). Although clonal growth could also produce aggregated patterns, none of the species studied exhibits such kind of asexual reproduction. Also, seeds are wind dispersed in both species, so dispersal limitation is unlikely. Moreover, even though grazing can influence the spatial distribution of plants in different ways (Adler *et al.* 2001), domestic and native herbivores do not browse on the studied species (Siffredi 2012; Bär Lamas *et al.* 2013). This rules out the existence of any direct effect of above-ground herbivory by vertebrate herbivores on plant patterns. However, it should be mentioned here that indirect effects cannot be discarded. For example, Bisigato and Lopez Laphitz (2009) have found that soil water increases under grazing pressure, which could reduce the water stress to which these shrubs are subjected and modify the interrelationship between the species.

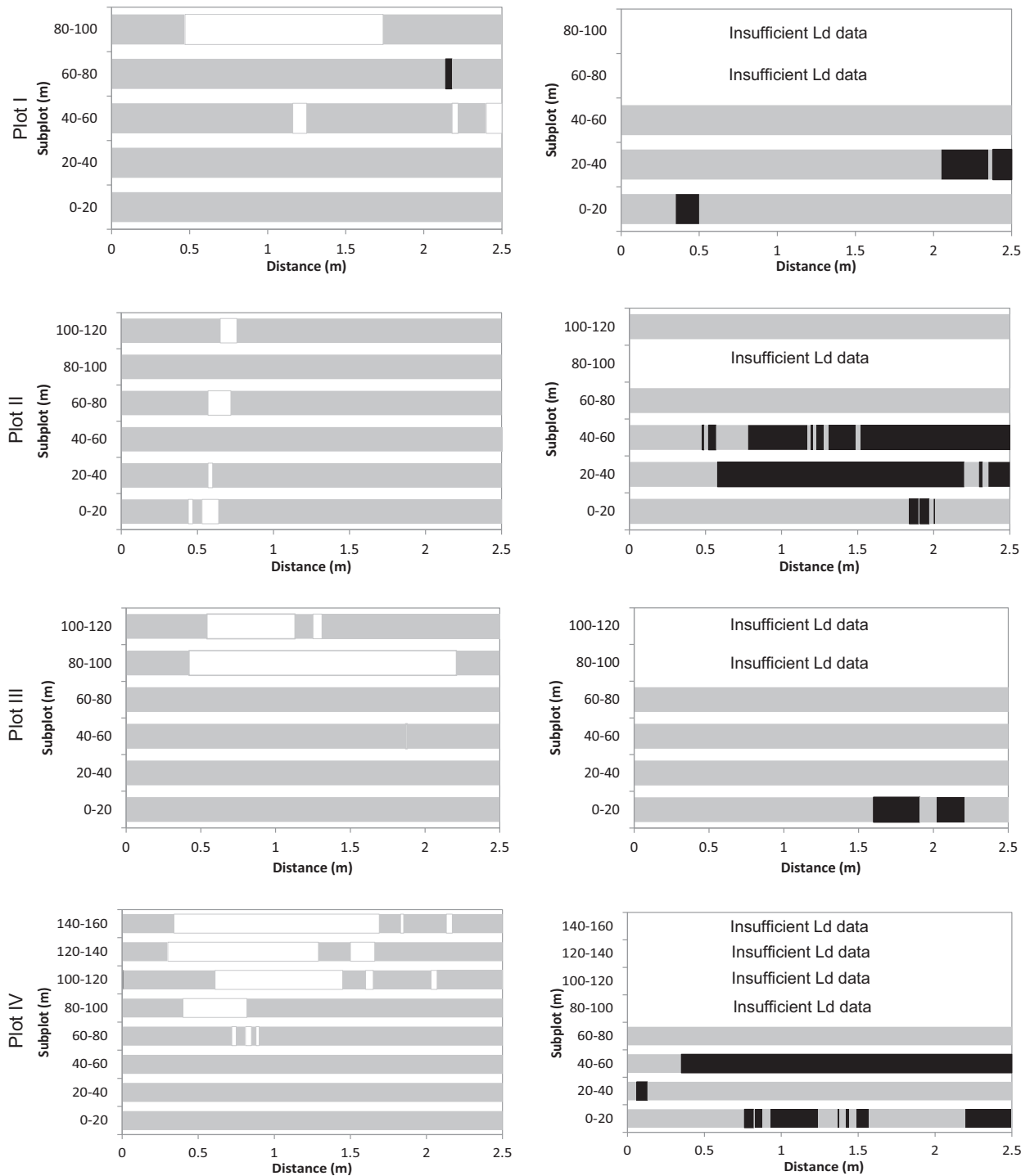
Spatial heterogeneity could also produce aggregated patterns. This heterogeneity coexists with the interactions between species and the resulting pattern

will depend on whether or not they are stronger than the underlying heterogeneity. In arid environments, environmental heterogeneity follows the pattern of patches in which the soil is more fertile, has lower bulk density and presents different microbiota than interpatches (Garner & Steinberger 1989). In fact, all these variables are strongly affected after shrubs colonize bare soil areas (Schlesinger & Pilmanis 1998).

Our results provide preliminary support for the model proposed by the SGH. More direct methods of studying competitive and facilitative interactions include the removal/addition of individuals. These kinds of designs are useful to demonstrate that the species of interests actually compete (Morin 1999). More complex experiments allow the discrimination of below/above-ground competition (Aguar & Sala 1994), or the identification of the mechanisms involved in facilitative interactions (Franco-Pizaña *et al.* 1996; Smit *et al.* 2006; Busso *et al.* 2010; Catorci *et al.* 2014; Leder *et al.* 2017).

