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3   **Post-dispersal seed anchorage to soil in semiarid plant communities, a test of the hypothesis of**

4   **Ellner and Shmida**

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21   **Abstract**

22   In this paper we aim to test the Ellner-Shmida's hypothesis that in water-limited environments

23   seed anchorage mechanisms are a response of plants to post-dispersal selective forces such as soil

24   erosion, seed predation or limitations to water uptake by seeds but not a seed dispersal response of

25   plants to selective forces related to the spatially heterogeneous distribution of resources as a

26   consequence of aridity, which shapes the lack of seed dispersal mechanisms (atelechory) of many

27   plants in these environments.

1   To test this hypothesis, we analyzed both the proportion of species with seed anchorage

2 mechanisms and that of atelechoric species in shrublands colonizing flat areas and hillslopes in two

3 sites differing in climate dryness. Their relation with several soil properties involved in runoff

4 generation, seed-soil contact and water uptake by seeds and with nest density of granivorous ants was

5 also explored.

6   Our results support the hypothesis that the proportion of species with seed anchorage

7 mechanisms in semiarid shrublands increases because soil erosion, but it is not affected by climate

8 dryness. This is the first time that a direct relation between the proportion of species with seed

9 anchorage mechanisms and soil erosion is shown in plant communities. It supports the view that

10 intense soil erosion shapes species composition in communities.

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1.   Introduction

It has been repeatedly observed that long-distance seed dispersal syndromes are less frequent in arid and semi-arid than in mesic habitats and even that mechanisms constraining spatial seed dispersal are a common trait of arid and semiarid floras (Van der Pijl 1972; Ellner and Shmida 1981; Van Rheede van Oudtshoorn and Van Rooyen 1999, and references herein).

Contrary to the theory that predicts that in spatially heterogeneous environments plants benefit from long-distance seed dispersal because it enables them to reach distant favourable patches and spread extinction risk in space (Levin et al. 1984; Cohen and Levin 1987), some authors proposed that the continued occupation of the few favourable sites for plant development that exist in open deserts and semiarid landscapes may be the best adaptative strategy for plants to survive, and that the most predictable sites that fit these conditions are those occupied by previously established mother plants (mother-site theory) (Stebbins 1971; Friedman and Stein 1980). Accordingly, these authors suggested that, in plant communities inhabiting open environments, long-distance seed dispersal syndromes (telechory) should be selected against whereas short-distance seed dispersal syndromes, including both the lack of syndromes for seed dispersal (atelechory) and the presence of syndromes to avoid seeds to disperse (antitelechory), should be favoured. On the grounds of these arguments, spatial restrictions to seed dispersal have been widely used to explain the origin and maintenance of patches in semiarid vegetation (Kefi et al. 2008; Pueyo et al. 2008).

There are two groups of antitelechoric mechanisms used by plants to avoid seed dispersal. One of them is based in the control of the time that seeds disperse and the other is based in mechanisms that anchor the seeds to the ground. Ellner and Shmida (1981) suggested that seed anchoring mechanisms should not be considered adaptations to claim the mother site in the same way that atelechory does, as the mother site theory proposed, because in plants with seed anchorage mechanisms seeds need to be dispersed before seed anchoring mechanisms can operate. They argue that "the openness of desert vegetation and the patterns of climatic variation favour atelechory while antitelechory is generally a side-effect of mechanisms whose adaptative value is not directly related to seed dispersal". They maintain that anchoring mechanisms are adaptative, given that providing fruits or seeds with mechanisms that actively restrict post-dispersal movement has an additional cost to

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1   plants in terms of carbon allocation during their development, but they also argue that these

2   mechanisms may be related to post-dispersal events, such as the loss of opportunities for seeds to

3   germinate derived from seed removal by erosion, seed predation or insufficient seed-soil contact in

4   coarse textured soils.

5   There are only two reputed mechanisms related to seed anchorage on the ground surface in

6   plants living in semiarid areas, trypanocarpy and myxospermy (Van Rheede van Oudtshoorn and Van

7   Rooyen 1999). Trypanocarpic diaspores have the ability to sink into the cracks or holes of the soil

8   surface by means of hygroscopic movements of appendages attached to the upper part of the diaspore.

9   This mechanism keeps diaspores safe from seed harvesters and removal by wind or water erosion, and

10   also increases the chance for seed germination by increasing the contact surface of seeds with soil

11   particles in coarse textured soils (Stamp 1989; Schöning et al. 2004). Typical examples of

12   trypanocarpic species can be found in the Geraniaceae and Graminae families. Myxospermy is the

13   ability of seeds or fruits to secrete mucilage from their testa or pericarp respectively, once they become

14   moistened. It is a common feature in many families of Angiosperms (Grubert 1974; Western 2012).

15   Rain, fog, dew or even soil moisture when soil is at field capacity are effective enough to stimulate the

16   secretion of mucilage (García-Fayos and Cerdà 1997; Huang et al. 2004). The increase of the diaspore

17   surface due to mucilage secretion reduces the probability of the diaspore being removed (García-Fayos

18   et al. 2010) because when the mucilage turns dry, it strongly anchors the diaspore to the surface it is in

19   contact with. Further research proved that mucilage secretion highly reduces seed predation by

20   granivorous ants (Fuller & Hay 1983; Gutterman and Shem-Tov 1997; Engelbrecht and García-Fayos

21   2012), significantly reduces seed losses by runoff (García-Fayos and Cerdà 1997; García-Fayos et al.

