**ORIGINAL PAPER**

# Soil arthropods indicate the range of plant facilitation on the soil of Mediterranean drylands

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**Abstract**

Drylands are ecosystems, where lack of rains imposes harsh conditions for the survival of organisms. These ecosystems are also susceptible to degradation and desertification. Their conservation depends on the understanding of the ecological functioning of vegetation and soil. In drylands, the vegetation is spatially structured as a mosaic of patches (vegetation) and interpatches (bare soil). This structure is a consequence of plant-plant interactions (facilitation and competition). Empirical data and modeling approaches reinforce the role of ecological facilitation for the maintenance of all organisms in drylands. However, the true range of facilitation is still poorly known. Here, we explored data of meso- and microarthropods living in soil, as bioindicators, to infer the range of facilitation provided by plants to soil. As dependent variables, we regard data of abundances and species richness collected in random patches (independent samples) and bare soil places. Data from patch size and distances between bare soil and patches were arranged in a single chute. Thus, one may consider a one-dimensional coordinate system, where zero is the border; negative coordinates are distances between bare soil and the border, while positive coordinates represent patch sizes. Discrete portions of this system are taken to calculate averages and variances of abundance and species richness. With these statistics, we investigate how soil communities vary across the patch border. Techniques of data transformation and signal analysis allowed us to reduce the data noise, reveal a continuous mean behavior, and fit a logistic function. Our findings indicate that soil communities change suddenly from simple patterns to numerous and diverse communities in bare soil regions. This abrupt change of fauna quantities, around 0.35 and 0.5 m outside the patch border, means that the facilitation of vegetation on soil goes beyond the patch border. However, the abundance and richness of soil communities in bare soil are small in comparison to overall quantities of soil arthropods. Consequently, variations in quantities of arthropods on bare soil do not necessarily reflect the main role of these soil arthropods for soil functions, which mainly occurs under the patches. Also, we found a minimum patch size (radius $\approx$ 0.5 m) able to maintain high diverse communities in soil. Accordingly, our results reveal information that can be interpreted in terms of soil amelioration, and, therefore, it indicates the range of plant facilitation, and the minimum patch size able to produce soil amelioration. These findings provide objective values that can be employed to update the general understanding of the ecological dynamics of drylands, as well as to better plan restoration and conservation actions.

**Keywords** Ground arthropods · Spatial ecology · Logistic function · Biological diversity · Ecological functioning · Desertification · Conservation

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## Introduction

Drylands (e.g., the arid and semiarid ecosystems) cover approximately 40% of the planet, and are characterized by the low precipitation, long dry periods, high luminosity, and relatively warm temperatures (Whitford 2002). These natural features bring consequences for the ecological regime, such as poor soil moisture, low rates of nutrient cycling, and low primary production, which may bring consequences for their capacity of regeneration (Delgado-Baquerizo et al. 2016; Maestre et al. 2016; Bestelmeyer et al. 2013). The

severe environmental conditions impose ecological constraints to the living organisms of drylands. Their survival are mainly conditioned (a) to their physiological adaptations and also (b) to the ecological interactions with further organisms (Stachowicz 2001; Laliberté et al. 2014; Delgado-Baquerizo et al. 2019; Berdugo et al. 2019a, b; Baruah et al. 2020). Although the items (a) and (b) are not completely independent components, our focus relies on the role of ecological interactions. The Stress Gradient Hypothesis (SGH) predicts that positive biological interactions like ecological facilitation are more common in harsh environments (Bertness and Callaway 1994; Maestre et al. 2009; McCluney et al. 2012). Facilitation relies on positive non-trophic interactions between different organisms, where the ecological activity of one brings benefits for the fitness of another (Bruno et al. 2003). Although the mechanisms and drivers may greatly vary, the most common for harsh environments embrace resource availability, niches, shelters, and amelioration of abiotic conditions (Cortina and Maestre 2006; Brooker et al. 2008; Pugnaire et al. 2011; Michalet and Pugnaire 2016). The current literature about drylands attributes great importance to facilitation as driver of vegetation spatial patterns, which is often discussed in terms of the general functioning and collapse of these systems (Kéfi et al. 2007; Maestre et al. 2016).

In drylands, the vegetation is not continuous. Instead it is often arranged in a mosaic structure (patches, for short), where plants occur as well-defined vegetation patches surrounded by bare soil regions, named as interpatches (Gandhi et al. 2019). The spatial organization of patches and interpatches arises from the interplay between plant-plant facilitation and competition in the context of water limitation of drylands (Escudero et al. 2004; Kéfi et al. 2007). For plants, one of the most usual indicators of facilitation in harsh environments concerns the spatial aggregation of individuals (Fuentes et al. 1984; Stachowicz 2001), which has been employed to evaluate facilitation in worldwide drylands (Xu et al. 2015). This indicator relies on the proper concept of facilitation: the presence of an organism (facilitator), which (a) is adapted to more stressful conditions, (b) attenuates the local conditions, and (c) enables that organisms (facilitated) grow in rates significantly higher than they would do in the absence of the facilitator (Brooker et al. 2008). This process results in a biased spatial distribution of organisms and also species, which can be assessed and measured. It is important to address this topic, because it may improve the understanding of the ecological dynamics of drylands, and the formulation of efficient strategies of conservation and restoration (Brooker et al. 2008; Synodinos et al. 2015; Uselman et al. 2018).

Accordingly, specific consortia between pioneer and secondary species may be regarded in proper timing and spacing sequence. These factors can foster the ecological

dynamics necessary for restoring these places. Bearing this in mind, one expects that the fine grain understanding about facilitation may improve our comprehension about "the way organisms mutually contribute to the functioning of ecological processes in dryland" (Synodinos et al. 2015). This rationale surpasses the plant-plant interactions, because plants also affect further organisms living in these places (Pugnaire et al. 2011; McCluney et al. 2012). Although the current scientific literature testifies the role of plants as a broad facilitator, an important question arises: How far can facilitation effects reach? Indeed, one expects that facilitation results in an umbrella radius, which shall define the chances of seedlings and further organisms to survive (Escudero et al. 2004; Pugnaire et al. 2011; Trautz et al. 2017). While answering this question is not a trivial task, a first guess can be revealed by the influence of plants on the upper layer of soil (Steven et al. 2017). The presence of plants can locally improve the water absorption and organic content in soil layers (Bochet et al. 1999a; Escudero et al. 2004; Pugnaire et al. 2011, Mayor et al. 2013, 2019), meaning that the soil moisture could be used to reveal the facilitation range. However, the assessment of long term effects of plants on the soil by direct measures of soil moisture can produce contrasting results (Michalet and Pugnaire 2016). In fact, drylands show scarce rains and high evaporation rates, meaning that soil moisture of the upper layers tend to persist only for short periods (Steven et al. 2017). The organic carbon content in the soil is a practical and cheap tool often employed to indicate the positive effects of plants on their neighborhood (Bochet et al. 1999b), but it cannot directly testify the functioning of soil processes. Aware of this fact, some light could be shed on the problem by alternative indicators, like the soil organisms. Soil organisms like arthropods can form highly diverse communities and survive for long periods of dryness, and yet are still sensitive to permanent changes in the environment (McGeoch 1998; Tiede et al. 2017; Meloni 2012). Particularly, the ecological patterns of meso- and microarthropods of soil provide great contribution to the understanding of more general processes of soil, such as water and air infiltration, vertical movement of sediments, microorganism dispersion, and facilitation, among others (Coleman et al. 2018). Many of these processes contribute directly or indirectly with nutrient cycling and contribute for the maintenance of biological communities. For these reasons, soil arthropods are considered good indicators of soil health (Parisi et al. 2005; Menta et al. 2018).

In turn, we conjecture that soil arthropods could also provide rich information about the spatial range of soil amelioration produced by plants. This hypothesis finds support in previous findings that link soil arthropods, soil health, and vegetation patterns. The quantity, diversity, and taxonomic balance of arthropods are intrinsically related to

ecological functions of soil (Coleman et al. 2018). In drylands, as in other harsh environments, soil arthropods are greatly affected by the amount of vegetation (e.g., biomass and vegetation cover) (Delgado-Baquerizo et al. 2019). Independent studies carried out in drylands confirm the correlation between the abundance, diversity, and species composition of ground arthropods and the vegetation spatial pattern (Doblas-Miranda et al. 2009; Liu et al. 2012, 2016; Civieta 2015; Meloni et al. 2020b). Soil layers under patches bear arthropod communities with large abundance and species richness, while bare soil regions show scarce organisms, also belonging to fewer taxa. Long distances between patches tend to isolate soil arthropods and it can affect their taxonomic balance. Hence, the patch border defines an important constraint for the activity of soil arthropods in drylands, but the amelioration provided by plants may reach some bare soil regions (Michalet and Pugnaire 2016). The manner that the soil amelioration decays in bare soil is still unclear. A recent study suggests that arthropods quantities asymptotically decreases as farther they are from patches (Meloni et al. 2020b), and it provides insights for an alternative approach. For instance, patch and interpatch are often considered as different spatial compartments, a dichotomic view. Then, we hypothesize to analyze patches and interpatches as different parts of the same compartment. In these terms, patches and interpatches are opposite sides of a continuous spatial system, which is subject to a switching close to the patch border. If this hypothesis is consistent, one would be possible to propose a unique mathematical description to predict quantitative variations of soil arthropods across the patch border. Most importantly, these variations could be used to infer the range of plant influence on bare soil. Summarizing, this achievement would allow us to analyze and interpret data of soil arthropods as the result of a well-behaved function. Thus, the faunal patterns could finally reveal the range of influence of plants on bare soil. However, this hypothesis is still untested.

