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Plant clonal morphologies and spatial patterns as self-organized responses to resource-limited environments

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We propose here to interpret and model peculiar plant morphologies (cushions and tussocks) observed in the Andean Altiplano as localized structures. Such structures resulting in a patchy, aperiodic aspect of the vegetation cover are hypothesized to self-organize thanks to the interplay between facilitation and competition processes occurring at the scale of basic plant components biologically referred to as 'ramets'. (Ramets are often of clonal origin.) To verify this interpretation, we applied a simple, fairly generic model (one integro-differential equation) emphasizing via Gaussian kernels non-local facilitative and competitive feedbacks of the vegetation biomass density on its own dynamics. We show that under realistic assumptions and parameter values relating to ramet scale, the model can reproduce some macroscopic features of the observed systems of patches and predict values for the inter-patch distance that match the distances encountered in the reference area (Sajama National Park in Bolivia). Prediction of the model can be confronted in the future with data on vegetation

patterns along environmental gradients so as to anticipate the possible effect of global change on those vegetation systems experiencing constraining environmental conditions.

1. Introduction

It is now widely acknowledged that interactions between plants can result in self-organized vegetation patterns, the scale of which is one to several orders of magnitude above the range over which an individual plant may exert facilitative as well as competitive influences on its neighbours [1,2]. The ranges of such influences are typically of tens of centimetres for herbs to metres for shrubs and trees, while the patterns observed at landscape scale may be characterized by a dominant scale over tens to hundreds of metres [3,4]. Yet models of self-organization have shown that plant–plant interactions in environments deprived of resource (water and nutrients) can indeed result in such landscape-scale patterns. The patterns that have so far received most attention display striking spatial alternation of vegetation and bare soil and a dominant wavelength can be detected [3–8]. Observed morphologies are made of bands, spots, labyrinths or gaps. Such patterns show a worldwide distribution [9] and are typically observed under arid or semiarid climates at the fringes of deserts, which suggest an analogy with phase transition between continuous vegetation cover (e.g. savannah) and desert. Broad scale monitoring of such systems thanks to remote sensing has moreover shown that the periodic patterns do react to the variation of rainfall over decades in a way which qualitatively accords with predictions of the diverse self-organization models which have been proposed [3,4]. This provides ample evidence that those systems are not dependent on inherited geological or soil properties but are instead dynamical and react to ongoing rainfall variation, a fact that corroborates the hypothesis of self-organization under resource limitation.

However, biphasic mosaics associating vegetation and bare ground are a very widespread feature of vegetation cover in drylands [10–12], which is far more ubiquitous than the specific subclass of spatially periodic patterns. The processes from which such mosaics originate and perpetuate are qualitatively well understood and described by many authors: vegetation traps nutrients and helps water infiltrate into the topsoil thereby creating ‘fertile islands’ within a resource deprived area [11–13]. Conversely, the crusted surface of bare areas prevents water from infiltrating, while nutrients, soil particles and plant propagules are moved along with water or wind towards vegetated places. Resource concentration also fosters the development of soil fauna, which contributes to the overall biological activity observed in vegetation patches [12]. In addition, the overall lack of resources leads plants growing in fertile patches to extend their root systems under adjacent bare grounds thereby decreasing the already insufficient soil resources and reinforcing the contrast within the biphasic mosaic. This interplay between the positive feedback associated with vegetation and biological activity (i.e. facilitation in the broadest sense) and the negative feedback represented by the competition for limited resources (and/or the transfer of those resources towards vegetated places) qualitatively explains the emergence and perpetuation of biphasic mosaics thanks to self-organization processes. Several models have been designed to explain spatially periodic vegetation patterns (e.g. [14–17]; see [18] for a review; [19,20]). They have been inspired by the study of self-organization in physical and chemical systems [21,22]. They all conceptually feature the interplay between positive and negative feedbacks [23], while a necessary condition for stable patterns to occur is that positive processes are shorter ranged (or implying lower diffusion) than negative processes [18,24].

But biphasic mosaics quite often correspond to aperiodic systems or even isolated structures. Trying to interpret such patterns as self-organized structures is nevertheless sensible since several models able to simulate self-organized periodic systems also yield aperiodic or isolated vegetation structures for particular domains in the parameter space. It therefore makes sense to investigate the origin and dynamics of dryland contrasted mosaics in reference to the physical concept of ‘localized structures’ (LSs) [25]. Indeed, recent applications proved fruitful [26–29],

although the concept has so far barely percolated into vegetation science. For instance, circular bare ground spots in a continuous grassy cover (as observed in Namibia and therein called ‘fairy circles’) have been modelled as LSs, and the model was able to yield sets of interacting circles as well as isolated ones (i.e. solitons) as is indeed observed in the field [29]. Phase transitions at the interface between tropical grasslands and forests have also been addressed via the LS concept to explain systems of isolated circular tree groves within seasonally flooded, yet fire-prone grasslands [26].

Besides systems which are spectacular because of the structure size that may reach 10–20 m [26,29], there is however another very broad and ubiquitous class of vegetation patterns for which an interpretation as LSs appeared relevant [27]. While occurring most frequently at small spatial scales (from tens of centimetres to several metres), it relates to a very pervasive feature of plant development, namely clonal reproduction. Many plants or plant structures are made of elementary components often referred to as ‘ramets’ that clonally duplicate and grow to form larger vegetal entities, i.e. patches, which are frequently called ‘genets’. Ramets are basic plant ‘architectural’ units, built upon one main axis (stem) and featuring leaves, roots and buds. The main ramet axis may ramify or extend (organogenesis versus extension) as in any plant development scheme, but the most peculiar property of clonal plants, which is part of the broader category of reiteration processes [30], is that ramets replicate themselves many times to extend the size of the patch (genet). In doing so, genets may not only extend in area but also modify their overall shape. In two-dimensional space, this may lead either to the fractioning of the genet (for instance, due to dieback of the central part) or to the possible merging of different genets [31]. The first possibility leads to vegetation patches apparently distinct yet genetically homogeneous, whereas the second outcome may result in vegetation patches of heterogeneous genetic identity [31]. Both cases result in the blurring by clonal reproduction of the notion of ‘individual plant’.

