1 **Ecological and socio-economical thresholds of land and plant-community degradation in semi-**

2 **arid Mediterranean areas of southeastern Spain**

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11 **Abstract**

12 The climate of semi-arid Mediterranean areas is characterized by highly variable rainfall and

13 seasonal droughts, which favor highly specialized flora, high biodiversity, and the emergence of a

14 large number of endemic species. Such highly specialized complex ecosystems are expected to be

15 more difficult to return to a previous state following perturbation than are more mild ecosystems and

16 lead to dramatic transitions in vegetation. An understanding of the circumstances under which

17 irreversible transition shifts occur is vital in an age of climate change and socio-economic

18 globalization, which will have significant consequences for those highly specialized areas unless

19 management practices, conservation, and preventive measures are increased. Within ecosystems, the

20 interactions between multiple factors acting at multiple temporal and spatial scales, and the inertia of

21 ecological processes, make the consequences of current management practices persist for a long

22 time. With the task of understanding the relative importance of the underlying mechanisms that

23 influence the resilience of drylands in southeastern Spain, we reviewed what is known about plant-

24 soil interactions and the role of the self-organizing capacity of vegetation in the formation of

25 vegetation spatial patterns at multiple spatial scales. In addition, we evaluated the importance of

26 threshold indicators as early detectors of transition shifts in dryland ecosystems.

27

28 **Biophysical and socio-economical factors that influence landscape configurations**

29 Landscape configurations result from processes that act at multiple spatial and temporal scales.

30 Abiotic factors have a significant influence on the distribution of plant communities within a

31 landscape and act as the first species filter. Long-standing human management of the land,

32 particularly livestock grazing, acts as a secondary successional species filter (Swanson et al., 1988;

33 Cingolani et al., 2003; Sebastià et al., 2008). Humans have been modifying the landscape in

34 southeastern Spain since they began occupying it in remote period, constrained only by the physical

1   limitations imposed by the landscape. There are, however, uncertainties about the relative importance

2   of biophysical and socioeconomic factors and the dynamics of desertified and desertification-prone

3   areas (Herrmann and Hutchinson, 2005; Verón et al., 2006; Reynolds et al., 2007).

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5   *Factors in the development of the Mediterranean landscape*

6   Like other Mediterranean coastal areas, the landscape of the southeastern region of the Iberian

7   Peninsula was affected by the widespread climate change that occurred at the end of the Tertiary

8   Period, which led to the region's characteristic summer drought, and tectonic activity of its

9   orographic systems, which increased erosion on hillslopes and sedimentation in drainage networks.

10   During the Holocene Epoch, arid conditions established in the basin; the area was particularly dry 6

11   ky and 4 ky BP, and humid periods occurred 3 ky and 250 y BP (Rognon, 1987). Carbon isotopes in

12   grain cereals from throughout the Iberian Peninsula indicated that the N-S aridity gradient tended to

13   become pronounced during the last 5 ky (Araus et al., 1997). A growing body of paleobotanical

14   evidence indicates that xeric plant species have been displacing mesic woodlands northward to

15   higher elevations (Parra, 1993). The activities of humans have influenced the current composition

16   and distribution of the vegetation in the Mediterranean region (Pons, 1981; Pons and Reille, 1988).

17   Humans have aided the expansion of sclerophyllous vegetation, e.g., evergreen oaks and pines in dry

18   soils at the expense of deciduous and semi-deciduous oaks. In that way, humans have created a

19   mosaic-like landscape that has a very complex spatial structure and high biodiversity (Naveh, 1991).

20   The changes that occurred over the long-term were at rates that were several orders of magnitude

21   lower than those that are occurring today. In the distant past, the influence of humans was absent or

22   very limited. In the last few hundred years, however, in southeastern Spain, the amount of land

23   degradation influenced by climatic and sociological factors acting synergistically has been significant

24   (Puigdefabregas and Mendizabal, 1998).

25   During the Little Ice Age (LIA) the Iberian Peninsula had a climate that was cooler and more humid

26   that it does today, but it was a period of high variability. The lowest maximum annual temperatures

27   occurred in the second half of the 17th C., which were about -0.5 ºC below the average for the

28   Medieval Period (Creus, 1983). Since that time, temperatures have been slowly increasing as the

29   amount of precipitation has been decreasing (with the exception of a small increase at the beginning

30   of the 21st C. Since 1900 the rate of the decrease in annual rainfall has been about 3 mm/yr (Brandt

31   et al., 1991; Oñate Rubalcaba, 1993).

32   In Spain, socio-economic systems underwent three significant events, which led to changes in land

33   use over the last 500 yr. The first occurred in the 16th and 17th C. because of the establishment of

34   complete Christian rule throughout the Iberian Peninsula, which favored the southward expansion of

1 the dryland agriculture, and the colonization in America, which increased the demand for wool and

2 wood products to meet the needs of the settlements in America (Elliot, 1965) and the growing ship-

3 building industry (Dupre Ollivier, 1990). As a result, the area dedicated to grain crops and large scale

4 sheep industries expanded and the amount of forest was reduced. The population increase that began

5 in the 18th C. brought about the second phase (Dupre Ollivier 1990), which overcrowded the rural

6 area during the first half of the 20th C. The major technological, social, cultural, and economic

7 changes that occurred in rural areas in the 1960s led to the third significant period.

8 In the period encompassed by the 16th and 18th C., the cold and humid climate (at the peak of the

9 LIA) and extensive changes in land use that left large areas exposed to erosion had a significant

10 impact on the landscape (Hoffmann, 1988).

11

12 *Patterns of land degradation*

13 In the 19th and early 20th C., the growth of human populations in rural areas, which caused a need

14 for the expansion of agriculture, led to the degradation of the land. In the second half of the 20th C.,

15 the expansion of industry in urban areas reduced the rural population, and agriculture was

16 concentrated in the most productive areas; namely, within irrigation developments. Since the mid-

17 20th C., inland populations have decreased as populations increase in coastal areas. The

18 'litoralization' of the economy is particularly acute in Spain, where the population density in the

19 coastal Mediterranean region is twice the national average (Grenon and Batisse, 1988). Marginal

20 and irrigated lands are the current hot spots of land degradation. In the semi-arid regions of

21 southeastern Spain, mining, extensive agriculture, and livestock production date to the Bronze Age

22 (Chapman, 1978). Those practices and the scarcity and irregularity of rainfall have created the

23 current landscape, which is dominated by xeric steppes on hillslopes with a few areas in the wetter

24 sites that have open shrublands and some pinewood forests at the higher altitudes. Those areas had

25 low productivity and, in the second half of the 20th C., anthropomorphic forces were exerted through

26 the use of hillslopes for extensive livestock grazing and the use of valley basins for rain-fed

27 agriculture, mainly cereal crops. Although humans have existed in the area since the Neolithic

28 Period, the low productivity has favored a reduced population density. With the aid of agricultural

29 technologies that were developed in the last 20 yr, the use of ground-water from aquifers and

30 desalinization plants has enabled the rapid development of greenhouses and tourism in the coastal

31 plains of Almeria (Tout, 1990). The expansion of irrigation projects in the area relies mainly on

32 ground-water sources. The risks include overdrafting, degradation of aquifers by marine intrusion,

33 land degradation caused by salinization, topographic reshaping, and surface-mining of sand to meet

34 the demand from greenhouses (Puigdefabregas and Mendizabal, 2004). With the exception of the

latter human impact, the scarcity of water in the area has discouraged exploitation by humans, which has led to a well preserved and well adapted xeric vegetation that has remained in a state similar to that described in the scientific botanical explorations of Simón de Rojas 200 yr ago (Gil Albarracín, 2002). In some of the badlands in southern Spain, archaeological evidence indicates that conditions existed 5 ky ago (Wise et al., 1982).

The abandonment of agricultural and mining activities in the 1960s did not lead to the recovery of the shrubland vegetation. Resilience (the ability to return to a previous state after perturbation) (Holling, 1973) in those semi-arid ecosystems is low because of the scarcity of resources and the pronounced fluctuations in precipitation (Noy-Meir, 1990; Milton and Hoffman, 1994). Thus, in Cabo de Gata-Nijar N.P., between 1957 and 1994, 45% of croplands in the area were abandoned and was not transformed into shrubland (Alados et al., 2004b); only the amount of tallgrass steppe of *Stipa tenacissima* (19%) and arid garrigues (24%) increased. The slow recovery of the vegetation that is associated with xeric slopes was also reported by Cerdá (1998) in southeastern Spain. More recently, an increase in the demand for biomass for biofuels has caused some reversal of this trend and many set-a-side areas have become cultivated again. A large-scale survey of the state of the land on the Iberian Peninsula (Barrio del et al., 2010) indicated an increase in land degradation in the southeast, but it was associated with the decrease in annual rainfall, rather than to an intrinsic worsening of the condition of the land, which is much less widespread. Mitigation programs have to distinguish between active desertification and relict desertification. In the former, stressors must be relieved, whereas in the latter, the rehabilitation or restoration of threatened areas, or even doing nothing is sufficient.