Here, we demonstrate that the spatial distribution of soil fauna in drylands is continuous along the patch border, and that their abundance and richness can indicate the range of soil amelioration produced by plants. For this, we assess how the patch size (radius) and distance from patch borders are associated with communities of ground arthropods in patches and inter patches. We focus on whether quantitative information of fauna is linked to the range of influence produced by vegetation on the surrounding bare soil, which is a halo of influence (soil amelioration) produced by plants. To obtain this result, we regard data of arthropods, abundance and species richness, and data of vegetation, patch size (radius) and distance between patches. Logistic functions are used to fit the faunistic quantities. The facilitation range is obtained from derivative values from the fitted curves. We discuss the implications of our findings

in ecological terms, indicating how the patterns of ground arthropods observed in different scales (logarithmic and observable) respectively indicate the plant facilitation and the activity of soil processes in drylands. This information is paramount for planning restoration projects in drylands, and it can improve our understanding of the relationship between vegetation spatial patterns and the range of soil amelioration provided by plants.

## Materials and methods

This study investigates data of soil fauna and vegetation spatial patterns collected in Cabezo de la Plata, Murcia, Spain. The region is characterized as semiarid, with precipitation $\approx$ 300mm/year, and subject to long dry periods. The soils are Haplic Calcisols and Lithic Leptosols (United Nations 2014), influenced by long term land use for agriculture and grazing (Oñate and Peco 2005). The statistical distribution of patch sizes found in this region (Meloni et al. 2017) stresses the role of vegetation cover to predict desertification (Meloni et al. 2019), the effect of grazing and dryness on plant-plant interactions (Verwijmeren et al. 2014, 2019), the influence of patch sizes and distance between patches on the abundance and richness of soil fauna (Meloni et al. 2020b).

All samples were obtained in a short time interval, between June and August, to avoid important seasonal variations. The data set includes samples obtained in patches (79) and in interpatches (70). The data are almost all formed by registers explored in Meloni et al. (2020b), with some additional entries, all them located close or into the UTM 23 S, coordinates 673831 E to 675919.78 E; 42030440 N to 42011716 N.[1] In the studied region, patches are predominantly constituted by the species *Stipa tenacissima* L. A., sometimes associated with some additional common species in small proportion. The new entries were obtained in patches also bearing a small individual of *Pinus* sp. (between 80 and 200 cm height). Although we have no detailed information about the plant composition of each patch, a recent study shows that plant diversity poorly affects the diversity of soil arthropods in harsh environments like drylands (Delgado-Baquerizo et al. 2019) and that the vegetation cover is the most important influence under such circumstances. We carried a preliminary test to compare arthropods from samples bearing *Pinus* and samples free

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[1]New data entries were necessary because the registers explored in Meloni et al. (2020b) contained only few samples of large patches (radius $R > 1.0$ m), which could limit our analyses. Hence, the data set was complemented with 10 additional samples, all of them representing large patches from the same region.

of *Pinus*. This test discharged any possibility of important differences in quantities or taxonomic composition of arthropods related to the presence of *Pinnus*. Hence, this factor was not explicitly addressed by our analyses.

The samples were collected in 14 independent semiarid plots with wide spectra of vegetation cover (from 2.2 to 85.7%). For each plot, 5 patches were randomly selected to be measured and to obtain a soil sample; while 5 soil samples were obtained from interpatch regions located beside the sampled patches (Fig. 1a). For each interpatch sample, we delimited a four-side polygon formed by the four-nearest neighbor patches, which were the vertices of this polygon. The interpatch sample was taken at the middle coordinate (centroid; Fig. 1b). Each soil sample taken in patch and interpatch is equivalent and represents 1L of top soil layer (until 10 cm deep), plus the litter layer immediately above (if present) (Meloni 2012, 2015). In laboratory, the meso- and microarthropods of soil were extracted using modified Berlese-Tullgren funnels, counted and identified. Further details concerning the sampling scheme, identification process, and taxonomic groups can be found in the Ref (Meloni et al. 2020b).

From each soil sample, we obtained data of ground arthropods, abundance $A$ and species richness $\rho$; and two descriptors of vegetation spatial pattern, the patch radius $R$ (meters), as the size of the patch immediately above the sample; and $\bar{D}$ (meters), as the average distance to the four-nearest points showing any vegetation. Because $\bar{D}$ depends on multiple distances of neighbor patches, it carries information about the spatial isolation of the interpatch, and also the collective influence of vegetation in its neighborhood. The values of $A$ and $\rho$ are obtained by counting individuals and species of each soil sample (densities). Previous findings (Meloni et al. 2020b) suggest that the influence of vegetation spatial pattern on soil fauna is more evident if data is assessed in the logarithmic scale. Thus, we introduce the transformed quantities $N = \ln(A)$ for abundances, and $S = \ln(\rho)$ for species richness. According to the definitions of $R$ and $\bar{D}$, a sample $m$ obtained in the soil under a patch shows $R_m \neq 0$ and $\bar{D}_m = 0$ (no distance from vegetation); while a sample $n$ obtained in the bare soil shows $R_n = 0$ (no patches immediately above) and $\bar{D}_n \neq 0$ (Fig. 1b). Hence, the patch size is assumed as the most important influence for $A$, $N$, $\rho$, and $S$ observed in patch samples[2], while the distance between the bare soil sample and the neighbor patches is assumed as the most important descriptor of the same faunistic quantities found in the soil of interpatches.

## Data organization

Our main hypothesis is that plants exert a positive influence on the establishment of soil organisms in bare soil regions. This influence can be interpreted as the facilitation effect generated by plants, which broadly affects organisms in drylands (Pugnaire et al. 2011; Delgado-Baquerizo et al. 2016). Concerning the link between plants and soil arthropods, it is necessary to consider a two way process. On one hand, the meso- and microarthropods of soil are very sensitive to the environmental filters, and they are benefited by the resources and shelters provided by plants already established (Doblas-Miranda et al. 2009; Delgado-Baquerizo et al. 2019; Meloni et al. 2020b). Although the core benefits for arthropods would occur under the patch, facilitation might reach regions beyond the border and also affect arthropods in bare soil (even in lesser intensity). On the other hand, soil arthropods directly or indirectly contribute for the well functioning of soil processes, and, therefore, they positively contribute for the establishment and growth of plants (e.g., including new sprouts and propagules).

Thus, we conjecture that the ground arthropod community could reflect the effects of plant facilitation on soil, which would be revealed by the spatial variation of its abundance and number of species. If so, measures of fauna could inform about the average range of plant facilitation. For this, we assess how the patterns of soil fauna found around the border respond to patch sizes and the distance between patches. We expect to use the collective variation of $N$ and $S$ values to reveal how far facilitation can reach in bare soil. Our hypothesis considers, as $H_0$, that $N$ and $S$ decay exactly at the border, or even inside the patch, meaning that the long term influence of plants on the maintenance of arthropods and the soil processes mediated by them do not reach bare soil regions. If $H_0$ is true, arthropods would be poorly sensitive to the amelioration produced by plants in bare soil, and they cannot be used to indicate the range of facilitation. Alternatively, $H_1$ considers the possibility that arthropods are sensitive to the long term amelioration of bare soil regions, which is produced by plants. This influence would result in large values of $N$ and $S$ of arthropods even for some interpatch regions, sometimes with similar values those found under patches. Furthermore, this region would be limited to a short-range halo around the patch border, and it would be indicated by sudden variations of $N$ and $S$. If $H_1$ is confirmed, then arthropods are sensitive enough to the soil amelioration, and their quantities can be used to indicate the range of influence exerted by plants.

To test these hypotheses, we explicitly addressed the spatial coordinates joining $R$ (meters) and $\bar{D}$ (meters) into

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[2]The distribution of $A$ and $\rho$ inside patches are assumed to be negligible.