22   2010) and, similar to trypanocarpy, increases the amount of surface contact between the seed coat and

23   soil, aiding seed hydration and thus facilitating germination (Harper and Benton 1966; Gutterman and

24   Shem-Tov 1996; Chambers et al. 1991).

25   Rainfall in arid and semi-arid regions of the world is mostly concentrated into a small number

26   of high intensity events (Rodríguez-Iturbe and Porporato 2004) with the potential to trigger strong soil

27   erosion processes, mainly on steep hillslopes (Poesen and Hooke 1997). In these situations, seeds on

28   the soil surface are at risk of being removed downslope by runoff water and dispersed downstream or

1   deposited in the lower parts of the slopes where they can get deeply buried (García-Fayos et al. 1995;

2   Han et al. 2011) or where seedlings, once seeds have germinated, can be affected by stronger

3   competition than those seedlings emerging on the upper or medium parts of the hillslopes with sparse

4   vegetation (Cantón et al. 2004; Alados et al. 2006). Although there has been less research on the

5   subject, wind erosion also has the potential of putting seeds at risk in the same way as surface runoff

6   (Whitford 2002). Erosion also affects important soil properties related to plant establishment and

7   development. Raindrop splashes break soil aggregates and sheet flow removes the finest particles and

8   organic debris from the upper layer of soil, thus reducing soil fertility, the rate of water infiltration into

9   the soil and the amount of available water for plants (Calvo-Cases et al. 2003; Monger and

10   Bestelmeyer 2006). In addition, granivorous animals, mainly harvester ants, have a strong impact on

11   seed survival in arid and semiarid ecosystems (Louda 1995; Hulme and Benkman 2002).

12   In consequence, the loss of seed germination opportunities in semiarid slopes because seed

13   removal by erosion, predation or soil degradation can be a major difficulty for plants to overcome and,

14   consequently, post-dispersal mechanisms allowing diaspore anchorage to the ground, burying the seed

15   into the soil or increasing the amount of contact of the surface of seeds with soil particles could be, for

16   all them, favourable adaptations.

17   If, as Ellner and Shmida (1981) proposed, seed anchorage mechanisms, such as myxospermy

18   and trypanocarpy, are the outcome of agents of selection that operate after seed dispersal, but not the

19   outcome of selective forces shaping seed dispersal, then it should be predicted that an increase in the

20   intensity of all, or some, of the agents of selection that operate on seeds once they have dispersed (i.e.

21   soil erosion, seed predation) must lead to an increase in the proportion of plants with seed anchorage

22   mechanisms, but should not affect the proportion of plant species with atelechory seed dispersal

23   syndromes. On the contrary, increasing the intensity of selective forces that shape seed dispersal only

24   (i.e. climate aridity) must lead to an increase in the proportion of species with mechanisms atelechory

25   syndromes, but should not affect the proportion of plant species with seed anchorage mechanisms.

26   To test this hypothesis we compared the proportion of plant species with atelechory seed

27   dispersal syndromes and the proportion of species with seed anchorage mechanisms (myxospermy

28   plus trypanocarpy) in plant communities colonizing flat areas and steep hillslopes at both extremes of

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an aridity gradient that has been proved to negatively affect soil properties (García-Fayos and Bochet

2009). We also explored the relationships between these proportions of species and physical soil

properties related to runoff generation (bulk density, as a surrogate of the rate of water infiltration in

soils) and to water uptake by seeds (fine sand content, indicative of the amount of contact between the

seed surface and the ground, and soil water availability as a surrogate of the amount of available water

for seeds to germinate and establish). At the same time, because seed harvesting pressure by ants may

also influence our results, we analyzed the current nest density of granivorous ants in the study area as

a surrogate of seed harvesting pressure. We assumed that harvesting pressure by ants should not mask

the outcome of the selective forces exerted by climate dryness and erosion. All other factors being

similar, the density of granivorous ants in semiarid areas of Spain, depends highly on vegetation

structure, food availability and microsite conditions for winter survival (Diaz 1991; Arnan et al. 2007)

that we expect does not covary with the analyzed factors. We predict that (i) an increase in climate

dryness, but not an increase in soil erosion, should increase the proportion of species with atelechory

syndromes; (ii) an increase in soil erosion, but not an increase in climate aridity, should increase the

proportion of plant species with seed anchorage mechanisms in plant communities; and (iii) the effect

of soil erosion on physical soil properties related to runoff generation and water uptake by seeds may

explain the effect that soil erosion has on the proportion of plant species with seed anchorage

mechanisms.

2. Material and Methods

2.1 Study Area

The study area is located in the Alfambra river basin (province of Teruel, Spain). The basin is

4000 m^2 in area and lies at an altitude of 900 to 1100 m a.s.l. It is composed mainly of calcareous

marls. While the seasonal pattern is homogeneous in the whole basin, the amount of precipitation and

average temperature differ between the southern and northern extremes of the basin with marked

consequences on the plant communities (García-Fayos and Bochet 2009). The extreme northern area,

hereafter "cool & wet" area, has year average temperature and total precipitation of 10.3 ℃ and 484

mm, respectively, and the southern area, hereafter "warm & dry" area, 11.9 ℃ and 368 mm,

1 respectively (data of the 1990-2009 period, provided by AEMET: www.aemet.es). Both areas share

2 almost 50% species of their local floras (see also García-Fayos and Bochet 2009, for a wider

3 description of the study area).

4 In spring 2006, we selected and marked one sampling plot (1 x 20 m) perpendicular to the

5 main slope direction in each of 30 hillslopes in the "cool & wet" and in the "warm & dry" areas, all of

6 them south-oriented. In each area, 15 plots were placed in flat sites (hereafter "no erosion" sites) and

7 15 in 25-30º steep hillslopes (hereafter "severe erosion" sites). Marked differences in erosion severity

8 exist between flat and steep sites, varying from 0 to 25% rill development respectively (see García-

9 Fayos and Bochet 2009); the latter rill density indicates a notorious sign of erosion processes on steep

10 sites (Cerdan et al. 2010). Wind erosion has not been taken into account in our experimental design,

11 because it has been reported as unimportant in the eastern part of the Iberian Peninsula (Solé-Benet

12 2006). Vegetation cover in all the plots was low (less than 50%) and it was mainly composed of dwarf

13 shrubs and some herbs.