Vegetation spatial patterns at multiple scales

A characteristic of complex biological systems is that they are governed by processes that act at multiple spatial and temporal scales, and it is in the cross-scale interactions where irreversible positive feedback processes can be triggered (Peters et al., 2004) and where higher levels constrain the structure and function of lower levels (Brown and Allen, 1989; Holling, 1992). For example, when the distance between ecosystem fragments exceeds a dispersal threshold, the disruption in connectivity can lead to metapopulation extinction (Alados et al., 2009b). Species richness and spatial patterns can depend on forces that operate across a wide range of temporal and spatial scales (Brown and Lomolino, 1998). Grazing can enhance plant diversity at fine scales by reducing plant competition, but it can inhibit diversity at coarse scales depending on the supply of propagules from neighbouring areas Olff and Ritchie (1998). This is especially relevant in arid areas where species that have a restricted spatial dispersal are abundant because the space suitable for germination is

scarce and it is advantageous to germinate close to the mother plant (Van Rheede van Outshoorn and Van Rooyen, 1999). Consequently, species that have restricted spatial dispersal (reduction of dispersal mechanisms or have anchorage mechanisms), which are predominant in arid regions (Ellner and Shmida, 1981; Gutterman, 1993; Navarro et al., 2009), are very sensitive to habitat fragmentation (Alados et al., 2010). In semi-arid areas in southeastern Spain, the isolation of remnant fragments had a negative effect on plant species richness (Alados et al., 2009a) and led to an increase in the differences in species composition among fragments (spatial variability in species distributions was greater than that expected from a random spatial distribution). Indeed, species distributions became more homogenized among large fragments because of diffusion processes.

The negative effects of habitat fragmentation on plant dispersal can be ameliorated by traditional grazing practices because, in many areas, livestock are essential for the dispersal of many plant species (Fisher et al., 1996). In dry environments, livestock are the primary dispersal agents of plants and can increase seedling success through consecutive stages of establishment throughout seed ingestion and deposition (Manzano et al., 2005; Robles et al., 2005; Ramos et al., 2006). In Spain, free-ranging sheep traveled > 25 km per day during transhumance (Klein, 1981), thereby spreading seeds over a large area. Although transhumance has almost disappeared in Spain, the daily movements of free-ranging sheep are still important because they travel about 6 km per day. Comparisons between fragmented and non-fragmented landscapes in the semi-arid regions of the Middle Ebro Valley, where gypsophilic species exhibited dispersal patterns that are associated with short dispersal distances (i.e., myxospermy (Escudero et al., 1999)), showed that grazing ameliorated the detrimental effects of habitat fragmentation on species diversity (Pueyo et al., 2008b).

While landscape spatial patterns influence the spatial distribution of species, organisms can shape their ecosystem by acting at the local scale, and influencing large-scale contagious processes such as insect outbreaks and spreading fire (Holling, 1992). In semi-arid ecosystems, local interactions between organisms and their environment, such as facilitation mechanisms (Bertness and Callaway, 1994; Pugnaire et al., 1996; HilleRisLambers et al., 2001), and limited dispersal ability (Miller et al. 2002), promotes the development of self-organized spatial patterns (Aarssen and Turkington, 1985; Soro et al., 1999; Solé and Bascompte, 2006) that emerge at larger scales (Rietkerk (Rietkerk and van de Koppel, 2008; van de Koppel et al., 2008). For example, woody species act as landscape modulators by altering the structure of the soil and the redistribution of nutrients (Rietkerk et al., 2002; Gilad et al., 2004; Meron et al., 2004), and provide refuge for grazing species (Rebollo et al., 2002). Those species are important landscape modifiers that can generate a two-phase mosaic of patches of woody phytomass and open space. In addition, the combined effects of spatial self-structuring and epigenetic selection can result in niche complementarity. Communities assembled by

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self-organizing processes such as niche complementarity, which includes niche differentiation and facilitation interactions, develop an increase in the efficient use of resources (Venail et al., 2008) and plant diversity has a positive effect on primary production (Loreau and Hector, 2001). In addition, the greater likelihood of relatedness among neighbors favors community-level selection (Johnson and Boerlijst, 2002) The destruction of the spatial structure of the community disrupts the self-organized gene-complex of long-standing stable communities. Microcosm experiments demonstrated that uniform populations rapidly diversified when distributed within spatially structured microcosms. Diversity was lost when the spatial structure was broken by shaking the microcosms (test tubes) (Rainey and Travisano, 1998).

Detecting vegetation transitions from spatial patterns

Most indicators of ecosystem-level stress are merely descriptors of past transitions between ecosystem stages (Westoby et al., 1989); however, changes in ecosystem attributes should be detected when management actions are cost-effective. In addition, in semi-arid regions, the transition from vegetated to desert zones is not always gradual; rather, they can occur suddenly and irreversibly (Scheffer et al., 2001; Rietkerk et al., 2004; Kéfi et al., 2007). Although, the random inter-annual variations in precipitation that are typical of Mediterranean semi-arid environments (Noy-Meir, 1973) might result in an intermediate, statistically stable configuration between the two states (D'Odorico et al., 2005). The ability to forecast system dynamics is limited; at least the emergent patterns that reflect gradual or imminent transition shifts can be detected. The objective is not to identify when the transition occurred, but to confirm whether the system is being pushed towards a new trajectory, and to detect any threats to the integrity of the ecosystem. Models of complex systems cannot predict where critical transitions will occur, but the vulnerabilities of the ecosystem to critical thresholds can be identified (Guttal and Jayaprakash, 2009; Scheffer et al., 2009). Indeed, complex systems need considerable time to manifest patterns in oscillations and, at the early stages of colonization, species are randomly distributed (Solé and Bascompte, 2006; Cutler et al., 2008). As the ecosystem develops, positive interactions between neighbours and population growth cause patch nucleation and coalescence (Yarranton and Morrison, 1974; Cutler et al., 2008). On the other hand, an increase in disturbance often leads to unpredictability (randomness) in species distributions (Alados et al., 2003; Alados et al., 2004a). Spatial interactions in natural plant communities can produce emergent patterns at higher spatial scales (Martens et al., 2000; Peterson, 2000; Rietkerk and van de Koppel, 2008). Different kinds of models resulted in plant spatial pattern formation (HilleRisLambers et al., 2001; Lejeune et al., 2002; Meron et al., 2004; Barbier et al., 2006). All of those models are limited because they cannot incorporate all of the sources of the variability of the

system. In statistical models, however, signs that occur close to transition shifts can be used; e.g., a model of changes in desert vegetation indicated that regular patterns change in a predictable way as the critical transition threshold to bare soil is approached (Rietkerk *et al.*, 2004), which has increased the use of the spatial distribution of vegetation to detect early warning signs of desertification (Kéfi et al., 2007; Scanlon et al., 2007; Maestre and Escudero, 2009).