Clonal reproduction is particularly notable regarding plant forms of small size such as grasses, herbs and shrubs. It also appears of increasing importance in ecosystems that are resource deprived and/or that experience strong climatic constraints (e.g. clonal propagation of *Olea europaea* subsp. *laperrinei* in the current climatic conditions in the Saharan mountains [32]) or frequent disturbance (e.g. grazing [33]). A pioneer work aiming at investigating clonal plant as self-organized LSs was carried out in reference to a desert grass in the Negev desert [27,28]. In this paper, we shall consider another constraining environmental context that corresponds to high altitude tropical drylands (tropical alpine regions) with a special reference to the Andes. Plants are there constrained by both cold temperature and a low rainfall-to-evapotranspiration ratio, while often experiencing grazing pressure from camelids (llamas, alpagas) [34]. In this environment, tussock-forming grasses and cushion-forming plants are important constituents of the vegetation cover [35]. In both cases (figure 1), vegetation patches appear made of many tiny ramets that are called tillers in the case of grasses and rosettes for cushions [36]. For each type of plant, we focus on a reference species: *Festuca orthophylla* (Poaceae) for grasses and *Pycnophyllum tetrastrichum* (Caryophyllaceae) for cushions. Each species can locally dominate the vegetation within the study area by forming largely monodominant patches contrasting with bare soils (figure 1; see also [37,38]).

We hypothesize that such patches can be modelled as self-organized LSs that are dynamical outcomes of the interactions occurring between ramets. Competitive interactions stem from the need for each ramet to track insufficient soil resource by developing lateral root systems (figure 2) thereby overlapping with the area that neighbouring ramets need to prospect. Facilitative interactions result from the influence that vegetation exerts on the physical environment (by mitigating harsh temperature, reducing evaporation and improving water infiltration) as well as on the biotic conditions, notably when plants reduce the negative effects of herbivores on other plants [39]. Such facilitative influences are extensively described in the literature [40], and more specifically for the two particular plant systems we are dealing with (see [38,41] regarding *F. orthophylla* and [42,43] regarding cushions).

We aim here to model and interpret clonal morphologies in the Andes as LSs by referring to the modelling framework introduced by Lefever & Lejeune [14] and further developed by Lefever

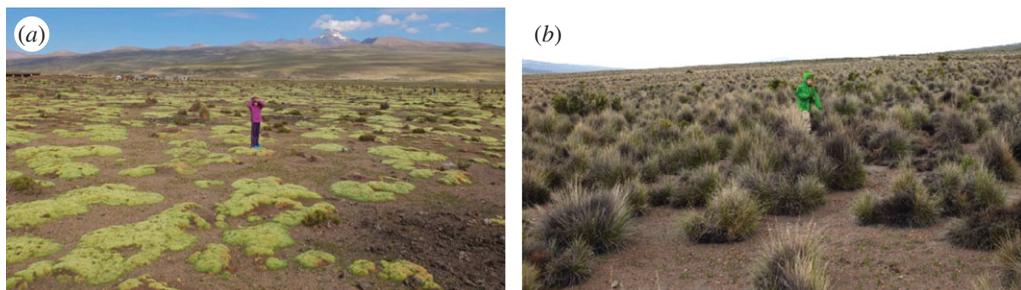


Figure 1. The two vegetation systems under study. Both display strong contrasts between bare ground and vegetation structures. (a) The cushion plant *Pycnophyllum tetrastichum*. (b) *Festuca orthophylla* also known as paja brava. Photos: F. Anthelme. (Online version in colour.)

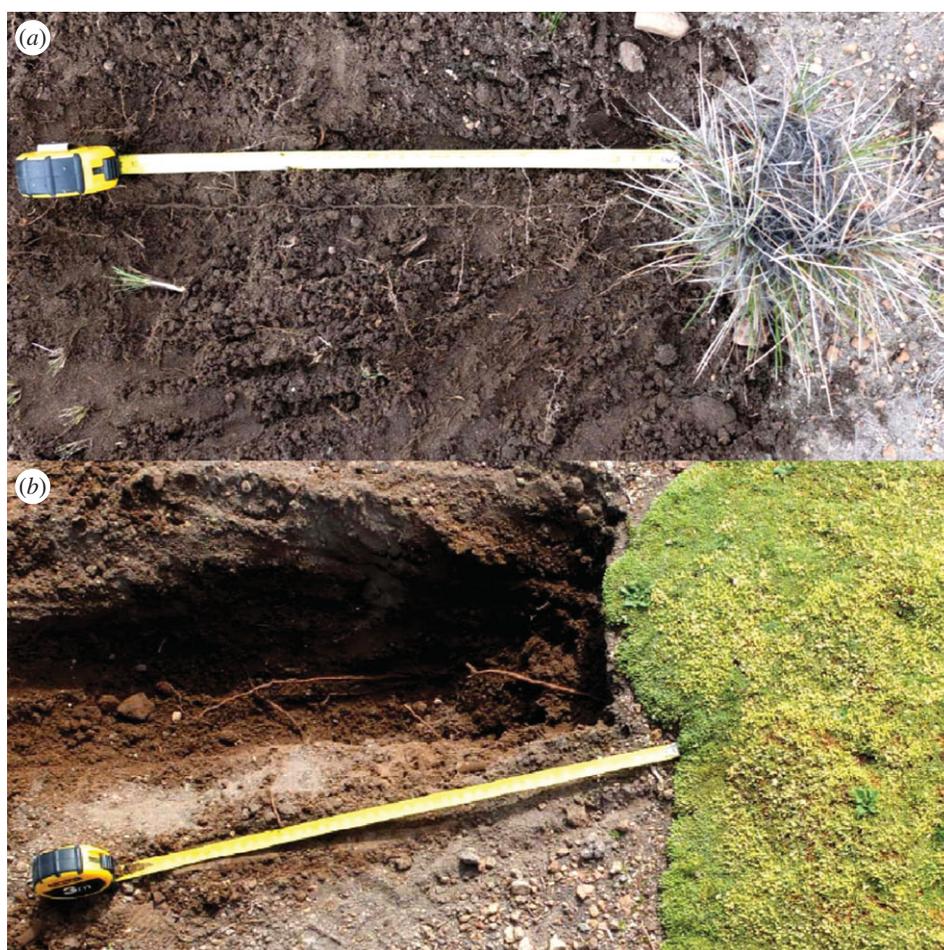


Figure 2. Lateral extent of the superficial rooting system at the periphery of the two plant forms under study. (a) A small tussock of *Festuca orthophylla*. (b) A large cushion of *Pycnophyllum tetrastichum*. Photos: F. Anthelme. In both cases, the measuring tape parallels one of the lateral roots and indicates 35 cm and 45 cm for (a) and (b), respectively. Note that the boundaries of the tussock/cushion have been preserved during root excavation. (Online version in colour.)

et al. [44] (see also [1]). This framework models the dynamics of the plant biomass using a single integro-differential equation that features logistic growth and non-local modulations expressing facilitative and competitive feedbacks of the biomass on its own developments. Such modulations are modelled via kernels that directly relate to plant morphology: the kernels embodying competitive and facilitative modulations have ranges of influences commensurate with the dimensions of the plant rooting system (rhizosphere) and above-ground part, respectively. In order to consider the dynamics of clonal systems, the emphasis will be here shifted from the plant to the ramet and the ranges of facilitative and competitive influences assessed accordingly.