14 Plant species present in each plot were identified and, when necessary, the plots were surveyed

15 several times during the growing season to assure that all plant species were recorded. From 2006 to

16 2009 we collected seeds from all species and 10 mature and full developed seeds per species were

17 checked and assigned to the following categories: trypanocarpy, myxospermy and atelechory.

18 Trypanocarpy corresponds to diaspores with hygroscopic awns or hairs that are able to enter into the

19 soil; myxospermy corresponds to diaspores that secrete mucilage from their testa or pericarp when

20 wet; and atelechory corresponds to diaspores with mechanisms for short-distance seed dispersal

21 (ballistic, barochory, etc.) or diaspores lacking such mechanisms but also lacking mechanisms for

22 long-distance seed dispersal. Since trypanospermy and myxospermy act after seed dispersal, a species

23 can be classified at the same time into the atelechory category and one of the two seed anchoring

24 categories.

25 At the end of the summer of 2006, we took five soil subsamples 5 cm deep and 300 cm^3

26 volume at regular distances in each plot, that were mixed up in a single sample per plot. Then, they

27 were air-dried and sieved through a 2 mm mesh and fine sand content (mineral fraction size between

28 0.10 and 0.25 mm) and the soil moisture content available for plants was determined following the

1   methodology proposed by Klute (1986). Additionally, we took three 57.7 cm^3 soil cores per plot for

2   bulk density determination at the same depth as previous soil sampling and the average value per plot

3   was used for comparisons. These soil properties were significantly and negatively affected by both

4   climate dryness and soil erosion in our study area (García-Fayos and Bochet 2009). Bulk density is a

5   key property influencing water infiltration into the soil and it was chosen as a surrogate of runoff

6   generation. The higher the soil bulk density, the lower the soil water infiltration and consequently, in

7   steep hillslopes, the faster and higher the runoff generation (Calvo-Cases et al. 2003). Fine sand

8   content and water availability were chosen respectively as surrogates of the extent of seed-soil contact

9   and the amount of water stored in soils. The relation of these soil properties with the energy that seeds

10   need to obtain water from soils was considered to be direct for fine sand content and inverse for water

11   availability (Williams and Shaykewich 1971). So, the higher the fine sand content and the lesser the

12   water availability in soils, the higher the pressure that seeds need to exert in order to obtain enough

13   water for germination and establishment (García-Fayos et al. 2000; Bochet et al. 2007).

14   To analyze the current nest density of granivorous ants in the study area, we sampled six

15   hillslopes per treatment and counted all the ant nests of granivorous species in an area of 250 m^2. Ant

16   nests were attributed to granivorous ants after identification of the worker ants or inspecting the vast

17   pile when direct ant identification was not possible.

18   Analyses of the influence of climate dryness and soil erosion treatments on the proportion of

19   species with seed anchorage mechanisms and the proportion of atelechoric species per plot were

20   performed with Linear Models, considering climate dryness and erosion as main factors and the

21   proportions of atelechoric species and of species with seed anchorage, as response variables. Analyses

22   were firstly performed on the total set of species with seed anchorage mechanisms, either

23   myxospermic or trypanocarpic, and secondly, separately on each of both categories. We checked

24   residuals for departure from normal distribution.

25   Because the size of the plots used to sample ant nest density was greater than that used to

26   sample plant species composition, it was not possible to directly analyze the effect of nest density on

27   the proportion of plant species with any dispersal or seed anchorage mechanism. Instead, we analyzed

28   the effect of climate dryness and seed erosion on ant nest density per hillslope, and compared the

1 results with those obtained from the analysis of the effect of the same factors on the proportion of

2 species with the considered dispersal and seed anchorage mechanisms per plot. Statistical analyses

3 were performed with the *lm* function of the R package v. 2.14.1 (R Development Core Team at

4 http://cran.r-project.org/ last accessed 25/05/2012).

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6 **3.   Results**

7   We found a total of 167 plant species in the study area. Of them, 139 were unambiguously

8 assigned to the different dispersal and seed anchoring diaspore categories (see Appendix). Among

9 these, 108 (77%) were considered to be atelechoric and 31 (22%) having any seed anchorage

10 mechanism (26 myxospermic species -several Brassicaceae, Cistaceae, Lamiaceae, Asteraceae,

11 Linaceae, Rosaceae, Plantaginaceae and Aristolochiaceae species- and only 5 trypanocarpic species -

12 four Graminae, *Stipa parviflora*, *S. celakowsky*, *S. lagascae*, *Avenula pratensis* and one Geraniaceae,

13 *Erodium cicutarium*). At the plot level, 67 to 94% of the species have atelechoric diaspores (79% in

14 average, see Table 1) and 17 to 45% of the species have diaspores with anchorage mechanism (30% in

15 average) and the proportion of myxospermic species is higher (15-44%, 26% in average) than that of

16 trypanocarpic species (0-8%, 2.4% in average).