The ways to identify the early-warning signs of critical transitions range from analyses of the autocorrelation and variance of the fluctuations (Scheffer *et al.*, 2009) to the long-term autocorrelation that measures the memory of the process as one approaches to vegetation transitions (Alados et al., 1996; Alados et al., 2003). To detect transition states in semi-arid ecosystems, recent studies have examined the spatial variance or spatial skewness of the vegetation (Guttal and Jayaprakash, 2009), or the change in the distribution of the sizes of patches of vegetation (Kéfi et al., 2007; Scanlon et al., 2007). Indeed, scaling relationships and fractals provide a powerful analytical framework that incorporates the structural complexity of plant communities and can be used to analyze "emergent patterns" of the ecosystem across a range of scales to predict catastrophic shifts. The change in the fractal dimension of the spatial pattern can indicate a significant change in the processes that generate plant spatial patterns (Sugihara and May, 1990; Li, 2000). For example, the Information Fractal Dimension of a species distribution quantifies the relationship between species diversity and area, and is equivalent to the exponent of the species-area relationship (Borda-de-Agua et al., 2002). The proportion of all possible species that are in a given area depends on the size of the area sampled. Thus, the Shannon Diversity Index (H') (Shannon, 1948) changes with the size of the area sampled, and the rate of change at several scales measures the Information Fractal Dimension (IFD) (Farmer et al., 1983). If the distribution of species is homogenous, the IFD is high, and decreased as patchiness increased in semi-arid shrubland ecosystems (Alados et al., 2003; Alados et al., 2006). IFD and species diversity are inversely correlated (Alados et al., 2006), which is consistent with the general phenomenon that spatial diversity is greater in heterogeneous habitats than it is in analogous homogeneous habitats, and with the community assembled by self-organizing processes, which results in an increase in the efficient use of resources (Venail *et al.*, 2008). IFD increases when the community assemblage changes to a more degraded state; e.g., when the dwarf matorral of Cabo de Gata N.P. degraded to alpha steppe dominated by *Stipa tenacissima* (Alados *et al.*, 2003). At sites of natural vegetation in Cabo de Gata-Nijar National Park, Spain, the vegetation was sampled along 69 500-m-long linear transects (Fig. 1). At those sites, the IFD of the dwarf matorral (x ± se = 0.629±0.002, n =37) and the alpha steppe (x ± se = 0.725 ±0.007, n =32) differed significantly ($F_{1, 58} = 237.13$, p < 0.001) (Fig. 2).

When examining plant spatial distributions, it is important to distinguish between those that result from external perturbations and those that are caused by dynamics intrinsic to the system (Cutler et al., 2008); e.g., distinguishing between those patterns influenced by the topography of the terrain and those patterns that originate at the level of the individual, but become apparent at larger scales, but at scales that are lower than the environmental heterogeneity of the landscape. Those conditions pose a problem in power spectrum calculations because the latter assume stationarity and cannot distinguish between stationary and non-stationary signals (Ivanov et al., 2002). Separating spatial patterns caused by pre-existing environmental heterogeneity from self-organizing processes allow us to detect intrinsic changes in the control mechanisms. Detrended Fluctuation Analysis (DFA) removes the trends (Peng et al., 1992) and avoids any spurious correlations caused by non-stationarities (Bunde et al., 2002). DFA, which describes spatial autocorrelation and patchiness, can detect long-range spatial autocorrelations in plant species' distributions (Alados *et al.*, 2003), which influence the degree of spatial clustering of the vegetation cover, independent of the scale of measurement. Long-range autocorrelations imply that positive feedback mechanisms dominate the system and provide valuable information about the inherent memory of the process under examination.

In several Mediterranean rangeland ecosystems, evaluations of degradation gradients caused by livestock grazing and associated increases in bare soil indicated that the long-range spatial autocorrelations of the characteristic species of each community were highest in the most preserved areas. As grazing pressure increased, most of plant species became more randomly distributed; species adapted to perturbed ecosystems experienced an increase in spatial organization (Alados *et al.*, 2004a). In addition, the slope of the negative correlation between grazing disturbance and long-range spatial autocorrelation (high α values) appeared to be most pronounced among the most perturbation-sensitive species; e.g., *Quercus coccifera, Phlomis purpurea, Cistus. albidus*, and even the grazing-tolerant *Periploca laevigata* exhibited a drastic reduction in spatial organization (Alados *et al.*, 2003). Grazing-resistant species such as *S. tenacissima*, which have buried renewal buds that livestock cannot reach, and species that have a capacity for persistence and colonizing unoccupied microhabitats (e.g., annuals or pioneer plants) exhibited little change in spatial distribution along a grazing pressure gradient (Alados *et al.*, 2003).

A reduction in the number and size of vegetation fragments and the degree of isolation had a negative influence on the long-range spatial distributions of the characteristic plant species in Cabo de Gata-Nijar N.P., Spain (Alados *et al.*, 2006). In particular, forest-gap species that have restricted dispersal (*Phlomis purpurea, Cistus albidus, Teucrium pseudochamaepytis, Genista spartioides, Brachypodium retusum*) and species that actively restrict or hamper dispersal (antitelechory) by myxospermy (*Helianthemum almeriensis* and *Linum strictum*) were very sensitive to the effects of

habitat fragmentation and exhibited a significant positive correlation between patch size and the long-range spatial autocorrelations. In general, changes in the long-range spatial autocorrelations of plant species in response to different degrees of land degradation indicated that spatial self-organizing processes are important in the conservation of the ecosystem, and the most effective way to protect against land degradation in semi-arid ecosystems is to reinforce self-organizing processes as positive feedback interactions, which will allow self-structuring mechanisms to operate.

Monitoring vegetation transitions using patterns in NDVI

The use of remote sensing to monitor desertification processes has become common (Prince et al., 1998; Asner and Heidebrecht, 2005; García et al., 2008; Weber et al., 2009; Hall et al., 2010) and the availability of high-resolution satellite images permits an estimation of the relationship between vegetation spatial patterns and the effects of environment. The satellite-derived vegetation index the Normalized Difference Vegetation Index (NDVI) provides estimates of vegetation productivity (Pettorelli et al., 2005) and can be correlated with the amount of green vegetation cover, vegetation abundance, chlorophyll content, and leaf area index (Harrison et al., 2006). The NDVI, an expression of the contrasting reflectance between the red and near-infrared wavelengths of a surface spectrum (Rouse et al., 1974; Tucker, 1979), is given by the following formula: NDVI = (RNIR-RRED)/(RNIR+RRED), where RNIR is near infrared reflectance (NIR) and RRED is red reflectance. Values range between -1 and 1, with 0 representing the approximate value of no vegetation. Thus, negative values usually indicate non-vegetated surfaces. A high NDVI indicates high vegetation activity because of the strong relationship between the NDVI and the amount of radiation absorbed in photosynthetic processes (Gallo et al., 1985). The NDVI can be used to estimate species richness and vegetation spatial heterogeneity (Gould, 2000; Fairbanks and McGwire, 2004; Gillespie, 2005; Levin et al., 2007); however, the ecological significance of vegetation spatial patterns depends on the scale of the analyses, which can produce apparently contradictory results. While some studies found a positive correlation between landscape heterogeneity and species richness (Fairbanks and McGwire, 2004; Gillespie, 2005), others did not find a clear relationship (Levin *et al.*, 2007). In general, studies conducted at higher scales observed a positive correlation between species diversity and landscape heterogeneity because, accordingly to habitat heterogeneity hypothesis (Simpson, 1949; MacArthur and Wilson, 1967), structurally complex habitats might provide more niches and diverse ways of exploiting the environmental resources and thus increase species diversity (Fahrig, 2003; Hobbs and Yates, 2003; Harper et al., 2005). Depending on the spatial scale of the analysis, and the way organisms perceive the habitat, species diversity can appear to decrease as habitat heterogeneity increases (Tews et al., 2004)

1 (ecosystem fragmentation). Thus, analyses at multiple scales are needed before spatial heterogeneity

2 can be advocated as a reliable means of monitoring ecosystem degradation.

3

4 **A case study of NDVI variation across a degradation gradient**

5 Coordination between ground- and remote sensing-based research and the implementation of sound,

6 cost-effective methods have promise as tools for monitoring desertification. To use the spatial

7 patterns in the NDVI index to monitor desertification, we need to know whether the average values

8 and spatial variability of NDVI differ depending on the ecosystem features. We compared the spatial

9 distribution of vegetation derived from ground transects and the NDVI values obtained from satellite

10 images of Cabo de Gata-Níjar Natural Park, in southeastern Spain, which was established in 1987.

11 Much (54%) of the 376-km^2 park is natural semi-arid vegetation on hillslopes within a matrix of

12 abandoned crop fields (Alados *et al.*, 2004b). The habitat in the northern part of the national park is

13 alpha steppe, which is dominated by *Stipa tenacissima* and, in the southern part, there is a dwarf

14 matorral of *Ulex baeticus, Phlomis* spp. and *Chamaerops humilis* on volcanic soils.