In this paper, we will specifically refer to the version of the model proposed by [44] in relation to the modelling of spatially periodic bare ground areas or ‘gaps’ punctuating a vegetation matrix of comparatively high biomass (i.e. ‘deep gaps’). This model was also applied in [29] to the modelling of circular gaps or ‘fairy circles’ [45] occurring as isolated structures as well as aperiodic systems of gaps within a continuous grass matrix as observed in the drylands of Namibia. It demonstrated the potential of the model to produce LSs and to predict some of their characteristics. We will here explore how the model may account for LSs occurring as ‘bumps’ instead of ‘troughs’, to render clonal vegetation patches isolated within a bare soil matrix. We will show that considering the available data on ramet morphology and biomass dynamics in the reference ecosystem, the model is able to predict macroscopic features of the observed patterns, notably modal tussock size and inter-tussock distance. We will carry out a thorough interpretation of the available information to provide realistic values for the model parameters. On this basis, we intend to show that using this array of parameter values relating to processes at ramet scale, the model is able to provide predictions at the scale for which plant biomass displays the maximum level of spatial variation (as illustrated in figure 1).

2. Mean-field model for vegetation dynamics

It is well known in the literature that the concept of self-organization based on the idea of Turing [21], then Prigogine & Lefever [22], involves large spatial scales, in the sense that the macroscopic spatial scale resulting from a self-organization could be several orders of magnitude larger than the size of individual elements such as atoms, molecules, or trees, the interactions of which can be at the basis of self-organization. This universal process has been experimentally proved in several physical and chemical systems, including optics and lasers (see recent overviews on this issue [46–49]). The self-organization mechanism was applied to the context of plant ecology to explain spatially periodic vegetation patterns displaying large-scale periodicity compared to individual plant sizes and the ranges of spatial scales at which the elementary processes resulting from plant–plant interactions may take place in the field [1]. For instance, patterns involving grasses may reach a dominant wavelength of up to 10 m. When shrubs and trees are involved, the order of magnitude of the wavelength is often in the range of 40–100 m and may exceed 120 m [4].

Several families of models have been proposed to deal with self-organization in vegetation (see [18] for a review). All conceptually relate to the interplay between facilitative and competitive feedbacks of vegetation biomass on its own dynamics acting at distinct spatial scales [23]. We here refer to the modelling framework introduced in the seminal paper by Lefever & Lejeune [14] and more precisely to the development proposed in [44]. This variant of the model has been specifically applied to the modelling of ‘deeply gapped vegetation’ often observed in the sub-Saharan Sahel, where patches of bare ground regularly punctuate shrubby vegetation of comparatively high biomass. In a first application, Barbier *et al.* [50] assessed the parameters of the model in reference to deeply gapped vegetation observed in Niger and discussed in depth the meaning of the parameters while confronting field measurements to theoretical predictions.

The model consists of a single integro-differential equation governing the dynamics of the vegetation biomass density through the balance between biomass growth and death. Let $b = b(\mathbf{r}, t)$ be the above-ground plant biomass density at time t and at the point $\mathbf{r} = (x, y)$, we have

$$\partial_t b = b(1 - b)\mathcal{M}_f - \mu b\mathcal{M}_c + D\mathcal{M}_d. \quad (2.1)$$

The first term on the right-hand side of the equation expresses the logistic increase and saturation of the biomass density. The gain corresponds to the natural production of plants via seed production, germination and development of shoots into new mature plants. The second term models the biomass losses resulting from natural death of tissues or destruction by herbivores or other disturbances. In this second term, the parameter μ measures the scarcity of resources, and more generally the environmental adversity. In equation (2.1), non-local interactions are taken into account using the functions \mathcal{M}_f , \mathcal{M}_c , \mathcal{M}_d . Facilitative interactions between plants are modelled by the function \mathcal{M}_f which expresses the positive feedback favouring vegetation development. \mathcal{M}_c expresses competitive influences: when the soil water becomes scarce, plants strive to maintain their water uptake by adapting and extending their root systems (figure 2). They thus compete with other plants at long distance L_c . This is a negative feedback that tends to reduce the biomass density. The parameters ξ_c and ξ_f model the interaction strength associated with the competitive and facilitative processes, respectively.

In the following, we use the Gaussian-type kernel for both competitive and facilitative non-local interactions, i.e.

$$\mathcal{M}_{c,f} = \exp \left[\xi_{c,f} \int K_{c,f}(|\mathbf{r}' - \mathbf{r}|) b(\mathbf{r}', t) d\mathbf{r}' \right], \quad \text{with } K_{c,f}(|\mathbf{r}' - \mathbf{r}|) = N_{c,f} \exp \left(-\frac{|\mathbf{r}' - \mathbf{r}|^2}{L_{c,f}^2} \right), \quad (2.2)$$

where $N_{c,f}$ are the normalization coefficients:

$$N_{c,f} = \frac{1}{\int \exp(-|\mathbf{r}|^2/L_{c,f}^2) d\mathbf{r}}. \quad (2.3)$$

Note however that the ranges of the competition and the facilitation have been modelled as depending on the allometric exponent in [1,44]. But in what follows, we consider that both these characteristic lengths are constant, and therefore we do not model the role of ramet age/size classes in the community.