17   Table 1 shows the variation among plots in the proportion of atelechory and seeds with

18 anchorage mechanisms. The linear model significantly explained the variation in the proportion of

19 atelechoric species (Adjusted R^2 = 0.1366; $F_{3, 56}$ = 4.112; p-value = 0.0105) indicating that it is

20 affected by climate dryness, although marginally (81.2 ± 4.5% in the "warm & dry" plots vs. 77.5 ±

21 3.9% in the "cool & wet" plots (Mean ± Standard deviation), t-value = 1.813; p-value = 0.0753), but

22 that neither soil erosion (t-value = -0.928; p-value = 0.3572) nor the interaction of both factors (t-value

23 = 0.816; p-value = 0.4178) affected the proportion of atelechoric species.

24   Relative to the proportion of species with seed anchorage mechanisms, the linear model

25 significantly explained a moderate proportion of the variance (Adjusted R^2 = 0.3481; $F_{3, 56}$ = 11.5; p-

26 value < 0.0001) showing that the proportion of species whose diaspores have anchorage mechanisms

27 is positively affected by soil erosion (t-value = 3.908; p-value = 0.0002) but neither by climate dryness

28 (t-value = -0.440; p-value = 0.6616) nor by their interaction (t-value = 0.330; p-value = 0.7426). On

1   average, the proportion of species with seed anchorage mechanisms is 26.7 ± 4.3% in the "no erosion"

2   plots and 33.5 ± 4.6% in the "severe erosion" ones.

3   When the proportion of species with myxospermic and trypanocarpic mechanisms was

4   analyzed separately, we found in the case of myxospermy that the model significatively explained

5   almost 41% of the variance ($F_{3, 56}$ =14.62; p-value < 0.0001) indicating that soil erosion (t-value =

6   2.744; p-value = 0.0081), but not climate dryness (t-value = -0.245; p-value = 0.8075), significantly

7   increased the proportion of myxospermic species in plots. However, the significant interaction term (t-

8   value = 2.130; p-value = 0.0376) indicates that the increase in the proportion of myxospermic species

9   due to the effect of soil erosion is higher when climate dryness is greater. In the case of trypanocarpy,

10   the model (Adjusted R^2 = 0.3033; $F_{3, 56}$ = 9.561; p-value < 0.0001) shows that climate dryness does not

11   have a significant effect (t-value = -0.436; p-value =0.6645) but that soil erosion increases the

12   proportion of trypanocarpic species (t-value =2.725; p-value = 0.0086). However, again, the

13   significant interaction term between climate dryness and soil erosion (t-value = -3.456; p-value =

14   0.0010) indicates that the proportion of trypanocarpic species in the "cool & wet" end of the climate

15   gradient, is a little higher in the "no erosion" plots than in the "severe erosion", but that the contrary

16   occurs in the "warm & dry" end of the climate gradient (see Table 1).

17   As hypothesized, both seed anchorage mechanisms (myxospermy and trypanocarpy together)

18   and myxospermy were significantly and directly related to fine sand content and bulk density and also

19   significantly but inversely related to water content (Table 2) indicating that there is an increase in the

20   proportion of species with anchoring mechanisms (mainly myxospermy) when physical soil properties

21   related to runoff generation and water uptake worsen. Atelechory was only positive and significatively

22   related with fine sand content and trypanocarpy was positively related with water availability (Table

23   2).

24   Nests of ants collecting diaspores in the studied hillslopes can be attributed mainly to genus

25   *Messor* (granivorous) and in a lesser extent to *Aphenogaster* (omnivorous). The total density of nests

26   of these ants in hillslopes was highly variable (from 0 to 317.5 nests.ha^{-1}) (see Table 1) and the linear

27   model that fitted our data (Adjusted R^2 = 0.2668; $F_{3, 24}$ = 4.276; p-value = 0.0149) showed that climate

28   dryness (t-value = -2.315; p-value = 0.0295), soil erosion (t-value = -3.488; p-value = 0.0019) and

their interaction (t-value = 2.327; p-value = 0.0287) significantly affected the density of ant nests on the hillslopes. Ant nest density decreased due to climate dryness and soil erosion, but the difference in ant nest density caused by soil erosion was higher in the "cool & wet" than in the "warm & dry" treatment (Table 1).

## 4.	Discussion

The proportion of species with diaspore anchorage mechanisms in our study area is similar, or even higher, to that found in desert and semi-desert areas of Africa (Van Rheede van Oudtshoorn and Van Rooyen 1999). At least 18.6% of the plant species in our study area and 17.0% of the species living in Namaqualand (Namibia) have anchorage mechanisms in their diaspores and 15.6% of the species in our study area, 15.7% in southeast Spain, 11.3% of the species in Namaqualand and 11.1% in northwest Africa are myxospermic (Van Rheede van Oudtshoorn and Van Rooyen 1999; Navarro et al. 2009). In relation to trypanocarpy, only 3.0% of the species in our study area are trypanocarpic, a similar value as in Namaqualand (5.7%) and in semi-desert areas of southeast Spain (less than 4%, Navarro et al. 2009). The proportion of species with short-distance dispersal syndromes (atelechory) was very high, approximately 80%, and is similar to that of desert areas of Israel (75.0%) but higher than that of Mediterranean and semi-desert areas of Israel (50.0%) and semiarid areas of Namaqualand (21.6%) (Ellner and Shmida 1981; Van Rheede van Oudtshoorn and Van Rooyen 1999). Interestingly, 100% of the myxospermic species also has short-distance dispersal mechanisms and 22% of atelechoric species are myxospermic (see Appendix). Ant nest density was also in the range of values reported for other semiarid shrublands (Diaz 1991; Azcárate and Peco 2003).