15 Values of the Normalized Difference Vegetation Index (NDVI) were derived from an image captured

16 on 2005-04-11 (11:10 GMT) by the Ikonos-2, a satellite-borne sensor (launched in 1999) that detects

17 four multi-spectral bands (blue, green, red, near infrared), simultaneously, at a spatial resolution of 4

18 m, and a panchromatic band (the entire range covered by the four multi-spectralbands) at a 1-m

19 resolution (Dial et al., 2003). The analysis was based on an image captured in April (see Fig. 1)

20 because that is the month in which the vegetation exhibits its greatest phenological development at

21 the study area in Almeria, Spain. The image of the 74-km^2 area was orthorectified into a UTM

22 projection with a high precision (RMS <1 pixel). For the geometrical corrections, we used a Digital

23 Elevation Model (DEM), georeferenced aerial orthophotos, and Ground Control Points (GCPs). To

24 preserve the original image values, we used the nearest-neighbor re-sampling procedure.

25 The ground reflectance data retrieved from satellite images can be compared to ground-based

26 measurements, although haze removal and atmospheric-topographic corrections were required,

27 which reduce atmospheric effects and variation in solar illumination (sunny and shady hills). The

28 corrections were applied using algorithms implemented in the ATCOR software (Geosystem, 2008),

29 which was available as an extension to the remote sensing software ERDAS IMAGINE 9.2. To

30 remove any bias caused by the sensor's parameters (calibration files), the digital numeric values (raw

31 data) were converted into estimates of the radiance reaching the sensor. The radiance values were

32 converted into real surface reflectance values using standard estimates of atmospheric conditions

33 (e.g., visibility, aerosol type, water vapor content) in the study area. ATCOR consists of ATCOR2

34 and ATCOR3, and is based on MODTRAN-4 code. Typically, ATCOR-2 is used to correct for

atmospheric effects in the data from spaceborne optical sensors and assumes flat terrain and Lambertian reflectance. The algorithm works with a database of atmospheric correction functions that are stored in look-up tables (Richter, 2000b; a). ATCOR-3 accounts for rugged terrain effects by incorporating DEM data and their derivatives, such as slope and aspect, sky view factor, and shadow cast. The algorithm accounts a compiled database that contains the results of the radiative transfer calculations for a wide range of weather conditions and sun angles (Richter, 1997; Richter, 1998; 2000a).

After the geometric and radiometric corrections, the NDVI was calculated at 4–m intervals (Fig 1d) along the 500-m-long transects that were extracted from the satellite image. The results were laid over the data collected from the ground-based transects in Cabo de Gata-Nijar N.P. For each transect on the ground, six random transects were taken from the satellite-based image (Fig 1c), which provided information from 36 and 48 transects in dwarf matorral and alpha steppe, respectively (Fig 1b). At the alpha steppe site, transects were placed on either shallow (<10°) or steep (20°-30° slopes. The critical slope for incipient rill formation is 9 ° (Hudson, 1975; Berael et al., 1995). On the transects (n = 84), the average NDVI and the bare-soil ratio were significantly negatively correlated (R^2 =0.58, slope = -0.62, P < 0.001). As in studies elsewhere (Fairbanks and McGwire, 2004; Harrison et al., 2006; Levin et al., 2007), in southeastern Spain, average NDVI and species richness were significantly positively correlated (R^2 = 0.28, slope = 0.002, P < 0.001).

The variation in NDVI within transects, as estimated by the coefficient of variation, increased significantly with the amount of bare soil (R^2 =0.42, slope = 0.72, P < 0.001); i.e., the heterogeneity of the spatial distribution of NDVI increased with an increase in the bare-soil ratio. However, the spatial pattern of the variation differed among plant communities. To calculate the spatial pattern of the variation in the long-range spatial autocorrelation of NDVI values of each transect, we used Detrended Fluctuation Analyses (DFA). The NDVI data sequence $y(s) = \sum_i^s x(i)$ is integrated directly from the NDVI values. The sequence was subdivided into non-overlapping sequential sets or 'boxes' of size b. A regression line was fit to each box of size b, ($y_b(s)$ was regressed on s) and the residual variance per each box size was calculated from $F^2(b) = \frac{\sum (y_b(s) - \hat{y}_b(s))^2}{N}$; to provide the scale of the relationship $F_{(b)} \propto b^\alpha$. The α parameter reflects the long-range autocorrelations of the NDVI distribution sequences. Theoretically, α is unaffected by the magnitude of the fluctuations in the sequences, but is affected by the sequential ordering of the fluctuations. If $\alpha > 0.5$, the sequence depends on the history of the distribution and, when $\alpha = 0.5$, the sequence is randomly distributed.

As the amount of bare soil increased α-DFA of NDVI increases ($R^2 = 0.39$, slope = 1.04, P < 0.001) in the dwarf matorral, but not in alpha steppe ($R^2 = 0.03$, slope = 1.04, P > 0.05) (Fig. 3). In dwarf matorral, although a patchy vegetation distribution maximizes vegetation growth because vegetation patches capture rainfall and nutrients in the patches and reduce inter-patch run-off (Ludwig et al., 1999; Pueyo et al., 2008a), the contagious spread of erosion processes can dominate vegetation dynamics when the system becomes over-connected and rapid change is triggered. Thus, the positive feedback triggered by run-off and erosion tend to destabilize the system when the patchy distribution of vegetation reaches a certain threshold beyond which the processes become irreversible (Rietkerk *et al.*, 2004). In the alpha steppe, the lateral root expansion of *S. tenacissima* favor to a stronger spatial autocorrelation on bare soil, coincident with the spatial distribution of *S. tenacissima* ($R^2 = 0.84$, slope = 1.02, P < 0.001, for the regression between α-DFA of *S. tenacissima* vs. that of bare soil from the ground-based transects). The effect was not as evident in the dominant species of the dwarf matorral, e.g., *Ch. humilis* ($R^2 = 0.27$, slope = 0.57, P < 0.001) and *Ph. purpurea* ($R^2 = 0.21$, slope = 0.39, P < 0.001). In the alpha steppe, effects of two opposing trends cancel out each other: (i) the self-organization of bare soil because of the self-organization of the dominant species *S. tenacissima* and (ii) the run-off process that increases with the bare-soil ratio.

To distinguish between those effects, we compared shallow and steep slopes in alpha steppe habitats, where the effect of *S. tenacissima* on pattern formation is greater because it occupied 48% of the area, whereas it occupied 24% on the dwarf matorral. Shallow slopes are very favorable to perennial bunch grasses such as *S. tenacissima* because source and sink patterns of water and sediments develop from bare ground areas into tussock (Sánchez and Puigdefábregas, 1994; Cerdá, 1997). The effect is reduced on steep slopes where there is an increase in run-off and erosion when the slope is >9º (Berael *et al.*, 1995), which produces a contagious spread of erosion processes. Along a degradation gradient, the long-range spatial autocorrelation of NDVI (α-DFA) was greater on high (1.081 ± 0.024, n = 24) than on low (0.865 ± 0.023, n = 24) slope (one way ANOVA $F_{1, 46} = 41.85$, P < 0.001) (Fig 4), which reflects the stronger effect of run-off processes on high slopes. NDVI self-organization (α-DFA) declined with the amount of bare soil equally on high and low slopes, but the effect was more pronounced on low slopes ($R^2 = 0.19$, slope = -0.81, P < 0.05) than on high slopes ($R^2 = 0.07$, slope = -0.34, P > 0.05). In steep-sloped areas, the shallow roots of *S. tenacissima* are exposed as the fine soil is lost during rain run-off, which reduces the competitiveness of this species (Alados *et al.*, 2006) and the negative relationship between α-DFA of NDVI and bare soil rate. In contrast, in shallow-sloped areas in alpha steppes dominated by *S. tenacissima,* the species plays a more important role in the organizing process.

The ecological strategy of the species occupying the habitat mediates the relationship between species richness and NDVI spatial organization. In the dwarf matorral, the long-range spatial autocorrelation of NDVI (α-DFA) declined as species richness increased ($R^2 = 0.14$, slope = -0.008, P < 0.05) (Fig. 5). Thus, when the spatial autocorrelation of NDVI is the result of run-off processes that occur in slope areas, species richness declines as the contagious spread of erosion processes increase. In contrast, as the spatial autocorrelation of NDVI in alpha steppe increases, the number of species increases, particularly in shallow-sloped areas, where the contribution of *S. tenacissima* to NDVI spatial organization is most apparent, which results in an increase in species diversity with α-DFA of NDVI ($R^2 = 0.25$, slope = 0.004, P < 0.05). The effect in high-slope areas is less evident (data not shown). Thus, the NDVI spatial pattern is not always associated with a significant change in species richness. While our study demonstrated a significant relationship between satellite-based and ground-based data, some of the variance documented in the ground-based data remain unexplained by the satellite-based methods (see also Hall et al. 2010). Other studies in semi-arid Mediterranean ecosystems did not detect a relationship between spatial heterogeneity of NDVI and species richness (Levin *et al.*, 2007).