The third term in equation (2.1) is based on the function \mathcal{M}_d and is a source term that expresses biomass gains due to seed arriving in the focal location from adjacent vegetation. D is a phenomenological constant, which fixes the rate of propagation of the vegetation relative to the rate of local biomass growth and decay embodied by the two first terms of (2.1).

$$\mathcal{M}_d = \int K_d(|\mathbf{r}' - \mathbf{r}|) (b(\mathbf{r}', t) - b(\mathbf{r}, t)) d\mathbf{r}', \quad \text{with } K_d(|\mathbf{r}' - \mathbf{r}|) = \frac{\sigma}{\pi} \exp(-\sigma|\mathbf{r}' - \mathbf{r}|^2). \quad (2.4)$$

The homogeneous steady states (HSSs) of equation (2.1) are the branch of trivial solutions $b_0 = 0$ that represent territories devoid of vegetation: $b_0 = 0$ is unstable for $0 < \mu < 1$ and stable for $\mu > 1$. The two other homogeneous solutions comply with

$$\mu = (1 - b_s) \exp(\Lambda b_s). \quad (2.5)$$

They represent spatially uniform plant distributions. For $\Lambda > 1$ and $1 \leq \mu \leq \exp(\Lambda - 1)/\Lambda$, equation (2.5) admits two non-trivial solutions b_{s-} and b_{s+} . The uniform state b_{s-} is always unstable.

We now look for the conditions under which spatially uniform distributions of vegetation b_{s+} are unstable with regard to inhomogeneous perturbations. In the Fourier representation, growing modes are characterized by a finite interval of wavenumbers. This Turing kind of symmetry-breaking instability produces patterns characterized by an intrinsic wavelength determined by the system's dynamics rather than by geometrical factors and/or boundary conditions. Small amplitude deviations from b_{s+} in terms of Fourier modes in the space of wavevectors

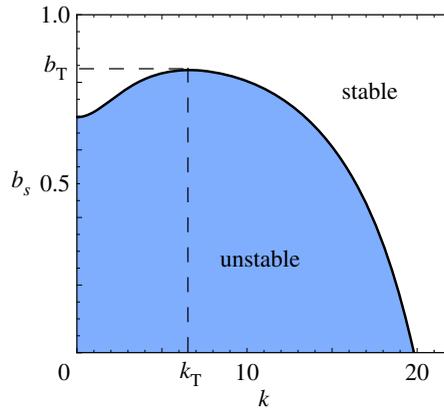


Figure 3. Marginal stability curve for the HSS solutions. Parameters used are: $\xi_c = 5.9$, $\xi_f = 9.1$, $L_c = 0.4$ and $L_f = 0.15$. The domain of instability is represented by the grey (blue online) area in the (b_{s+}, k) -plane. b_s is the HSS biomass density. The stability versus instability domains are separated by a solid line. b_T and k_T correspond to the threshold at which the symmetry breaking instability appears. (Online version in colour.)

$\exp(i\mathbf{k} \cdot \mathbf{r} + \lambda t)$ are considered. This analysis yields the eigenvalues of the linear operator

$$\lambda = (1 - 2b_s) \exp(\xi_f b_s) + (b_s - 1) b_s \xi_f \exp\left(\xi_f b_s - \frac{k^2 L_f^2}{4}\right) - \mu \exp(\xi_c b_s) \left(-1 + b_s \xi_f \exp\left(-\frac{k^2 L_c^2}{4}\right)\right) + D \left(\exp\left(-\frac{k^2 \sigma}{4}\right) - 1\right). \quad (2.6)$$

The wavelength of the first non-zero Fourier mode to become unstable is

$$\lambda_T = \pi \sqrt{\frac{L_f^2 - L_c^2}{\log(L_f^2 \xi_f / L_c^2 \xi_c)}}. \quad (2.7)$$

The threshold state at which the symmetry breaking instability appears on the b_{s+} branch of solutions is

$$\left. \begin{aligned} \left(1 + b_T \xi_c \exp\left(-\frac{k_T^2 L_c^2}{4}\right)\right) &= b_T (b_T - 1) \xi_f \exp\left(-\frac{k_T^2 L_f^2}{4}\right) + (1 - 2b_T) \exp(\xi_f b_T) \\ \text{with } \mu_T &= (1 - b_T) \exp(\lambda b_T) \quad \text{and} \quad k_T = \frac{2\pi}{\lambda_T}. \end{aligned} \right\} \quad (2.8)$$

The domain of instability includes the wavenumber of the fastest growing modulation. The critical wavenumber k_T corresponds to the situation where the HSS b_{s+} exhibits a pattern forming (Turing) instability as shown in figure 3. The coordinates in parameter space at which the symmetry-breaking instability takes place are $b_T = 0.78$ and $k_T = 4.6$. The corresponding aridity parameter at this instability is $\mu_T = 2.28$ and the wavelength $\lambda_T = 2\pi/k_T = 1.36$ m.

3. Reference vegetation patterns and parameter assessment

Large areas experiencing tropical alpine environments (TAE) are encountered in Africa and South/Central America, Southeast Asia and various islands, while 90% of these environments is observed in the Andes [51]. TAE experience cold minimum temperatures that constrain plant development [52], along with some distinctive features: (i) an inversion of rainfall gradients in the form of increasing aridity at higher elevation, (ii) strong nyctemeral variations (exceeding annual variations) in temperatures, and (iii) the absence of persisting snow cover contrary to most

alpine environments [52,53]. In this study, we will specifically refer to the Sajama National Park (SNP) in Bolivia for which climatic features, as described in [54], fit to the overall descriptions of TAE. Notably, the annual precipitation is around 350 mm and is concentrated between November and March. Locations in the SNP where direct observations have been carried out by one of us (F. Anthelme) experience the same climate.

The singular characteristics of TAE make some plant life forms specific to these regions, or at least let them be found there at higher abundance. Among them, cushion-forming plants (hereafter termed as cushions) are incredibly diverse and may reach giant sizes. Their abundance can reach 50% of the soil surface in dry alpine areas where vegetation is fragmented (figure 1), notably in the Chilean high Andes [55]. However, the relative cover of cushions in dry areas never approaches 100% and the patterns are biphasic. The three-dimensional shape of cushions is variable, but in general it can be described as relatively flat, with a low growth rate. The facilitative effects of cushions on plant communities in dry alpine environments are well known [55]. Cushions ameliorate minimum temperature, water and nutrient availability. Though intraspecific facilitation within cushion populations and between ramets of cushions has not been tested explicitly so far, it is highly probable that their structure, often composed of a large number of small rosettes (ramets) generating a compact cover [36], determines intense interactions between neighbouring rosettes, both positive and negative. Tussock grasses are frequently observed and often are a dominant life form in TAE [36,56,57]. There, tussock grasses display a typical two-phase structure with tussocks having a limited lateral growth and a high density of tall stems at tussock centre (figure 1). Although providing more humidity and nutrient than available in adjacent bare areas (see below), tussocks in dry environments are also thought to have a negative impact on other plants, because of strong competitive traits [58].