**Fig. 1** Schematic representation of sampling and the spatial transposition used by the present study. Panel **a** illustrates the field conditions (Created with BioRender.com). Panel **b** depicts a general configuration of patches in dryland landscapes. Soil samples (filled black circles) were acquired in patches (color circles) and in interpatches (matrix), from which arthropods abundance and species richness are measured. $R$ is the patch radius, and it assumes a nonzero for a given patch sample (e.g., $R_k$ and $R_m$), or zero for an interpatch sample (e.g., $j$ and $n$). $\bar{D}$ is the average distance between the sample and the 4-nearest patches, which assumes nonzero for an interpatch sample, or zero for a patch sample. Panel **c** depicts the 1-d transposition of all samples in terms of a unified and continuous behavior, which is addressed as $x$-coordinates. The nonzero values of $R$ determine $+x$ coordinate where patch samples take place, while the nonzero $\bar{D}$ determines the positions $-x$ for interpatch samples. For the analysis, samples are taken into non-overlapping regular intervals of $\Delta x = 0.10$ m
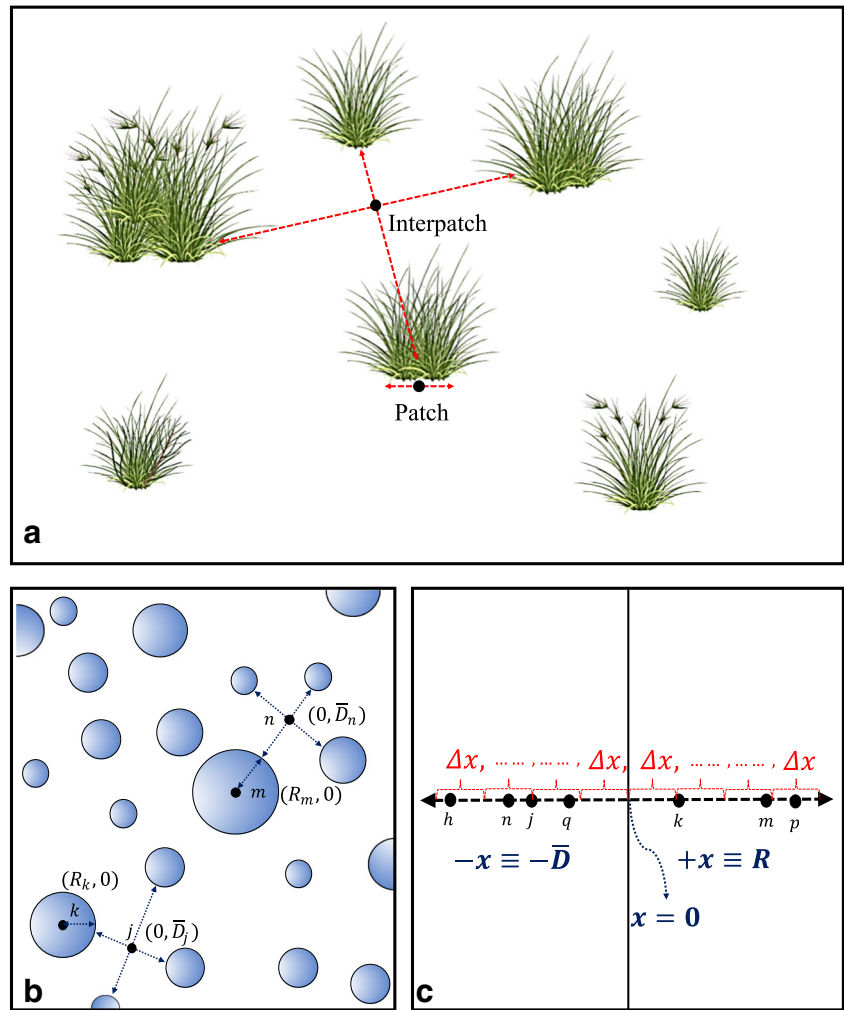


one single variable $x$. The $x$ values are the subtraction of $R$ and $\bar{D}$ of each sample, obtained as

$$x_j = R_j - \bar{D}_j, \tag{1}$$

where $j$ is a random sample taken in patch or interpatch, $R_j$ is the respective patch size, and $\bar{D}_j$ is the average distance from four-nearest vegetated regions. Note that samples of patches show $\bar{D}_j = 0$, while samples of interpatches show $R_j = 0$, so that Eq. 1 produces $x < 0$ if the j-*th* sample represents an interpatch, and $x > 0$ if it represents a patch, and $x = 0$ is represents the border (Fig. 1c). Accordingly, $x$ stores all values of $R$ and $\bar{D}$ in only one axis using same unit (meters), while the signal preserves information about origin (patch:$+x$; interpatch:$-x$). Therefore, $x$ is a 1-d spatial representation deduced from different sources ($R$ and $\bar{D}$) that allows all samples (that were randomly acquired) to be represented in the same 1-d chute (Fig. 1b). This approach enables one to plot all values of $A$, $N$, $S$, and $\rho$ against $x$, in a continuous

representation that crosses the patch border and it allows us to explicitly interpret the multivariate influences of $R$ and $\bar{D}$ on the soil arthropods (Fig. 1c). Note that $\bar{D}$ relies on measures of multiple neighbor patches, while $R$ addresses only one of them. However, this is not a problem for the studied region, because previous findings (Meloni et al. 2017, 2019) report that the statistical distribution of patch size is parametric for the most common vegetation covers in the region. Additionally, the individual and collective influence of patches on soil arthropods, at a local scale, show a strong positive correlation between themselves (Meloni et al. 2020b). As indicated in Meron et al. (2019), the advantage of the continuous representation against the discrete description of drylands relies on the possibility of employing mathematical analyses to reveal and predict patterns and behaviors.

We formulate a data pretreatment before to perform our analyses. The first step removed all registers showing zeros and missing data (12 samples). The motivation relies on the adopted methods that employ logarithm transformation to

data. Aware about possible implications of removing zeros, we employed a preliminary test to certify that this step could not affect our results and conclusions.[3] Next, we applied moving averages to reduce the noise of our data. Soil samples usually show data with high noise, a consequence of random effects and uncontrolled variables under common field conditions (Moreira et al. 2008). This condition may puzzle the search for main patterns, and moving averages can be useful for these cases. The technique is employed in different areas, like price analysis, and it aims to smooth data to reveal general tendencies, despite the local fluctuations are very important. We employed five independent rounds of moving averages that respectively considered 3, 4, 5, 6, and 7 points to calculate averages. The multiple rounds aimed (i) to reinforce the signal around the mean behavior, and (ii) to mitigate possible bias created by adopting only one. Each round generated further data points based on the calculated averages that were joined to the original registers. Overall, this data pretreatment increased the number of useful registers from 149 to 794 (original + calculated), and it greatly improved the signal-noise ratio. The final data set shows a large cloud of points centered on the mean behavior for both, $N$ and $S$ along $x$ (Appendix).

Considering the 794 data points, the following step consisted in to discretize $x$ at regular small intervals of $\Delta x = 0.10$ m (Fig. 1c). The discretization allows calculating different and complementary statistics for each interval, like the average and variance. The average values point the general tendency of quantities through the $x$-coordinates. Variance values permit to follow the uncertainty level. Indeed, we search out for a characteristic peak in variance values, which reveals the possible existence of abrupt changes in faunal quantities and, if so, which $x$-coordinate it takes place. Therefore, it is expected that the variance peak overlaps a sudden change of average values. This approach and interpretations find support on the theoretical concepts and mathematical tools of statistical mechanics and thermodynamics (Stanley 1971; Papon et al. 2007; Hillert 2007),

and we employ this technique to define where the community of arthropods switch its pattern. [4]

In turn, each discrete interval $k$ delimited by $x_k + \Delta x$ contains $v$ samples, and the respective values of $N$ and $S$ are used to calculate the averages $\bar{\mu}_N^{(k)}$ and $\bar{\mu}_S^{(k)}$ respectively as

$$\bar{\mu}_N^{(k)} = \sum_{q=1}^{v} N_q^{(k)}/v \qquad (2)$$

and

$$\bar{\mu}_S^{(k)} = \sum_{q=1}^{v} S_q^{(k)}/v; \qquad (3)$$

while variances $\bar{\sigma}_N^{2(k)}$ and $\bar{\sigma}_S^{2(k)}$ respectively as

$$\bar{\sigma}_N^{2(k)} = \sum_{q=1}^{v} (N_q^{(k)} - \bar{\mu}_N^{2(k)})/v \qquad (4)$$

and

$$\bar{\sigma}_S^{2(k)} = \sum_{q=1}^{v} (S_q^{(k)} - \bar{\mu}_S^{2(k)})/v; \qquad (5)$$

where $q$ is a given sample taken into the $k$th interval of $x$. Mean values and variances are finally used to assess how the arthropod communities vary throughout $x$. The data organization can be reproduced by accessing Meloni (2020a).

## Analyses

We are particularly concerned about how the soil community varies along the spatial coordinates represented by $x$. Previous findings indicate that abundances and species richness found in patches and interpatches are very different (Doblas-Miranda et al. 2009; Meloni et al. 2020b), which suggest that average values across the patch border tend to abruptly vary in a short interval of $x$. In turn, we search for a possible transition of the community patterns, $N$ and $S$, plotting $\bar{\sigma}_N^2$ and $\bar{\sigma}_S^2$ against $x$. We searched for a well-defined peak formed by the variance values. A peak of variance may reveal an interval of $x$ bearing high level of uncertainty about soil communities (values greatly vary in comparison with further ranges of $x$). This is the remarkable sign that both patch and interpatch are influencing the interval (Stanley 1971; Meloni et al. 2019; Majumder et al. 2019), and may infer where the patterns of soil community

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[3]We tested if samples showing zeros could change our results. Although both results (with $vs$ without zeros) are very similar, an important problem arises if zeros are maintained. Because we employ moving averages, some values assume values between 0 and 1, and our analyses consider data in the logarithmic scale. Consequently, the inclusion of zeros produce a set that (a) overestimates differences for small values of abundance and richness, and (b) produces negative values. Both aspects hamper the modeling and the interpretation. We have tried to avoid (a) and (b) by adding a constant $c \gg 1$ to each register, as $N = \log(A+c)$ and $S = \log(\rho+c)$. Despite this procedure enabled us to carry out our analysis, the additional mathematical steps also hampered the interpretation of results to the broad audience. Bearing all aspects in mind, we opted for removing the zeros.

[4]Because this approach is not widely known, we advise interested readers to find out more in the specialized literature. We indicate the Refs. Stanley (1971) and Papon et al. (2007), and Hillert (2007) as good starting points.

switching from a community of few individuals and species to a more structured community. Therefore, we interpret this interval as an indicator of the region where the effects produced by facilitation on the soil arthropods suddenly change.