Before landscape satellite images can be used to monitor ecosystems, we need to understand the relationship between the spatial patterns in the satellite-derived vegetation index and ground-based data and the mechanisms that trigger the self organizing positive feedback process. Once that is understood, we can use the changes in the spatial autocorrelation of NDVI to monitor the thresholds of change associated with irreversible desertification.

References

Aarssen, L.W., Turkington, R., 1985. Vegetation dynamics and neighbour associations in pasture-community evolution. Journal of Ecology, 73, 585-603.

Alados, C.L., ElAich, A., Papanastasis, V.P., Ozbek, H., Navarro, T., Freitas, H., Vrahnakis, M., Larrosi, D., Cabezudo, B., 2004a. Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. Ecological Modelling, 180, 523-535.

Alados, C.L., Escos, J.M., Emlen, J.M., 1996. Fractal structure of sequential behaviour patterns: an indicator of stress. Animal Behaviour, 51, 437-443.

Alados, C.L., Gotor, P., Ballester, P., Navas, T., Escos, J., Navarro, T., Cabezudo, B., 2006. Association between competition and facilitation processes and vegetation spatial patterns in alpha steppes. Biological Journal of the Linnean Society, 87, 103-113.

Alados, C.L., Navarro, T., Komac, B., Pascual, V., Martínez, F., Cabezudo, B., Pueyo, Y., 2009a. Do vegetation patch spatial patterns disrupt the spatial organization of plant species? Ecological Complexity, 6, 197-207.

Alados, C.L., Navarro, T., Komac, B., Pascual, V., Rietkerk, M., 2010. Dispersal abilities and spatial patterns in fragmented landscapes. Biological Journal of the Linnean Society.

Alados, C.L., Pueyo, Y., Barrantes, O., Escós, J., Giner, L., Robles, A.B., 2004b. Variations in landscape patterns and vegetation cover between 1957 and 1994 in a semiarid Mediterranean ecosystem. Landscape Ecology, 19, 543-559.

Alados, C.L., Pueyo, Y., Escós, J., Andujar, A., 2009b. Effects of the spatial pattern disturbance on the patch-occupancy dynamics of juniper-pine open woodland. Ecological Modelling, 220, 1544-1550.

Alados, C.L., Pueyo, Y., Giner, M.L., Navarro, T., Escos, J., Barroso, F., Cabezudo, B., Emlen, J.M., 2003. Quantitative characterization of the regressive ecological succession by fractal analysis of plant spatial patterns. Ecological Modelling, 163, 1-17.

Araus, J.L., Febrero, A., Buxo, R., Camalich, M.D., Martin, D., Molina, F., Rodriguez-Ariza, M.O., Romagosa, I., 1997. Changes in carbon isotope discrimination in grain cereals from different regions of the western Mediterranean Basin during the past seven millenia. Palaeoenvironmental evidence of a differential change in aridity during the late Holocene. Global Change Biology, 3, 107-118.

Asner, G.P., Heidebrecht, K.B., 2005. Desertification alters regional ecosystem–climate interactions. Global Change Biology, 11, 182-194.

Barbier, N., Couteron, P., Lejoly, J., Deblauwe, V., Lejeune, O., 2006. Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems. Journal of Ecology, 94, 537-547.

Barrio del, G., Puigdefabregas, J., Sanjuan, M.E., Stellmes, M., Ruiz, A., 2010. Assessment and monitoring of land condition in the Iberian Peninsula, 1989–2000. Remote Sensing of the Environment.

Berael, C., Poesen, J., Van Wesemael, B., Fantechi, R., Peter, D., Balabanis, P., Rubio, J.L., 1995. Rill and gully erosion in relation to rock fragment cover and surface slope along a hill slope in south eastern Spain., Proceedings of the European School of Climatology and Natural Hazard.

1   Desertification in a European context: physical and socio economic aspects. El Campello. Pueblo
2   Acantilado, Alicante, Spain, pp. 371-375.

3   Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. Trends in Ecology and
4   Evolution, 9, 191-193.

5   Borda-de-Agua, L., Hubbell, S.P., McAllister, M., 2002. Species-area curves, diversity indices, and
6   species abundance distributions: A multifractal analysis. The American Naturalist, 159, 138-155.

7   Brandt, J., Thornes, J.B., Lopez-Bermudez, F., Romero-Diaz, M.A., 1991. Recent rainfall variability
8   in South East Spain and its implications for cereal growth. EC Conference on Mediterranean
9   desertification Florence.

10   Brown, B.J., Allen, T.F.H., 1989. The importance of scale in evaluating herbivory impacts. Oikos,
11   54, 189-194.

12   Brown, J.H., Lomolino, M.V., 1998. Biogeography. 2nd edn. Sinauer Associates, Sunderland, MA,
13   692 p.

14   Bunde, A., Havlin, S., Koscielny-Bunde, E., Schellnhber, H.J., 2002. Atmospheric persistence
15   analysis: novel approach and applications. In: A. Bunde, J. KroppH.J. Schellnhuber (Editor), The
16   sicience of disasters: climate disruption, heart attacks, and market crashes. Springer, Berlin, pp.
17   171-191.

18   Cerdá, A., 1997. The effect of patchy distribution of Stipa tenacissima L. on runoff and erosion.
19   Journal of Arid Environments, 36, 37-51.

20   Cerdá, A., 1998. The influence of aspect and vegetation on seasonal changes in erosion under rainfall
21   simulation on a clay soil in Spain. Canadian Journal of Soil Science, 78, 321–330.

22   Chapman, R.W., 1978. The evidence for pre-historic water control in south-east Spain. . Journal of
23   Arid Environments, 261–274.

24   Cingolani, A.M., Cabido, M.R., Renison, D., Solís Neffa, V., 2003. Combined effects of
25   environment and grazing on vegetation structure in Argentine granite grasslands. Journal of
26   Vegetation Science, 14, 223-232.

27   Creus, J.a.J.P., 1983. Climatología histórica y dendrocronología de *Pinus nigra*. In: A. Blanco de
28   Pablos (Editor), Avances de Investigación en Bioclimatología. Consejo Superior de
29   Investigaciones Cientificas, Zaragoza, pp. 121-128.

30   Cutler, N.A., Belyea, L.R., Dugmore, A.J., 2008. The spatiotemporal dynamics of a primary
31   succession. Journal of Ecology, 96 231-246.

32   D'Odorico, P., Laio, F., Ridolfi, L., 2005. Noise-induced stability in dryland plant ecosystems.
33   Proceedings of the Academy of Natural Sciences of Philadelphia, 102, 10819-10822.

Dial, G.F., Bowen, H., Gerlach, B., Grodecki, J., Oleszczuk, R., 2003. IKONOS satellite, sensor, imagery, and products. Remote Sensing of Environment, 88, 23-36.

Dupre Ollivier, M., 1990. Historical antecedents of desertification: climatic or anthropological factors? In: J.L. RubioR.J. Rickson (Editor), Strategies to combat desertification in Mediterranean Europe. Commission of European Communities. Directorate General Telecommunications, Information Industries and Innovation, Brussels, pp. 2-39.

Elliot, J.H., 1965. Imperial Spain 1469-1716. Edward Arnold, London.

Ellner, S., Shmida, A., 1981. Why are adaptation for long-range dispersal rare in desert plants? Oecologia, 51, 133-144.

Escudero, A., Somolinos, R., Olano, J.M., Rubio, A., 1999. Factors controlling the establishment of *Helianthemum squamatum*, an endemic gypsophile of semi-arid Spain. Journal of Ecology, 87, 290-302.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology and Systematics, 34, 487-515.

Fairbanks, D.H.K., McGwire, K.C., 2004. Patterns of floristic richness in vegetation communities of California: regional scale analysis with multi-temporal NDVI. Global Ecology and Biogeography, 13, 221–235.

Farmer, D., Ott, E., Yorke, J.A., 1983. The dimension of chaotic attractors. Physica, 7D, 153-180.

Fisher, S.F., Poschlod, P., Beinlich, B., 1996. Experimental studies on the dispersal of plant and animals on sheep in calcareous grasslands. Journal of Applied Ecology, 33, 1206-1222.

Gallo, K.P., Daughtry, C.S.T., Bauer, M.E., 1985. Spectral estimation of absorbed photosinthetically activeradiation in corn canopies. Remote Sensing of Environment, 17, 221-232.