(a) Interpretation of the tussock pattern in the Sajama National Park

We here equate b (equation 2.1) with the above-ground biomass density (referred to hereafter as 'biomass') irrespective of the below-ground part. The density is defined with respect to the maximal local biomass observed, which is generally observable in the middle of a vegetation patch. In the case of *F. orthophylla*, we assume accordingly that a density of 1 is reached in the centre of every mature, non-senescent tussock, while the density is decreasing towards the periphery as described in [41]. For simplicity, the model does not distinguish the 'live' and 'dead' fractions of the biomass as in [41] and b can thus be considered as a 'phytomass' *sensu* [41]. The average biomass density over a tussock is estimated at *ca* 0.5. The overall basal area of the tussocks is reported to be *ca* 15–20%, a range of values which appears stable across space from both the literature [41] and direct measurements carried out by one of us in the SNP. We therefore assess the overall biomass density of this typical pattern as $\bar{b} = 0.18 \times 0.5$, i.e. *ca* 0.1.

In the model, non-local modulations express how the balance between biomass build-up and decay at the scale of a given ramet is affected by the influences, either competitive or facilitative, exerted by neighbouring ramets. Associated parameters are, first, the ranges of interactions (L_f and L_c , i.e. the ranges of the Gaussian kernels) which reflect ramet morphology and, second, the intensity of the modulations (expressed by ξ_f and ξ_c) of the overall biomass dynamics as ruled by μ .

(b) Morphological parameters

Based on the available published data and direct field observations (figure 2), we set L_c to the observed length of lateral roots (i.e. 40 cm for both the observed plant forms). We assessed the range of the facilitation effect resulting from lateral shading (integrating the effect of dusk and dawn sun inclinations) and protection from grazing as approximately half the height of an average mature ramet. In the case of the *F. orthophylla* grass, the average height of live tiller leaves is about 20–30 cm, and in accord with the modelling of interactions through Gaussian kernels, we set L_f to 10–15 cm.

(c) Facilitative and competitive feedbacks from the above-ground biomass

The intensity of facilitative and competitive modulations (parameters ξ_f and ξ_c) is first assessed with reference to the influence of vegetation on soil moisture (considered via the volumetric soil moisture content, vol%) within the shallow rooting zone. In the topsoil that is actually explored by tussock roots (<40–50 cm), soil moisture proved to be virtually undetectable during the dry season whatever the location [41]. But during the rainy season, strong variations were observed in time (depending on the occurrence of rain showers) as well as in space (under vegetation cover versus in open ground). Maximal values of soil volumetric moisture were reported to be above 5.5% under a grass tussock while they never exceeded 1.5% in the absence of vegetation. Moreover, a mulching experiment let soil moisture content reach as much as 19.4% [41], emphasizing the pervasive role of evaporation in depleting the scarce topsoil water resource. Moreover, the latter authors reported that the tussock aerial part was at least as efficient as the mulch in decreasing the hottest mid-day soil surface temperature and henceforth the evaporative demand. Hence, reinterpreting the published results allowed us to separate the relative effects of soil water consumption by grass tillers (competition) from the protection against evaporation (facilitation). It thereby appears that the reduction of evaporation by grass cover represents a possible increase in maximal volumetric soil moisture content up to 12 times the maximal content found in bare areas. Conversely, the potential water demand from well-developed tillers represents *ca* 9 times the bare soil content. The overall balance appears thus positive thereby illustrating the predominance of facilitation over competition that helps tillers survive adverse climatic conditions as soon as they are part of a tussock.

From those figures, it looks as if at the centre of a modal tussock the soil moisture was *ca* 2.5 times the level it reached under bare ground, far away from any vegetation influence. Reasoning on moisture values averaged over a rainy season instead of maximal values yields a lower, yet positive figure of *ca* 1.5 under vegetation. It is however reasonable to think that maximal values better render the functioning of the system, which is probably based on pulses of vegetation development triggered by discrete rainfall events. For instance, Barbier *et al.* [50] described the functioning of a semiarid system where the most striking difference in terms of water budget between vegetated and bare locations was mostly noted during the days following a rain shower before progressively fading away as the topsoil water dries up everywhere.

To transfer the above values into the parameters of the model (i.e. ξ_f and ξ_c), we can refer to the effect of unusually low rainfall, as reported by Monteiro *et al.* [41], who compared biomass production between 2007–2008 (considered as a ‘normal’ rainy season, 384 mm) and 2006–2007 (poor season, 327 mm, minus 15%). As a response of *F. orthophylla* to the decrease in rainfall, the mean standing tussock biomass dwindled by 40% (table 5 in [41]). But so strong a decrease was not a direct result of tiller death but rather reflected a reduction of the green fraction in the well-developed tillers [41], and caution is needed when interpreting it. On the other hand, studies of water-limited ecosystems with annual rainfall around 350 mm per year reported that grass biomass reduction accompanying a 15% rainfall decrease is about 30% [59]. From this observation and assuming a linear response of biomass production to any water resource fluctuations of reasonable amplitude, we set a ratio of 2 (0.3/0.15) and apply it to the modulation in soil moisture determined by a tiller bunch of modal size, as described above. According to the model, this modulation is to be equated to $\exp(\xi_f b^f)$ for moisture increase and $\exp(\xi_c b^f)$ for moisture decrease, where b^f is the mean biomass density of tillers over a tussock that is *ca* 0.5. This yields for the two parameters, $\xi_f = 6.3$ and $\xi_c = 5.8$. Λ therefore amounts to *ca* 0.5 making the vegetation system look as weakly cooperative considering the only aspect of vegetation feedbacks on biomass production through soil water resource. This weakness of the positive balance is due to the strong demand of the grassy cover for transpiration. However, plant biomass also exerts another kind of positive feedback since it acts as a protection against grazing. This second source of facilitation can be considered as additive to soil moisture modulation since it is independent from the soil water resource. We will assess it in the subsequent discussion as part of the overall biomass dynamics.

(d) Overall biomass dynamics

μ is basically the ratio of the plant biomass lost to the biomass produced at low biomass levels (i.e. far under the logistic saturation). In the considered ecosystem, biomass loss features two components, which are senescence of live plant material as well as live biomass destruction by grazing. Those two causes each determine additive fractions of μ , i.e. $\mu = \mu_0 + \mu_g$ relating to senescence and grazing, respectively.