Next, we plotted the $\bar{\mu}_N$ and $\bar{\mu}_S$ as functions of the $x$-coordinates to achieve two main objectives. The first one is whether to confirm or deny the possibility of abrupt changes in the considered quantity, as indicated by the respective variances. The second aim is to construct a predictive curve using a known function and revealing specific thresholds. For this, we assumed the behavior of $\bar{\mu}_N$ and $\bar{\mu}_S$ along $x$ varying as a logistic function (Cramer 2004). Although the logistic function is just a first approximation to describe the problem, this function can provide great intuition about the average behavior of arthropod quantities along $x$, as detailed below.

The logistic function is expressed as

$$\mu(x) = \frac{\mu_{max}}{1 + be^{-c(x)}} + \mu_{min}, \qquad (6)$$

where $\mu(x)$ represents one of the faunistic variables ($\bar{\mu}_N$ or $\bar{\mu}_S$), $\mu_{max}$ and $\mu_{min}$ are respectively the maximum and minimum values achieved by $\mu$; $b$ and $c$ are the growth parameters that mold the $S$-shape. This function is usually employed to fit population growth, which regards time as the independent variable, but we interpret its parameters in terms of the spatial variable. One expects that $\mu \rightarrow \mu_{min}$ for samples taken in interpatches coordinates located very far from the patch border ($x \ll 0$), while $\mu \rightarrow \mu_{max}$ for samples obtained in very large patches ($x \gg 0$).

The variation of $\mu$ along $x$ is not homogeneous for the logistic function that shows three regions of interest. The first-order derivative $\mu'(x)$ and the second-order derivative $\mu''(x)$ are useful to reveal these main $x$ regions of interest. The inflection point $x^*$ takes place at the $x$-coordinate where $\mu''(x)$ changes its signal from positive to negative. It marks the place where $\mu(x) = \frac{\mu_{max} - \mu_{min}}{2}$, revealing where the soil arthropod community suddenly change their quantities, and, consequently, the range of facilitation provided by plants. According to the region where $x^*$ takes place, the following interpretation can be done:

– $x^* = 0$: the quantities of soil arthropods decay at the patch border. It indicates that facilitation is constrained to regions close to the patch border, which we name as **edge facilitation**;

– $x^* < 0$: the quantities of soil arthropods decay in bare soil regions. The case infers that patch influence (facilitation) persists beyond the patch border. We name it as **long-range facilitation**.

– $x^* > 0$: the quantities of soil arthropods decay even inside patches. In that case, the positive influence occurs only for regions covered by the plants, and that interpatch regions negatively affect the conditions inside patches. We name as **constrained facilitation**.

Furthermore, two other regions of interest, $x_a^*$ and $x_b^*$, are also expected for the $\mu''(x)$. The maximum value achieved by $\mu''(x)$ points the $x_a^*$ value, while the minimum $\mu''(x)$ determines $x_b^*$. Interpreting the logistic function, the $x_a^*$ indicates the $x$ coordinates where $\mu$ values start to differ from $\mu_{min}$ (found in interpatches), while $x_b^*$ where $\mu$ values become close to $\mu_{max}$ (found in patches). Hence, they are also important reference values to interpret the influence of vegetation on soil arthropods, and soil amelioration. Considering the $\bar{\mu}_N$ and $\bar{\mu}_S$ values, the respective $x_a^*$ is interpreted as the maximum range of the facilitation, and $x_b^*$ as an effective patch radius, that is the minimum patch size able to support a soil community with high abundance and richness.

The parameters were set by coupling a recurrent human supervised process, which coupled initial guess and optimization by Generalized Reduced Gradient (MS Excel and Python). Concerning Eq. 6, we fitted the logistic curves $f_1(x)$, $f_2(x)$, $f_3(x)$ for values of $\bar{\mu}_N$, and $g_1(x)$, $g_2(x)$, and $g_3(x)$ for values of $\bar{\mu}_S$, where the indexes $1 \rightarrow 3$ represent: 1—curves fitted for lower bound values; 2—curves fitted for the average behavior (middle); and 3—represent curves for upper bound values. The curves of indexes 1 and 3 are interpreted as "intervals of confidence", although they do not truly match such formalism.[5] For clarity, we shall refer the respective second-order derivatives as $f''_{1 \rightarrow 3}(x)$ and $g''_{1 \rightarrow 3}(x)$.

Last, we plot $f(x)$ and $g(x)$ in the observable scale ($A = e^N$ and $\rho = e^S$) to elucidate the role of the patch sizes and the carrying capacity on the effective shift produced by the scale conversion. Concerning the nature of $N$ and $S$, the analysis addressing $A$ and $\rho$ consider Eq. 6 as a reference to obtain

$$\Phi(x) = \exp[\mu(x)] = \exp\left(\frac{\mu_{max}}{1 + be^{-c(x)}} + \mu_{min}\right), \qquad (7)$$

where $\Phi(x)$ represents $\bar{\mu}_{A,x} = \exp(\bar{\mu}_{N,x}) = \exp[f(x)]$ or $\bar{\mu}_{\rho,x} = \exp(\bar{\mu}_{S,x}) = \exp[g(x)]$. Note that Eq. 7 is a Gompertz like function, which differs in symmetry from the logistic function. Therefore, the inflection point obtained for $\Phi''(x)$ is given as $x^{(o)}$ to also differ from $x^*$. By observing the behaviors of $x^*$ and $x^{(o)}$, we provide differentecological interpretations for the quantities observed in soil communities. The $x^*$ (logarithm scale)

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[5]The employment of moving average prevents the calculation of true confidence intervals from the statistics.

discloses the region around the border where the chances of soil arthropods to establish and maintain a viable community abruptly change, while $x^{(o)}$ (observable scale) reveals where the community increases its ecological activity. Therefore, the threshold $x^{(o)}$ is important to complement our analyses and interpretations, mainly to show how the increase of the carrying capacity indicated by variables $N_{max}$ and $S_{max}$ (logarithmic scale) can affect the $x^{(o)}$ value. For this, we employed numerical simulations using Python, and we observe how the values of $N_{max}$ and $S_{max}$ can shift $x^{(o)}$.

This paper does not explore in detail the taxonomic balance and biological aspects of ground arthropods. Indeed, these topics were already explored by a previous study, and we invite readers interested in such topics to find more in Meloni et al. (2020b).

## Results

Concerning the discretization of $x$ by $\Delta x = 0.10$ m, the analysis of $\bar{\sigma}_N^2(x)$ and $\bar{\sigma}_S^2(x)$ along the $x$ coordinates reveals a characteristic region of high uncertainty ranging $-0.75$ m $< x < -0.35$ m (Fig. 2a, b). This interval is marked by $N$ and $S$ values showing large deviation among samples, meaning that samples with large and small values of $N$ and $S$ coexist in an interpatch region. Furthermore, the variances abruptly increase at the center of the interval, forming a characteristic peak. For abundances, the normalized variance $\bar{\sigma}_N^2(x)/\bar{\sigma}_{Nmax}^2$ indicated that a characteristic peak takes place in the neighborhood of $x \to -0.60$ m. For species richness $\bar{\sigma}_S^2(x)/\bar{\sigma}_{Smax}^2$ reveals that the peak takes place around $x \to -0.55$ m (Fig. 2a, b). Accordingly, soil arthropods shift from simple communities bearing few individuals belonging to few species, to a more structured pattern, with a larger number of individuals and species. These pieces of evidence indicate that the organization of soil communities markedly changes, and the negative values of $x$ where the peaks exist reveal that such changes occur outside of patches. This is an important indicator of the range of influence exerted by patches on the surrounding regions of bare soil. Additional tests with alternative values of $\Delta x$ confirm the patterns observed for $\Delta x = 0.10$ m, meaning that results depicted in Fig. 2 a and b are resilient to the grain size used for discretization.

The middle logistic functions $f_2(x)$ and $g_2(x)$ respectively adjusted for $\bar{\mu}_N$ and $\bar{\mu}_S$ were able to properly represent the general behavior of soil communities along $x$ (Fig. 2c, d). Both cases indicated that the curves reach their inflection point at $x^* \approx -0.35$ m (Fig. 2c, d). The threshold $x^*$ is coherent with the coordinate where $\bar{\mu}_N$ and $\bar{\mu}_S$ respectively reach half of $\bar{\mu}_{Nmax}$ and $\bar{\mu}_{Smax}$. The second-order derivative of $f_2(x)$ and $g_2(x)$, $f_2''(x)$ and $g_2''(x)$, confirm

the middle $x^*$ thresholds, which are revealed by the signal change of the respective curves (Fig. 2e, f). Concerning the variations related to the extreme values assumed $\bar{\mu}_N$, $f_1''(x)$ and $f_3''(x)$ indicated a range between $x^* \approx -0.95$ and $x^* \approx 0.05$ respectively as the lower and upper bounds. For $\bar{\mu}_S$, $g_1''(x)$ and $g_3''(x)$ indicated $x^* \approx -0.95$ and $x^* \approx 0.25$ respectively as the lower and upper bounds.