According to the prediction of the Ellner-Shmida's hypothesis, soil erosion but not climate dryness, increased the proportion of species with anchoring mechanisms living on hillslopes in our study area. Similarly, and in agreement with our prediction, atelechory increased, although slightly, with climate dryness, but soil erosion did not affect them. These results and the correlations between the proportions of atelechory and seed anchorage species with the studied soil properties strongly suggest that the need to resist seed removal by water runoff and to enhance the rate and the amount of water uptake by seeds are selective forces affecting the proportion of species with seed anchoring

1 mechanisms, mainly myxospermy, in our study area. However, the significant correlation of

2 atelechory with fine sand content (positive) and water availability (negative) and the fact that all

3 myxospermic species have also atelechoric syndromes, supports the idea that soil degradation because

4 of vegetation openness positively selects plant species with short-distance seed dispersal mechanisms

5 (Ellner and Shmida 1981; Kefi et al. 2008; Pueyo et al. 2008) but that myxospermy should be a

6 specific adaptation to soil erosion.

7   It is interesting to note that although the proportion of seed anchorage and myxospermic

8 species are positively correlated with bulk density and bulk density increased with both, climate

9 dryness and soil erosion, only soil erosion, but not climate dryness, positively affected the proportion

10 of species with seed anchorage mechanisms and myxospermy. This can be explained by the fact that

11 although bulk density decreased from the flat "warm & dry" plots to the flat "cool & wet" plots

12 (García-Fayos and Bochet 2009), the low slope angle recorded in these areas (less than 5º) prevents

13 water sheet flow from increasing in the same way. Therefore, plants of the flat "warm & dry" plots do

14 not suffer from more intense erosion than their equivalents in the "cool & wet" area and consequently

15 they do not need to increase mechanisms against seed removal by erosion.

16   Our results also shed some light on the different roles that myxospermy and trypanocarpy play

17 as seed anchorage mechanisms, although the very low frequency of trypanocarpic species (less than

18 1.5 ± 0.9 species.plot^{-1} in average) precludes obtaining strong conclusions. Whereas almost all the

19 conclusions about seed anchorage mechanisms are applicable to myxospermy, this is not the case for

20 trypanocarpy. In fact, the percentage of trypanocarpic species per plot is only significantly correlated

21 with water availability and this relationship is positive, unlike myxospermy. This reinforces the results

22 from the linear model indicating that trypanocarpic species seem to be selected by soil erosion only in

23 the wetter extreme of the climatic gradient, but that myxospermic species are selected positively in

24 both extremes of our climate gradient, although more intensely in the "warm & dry" extreme.

25   It is unlikely that our interpretation of the results on seed anchorage and myxospermy is

26 masked by a possible confounding effect of harvester ants. As assumed, ant nest density is negatively

27 affected by soil erosion, especially in the "cool & wet" extreme of the gradient, probably as a result of

28 the negative effect of soil erosion on standing biomass and productivity. So, the pattern we can expect

1   because of the pressure that ant harvesting exerts on plants is the opposite pattern that we found

2   relative to the proportions of seed anchorage and myxospermic species. This does not mean that ant

3   harvesting pressure cannot be a relevant force when selecting anti-predatory mechanisms for seeds,

4   such as myxospermy and trypanocarpy (see Schöning et al. 2004 and Engelbrecht and García-Fayos

5   2012 for recent reports on this issue), but it simply means that this pressure cannot explain the

6   proportion of species with seed anchorage mechanisms in our study design.

7   Our results have implications for the controversies on the role of seed dispersal in buffering

8   unpredictable small or medium-scale differences in patchy semiarid environments. Atelechory and

9   seed anchorage mechanisms have been repeatedly assumed to be in the origin and maintenance of arid

10   and semi-arid patchy landscapes (Schurr et al. 2004; Kefi et al. 2008; Pueyo et al. 2008) but to date

11   this assumption remains untested and needs to be directly verified. Siewert and Tielborger (2010)

12   found that in Mediterranean semiarid communities most species do not rely on seed dispersal

13   mechanisms to buffer unpredictable small-scale differences in patch quality, but rather that the major

14   contribution of plant species to population recruitment was through the investment in seed numbers

15   and dormancy. In this context, investing in seed anchorage mechanisms, such as those analyzed here,

16   can be another way for plant species to survive in semiarid landscapes where soil erosion plays an

17   important selection pressure.

18   In conclusion, our report is, to our knowledge, the first attempt to examine systematically the

19   importance of various factors associated with the selection of plant species whose diaspores have

20   anchoring mechanisms to soil. Although the role of myxospermy and trypanocarpy as mechanisms

21   enhancing seed-soil contact had been widely studied, it is the first time that a direct relation of soil

22   erosion with the proportion of myxospermy and trypanocarpy in plant communities has been shown,

23   supporting the hypothesis that anchorage mechanisms in diaspores play a role shaping species

24   composition in communities affected by intense soil erosion (see also Bochet et al. 2009 and García-

25   Fayos et al. 2010).The correlative approach of our study and the complex nature of the explanatory

26   characteristics used make it difficult to interpret unambiguously the ultimate causes behind the

27   observed associations. Nevertheless, the patterns that we detected support the idea that in water-

28   limited environments anchorage mechanisms can be a way for seeds to overcome the direct effects of

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1   soil erosion -seed removal- and the negative effects of soil erosion on soil properties related to water

2   uptake by seeds, an important limiting factor for plant establishment in such environments (García-

3   Fayos et al. 2000; Bochet et al. 2009; Moreno-de las Heras et al. 2011). Although seed predation by

4   ants cannot be completely discarded, it seems to play a minor role in the plant communities we

5   studied.

6

1   **References**

2   Alados C, Gotor P, Ballester P et al (2006) Association between competition and facilitation processes

3   and vegetation spatial patterns in alpha steppes. Biol J Linn Soc 87:103-113.

4   Arnan X, Rodrigo A, Retana J (2007) Uncoupling the effects of shade and food resources of

5   vegetation on Mediterranean ants: an experimental approach at the community level.