μ fundamentally expresses the potential development of a small amount of live plant biomass (typically a small bunch of young ramets) that does not benefit from facilitative retroaction from pre-existing developed plants. The young plant will either die out if the conditions are also unfavourable ($\mu > 1$) or develop at a rate which is a decreasing function of μ . Qualitatively, we expect μ to be a decreasing function of rainfall. From experimental results [41] and direct field observations, it appears that without any facilitative effects by large pre-existing biomass tiller development is very weak and may not completely balance decay. So μ_0 should be substantially larger than 1.

In the case of *F. orthophylla*, we shall rely on an experiment reported in [60, p. 31] that provides elements to assess the grazing-related part of μ : after experimental burning (i.e. removal of most of the above-ground biomass), the biomass regrowth is dependent on the root system which has been spared by fire. In fenced plots that were not accessible to camelids, the total biomass production during the first year of regrowth was seven times higher than in unfenced plots subjected to grazing. Assuming an exponential regrowth curve at plot scale, since the system restarts from virtually no above-ground biomass, it yields: $\mu_g = \log(b_f/b_u)/(t_f)$, where b_f/b_u is the ratio at the end of the first year after burning of biomass in fenced to unfenced plots and t_f is 1 year or *ca* 2 tiller generations [41]. Accordingly, we assess $\mu_g = \log(7)/2 = 1$.

Another aspect of the same experimental design also showed that fencing out camelids only determined a small increase in biomass production (*ca* 10%) at and around the biomass levels of the patterns usually observed in the studied area, i.e. \tilde{b} . This indicates that shielding a large share of young and productive tillers against grazing is an important component of the positive feedback that a grass stand exerts on its own dynamics. It is apparently as if this modality of facilitation cancels out a substantial part of the grazing impact. To assess the magnitude of such a protecting effect and deduce the final value of ξ_f , we relate the slight increase in biomass production Δ_s between fenced and unfenced situations to μ_g and ξ_f^0 as

$$\xi_f - \xi_f^0 = \frac{\exp(-\tilde{b}\xi_f^0)}{\tilde{b}(1-\tilde{b})} \left(\frac{\mu_g + \Delta_s}{\tilde{b}} \right), \quad (3.1)$$

where $\xi_f^0 = 6.3$ corresponds to the value assessed at the previous point and refers to the only aspect of vegetation feedback on soil moisture. This finally yields $\xi_f = 9.1$ and $\Lambda = 3.3$.

A last step is to assess μ_0 via μ . For this, we posit that the small-sized tussocks observable (as in figure 2a) represent the minimal concentration of biomass which allows the survival of a tussock in spite of environmental adversity. We then relate their biomass density (over an individual small tussock) to μ by assuming that equation (2.5) applies at individual tussock scale while it was previously applied to describe the homogeneous biomass density over the whole pattern. Small tussocks have a diameter of *ca* 10 cm against *ca* 35 cm for a modal tussock, and we estimate their average biomass density as half b^t , i.e. 0.25.

Such a figure associated with Λ (*ca* 3) as previously assessed leads to values of μ close to 4.5, that is μ_0 close to 3.5. We used all these values for simulations (figures 4–6).

4. Clustering and localized vegetation patterns

Localized vegetation patterns and clustering behaviour have been described in various arid regions or in nutrient-poor territories of South America, West Africa and Namibia [26,29]. Such patterns are ‘spatially localized’, in the sense that they are elemental structures (vegetation patches or holes in the vegetation cover) which have a well-defined size. On the theoretical side,

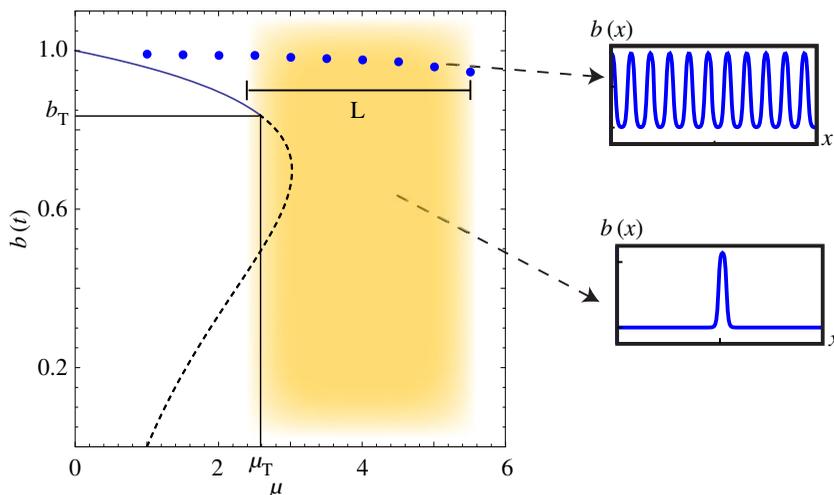


Figure 4. One-dimensional bifurcation diagram and LSs. Same parameter values as in figure 3. The bare HSS b_0 is stable for μ_T values above 1 and unstable below. The solid and dashed lines correspond to stable and unstable HSSs (b_{s+} and b_{s-}), respectively. The dots (blue online) are the maximal biomass density values obtained at the centre of the periodic structures for the one-dimensional simulations of the patterns along a gradient of increasing μ values (see illustration on the right-hand side of the figure). The domain where localized solutions exist is denoted by L (illustration of a soliton on the right-hand side). A value of $\mu = 4.5$ has been used for all the simulations. (Online version in colour.)

spatial localization is a patterning phenomenon better known in contexts of a physico-chemical rather than biological nature. It is established that various, quite different non-equilibrium systems exhibiting a modulational instability or a Turing type of bifurcation may display pinning phenomena generating the so-called LSs. In [26,29], the analysis has been restricted to a weak gradient approximation, while in what follows we investigate this phenomenon in the full integro-differential model (equation (2.1)).

A bifurcation diagram in the plane $(b-\mu)$ is shown in figure 4. The solid line corresponds to stable HSS and the dashed line to unstable HSS. The circles indicate the maximum values corresponding to the periodic structures that emerge subcritically from the Turing instability located at b_T, μ_T . We focus on the regime where the system exhibits a coexistence between the bare stable state b_0 and the periodic vegetation pattern. In this region of parameter space, there exists a domain denoted by L (figure 4) where localized vegetation patches are stable. Examples of stable localized vegetation patches with one, two or several peaks are shown in figure 5. The numbers of peaks in the localized patterns are determined solely by the initial conditions used. All the displayed LSs are obtained for the same parameter values. They can either be self-organized or randomly distributed in space as shown in figure 5. LSs or localized patterns are homoclinic solutions (solitary or stationary pulses) of partial differential equations among which reaction-diffusion models or integro-differential equations such as our model (equation (2.1)). The condition under which LSs and periodic patterns appear are closely related. Typically, when the Turing instability becomes subcritical, there exists a pinning domain where LSs are stable. LSs occur in various fields of nonlinear science, such as chemistry [61–65] and optics [25,66–68].