Furthermore, these curves also reveal two additional thresholds, $x_a^*$ and $x_b^*$, which are indicated by two distinct changes of behavior along $x$. The $f_2''(x)$ indicates a region of interest at $x_a^* \approx -1.15$ m for $\bar{\mu}_N$, while $g_2''(x)$ at $x_a^* \approx -1.25$ m for $\bar{\mu}_S$. Such values reveal where $\bar{\mu}_N$ and $\bar{\mu}_S$ assume values that are consistently different from values usually found in interpatch samples ($\bar{\mu}_N > \bar{\mu}_{Nmin}$ and $\bar{\mu}_S > \bar{\mu}_{Smin}$). Therefore, they provide an inference about the maximum range of facilitation produced by patches. Concerning deviations of $x_a^*$ for extreme values of $\bar{\mu}_N$, $f_1''(x)$ indicated a lower bound of $x_a^* \approx -1.75$, and $f_3''(x)$ a upper bound of $x_a^* \approx 0.55$. For $\bar{\mu}_S$, $g_1''(x)$ indicated a lower bound of $x_a^* \approx -1.75$, and $g_3''(x)$ a upper bound of $x_a^* \approx -0.35$. The region of interest $x_b^*$ infers where soil communities assume abundances and species richness close those observed into large patches ($\bar{\mu}_N \approx \bar{\mu}_{Nmax}$ and $\bar{\mu}_S \approx \bar{\mu}_{Smax}$). The $f_2''(x)$ indicates $x_b^* \approx 0.55$ m, and $g_2''(x)$ indicates $x_b^* \approx 0.45$ m. They suggest the minimum patch size (radius) necessary for soil arthropod communities reach the maximum local abundance and richness found in the studied region. Concerning deviations of $x_b^*$ for extreme values of $\bar{\mu}_N$, $f_1''(x)$ indicated a lower bound of $x_b^* \approx -0.15$, and $f_3'(x)$ a upper bound of $x_b^* \approx 0.75$. For $\bar{\mu}_S$, $g_1'(x)$ indicated a lower bound of $x_b^* \approx -0.15$, and $g_3'(x)$ a upper bound of $x_b^* \approx 0.95$.

Figure 3 a–d depict the results obtained for $\bar{\mu}_A(x) = \exp[f_2(x)]$ and $\bar{\mu}_\rho(x) = \exp[g_2(x)]$, indicating that the averages curves remain coherent even for the observable scale. As predicted by the change of scale, the smaller values $\bar{\mu}_A$ and $\bar{\mu}_\rho$ found in samples of interpatches produced better fit for $x < 0$, while $\bar{\mu}_N$ and $\bar{\mu}_S$ produced better fit for samples taken in patches. Values of $x^*$ obtained for $f_2(x)$ and $g_2(x)$ are poorly affected by variations of $N_{max}$ and $S_{max}$, which is indeed predicted for the logistic function. However, when the observable scale is recovered by $\bar{\mu}_A(x) = \exp[f_2(x)]$ and $\bar{\mu}_\rho(x) = \exp[g_2(x)]$, the new inflection point $x^{(o)}$ is shifted in relation to $x^*$ (Fig. 3c, d). Accordingly, while $\bar{\mu}_N$ and $\bar{\mu}_S$ produce $x^*$ as a resilient region of bare soil ($x < 0$), $\bar{\mu}_A$ and $\bar{\mu}_\rho$ result in $x^{(o)} > 0$, meaning that the inflection is shifted to the patch domain in the observable scale. Therefore, the change of scale leads to a clear shift of reference, suggesting that $A$ and $N$ reveal different aspects of abundances, while $\rho$ and $S$ indicate different aspects of species richness.

Finally, the numerical analysis revealed how changes in the carrying capacities indicated by $N_{max}$ and $S_{max}$ (log
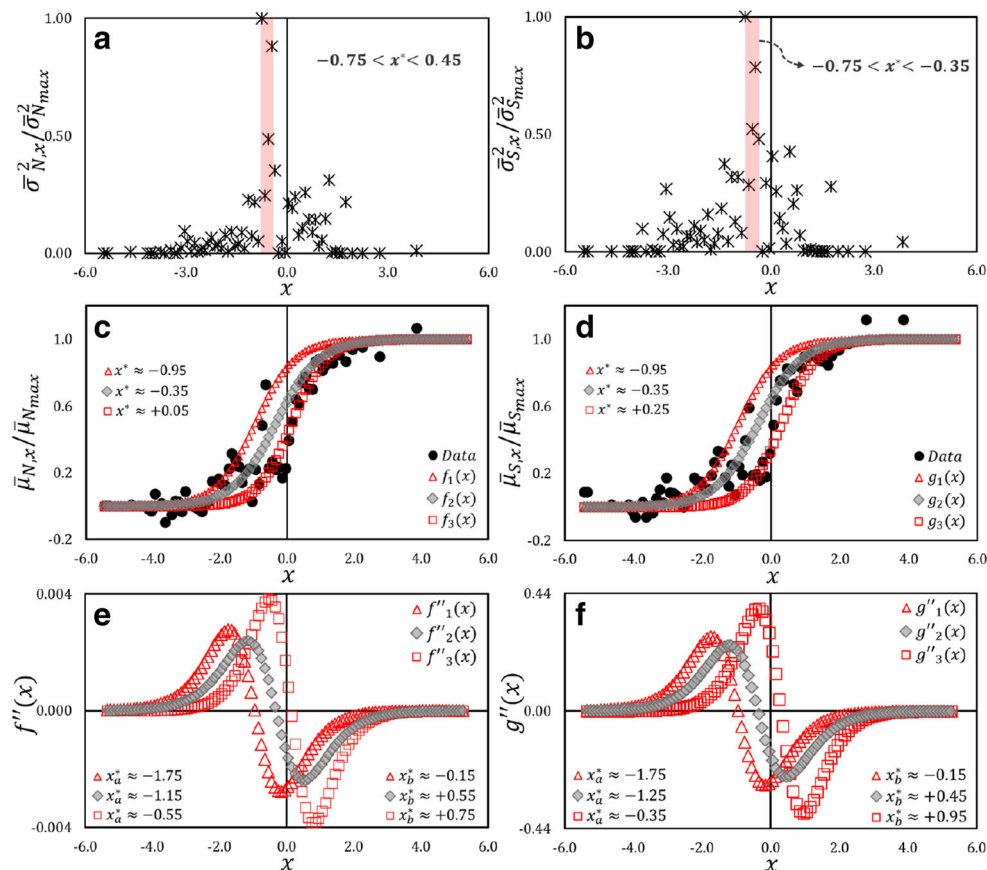
**Fig. 2** Analysis of the soil arthropods quantities $N = \ln(A)$ and $S = \ln(R)$ through a *1-d* spatial representation $X$ that crosses the patch border. Values of $N$ and $S$ are taking into intervals of $\Delta x = 0.10$ m, resuting in their averages and variances ($\bar{\mu}_N$ ; $\bar{\mu}_S$ ; $\bar{\sigma}_N^2$; $\bar{\sigma}_S^2$). The value $x = 0$ represents the patch border; $x > 0$ patch size (radius); $x < 0$ distances between the patch border and interpatch samples. From outwards to inwards the $\bar{\mu}$ and $\bar{\sigma}^2$ plots along $x > 0$ represent samples obtained in patches, and for $x < 0$, samples were collected in bare soil (interpatches). Panels **a** and **b** depict the peak of variance observed for $\bar{\sigma}_N^2$ around $x = -0.60$ m, and $bar\sigma_S$ around $x = -0.55$ m. The peaks and their neighborhood indicate where maximum rate of uncertainty takes place, and samples of large and small abundances and richness coexist. In panels **c** and **d**, $f_2(x)$ and $g_2(x)$ respectively indicate the logistic curves that better describe the behavior of $\bar{\mu}_N$ and $\bar{\mu}_S$ through the $x$ values. Both functions indicate inflection points (change

of growth rate) in $x^* \approx -0.35$ m. These inflections reveal the average distance from the patch border where soil communities reach half of $\bar{\mu}_{Nmax}$ and $\bar{\mu}_{Smax}$ values. In panels **e** and **f**, the second-order derivatives $f_2'(x)$ and $g_2'(x)$ confirm the patterns observed in panels **c** and **d** (signal change) at $x^*$, and point out two further inflection points. The threshold $x_a^* \approx -1.15$ m indicates the distance from patch border where soil communities starts to show consistent increasing of $\bar{\mu}_N$ and $\bar{\mu}_S$. It also suggests the maximum range of positive influence of patches on interpatches (facilitation). The $x_b^* \approx 0.50$ m suggests the average patch size (radius $\approx 0.50$ m) able to support soil communities with large values of $\bar{\mu}_N$ and $\bar{\mu}_S$. The curves $f_1(x)$, $f_3(x)$, $g_1(x)$ and $g_3(x)$ depicted in panels **c**, **d**, **e** and **f** indicate logistic curves fitted for extreme cases. They provide a reference of error associated with the average behavior described by $f_2(x)$ and $g_2(x)$

scale) shift the respective inflection points $x^{(o)}$ when data are considered in the observed scale ($A$ and $\rho$). Accordingly, the numerical integration of $exp[f_2(x)]$ and $exp[g_2(x)]$ for multiple values of $N_{max}$ and $S_{max}$ indicate that the inflection point $x^{(o)}$ always take place at positive coordinates of $x$, and it is shifted in direction to the patch border, $x \to 0$, as larger are $N_{max}$ and $S_{max}$ (Fig. 4a–d). Figure 4 depicts this behavior and indicates that the linear increase of $N_{max}$ and $S_{max}$ [$A = \exp(N)$ and $\rho = \exp(S)$] produces logarithmic variation of $x^{(o)}$ values. In turn, the exponential increase of the maximum values of $N$ and $S$ shifts the inflection of observable quantities in direction to the patch