6   Ecography 30:161-172.

7   Azcárate FM, Peco B (2003) Spatial patterns of seed predation by harvester ants (*Messor* Forel) in

8   Mediterranean grassland and scrubland. Insect Soc 50:120-126.

9   Bochet E, García-Fayos P, Poesen J (2009) Topographic thresholds for plant colonization on semi-arid

10   eroded slopes. Earth Surf Proc Land 34:1758-1771.

11   Bochet E, García-Fayos P, Alborch B, Tormo J (2007) Soil water availability effects on seed

12   germination account for species segregation in semiarid roadslopes. Plant Soil 295:179-191.

13   Calvo-Cases A, Boix-Fayos C, Imeson AC (2003) Runoff generation, sediment movement and soil

14   water behaviour on calcareous (limestone) slopes of some Mediterranean environments in

15   Southeast Spain. Geomorphology 50:269-291.

16   Cantón Y, del Barrio G, Solé-Benet A, Lázaro R (2004) Topographic controls on the spatial

17   distribution of ground cover in the Tabernas badlands of SE Spain. Catena 55:341-365.

18   Cerdan O, Govers G, Le Bissonnais Y, et al (2010) Rates and spatial variations of soil erosion in

19   Europe: A study based on erosion plot data. Geomorphology 122:167-177.

20   Chambers JC, MacMahon JA, Haefner JH (1991) Seed entrapment in alpine ecosystems: effects of

21   soil particle size and diaspore morphology. Ecology 72:1668-1677.

22   Cohen D, Levin SA (1987) The interaction between dispersal and dormancy strategies in varying and

23   heterogeneous environments. Lecture Notes in Biomathematics 71:110-122.

24   Diaz M (1991) Spatial patterns of granivorous ant nest abundance and nest site selection in

25   agricultural landscapes of Central Spain. Insect Soc 38:351-363.

26   Ellner S, Shmida A (1981) Why are adaptations for long-range seed dispersal rare in desert plants?

27   Oecologia 51:133-144.

1   Engelbrecht M, García-Fayos P (2012) Mucilage secretion by seeds doubles the chance to escape ant

2   removal. Plant Ecol 213:1167-1175.

3   Friedman J, Stein Z (1980) The influence of seed dispersal mechanisms in the dispersion of *Anastatica*

4   *hierochuntica* (Cruciferae) in the Negev Desert, Israel. J Ecol 68:43-50.

5   Fuller PJ, Hay ME (1983) Is glue production by seeds of *Salvia columbariae* a deterrent to desert

6   granivores? Ecology 64:960-963.

7   García-Fayos P, Bochet E (2009) Indication of antagonistic interaction between climate change and

8   erosion on plant species richness and soil properties in semiarid Mediterranean ecosystems.

9   Global Change Biol 15:306-318.

10 García-Fayos P, Bochet E, Cerdà A (2010) Seed removal susceptibility through soil erosion shapes

11   vegetation composition. Plant Soil 334:289-297.

12 García-Fayos P, Cerdà A (1997) Seed losses by surface wash in degraded Mediterranean

13   environments. Catena 29:73-83.

14 García-Fayos P, Cerdà A, Recatalá TM, Calvo A (1995) Seed population dynamics on badland slopes

15   in SE Spain. J Veg Sci 6:691-696.

16 García-Fayos P, García-Ventoso B, Cerdà A (2000) Limitations to plant establishment on eroded

17   slopes in southeastern Spain. J Veg Sci 11:77-86.

18 Grubert M (1974) Studies on the distribution of myxospermy among seeds and fruits of Angiospermae

19   and its ecological importance. Acta Biol Venezuelica 8:315-551.

20 Gutterman Y, Shem-Tov S (1996) Structure and function of the mucilaginous seed coats of *Plantago*

21   *coronopus* inhabiting the Negev Desert of Israel. Isr J Plant Sci 44:125-133.

22 Gutterman Y, Shem-Tov S (1997) The efficiency of the strategy of mucilaginous seeds of some

23   common annuals of the Negev adhering to the soil crust to delay collection by ants. Isr J Plant

24   Sci 45:317-327

25 Han L, Jiao J, Jia Y, Wang N, Lei D, Li L (2011) Seed removal on loess slopes in relation to runoff

26   and sediment yield. Catena 85:12-21.

27 Harper JL, Benton RA (1966) The behaviour of seeds in soil: II. The germination of seeds on the

28   surface of a water supplying substrate. J Ecol 54:151-166.

Huang Z, Gutterman Y, Osborne DJ (2004) Value of the mucilaginous pellicle to seeds of the sand-stabilizing desert woody shrub *Artemisia sphaerocephala* (Asteraceae). Trees 18:669-676.

Hulme Ph, Benkman CW (2002) Granivory. In Herrera CM, Pellmyr O (eds) Plant-Animal Interactions. An Evolutionary Approach. Blackwell Science, Oxford, pp 132-154.

Kefi S, van Baalen M, Rietkerk M, Loreau M (2008) Evolution of local facilitation in arid ecosystems. Am Nat 172:E1-E17.

Klute A (ed) (1986) Methods of soil analysis. Part 1. Physical and mineralogical properties. Agronomy Monograph 9, 2nd ed, American Society of Agronomy-Soil Science Society of America, Madison WI, USA.

Levin S, Cohen D, Hastings A (1984) Dispersal strategies in patchy environments. Theor Popul Biol 26:165-191.

Louda SM (1995) Effect of seed predation on plant regeneration: Evidence from pacific basin Mediterranean scrub communities. In Arroyo MTK, Zedler PH, Fox MD (eds) Ecology and biogeography of Mediterranean ecosystems in Chile, California and Australia. Springer-Verlag, NY, USA, pp 311-344.