For the tussock grass, we use the parameters estimated above to compute the wavelength expected for the pattern at the first non-zero Fourier mode to become unstable (equation (2.7)). It yields 0.95 m, i.e. within the range of distances between tussock centres measured in the field (0.8–1 m). λ_T strongly depends on the values taken for the ranges of facilitative and competitive interactions between ramets. Simulations that took $L_f = 0.1$ m and $L_c = 0.4$ m also reached a wavelength of *ca* 1 m and closely mimic the observed patterns as illustrated in figure 6. This indicates a certain robustness of the result against variations of the most influential parameters within a realistic range of uncertainty.

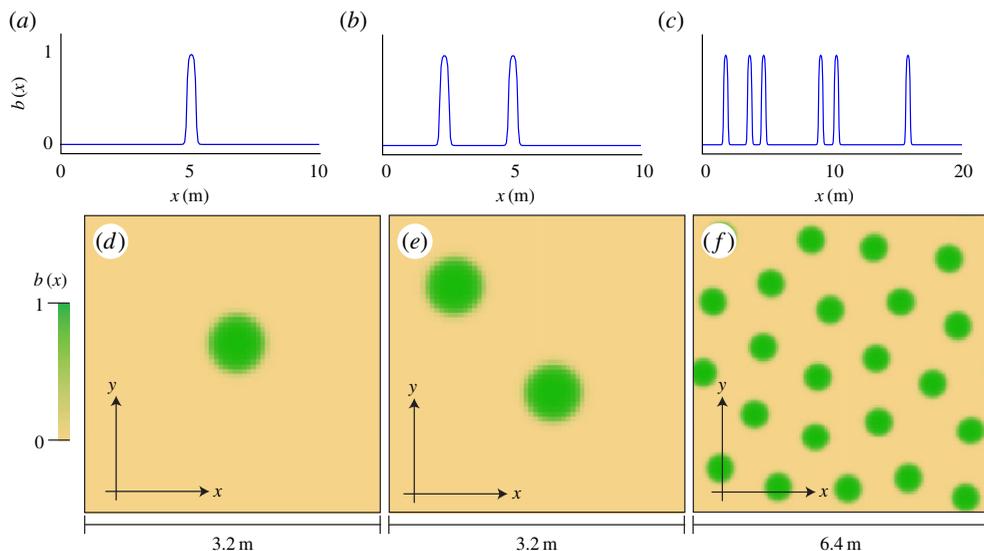


Figure 5. Localized vegetation patterns in one and two dimensions. The figure shows the variation of the number of LSs according to the initial conditions used for simulations, in one dimension (*a–c*) and in two dimensions (*d–f*). Note that the two series are independent. All panels display the variation of biomass density in one or two dimensions, and the results have been obtained for the same set of parameter values as in figures 3 and 4, for a fixed value of the aridity parameter $\mu = 4.5$. (Online version in colour.)

5. Discussion and conclusion

We have here proposed interpreting patchy patterns displayed by herbaceous, clonal vegetation in the tropical alpine regions of the Andes as self-organized LSs, in environments for which vegetated cover and bare soil appear simultaneously stable. Several elements encouraged us towards this type of interpretation. First, it is widely acknowledged from botanical observations that elementary plant units or ramets play a fundamental role from both the dynamical and functional points of view in what appears in figure 1 as ‘vegetation patches’ (e.g. [69,70]). Moreover, there is for many species no information on what the genetic structure of the patches may be and there is no *a priori* reason to consider the overall dynamics of a given patch as constrained or influenced by an overall genetic programme as for some other plant forms such as trees or annual herbs. For example, the subantarctic cushions formed by *Azorella selago* were demonstrated to be the result of the aggregation of several individuals with distinctive genetic material, and not only one single genet [31]. Several qualitative observations support such an interpretation. Patches are not permanent entities since they are known to change shape and even divide as part of their dynamics. Although we did not emphasize this aspect, senescence of the central part of the tussock grass *F. orthophylla* is also observable in our reference area, as was described and modelled for other grass species in various types of ecosystems, e.g. *Poa bulbosa* in the Negev desert [28] or *Scirpus holoschoenus* in eastern central Italy [71]. Clearly, such dynamics casts doubt on considering patches as ‘individuals’. Moreover, for certain species, the planar growth of a patch may appear as unlimited once the resource constraint and/or the competition from other species has been removed or alleviated. We may here quote the case of Andean cushion bogs, especially those dominated by *Distichia muscoides* (Juncaceae), a cushion plant found in the TAE of the Andes: on dry slopes it forms small, circular cushions while in wet bottomlands with saturating water conditions it can develop a continuous cover [72] (F. Anthelme 2014, personal observation). It therefore appears sensible to look at those patches strongly contrasting with bare ground as structures emerging from the interactions between the ramets in the context of environmental conditions unfavourable to plant growth.

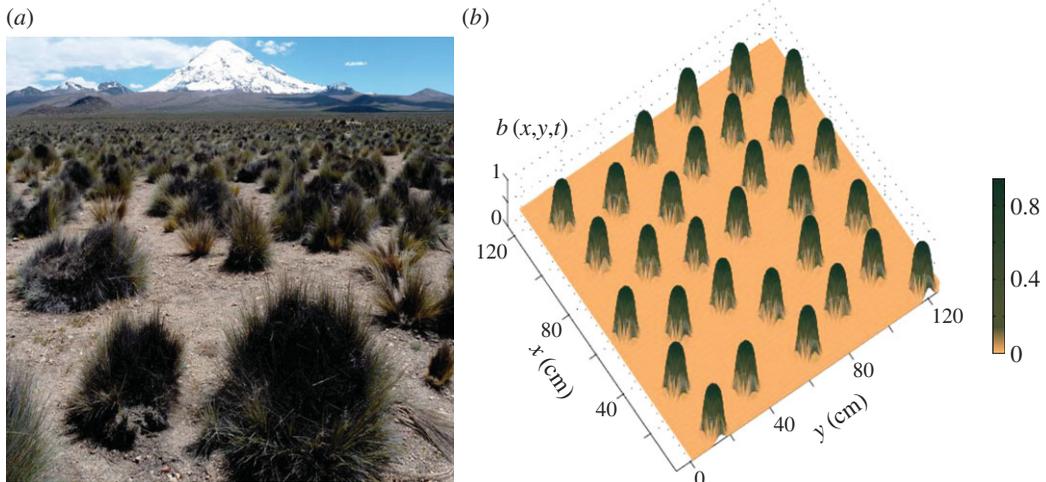


Figure 6. Overall comparison of (a) a system of tussocks of *Festuca orthophylla* (observed in the Sajama National Park, Bolivia) with (b) the simulation results. The simulated system displays a mean distance between tussock centres (xy coordinates in cm) that agrees with the range of values observed in the field (i.e. 0.8–1 m). (Online version in colour.)