Our results serve as a basis to understand the role of facilitative and competitive interactions in the functioning of communities and the possible responses to climate change and desertification. This information about ecotones in particular is of great value because of the susceptibility of these habitats to environmental variations (King *et al.* 2013; Gebrekirstos *et al.* 2014).

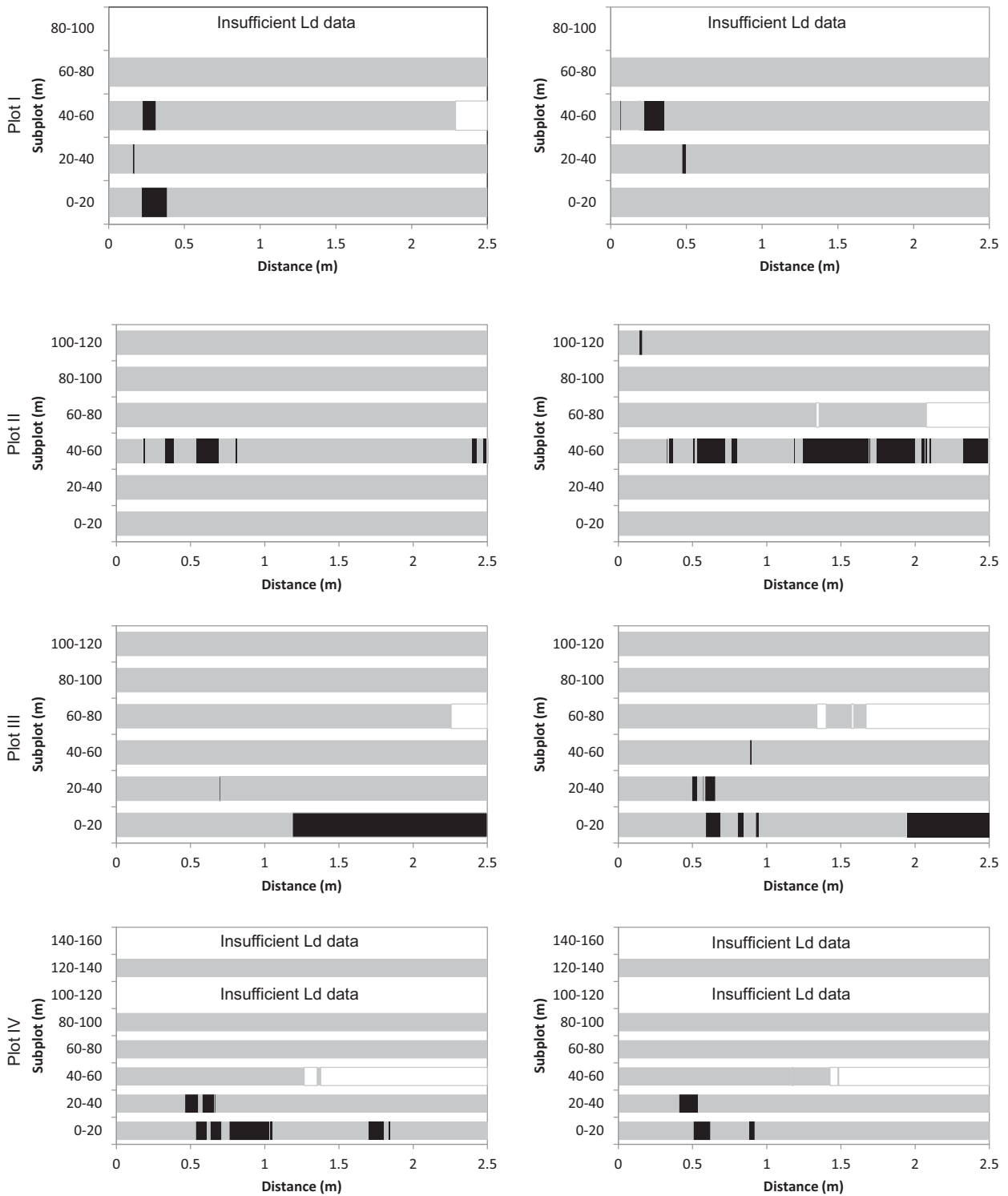
In conclusion, our results support the SGH at this arid ecotone where a gradient of water availability between landforms was found. Although the



**Fig. 4.** Summary of the spatial patterns detected by univariate Ripley's K for each subplot from each plot. Left and right columns indicate *Chuquiraga avellanadae* and *Larrea divaricata* distribution patterns, respectively. At each panel, the bar is at the bottom and the palaeochannel is on the top. Grey areas indicate that the distribution did not differ from CSR for that distance interval; white, that it is regular; and, black, that it is clustered. CSR was obtained by 39 computer-generated random realizations of a Poisson process within the subplot.

landscape is plain and the differences in height among landforms rarely exceed 2 m, bars are drier than palaeochannels. In accordance to the SGH, the

analysis of plant spatial patterns indicates plant competition at wetter palaeochannels, whereas interspecific facilitation appears to prevail at dry bars.



**Fig. 5.** Summary of the spatial patterns detected by bivariate Ripley's K for each subplot from each plot. Left column indicates *Larrea divaricata* relative to *Chuquiraga avellanae* and right column indicates *C. avellanae* relative to *L. divaricata*. At each panel, the bar is at the bottom and the palaeochannel is on the top. Grey areas indicate that species distribution did not differ from CSR for that distance interval; white areas indicate segregated patterns; and, black areas indicate aggregated patterns. CSR was obtained by 39 computer-generated random realizations using the null model of independence which assumes that the two patterns were produced by two independent processes.



## Species nomenclature

Flora Argentina Plantas vasculares de la República Argentina. (<http://www.floraargentina.edu.ar/>, accessed on 21 March 2018).

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