García, M., Oyonarte, C., Villagarcía, L., Contreras, S., Domingo, F., Puigdefábregas, J., 2008. Monitoring land degradation risk using ASTER data: The non-evaporative fraction as an indicator of ecosystem function. Remote Sensing of Environment, 112, 3720-3736.

Geosystem, 2008. ATCOR for IMAGINE 9.3. User Manual ATCOR 2 and ATCOR 3: Haze Reduction, Atmospheric and Topographic Correction. Germering, Germany: 218 pp. . http://www.yourgeo.de/atcor/manual/ATCOR_MANUAL_V93.pdf

Gil Albarracín, A., 2002. Viaje a Andalucía. Historia natural del reino de Granada (1804-1809). Griselda Bonet Girabet, Barcelona, 1247 p.

Gilad, E., von Hardenberg, J., Provenzale, A., Shachak, M., Meron, E., 2004. Ecosystem engineers: from pattern formation to habitat creation. Physical Review Letters, 93, 0981051.

Gillespie, T.W., 2005. Predicting woody-plant species richness in tropical dry forests: a case study from south Florida, USA. Ecological Applications, 15, 27-37.

Gould, W., 2000. Remote sensing of vegetation, plant species richness, and regional biodiversity hotspots. Ecological Applications.

Grenon, M., Batisse, M., 1988. El Plan Azul : El futuro de la Cuenca Mediterranea. Ministerio de Obras Publicas y Transportes, Madrid.

Guttal, V., Jayaprakash, C., 2009. Spatial variance and spatial skewness: leading indicators of regimen shifts in spatial ecological systems. Theoretical Ecology, 2, 3-12.

Gutterman, Y., 1993. Seed germination in desert plants. Adaptation of desert organisms Springer-Verlag, Berlin.

Hall, K., Johansson, L.J., Sykes, M.T., Reitalu, T., Larsson, K., Prentice, H.C., 2010. Inventorying management status and plant species richness in seminatural grasslands using high spatial resolution imagery. Applied Vegetation Science, 13, 221-233.

Harper, K.A., Macdonald, E., Burton, P.J., Chen, J., Brosofske, K.D., Saunder, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S., Esseen, P., 2005. Edge influence on forest structure and composition in fragmented landscapes. Conservation Biology, 19, 768-782.

Harrison, S., Davies, K.F., Safford, H.D., Viers, J.H., 2006. Beta diversity and the scale-dependence of the productivity-diversity relationship: a test in the Californian serpentine flora. Journal of Ecology, 94, 110-117.

Herrmann, S.M., Hutchinson, C.F., 2005. The changing contexts of the desertification debate Journal of Arid Environments, 63, 538-555.

HilleRisLambers, R., Rietkerk, M., van den Bosch, F., Prins, H.H.T., de Kroon, H., 2001. Vegetation pattern formation in semi-arid grazing systems. Ecology, 82, 50-61.

Hobbs, R.J., Yates, C.J., 2003. Impacts of ecosystem fragmentation on plant populations: generalising the idiosyncratic. Australian Journal of Botany, 51, 471-488.

Hoffmann, G., 1988. Holozänstratigraphie und Küstenlinienverlagerung an der Andalusischen Mittelmeerküste. Berichte aus dem Fachbereich Gewissenschaften der Universitat Bremen, 156 p.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics., 4, 1-23.

Holling, C.S., 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs, 62, 447-502.

Hudson, N.W., 1975. Field engeneering for agricultural development. Oxford University Press, London, 225 p.

Ivanov, P.C., Goldberger, A.L., Stanley, H.E., 2002. Fractal and multifractal approaches in physiology. In: A. Bunde, J. KroppH.J. Schellnhuber (Editor), The science of disasters. Springer, Berlin, pp. 219-258.

Johnson, C.R., Boerlijst, M.C., 2002. Selection at the level of community: the importance of spatial structure. Trends in Ecology & Evolution, 17, 83-90.

Kéfi, S., Rietkerk, M., Alados, C.L., Pueyo, Y., ElAich, A., Papanastasis, V., de Ruiter, P.C., 2007. Spatial vegetation patterns and imminent desertification in Mediterranean arid ecosystems. Nature, 449, 213-218.

Klein, J., 1981. La Mesta. Alianza Editorial, Madrid.

Lejeune, O., Tlidi, M., Couteron, P., 2002. Localized vegetation patches: A self-organized response to resource scarcity. Physical Review E, 66, 1-4.

Levin, N., Shmida, A., Levanoni, O., Tamari, H., Kark, S., 2007. Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices. Diversity and Distributions, 13, 692-703.

Li, B.-L., 2000. Fractal geometry applications in description and analysis of patch patterns and patch dynamics. Ecological Modelling, 132, 33-50.

Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. Nature, 412, 72-76.

Ludwig, J.A., Tongway, D.J., Marsden, S.G., 1999. Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. CATENA, 37, 257-273.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Maestre, F.T., Escudero, A., 2009. Is the patch size distribution of vegetation a suitable indicator of desertification processes? Ecology, 90, 1729-1735.

Manzano, P., Malo, J.E., Peco, B., 2005. Sheep gut passage and survival of Mediterranean shrub seeds. Seed Science Research, 15, 21-28.

Martens, S.N., Breshears, D.D., Meyer, C.W., 2000. Spatial distribution of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. Ecological Modelling, 126, 79.93.

Meron, E., Gilad, E., von Hardenberg, J., Shachak, M., Zarmi, Y., 2004. Vegetation Patterns Along a Rainfall Gradient. Chaos, Solitons and Fractals, 19, 367-376.

Milton, S.J., Hoffman, M.T., 1994. The application of state and transition models to rangeland research and management in arid succulent and semi-arid grassy Karoo, South Africa. African Journal of Range and Forestry Science, 11, 18-26.

Navarro, T., Pascual, V., Alados, C.L., Cabezudo, B., 2009. Growth forms, dispersal strategies and taxonomic spectrum in a semi-arid shrubland in SE Spain. Journal of Arid Environments, 73, 103-112.

Naveh, Z., 1991. Biodiversity and ecological heterogeneity of Mediterranean uplands. Linea Ecologica, 4, 47-60.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics, 4, 25-51.

Noy-Meir, I., 1990. Responses of two semiarid rangeland communities to protection from grazing. Israel Journal of Botany, 39, 431-442.

Olff, H., Ritchie, M.E., 1998. Effects of herbivores on grasslands plant diversity. Trends in Ecology and Evolution, 13, 261-265.

Oñate Rubalcaba, J.J., 1993. Caracterización de los cambios climáticos en la península ibérica y Canarias desde principios de siglo. , Autónoma de Madrid.

Parra, I., 1993. Desplaçaments latitudinals de la vegetacio al litoral mediterrani durant els darrers 8 500 anys. Un enfocament pollinic i climatic. Revista Catalana de Geografia, 21, 37-44.

Peng, C.-K., Buldyrev, S.V., Goldberger, A.L., Havlin, S., Sciortino, F., Simons, M., Stanley, H.E., 1992. Long-range correlations in nucleotide sequences. Nature, 356, 168-170.

Peters, D.P.C., Pielke, R.A., Sr., Bestelmeyer, B.T., Allen, C.D., Munson-McGee, S., 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. Proceedings of the National Academy of Sciences 101, 15130-15135.

Peterson, G.D., 2000. Scaling ecological dynamics: self-organization, hierarchical structure, and ecological resilience. Climatic Change, 44, 291-309.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenset, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change Tends in Ecology and Evolution, 20, 503-510.

Pons, A., 1981. The history of the mediterranean shrublands. In: F. Di Castri, D.W. GoodallR.L. Specht (Editor), Mediterranean-type shrublands. Elsevier., Amsterdam, pp. 131-138.

Pons, A., Reille, M., 1988. The Holocene and Upper Pleistocene pollen record from Padul (Granada, Spain): a new study. Palaeogeography, Palaeoclimatology and Palaeoecology, 66, 243-263.

Prince, S.D., Colstoun, E.B., Kravitz, L.L., 1998. Evidence from rain-useefficiencies does not indicate extensive Sahelian desertification. Global Change Biology, 4, 359-374.

Pueyo, Y., Kéfi, S., Alados, C.L., Rietkerk, M., 2008a. Dispersal strategies and spatial organization of vegetation in arid ecosystems. Oikos, 117, 1522-1532.