border ($x = 0$), which also defines lower limit for $x^{(o)}$. Note that this limit is marked by $A = \rho = 1$, quantity that reflects the minimum biological activity. Furthermore, any increase in the carrying capacity shall imply larger biological activity inside patches, but they poorly affect quantities of arthropods found in bare soil. Hence, the observable scale better reflects the activity of arthropods in soil than their dispersion along the bare soil. Therefore, these results point that the observable and logarithmic scales reflect distinct ecological aspects related to soil arthropods and their relation with vegetation in drylands (see "Patterns from different scales and their ecological implications").
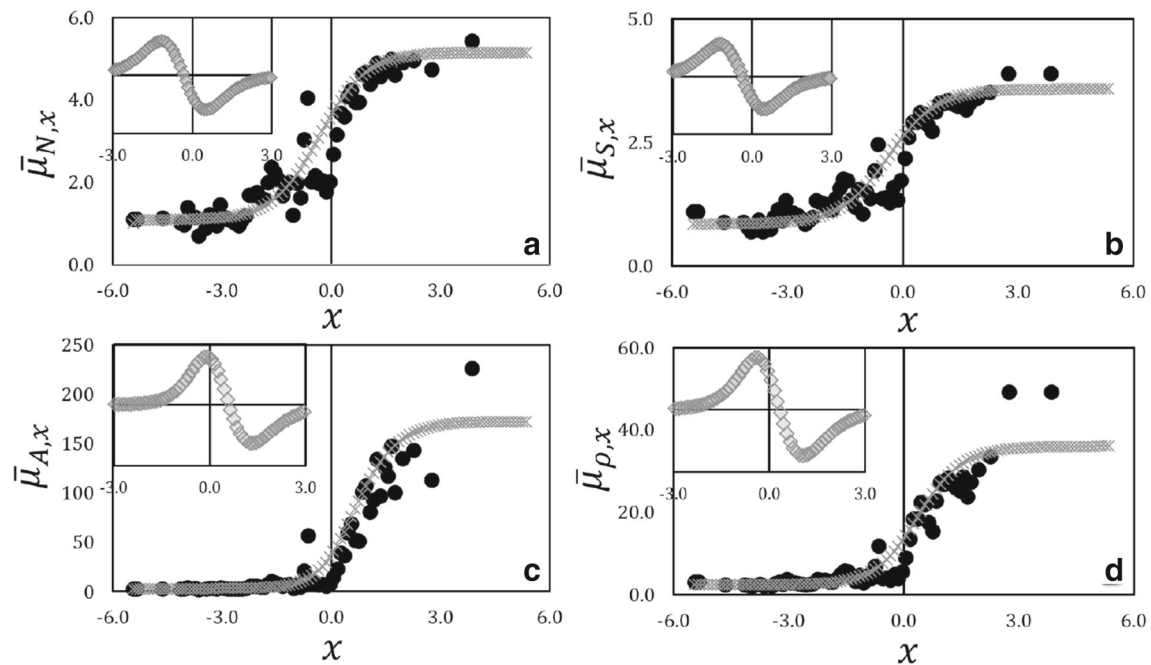
**Fig. 3** Comparing average abundances and species richness along a spatial representation that crosses the patch border ($x = 0$). $x > 0$: patch size (radius); $x < 0$: distance from patch border. Filled circles are data, and small marks are logistic functions. On top, the consensus curve describing $\bar{\mu}_N$ (left) and $\bar{\mu}_S$ (right), which consider data at log scale. In the bottom, the $\bar{\mu}_A = \exp(\bar{\mu}_N)$ (left) and $\bar{\mu}_R = \exp(\bar{\mu}_S)$ (right), meaning that data are at observable scale. In the logarithm scale, the consensus curve show higher imprecision for $x < 0$ than for $x > 0$. In the observable scale, the imprecision vanishes for $x < 0$. Insets in panels **a** → **d** depict the second-order derivative of average values and how the scale change shifts the thresholds
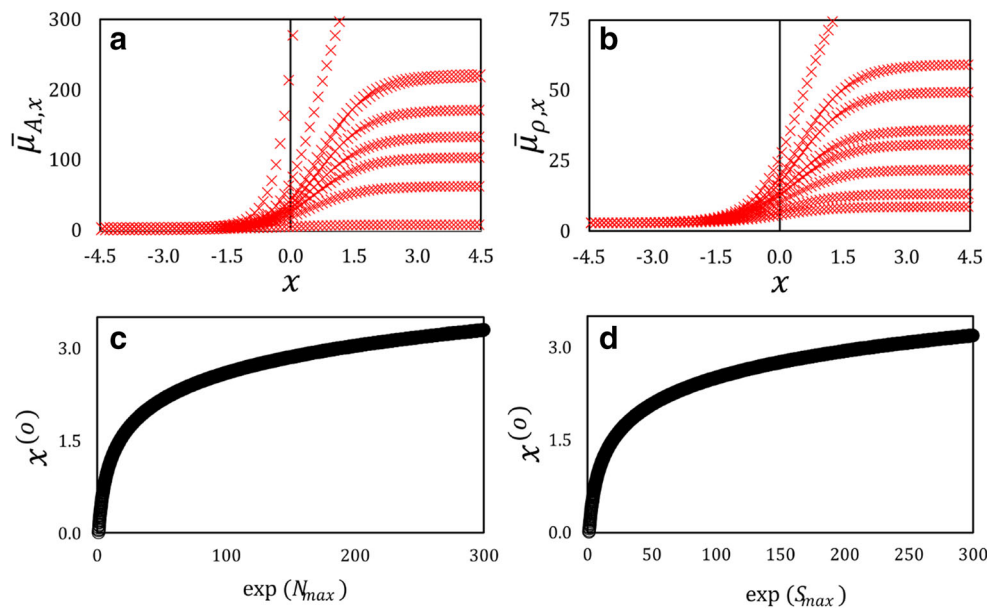


**Fig. 4** Effect of carrying capacity on the expected thresholds $x^{(o)}$ for observable (a) average abundances ($\bar{\mu}_A$), and (b) average species richness ($\bar{\mu}_\rho$) found in soil throughout the spatial representation. Different from $x^*$, which is not affected by variations in the carrying capacity, $x^{(o)}$ values are shifted by $\exp(N_{max})$ and $\exp(S_{max})$ as logarithm (c and d). Therefore, one is clear that the observable and the logarithm scale of arthropod communities represent distinct aspects of these communities

## Discussion

### Vegetation pattern, soil arthropods, and soil amelioration

Our findings confirm that variations in abundances and species richness of soil arthropods can be understood as a continuous space, which crosses the patch borders. Furthermore, they reveal the existence of a region of maximum uncertainty (validated by averages and variances), which is located in the bare soil. This interpatch coordinate reveals the bare soil region where soil communities switch, from a simple community, with few organisms and species, to a more diverse community, with larger abundance and species richness. Previous findings complement this information, suggesting that changes in soil communities is also structural (Meloni et al. 2020b). The explanation relies on the fact that soil arthropods depend on resources and protection provided by plants to live and explore their niches (Doblas-Miranda et al. 2009; Synodinos et al. 2015; Coleman et al. 2018). Accordingly, one expects that abundances and species richness would increase as closer the interpatch is from the patch border, as a consequence of the local amelioration produced by plants. Therefore, this evidence offers an objective indication of the range of long term effects provided by plants on the upper soil layers.

The previous investigation already pointed out the importance of patch sizes for the maintenance of biodiversity and the local amelioration of soil, as well as for some ecological processes in drylands (Escudero et al. 2004; Cortina and Maestre 2006; Pugnaire et al. 2011; Maestre et al. 2016). Furthermore, experimental results show that the organic content in the soil decays from the patch interior to interpatch regions, while the penetration resistance increases (Bochet et al. 1999a). Although we could not formally compare our findings with data of soil properties, there is strong evidence that variations in abundance and species richness of arthropods match the spatial variation in soil properties. As a highlight, even the threshold indicated in the litterature for soil properties (Bochet et al. 1999a), at 35 cm far from the patch border, is compatible with the changes in arthropods quantities indicated by our analysis. Therefore, our results and information from literature together (a) corroborate the role of plant facilitation for the soil amelioration and maintenance of soil communities, and (b) reveal the existence of a specific and measurable threshold in arthropods quantities, which also links the spatial pattern of vegetation and soil features. Accordingly, we have evidence that soil arthropods quantities can indicate the range of soil amelioration produced by plants in drylands.

Figure 5 depicts a schematic representation of the findings. The analysis of soil arthropods quantities taken in the logarithm scale revealed that plants provide long-range facilitation. The results point out that the positive influence remains important until $0.35 \rightarrow 0.50$ m far from the patch border in direction of bare soil, although the extreme case may overcome 1.00 m. This range is pointed by averages and variances of abundance and species richness, and it matches an average halo of influence of plants on bare soil amelioration. This can be interpreted as a reference for the range of facilitation provided by plants to soil arthropods. Although the results indicate that this threshold is poorly affected by patch size, they also showed that the absolute quantities of arthropods found into the halo are affected by patch size. Indeed, our findings indicate that such influence grows with the patch radius (even for logarithm scale), until a radius $\approx 0.5$ m, and it stabilizes for larger patches. Interestingly, the halo width in bare soil almost matches the minimum patch radius ($\approx 0.50$ m) able to support a large and rich community. Note that the maximum uncertainty found around $x^*$ indicates that there is large variability in arthropod communities found close to this limit. Accordingly, the abundance and richness of soil arthropods living in such range regions may vary from patterns commonly found in bare soil (smallest abundance and richness) to patterns commonly found in under small patches (largest abundance and richness). The uncertainty decreases as observations move away from $x^*$ (in both directions).