Monger HC, Bestelmeyer BT (2006) The soil-geomorphic template and biotic change in arid and semi-arid ecosystems. J Arid Environ 65:207-218

Moreno-de las Heras M, Espigares T, Merino-Martín L, Nicolau JM (2011) Water-related ecological impacts of rill erosion processes in Mediterranean-dry reclaimed slopes. Catena 84:114-124.

Navarro T, Pascual V, Alados CL, Cabezudo B (2009) Growth forms, dispersal strategies and taxonomic spectrum in a semi-arid shrubland in SE Spain. J Arid Environ 73:103-112.

Poesen J, Hooke JM (1997) Erosion, flooding and channel management in Mediterranean environments of southern Europe. Prog Phys Geog 21:157-199.

Pueyo Y, Kefi S, Alados CL, Rietkerk M (2008) Dispersal strategies and spatial organization of vegetation in arid ecosystems. Oikos 117:1522-1532.

Rodriguez-Iturbe I, Porporato A (2004) Ecohydrology of Water Controlled Ecosystems: Soil Moisture and Plant Dynamics. Cambridge University Press, NY, USA.

1   Schöning C, Espadaler X, Hensen I, Roces F (2004) Seed predation of the tussock-grass *Stipa*

2   *tenacissima* L. by ants (*Messor* spp.) in southeastern Spain: the adaptive value of

3   trypanocarpy. J Arid Environ 56:43-61.

4   Schurr FM, Bossdorf O, Milton SJ, Schumacher J (2004) Spatial pattern formation in semi-arid

5   shrubland: a priori predicted versus observed pattern characteristics. Plant Ecol 173:271-282.

6   Siewert W, Tielborger K (2010) Dispersal-dormancy relationships in annual plants: Putting model

7   predictions to the test. Am Nat 176:490-500.

8   Solé-Benet A (2006) Spain. In Boardman J, Poesen J (eds) Soil erosion in Europe. John Wiley & Sons

9   Ltd Chichester, UK, pp 479-488.

10   Stamp NE (1989) Seed dispersal of four sympatric grassland annual species of *Erodium*. J Ecol

11   77:1005-1020.

12   Stebbins GL (1971) Processes of organic evolution. Prentice Hall Inc, Englewood Cliffs N.J., USA.

13   Van der Pijl L (1982) Principles of dispersal in higher plants, 3rd ed, Springer-Verlag, Berlin,

14   Germany.

15   Van Rheede van Oudtshoorn K, Van Rooyen MW (1999) Dispersal Biology of Desert Plants.

16   Springer-Verlag, Berlin-Heidelberg, Germany.

17   Western T (2012) The sticky tale of seed coat mucilages: production, genetics, and role in seed

18   germination and dispersal. Seed Sci Res 22:1-25.

19   Whitford WG (2002) Ecology of Desert Systems. Academic Press, San Diego, CA, USA.

20   Williams J, Shaykewich CF (1971) Influence of soil matric potential and hydraulic conductivity of the

21   germination of rape seed (*Brassica napus*). J Exp Bot 22:586-597.

		"cool & wet"		"warm & dry"	
		"no erosion"	"severe erosion"	"no erosion"	"severe erosi
Atelechory	(n sp.20m^{-2})	39.3 ± 3.0	24.5 ± 4.5	21.6 ± 3.9	20.0 ±3.8
	%	79.2 ± 3.3	76.8 ± 4.3	81.0 ±5.8	81.3 ± 2.8
Seed anchorage mechanisms (n sp.20m^{-2})		13.5 ± 1.4	10.6 ± 1.7	7.0 ± 2.0	8.2 ± 1.9
	(%)	27.0 ± 3.1	33.5 ± 4.1	26.3 ± 5.3	33.5 ± 5.2
Myxospermy	(n sp.20m^{-2})	11.5 ± 1.5	8.6 ± 1.3	6.0 ± 1.6	8.6 ± 1.3
	(%)	22.9 ± 3.0	29.3 ± 3.0	22.5 ± 4.7	31.4 ± 5.7
Trypanocarpy	(n sp.20m^{-2})	1.1 ± 0.5	1.3 ± 0.5	0.6 ± 0.7	0.3 ± 0.5
	(%)	2.1 ± 1.0	4.2 ± 1.6	2.1 ± 2.6	1.1 ± 1.9
Ant nest density	(nests.ha^{-1})	186.7 ± 96.1	36.6 ± 40.6	97.6 ± 89.1	81.8 ± 38.

Table 1. Average and standard deviation of number of species and percentage of species with different

dispersal and soil anchorage mechanisms and ant nest density in hillslopes of the different treatments

(N = 15).

	Fine sand content (%)	Water availability	Bulk density
Atelechory	0.2713*	-0.3233*	0.0169
Seed anchorage mechanisms	0.2753*	-0.2948*	0.3479**
Myxospermy	0.3277**	-0.4260***	0.3745**
Trypanocarpy	-0.1048	0.2708*	-0.0489

Table 2. Pearson correlation indices between the percentage of species with different dispersal and soil

anchorage mechanisms and soil properties (** = p-value <0.01; * = 0.01> p-value <0.05; N = 60).