Pueyo, Y., L., A.C., Barrantes, O., Komac, B., Rietkerk, M., 2008b. Differences in gypsum plant communities associated with habitat fragmentation and livestock grazing. Ecological Applications, 18, 954-964.

Pugnaire, F.I., Haase, P., Puigdefábregas, J., 1996. Facilitation between higher plant species in a semi-arid environment. Ecology, 77, 1420-1426.

Puigdefabregas, J., Mendizabal, T., 1998. Perspectives on desertification : western Mediterranean. Journal of Arid Environments, 39, 209-224.

Puigdefabregas, J., Mendizabal, T., 2004. Prospects of desertification impacts in Western Europe. In: A. Marquina (Editor), Environmental Challenges in the Mediterranean 2000.2050. NATO Science Series. IV. Earth and Environmental Sciences, p. 155.

Rainey, P.B., Travisano, M., 1998. Adaptive radiation in a heterogeneous environment. Nature (London), 394, 69-72.

Ramos, M.E., Robles, A.B., Castro, J., 2006. Efficiency of endozoochorous seed dispersal in six dry-fruited species (Cistaceae): from seed ingestion to early seedling establishmnent. Plant Ecology, DOI 10-1007/s11258-005-9087-y.

Rebollo, S., Milchunas, D.G., Noy-Meir, I., Chapman, P.L., 2002. The role of a spiny plant refuge in structuring grazed shortgrass steppe plant communities. Oikos, 98, 53-64.

Reynolds, J.F., Maestre, F.T., Kemp, P.R., Stafford-Smith, D.M., Lambin, E., 2007. Natural and Human Dimensions of Land Degradation in Drylands: Causes and Consequences In: S.B. Heidelberg (Editor), Libro Terrestrial Ecosystems in a Changing World pp. 247-257.

Richter, R., 1997. Correction of atmospheric and topographic effects for high spatial resolution satellite imagery. International Journal of Remote Sensing, 18, 1099-1111.

Richter, R., 1998. Correction of satellite imagery over mountainous terrain. Applied Optics, 37, 4004-4015.

Richter, R., 2000a. Atmospheric and Topographic Correction: Model ATCOR3, DLR-IB 564-03/00 DLR-IB, Wessling, Germany.

Richter, R., 2000b. Atmospheric correction algorithm for flat terrain: Model ATCOR2. DLR-IB 564-02/00 DLR-IB, Wessling, Germany.

Rietkerk, M., Boerlijst, M., van Langevelde, F., HilleRisLambers, R., van de Koppel, J., Kumar, L., Prins, H., de Roos, A., 2002. Self-organization of vegetation in arid ecosystems. The American Naturalist, 160, 524-530.

Rietkerk, M., Dekker, S.C., de Ruiter, P.C., van de Koopel, J., 2004. Self-orgnized patchiness and catastrophic shifts in ecosystems. Science, 305, 1926-1929.

Rietkerk, M., van de Koppel, J., 2008. Regular pattern formation in real ecosystems. Ttrends in Ecology and Evolution, 23, 169-175.

Robles, A.B., Castro, J., Braun-Blanquet, González-Miras, E., Ramos, M.E., 2005. Effects of ruminal incubation and goats' ingestion on seed germination of two legume shrubs: Adenocarpus decorticans Boiss. and Retama sphaerocarpa (L.) Boiss. Options Méditerranéennes. Series A, 67, 111-115.

Rognon, P., 1987. Late Quaternary climatic reconstruction of the Maghreb (North Africa). Paleogeography, Paleoclimatology, Paleoecology, 58, 11-34.

Rouse, J.W., Haas, R.H., Schell, J.A., Deering, D.W., Harlan, J.C., 1974. Monitoring the vernal advancements and retrogradation (greenwave effect) of nature vegetation, NASA/GSFC

Sánchez, G., Puigdefábregas, J., 1994. Interaction betweenplant growth and sediment movement in semi-arid slopes. Geomorphology, 9, 243-260.

Scanlon, T.M., Caylor, K.K., Levin, S.A., Rodrı´guez-Iturbe, I., 2007. Positive feedbacks promote power-law clustering of Kalahari vegetation. Nature, 449, 209-212.

Scheffer, M., Bascompte, J., Brock, W.A., Brovkin, V., Carpenter, S.R., Dakos, V., Held, H., van Nes, E.H., Rietkerk, M., Sigihara, G., 2009. Early-warning signals for critical transitions. Nature, 461, 53-59.

Scheffer, M., Carpenter, S.R., Foley, J.A., Folke, C., Walker, B., 2001. Catastrophic shifts in ecosystems. Nature, 413, 591-596.

Sebastià, M.-T., de Bello, F., Puig, L., Taull, M., 2008. Grazing as a factor structuring grasslands in the Pyrenees. Applied Vegetation Science, 11, 215-222.

Shannon, C.E., 1948. A mathematical theory of communication. Bell System Technical Journal, 27, 379-423.

Simpson, E.H., 1949. Measurement of diversity. Nature, 163, 688.

Solé, R.V., Bascompte, J., 2006. Self-organization in complex systems. Princeton University Press, 373 p.

Soro, A., Sundberg, S., Rydin, H., 1999. Species diversity, niche metrics and species associations in harvested and undisturbed bogs. Journal of Vegetation Science, 10, 549-560.

Sugihara, G., May, R.M., 1990. Applications of fractals in ecology. Trends in Ecology and Evolution, 5, 79-86.

Swanson, F.J., Kratz, T.K., Caine, N., Woodmansee, R.G., 1988. Landform effects on ecosystem patterns and processes Bioscience, 38, 92-98.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F., 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography, 31 79-92.

Tout, D., 1990. The horticulture industry of Almeria Province, Spain. The Geographical Journal, 156, 304-312.

Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. Remote Sensing of Environment, 8, 127- 150.

van de Koppel, J., Gascoigne, J.C., Theraulaz, G., Rietkerk, M., Mooij, W.M., Herman, P.M.J., 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. Science, 322, 739-742.

Van Rheede van Outshoorn, K., Van Rooyen, M.W., 1999. Dispersal Biology of Desert Plants. Springer Verlag, New York, 242 p.

Venail, P.A., MacLean, R.C., Bouvier, T., Brockhurst, M.A., Hochberg, M.E., Mouquet, N., 2008. Diversity and productivity peak at intermediate dispersal rate in evolving metacommunities. Nature, 452, 210-214.

Verón, S.R., Paruelo, J.M., Oesterheld, M., 2006. Assessing desertification. Journal of Arid Environments, 66, 751-763.

Weber, K.T., Alados, C.L., Bueno, G., Gokhale, B., Komac, B., Pueyo, Y., 2009. Modeling Bare Ground With Classification Trees in Northern Spain. Rangeland Ecology & Management, 62, 452-459.

Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management, 42, 266-274.

Wise, S.M., Thornes, J.B., Gilman, A., 1982. How old are the badlands ? A case study from south-east Spain. In: R. BryanA. Yair (Editor), Badland geomorphology and piping, . Geo-Books (Geo Abstracts Ltd), Norwich, UK, pp. 259-278.

Yarranton, G.A., Morrison, R.G., 1974. Spatial dynamics of primary succession: nucleation. Journal of Ecology, 62, 417-428.

Legends

Fig. 1. a) Limits of Cabo de Gata-Nijar Natural Park (SE Spain). Black dots are ground-transects areas. The box in the north represents the study area covered by the Ikonos-2 Image. b) Ikonos-2 image acquired on 2005-04-11. The 84 random image-transects are overlapped. c) Detail of the six random image-transect replicas in one of ground-transect areas (Montano Low Slope). d) Detail of the extraction points of NDVI values\ every 4 meters along one of the image-transect.

Fig. 2. Box-plot of the Information Fractal Dimension (IFD) obtained from 69 500-m transects collected at Cabo de Gata –Nijar National Park, Spain, showing significant differences between dwarf and alpha steppe communities.