Having in mind the positive and negative influences respectively exerted by patches and interpatches on the soil arthropods of drylands, a previous study (Meloni et al. 2020b) interpreted that this kind of trade-off well matches the "Island Biogeography Theory" predictions (MacArthur and Wilson 1967). Accordingly, plants would match the concept of "islands", permitting the colonization of arthropods, and interpatches would match the "matrix", imposing restrictions to their dispersion. Indeed, the experimental evidence shows that patch sizes and distances between patches can affect the composition and structure of soil arthropod communities (Liu et al. 2012, 2016; Meloni et al. 2020b); only sites showing large patches can support some taxa considered as specialized to soil niches, and long distances between patches can impose restrictions to the dispersion of arthropods that show low mobility (Meloni et al. 2020b). Such evidence reinforces that the link between spatial arrangement of patches and the maintenance of the diversity of soil arthropods communities may be non-trivial in drylands, and our findings introduce important updates to the topic. Accordingly, the minimum patch sizes, radius $\approx 0.5$ m, and the fix range of soil amelioration, $\approx 0.5$ m, reveal the limits of the quantitative influence of plants on upper soil layers of interpatches. Following theoretical predictions (MacArthur and Wilson 1967) and modeling approaches (Filotas et al. 2010), they also can bring consequences for
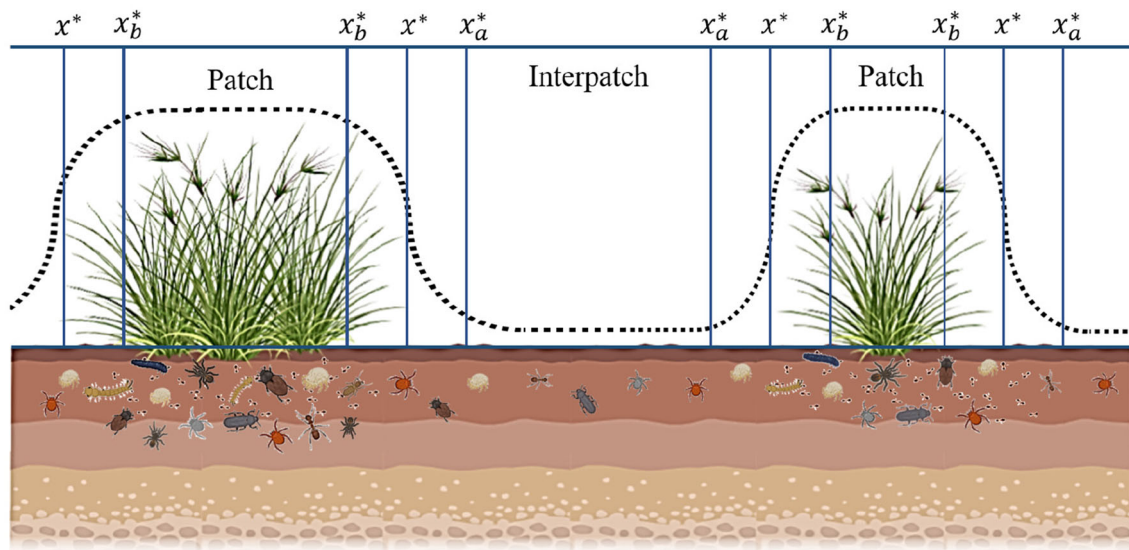
**Fig. 5** Schematic representation of the spatial distribution of soil arthropods across the border of patches. The abundance and richness of soil arthropods is larger under vegetation tussocks (patch) and decay in bare bare soil (interpatch). $x_a^*$ marks where soil communities assume pattern commonly found in bare soil regions; $x_b^*$ points the region where soil arthropods show patterns commonly observed under vegetated regions; $x^*$ marks where abundance and richness assume the half values, an indicative of soil amelioration provided by plants. Therefore, $x^*$ indicates the range of plant facilitation (created with BioRender.com)

the collective organization of soil organisms. For instance, the thresholds suggest that, on a site scale (several patches), the ameliorated soil regions may become continuous, even if vegetation remains discontinuous. Furthermore, the type and intensity of degradation may affect the continuity of regions of ameliorated soil. As soil arthropods directly or indirectly contribute to a large number of ecological processes, like the dispersion of microorganisms, revolving of sediments, nutrient cycling, among others, the thresholds here reported should be employed to explore "how the spatial organization of patches affects the collective functioning of soil processes", and "how degradation level may affect them".

It is important to highlight that there is strong support in the literature indicating that, in a general sense, soil arthropods communities positively contribute to the performance of plants (Bardgett and Wardle 2010, 2014; Rodríguez-Echeverría and Traveset 2015; Coleman et al. 2017; Menta and Remelli 2020). However, it is not clear whether such influence would sound for harsh environments, like drylands, or under which conditions this influence would be feasible for these ecosystems. Unfortunately, manipulative experiments focused on the role of arthropods as mediators of cooperative interactions in the plant-soil system are still rare (Bardgett 2014; Rodríguez-Echeverría and Traveset 2015). Because soil arthropods show great value as an indicator of soil amelioration, and they potentially may contribute to facilitative processes, we call attention to the necessity of future studies to investigate their weight as mediators of the soil amelioration in drylands.

## Patterns from different scales and their ecological implications

The results point that observable and logarithmic scales reflect distinct aspects of soil arthropods, which also show distinct ecological interpretations. Next, we shall discuss how mathematical and ecological aspects are connected and together support interpretations.

From a mathematical point of view, Eqs. 6 (logistic) and 7 (Gompertz like) show distinct symmetries, and their inflections are not compatible (Figs. 2 and 3; Figs. 3 and 4). As $\mu(x) \neq \exp[\mu(x)]$, the change of scale affects the forms of these curves in different ways, meaning that the thresholds $x^*$ and $x^{(o)}$ represent distinct behaviors. The logistic functions always consider $\bar{\mu}_N(x)$ or $\bar{\mu}_S(x)$ and, therefore, faunal quantities are taken in their logarithm form. In that way, the curve behaviors observed for smaller values are overestimated in comparison with behaviors observed for the larger ones. This expanded the resolution of patterns along the bare soil regions, allowing us to reveal how abundance and richness vary in response to patch proximity. The approach is often employed to distinguish between heavy tail probability distribution functions (Meloni et al. 2017; Cirillo 2013), and it was also useful to detect variations of soil arthropods quantities. Indeed, the abrupt changes found in the bare soil is highlighted by the logarithm scale and, although it is also present in the observable scale, it remains hidden (minor or imperceptible effect). Consequently, the scale change provided a higher "zoom" on a hidden part of the problem, and it has worked

analogously to a microscope that can amplify structures that cannot be detected the eye alone.

Hence, the distinct mathematical behaviors found for abundances and richness in different scales also suggests that each one better reflects an specific ecological feature. As aforementioned, abundances and species richness of soil arthropods from patches and interpatches differ in magnitude. Therefore, the employment of $N$ and $S$ allowed us to reveal some variations in bare soil regions that could not be found in another way. They are associated with the amelioration provided by plants to the soil (resources, protection, etc), so they are interpreted as the range of facilitation. According with the definitions adopted by this paper, the changes in soil communities verified at log scale fit the **long-range facilitation**.

However, the employment of $N$ and $S$ and the subsequent strain produced by this scale cannot reflect the actual activity of soil arthropods. Bearing in mind the absolute values of abundance and richness found in bare soil and patches, it is possible to conclude that variations associated with the long-range facilitation are minor effects in comparison with the overall patterns of these communities. Therefore, the observable scale, represented by $A$ and $\rho$, seems to better represent the general activity of soil arthropods.

As second aspect, meso- and microarthropods are often employed to indicate soil health (Menta et al. 2018). The indication of soil properties and processes employing soil arthropods usually address basic information of abundances, number of taxa, presence of particular taxa, ad hoc information, or even combination of metrics (Parisi et al. 2005; Moreira et al. 2008; Yan et al. 2012; Meloni 2012; Arajo et al. 2018). Even though the correlation between arthropods quantities and soil functionality is not always straightforward[6], the basic assumption of indication relies on the active role of arthropods to maintain soil processes, and that population levels and species diversity are linked to the niche availability (Seastedt 1984; Coleman et al. 2000, 2018; Fitter et al. 2005). However, this link may be masked by the log transformation. We have used log transformation to bring large and small communities to the same ground (scale) to study them. This procedure amplifies small events and restricts large ones. Large fluctuations in the measured quantities of biological communities are intrinsically related with their dynamics, and to the proper functioning of ecological processes. Log scale smooths this effect, reducing the effect of ecological dynamics on qunatities. We are also aware that this procedure indicates

multiplicative underlying processes which are out of the scope of this study.[7]

Thus, we may link this information with our results. It is expected that threshold $x^{(o)}$ from the observable scale ($A$ and $\rho$) could better reflect the arthropod's activity in soil processes than the log scaled ($N$ and $S$) can do. These arguments relies on fact that $A$ and $\rho$ better reflect the actual quantiative levels and fluctuations in arthropod communities, which is essential to state about the ecological functioning of soil processes. Following this rationale, the soil processes mediated by arthropods tend to be more efficient in large patches than in small patches or in bare soil (large patches show too larger abundance and richness). Different from the range of soil amelioration, the arthropods quantities are affected by patch sizes. Furthermore, the patch border marks the limit range for the threshold $x^{(o)}$, meaning that the main activity of soil arthropods is importantly delimited to the patch domain. Under definitions adopted by this study, the general activity of soil arthropods revealed by observable scale fits the **constrained facilitation**.