A large share of self-organization models that have been developed to account for spatially periodic vegetation patterns can also yield LSs within the part of the parameter space that corresponds to conditions harsher than for periodic patterns. Under such adverse conditions, plant LSs owe their existence and perpetuation to strong facilitative effects from pre-existing biomass and the locations of the structures are strongly dependent on initial conditions. With the model [44] on which we relied here, the adversity of the environment is measured by a single parameter μ , which should strongly exceed 1 (the level at which biomass production and destruction are balanced) if LSs are to be obtained. In addition, facilitative effects should markedly exceed competitive influences and a strongly positive value of Λ is expected. In the case of *F. orthophylla*, reinterpreting soil moisture data from Monteiro *et al.* [41] allowed us to assess Λ via the modulation coefficients ξ_f and ξ_c . It appeared, however, that the influence of the pre-established tussocks on the soil moisture, though globally improving the soil moisture budget does not yield strong enough values of Λ to match very strong values of μ . On the other hand, acknowledging μ as cumulating both aridity and grazing as additive sources of environmental adversity led to a strong overall value of Λ (*ca* 3). Grazing is indeed a crucial component of these ecosystems, as suggested by the experimental results of [60]: fencing out camelids appeared necessary to let the above-ground biomass rebuild from the root systems during the first year after burning. This experiment also qualitatively confirmed that the development of young ramets crucially needs the sheltering of extant biomass. The pervasive role of facilitation [39] is here illustrated all the more in that growing from preserved root systems is far less demanding than growing from isolated seed germination, i.e. virtually from scratch with no facilitation.

Hence facilitation appears here pervasive in the case of ramets belonging to the same species, while there is a growing body of literature emphasizing the role of interspecific facilitation in tropical alpine ecosystem vegetation (see [53] for a review). On the other hand, a fencing out experiment when applied to unburned tussock patterns of current biomass density resulted only in a modest biomass increase in the ungrazed compartment [60]. This pleads for strong constraints endogenous to a mature system, which reflect competition for limited soil resources and even for space. The central parts of the tussocks are indeed reported at saturating biomass levels (as rendered by the logistic term in the model), while at the periphery, competition from extended lateral root systems is evident (figure 2) and hinders ramet development at the fringes. (Besides, it is highly probable that not only soil moisture but also nutrients are limiting; see [60, p. 31].) As a consequence, the removal of the grazing pressure does not trigger a rapid development of the overall biomass of the system, which can however be considered of low density \tilde{b} with respect

to the maximal biomass encountered at the centre of most patches (ca 1): \tilde{b} was assessed in the range 0.08–0.15 since the basal area of the tussocks covers around one-fifth to one-sixth of the ground surface.

Low biomass density, strong facilitative and competitive effects and overall sensitivity to the initial distribution of biomass, all those conclusions are consistent with the interpretation of the patchy vegetation patterns on the Altiplano as systems of LSs. In this paper, we aimed to verify that interpretation by matching predictions of a simple, fairly generic model of vegetation dynamics with some macroscopic features of the observed systems. In the best documented case of *F. orthophylla* (thanks to the considerable work carried out by Monteiro [60]), both our analytical predictions and simulations yielded an inter-tussock distance λ_T within the range of values observed in the field (i.e. 0.8–1 m). Moreover, the equation predicting λ_T appears mainly sensitive to the ranges of facilitative and competitive interactions, i.e. L_f and L_c . Considering the morphology of cushions (figure 2), similar values of λ_T are probable for this life form, and indeed field measurements in the location where the picture of figure 1 was taken pointed towards mean λ_T values of 1.4 m.

In this paper, we show that the systems of vegetation patches made of clonal plants and observable in the tropical alpine region of the Andes are plausibly patterns self-organizing under the form of LSs. Yet, to progress in our understanding of the phenomenon, we need additional observations and data at both landscape and plant scales. At the broad scale, it would be useful to acquire aerial photographs of patterns (for this, drones now provide an efficient solution) to check pattern characteristics over rainfall gradients. In the SNP patterns look aperiodic while patches appear to have a modal size (figure 1), but this is to be systematically checked in diverse locations and conditions. Image analyses of patterns over ecological gradients proved fruitful in other contexts [3,6,8,73]. If our interpretation based on LSs is correct, tussock/cushion systems may shift towards periodic structures under wetter climates. Conversely, in drier or more heavily grazed situations, systems of LSs are expected to give way to more scattered LSs of highly random spatial distribution (as for simulations in figure 5). *Festuca orthophylla* is obviously a good opportunity for such analyses, especially because it is observed at regional scale of the Andean Altiplano along a gradient of increasing aridity, from Lake Titicaca to the Salar of Uyuni (F. Anthelme 2014, personal observation). At ramet scale, and since our reference model [44] emphasized plant morphology, more accurate values of interaction ranges should be deduced from an analysis of how ramets ramify and how bunches of ramets of common origin connect to the longest lateral roots (figure 2) that determines the competition range. Greater accuracy in model predictions, via enhanced measurements of interaction ranges L_f and L_c are strongly dependent on improved understanding of how above-ground architectural units connect to the different components of the patch rhizosphere. On the dynamical side, it is necessary to carry out experiments to verify how isolated small bunches of ramets react to variation in soil water resource and identify which level of soil moisture corresponds to the critical value of $\mu = 1$. It is at this stage really interesting to have a reference model and well-defined theoretical predictions to guide field data collection in the future. It is all the more interesting that vegetation patterns are known to react to changes in both climate and anthropic influences [3,15,16,23,74,75], and notably systems of LSs may be thought of as the last stage before a possible collapse of vegetation cover and associated ecological functions and services.

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