Fig. 3. Scatter plot and linear regression fit between the long range spatial autocorrelation of NDVI (α-DFA) and bare soil rate (a) and species richness (b) obtained from 36 500-m transects extracted from Ikonos-2 image at the dwarf matorral of Cabo de Gata –Nijar National Park, Spain.
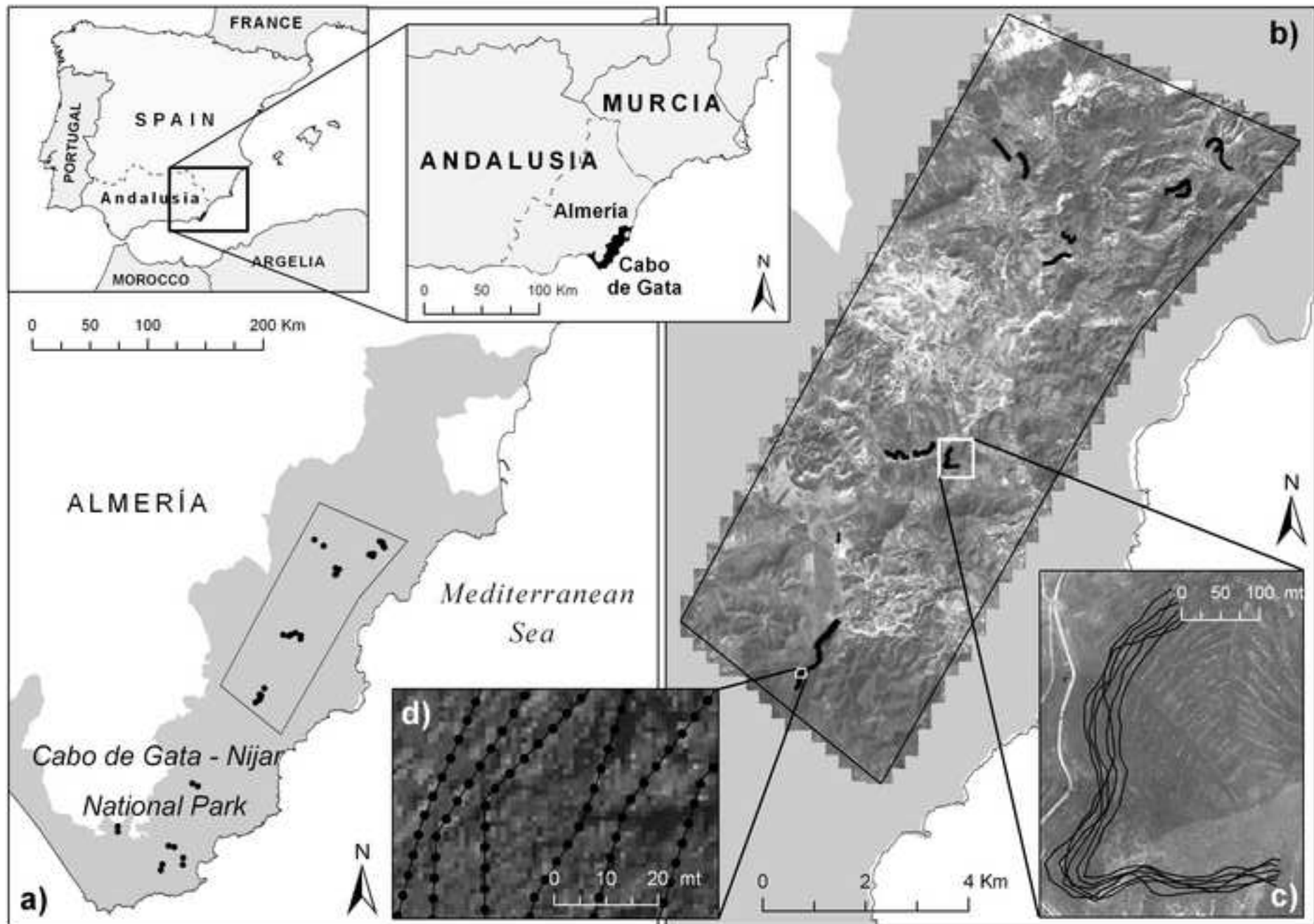
Fig. 4. Mean and standard error bar diagram of the long range spatial autocorrelation of NDVI (α-DFA) and bare soil rate obtained from 48 500-m transects extracted from Ikonos-2 image at the alpha steppe of Cabo de Gata –Nijar National Park, Spain, under high (20º-30 º) and gentle slope (< 10º) separately.

Fig. 5. Scatter plot and linear regression fit between the long range spatial autocorrelation of NDVI (α-DFA) and bare soil rate (a) and species richness (b) obtained from 24 500-m transects extracted from Ikonos-2 image at the gentle slope (< 10º) alpha steppe of Cabo de Gata –Nijar National Park, Spain.
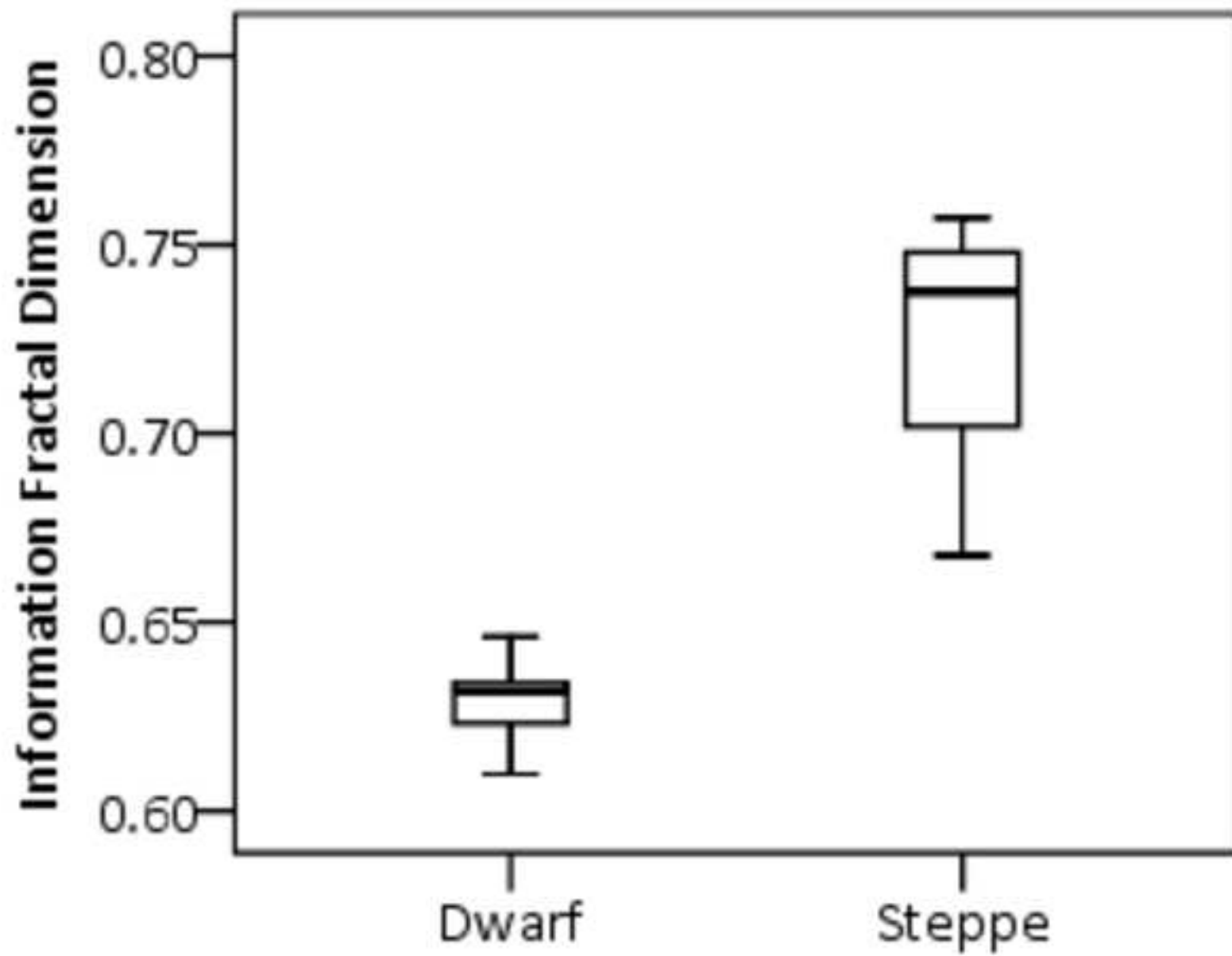
Figure

a)

Dwarf Matorral

y = 1.04x + 0.61
R² = 0.39

b)

Alpha steppe

y = -0.39x + 1.08
R² = 0.03

Fig. 3

Figure

Fig. 4

Figure

a)

Dwarf Matorral

y = -0.008x + 1.56
R² = 0.14

α-DFA (NDVI)

Species richness

b)

Alpha steppe

y = 0.004x + 0.76
R² = 0.063

α-DFA (NDVI)

Species richness

Fig. 5