*SPECIES	ATELECHORY	MYXOSPERMY	TRYPANOSPERMY
Allium senescens subsp. montanum	1	0	0
Alyssum simplex	1	1	0
Androsace maxima	1	0	0
Anthyllis montana	1	0	0
Anthyllis vulneraria	1	0	0
Aphyllantes monspeliensis	1	0	0
Arabis auriculata	1	1	0
Arctostaphyllos uva-ursi	0	0	0
Argyrolobium zanonii	1	0	0
Aristolochia pistolochia	1	1	0
Artemisia campestris	1	1	0
Asperula aristata subsp. scabra	1	0	0
Asphodelus ramosus	1	0	0
ASTERACEAE (undetermined)	0	0	0
Astragalus incanus	1	0	0
Astragalus stella	1	0	0
Atractylis humilis	0	0	0
Avenula pratensis subsp. gonzaloi	0	0	1
Biscutella alcarriae	0	0	0
Brachypodium retusum	1	0	0
Brassica nigra	1	1	0
BRASSICACEAE (undetermined)	1	1	0
Bromus erectus	1	0	0
Bupleurum fruticescens	1	0	0
Bupleurum rigidum	1	0	0
Carduncellus monspelliensium	0	0	0
Carex humilis	1	0	0
Centaurea aspera	1	0	0
Cephalaria leucantha	1	0	0
Cerastium sp 1	1	0	0
Cerastium sp 2	1	0	0
Cerastium sp 3	1	0	0
Convolvulus lineatus	1	0	0
Coris monspeliensis	1	0	0
Coronilla minima subsp lotoides	1	0	0
Coronilla minima subsp minima	1	0	0
Crucianella patula	1	0	0
Dactylis glomerata subsp hispanica	1	0	0
Dianthus algetanus subsp turolensis	1	0	0
Dianthus pungens subsp hispanicus	1	0	0
Digitalis obscura	1	0	0
Dipcadi serotinum	1	0	0
Dorycnium pentaphyllum	1	0	0
Echinops ritro	0	0	0
Erinacea anthyllis	1	0	0
Erodium ciconium	1	0	1
Eryngium campestre	0	0	0
Euphorbia exigua	1	0	0
Euphorbia isatidifolia	1	0	0
Euphorbia polygalifolia	1	0	0
Euphorbia serrata	1	0	0
Filago pyramidata	0	0	0
Fritillaria lusitanica	1	0	0
Fumana ericifolia	1	1	0
Fumana procumbens	1	1	0

Galactites tomentosa	0	1	0
Genista mugronensis	1	0	0
Genista scorpius	1	0	0
Globularia vulgaris	1	0	0
Helianthemum apenninum subsp stoechadifolium	1	1	0
Helianthemum marifolium	1	1	0
Helianthemum origanifolium subsp glabratum	1	1	0
Helianthemum salicifolium	1	0	0
Helianthemum violaceum	1	1	0
Helichrysum stoechas	0	1	0
Hieracium sp	0	0	0
Hippocrepis commutata	1	0	0
Hormatophylla lapeyroussiana	1	1	0
Hymenolobus procumbens	1	0	0
Iris germanica	1	0	0
Juniperus communis	0	0	0
Juniperus thurifera	0	0	0
Koeleria splendens	1	0	0
Koeleria vallesiana	1	0	0
Lavandula latifolia	1	0	0
Leuzea conifera	0	0	0
Linaria glauca subsp aragonensis	1	0	0
Linum narbonense	1	1	0
Linum suffruticosum	1	1	0
Lithodora fruticosa	1	0	0
Matthiola fruticulosa	1	1	0
Medicago minima	0	0	0
Muscari neglectum	1	0	0
Myosotis sp	1	0	0
Onobrychis viciifolia	0	0	0
Ononis fruticosa	1	0	0
Paronychia sp	1	0	0
Phagnalon saxatile	0	0	0
Phlomis lychnitis	1	0	0
Pilosella pseudopilosella	0	0	0
Plantago albicans	1	1	0
POACEAE (undetermined sp 1)	1	0	0
POACEAE (undetermined sp 2)	1	0	0
Potentilla cinerea	1	1	0
Potentilla neumanniana	1	1	0
Quercus faginea	1	0	0
Quercus ilex	1	0	0
Ranunculus gramineus	1	0	0
Rapistrum rugosum	1	0	0
Reseda lutea	1	0	0
Reseda phyteuma	1	0	0
Reseda undata	1	0	0
Rhamnus alaternus	0	0	0
Rhamnus saxatilis	0	0	0
Ruta chalepensis	1	0	0
Salvia lavandulifolia	1	1	0
Sanguisorba minor	1	0	0
Santolina chamaecyparissus	1	1	0
Satureja intricata	1	0	0
Scabiosa stellata	1	0	0
Scleranthus annuus	1	0	0

Scorzonera angustifolia	0	0	0
Scorzonera hirsuta	0	0	0
Sedum sediforme	1	0	0
Senecio gallicus	0	0	0
Serratula nudicaulis	0	0	0
Seseli montanum	0	0	0
Sideritis ilicifolia	1	0	0
Silene nutans	1	0	0
Sisymbrium irio	1	1	0
Sonchus tenerrimus	0	0	0
Spergularia diandra	1	0	0
Stipa celakowskyi	0	0	1
Stipa lagascae	0	0	1
Stipa parviflora	0	0	1
Stipa pennata	0	0	0
Teucrium capitatum	1	0	0
Teucrium chamaedrys	1	0	0
Teucrium gnaphalodes	1	0	0
Teucrium webbianum	1	0	0
Thalictrum tuberosum	1	0	0
Thesium humifussum	1	0	0
Thymelea pubescens	1	0	0
Thymus leptophyllus	1	1	0
Thymus vulgaris	1	1	0
Tribulus terrestris	0	0	0
Trinia glauca	1	0	0
Vicia sp	1	0	0
Viola willkommii	1	0	0

*Nomenclature follows Castroviejo S. (coord.) (1986-2012) Flora Iberica. CSIC, Madrid
but still unpublished families that follows Mateo G. (1992) Claves para la flora de la Provincia de Teruel.
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