As demonstrated by our numerical analyses, the increase in the carrying capacity shifts the inflection point $x^{(o)}$ to the center of the patch ($x \gg 0$). In fact, the increasing of carrying capacity means that large patches would present even higher functionality in soil, because they would also show more individuals and species, exploring more niches. If true, this would also introduce spatial heterogeneity inside the patches, in a process that finds similarity with the border effect in tropical forests (Corlett and Primack 2011). While this possibility seems plausible in theory, it also seems that does not hold for the studied region. From the best of our efforts, we could not find patches with so large carrying capacity, despite the number of individuals and species of arthropods greatly vary among samples obtained in large patches. Thus, the hypothesis raised by the numerical tests indicates that a so high carrying capacity (and consequent soil ecological processes, like the nutrient cycling) is only possible for environments with higher productivity and litter quality.

We call attention to the fact that the different behaviors presented by $x^*$ and $x^{(o)}$ are not mere mathematical artifacts, and the evidence suggests that they actually reveal information from different ecological effects, each one better observed on a specific scale. Note that the long-range facilitation, indicated by the logarithmic scale, and constrained facilitation, indicated by the observable scale, are not contrasting, but are indeed two complementary aspects of the facilitation produced by plants. On one hand, the long-range facilitation shows small effects for large relative area. On the other hand, the constrained facilitation shows intense

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[6]Exceptions may occurs, e.g., when aggressive species (invasive or native) is very abundant due to a degraded condition that favors its fitness.

[7]The log transformation makes also multiplicative terms become aditive, as $\log(a \times b \times c \times ...) = \log(a) + \log(b) + \log(c) + \log(...)$.

ecological effects, which are limited to the patch domain. The partitioning of facilitation provided by plants makes great sense for the understanding of the biological communities as whole, as well as for the ecological dynamics of drylands. In harsh environments, the ecological role of plants extrapolates the primary productivity, because the facilitation becomes essential for the establishment of further plants, invertebrates, vertebrates and microorganisms. Obviously, the species or guilds show physiological particularities and tend to explore different niches, meaning that they are impacted in different manners by the amelioration produced by plants (Fitter et al. 2005; Coleman and Whitman 2005, 2018; Menta and Remelli 2020).

Therefore, the thresholds here revealed are important for the understanding of how the spatial patterns of vegetation define the collective functioning of soil processes in drylands. They reinforce the necessity of analyzing facilitation by its components, information that can be used to understand the ecological dynamics of drylands and to formulate conservation and restoration actions. Concerning the spatial pattern of vegetation, the specific thresholds aforementioned should be employed to deeper explore the mechanisms that drive such dynamics. For instance, some important models used to investigate it consider facilitation as an underlying mechanism (Kéfi et al. 2007, 2011; Corrado et al. 2014; Meron 2012; Gilad et al. 2007; von Hardenberg et al. 2010), but the link between path sizes and the range of facilitation remains little understood. As a suggestion, these models could be updated in the future to incorporate the thresholds found here, which may bring some new insights about the formation of vegetation spatial patterns, and how desertification would be triggered. Concerning the conservation of drylands, the restoration of degraded sites could consider our findings to better plan the planting designs, incorporating the spatial distribution of patches to maximize regions of ameliorated soil. Furthermore, they may consider the distance between patches to produce functional connectivity of soil communities, improving the maintenance of soil organisms. Therefore, our findings show potential for contributing to the maintenance of drylands, by improving the chances of restoration and conservation strategies be successful.

# Conclusions

We demonstrate that variations in abundance and species richness of soil arthropods found in patches and interpatches of drylands can be described as a continuous pattern. This description also revealed where the community patterns change from simple communities to abundant and highly diverse communities, indicating the existence of a clear region of switching. This region takes place in bare soil,

between 0.35 and 0.50 m from the patch border, and it is inferred as the facilitation provided by plants on the bare soil regions. This is a halo of influence, and its width is poorly affected by the patch size. However, the quantity of arthropods is affected by patch size, and patches showing radius $\approx$ 0.5m or larger are able to support abundant and rich soil arthropod communities. Our findings also show that soil arthropods can reveal two distinct types of facilitation, long-range facilitation, with small effects for soil processes but long extension; and the constrained facilitation, with intense activity for soil processes but short extension. These findings bring important updates to the ecology of drylands and provide insights for projects focused on restoration and conservation of these ecosystems. They can also be used to improve the theoretical models aimed to explain the pattern formation of vegetation and the ecological dynamics of drylands.

**Availability of data and codes** The authors declare that data shall be made available.

## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Abbreviations** The following abbreviations are used in this manuscript: $A$, abundance; $N = \ln(A)$; $\rho$, species richness; $S = \ln(\rho)$; $R$, patch radius (m); $\bar{D}$:$\bar{D}$, average distance between interpatch middle region and its four-nearest patches (m); $x$, continuous 1-d representation of $R$ and $\bar{D}$ (m); $\Delta x$, regular discrete intervals of $x$; $\bar{\mu}_N$ and $\bar{\mu}_S$, average values of $N$ and $S$ in a given interval $\Delta x$; $\sigma_N^2$ and $\sigma_S^2$, variance of $N$ and $S$ in a given interval $\Delta x$; $\Phi(x)$, generic representation of $\bar{\mu}_A(x) = \exp[\bar{\mu}_N(x)]$ or $\bar{\mu}_\rho(x) = \exp[\bar{\mu}_S(x)]$; $f_{1\to3}(x)$ and $g_{1\to3}(x)$, logistic functions fitted for data; $f'_{1\to3}(x)$ and $g'_{1\to3}(x)$, second-order derivative of $f_{1\to3}(x)$ and $g_{1\to3}(x)$; $x^*$, inflection point of $f_{1\to3}(x)$ or $g_{1\to3}(x)$; $x_a^*$ and $x_b^*$, regions of interest of $f_{1\to3}(x)$ and $g_{1\to3}(x)$; $x^{(o)}$, inflection point for $\exp[f_{1\to3}(x)]$ and $\exp[g_{1\to3}(x)]$.

## Appendix: Figure 6

Figure 6 depicts results obtained after the inclusion of data obtained by the employment of moving averages to the raw data.

**Fig. 6** Abundances ($A$) and species density ($\rho$) plotted against $x$ as raw data, after the inclusion of *pseudo*-samples produced by moving averages. Continuous red lines are logistic functions and represent the average behavior of data
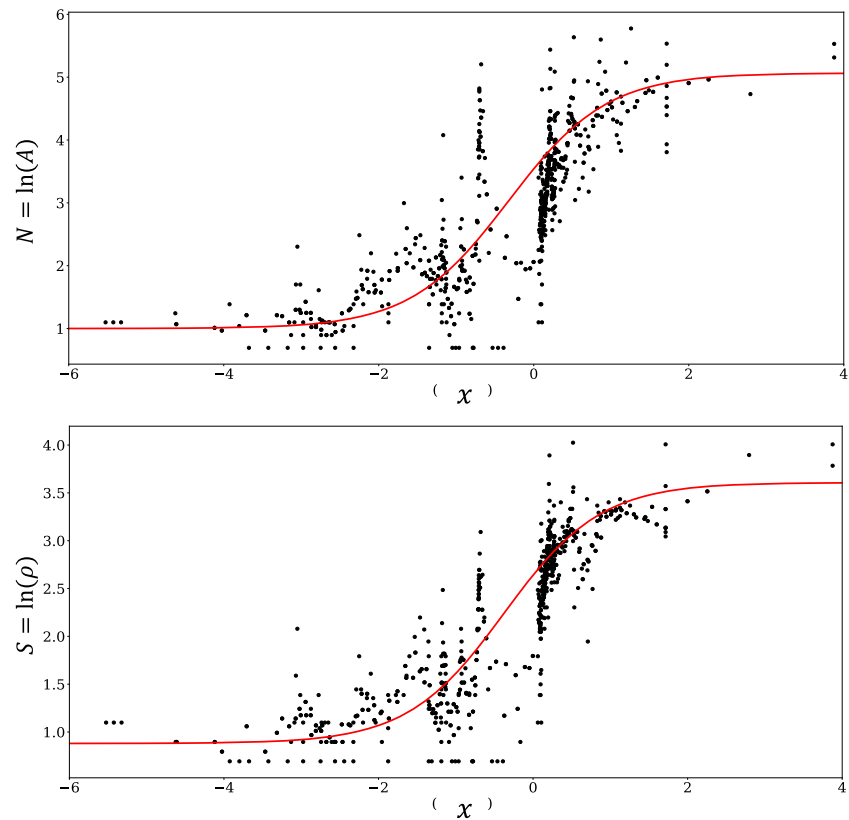
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