

What nurse shrubs can do for barren soils: rapid productivity shifts associated with a 40 years ontogenetic gradient

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Abstract

Aims We postulated that soil productivity shifts associated with the development of facilitation-driven plant patches in abiotically stressful ecosystems can be faster than currently assumed. This might be due to the effect of the nurse plant by promoting resource accumulation both directly and indirectly through facilitating a plant community underneath its canopy.

Methods We analysed a 40 year-ontogenetic gradient of *Ononis tridentata*, a colonizer shrub of barren gypsum soils in drylands. Soil fertility (chemical variables) and microbial productivity (microbial biomass, respiration

and enzymatic activities) were measured along the gradient. The contribution of the nurse plant and the facilitated community to the soil fertility and microbial productivity shifts were separated and quantified by regression commonality analysis.

Results Soil chemical fertility and microbial productivity rapidly increased during the first 20 years, with total organic carbon and microbial parameters rising six-fold along the *Ononis* ontogenetic gradient. This fast development of soil fertility was mostly explained by the unique effect of *Ononis* age (37.5 %) with an important contribution of the abundance of facilitated species (15.6 %).

Conclusions Facilitative interactions counterbalance the negative effect of harsh abiotic stress on the time rate and intensity at which plant and soil development occur in drylands.

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Introduction

Pedogenetic processes primarily occur on soil surface horizons, which at the same time are the most vulnerable layers to natural or human-induced soil degradation. Weathering rates are rock- and climate-dependent and are usually measured in geological time-scales (White and Brantley 1992; Keech et al. 2013). Plant-soil feedbacks operate on faster timescales and are mainly

dependent on plant litter and root exudates inputs (Kellman 1979; Wezel et al. 2000; Dakora and Phillips 2002), whose chemical content and decomposition rates are species-specific (Moro and Domingo 2000). The kinetics of organic matter decomposition is regulated by the local biological activity through moisture and temperature regimes (Schlesinger 1997; McTiernan et al. 2003), which thus synergistically control the evolution of soil and vegetation (Van Breemen and Finci 1998; Walker and del Moral 2003). This has brought about the hardly-assessed idea that natural soil nutrient enrichment is a very slow process in drylands (Bolling and Walker 2000; Verheye and de la Rosa 2005), which concurrently has been (intuitively) associated with a low plant cover and the displacement of tree life forms by dwarf plants. However, the time rate at which shrubby communities evolve and influence organic matter decomposition and nutrient cycling in stressful ecosystems has been hardly assessed.

Soil properties in arid lands show a marked spatial heterogeneity strongly associated with the patchy distribution of the vegetation. Patchy ecosystems usually determine soil fertility-unfertility mosaics associated to a plant-gap structure (Garner and Steinberg 1989; Pugnaire et al. 1996; Schlesinger et al. 1996; Aguiar and Sala 1999). Shrubs, dwarf scrubs or perennial grasses dominate the plant patches, whose diameter ranges from decimeters to meters. Underneath these plant patches, soils show ameliorated physical properties, as well as levels of organic matter, nitrogen and mineral nutrients that can be up to 4–10 times higher than in open spaces (Bochet et al. 1999; Ambatzis et al. 2003; Goberna et al. 2007a; Navarro-Cano et al. 2014). This fosters soil microbial activity in patches compared to gaps (Bolton et al. 1993; Moro et al. 1997; Goberna et al. 2007a). The formation of plant patches is driven by facilitative interactions among plant species (Brooker et al. 2008; Castillo et al. 2010). A nurse plant able to establish under abiotically stressful conditions founds the patch, enriches the soil by incorporating litter and exudates, and lessens the harsh micro-climatic conditions by shading and capturing circulating water (Aguiar and Sala 1999). This shapes a more suitable niche for the establishment of plant species with less stress tolerance, a process that leads to enhanced plant abundance and diversity (Callaway 2007). Nurse ability has been observed in very different plant life forms (Padilla and Pugnaire 2006). However, shrubs are among the most suitable nurse plants because they provide an

ameliorated micro-climate and increased soil fertility at minimum competitive costs compared to grasses or trees (Gómez-Aparicio 2009; Butterfield and Briggs 2011).

The use of short life forms (shrubs, scrubs, perennial herbs and grasses) as potential candidates to drive ecological restoration is increasingly recommended when stress-tolerance and nurse ability are required (Maestre et al. 2001; Castro et al. 2002; Barberá et al. 2006; Gómez-Aparicio 2009; Padilla et al. 2009). The time needed by a restoration action to reach the target ecosystem is fundamental to properly assess the technical and economic viability of restoration plans. It is known that factors such as the abundance of the nurse species in the early stages of ecosystem development following disturbance may determine the long-term result of restoration (Siles et al. 2008). Nevertheless, the time rates at which plant patches (dominated by short life forms) develop and improve soil properties in arid lands have not been tackled yet due to two main reasons. First, trees (mainly conifers) have had a dominant role in afforestation and restoration programs under semiarid to dry conditions throughout the world (Maestre and Cortina 2004; Cao et al. 2011). However, it is now accepted that tree species reduce influence on soil development as water stress increases (Padilla et al. 2009). In fact, 30–60-year-old pine stands, with their recalcitrant litter inputs, did not improve soil properties compared to neighbouring shrubby or perennial grass communities in semiarid environments (Goberna et al. 2007b; Ruiz-Navarro et al. 2009; Navarro-Cano et al. 2009). Second, there has been a historical lack of empirical knowledge on age determination in perennial growth forms other than trees. In recent years, dating short life forms has been revived as a useful method to detect former effects of climate on biological communities and predict future trends under ongoing global warming in areas above the survival limit of trees (Rayback and Henry 2005; Liang and Eckstein 2009; Weijers et al. 2010). Several age determination studies in humid environments suggest that around 9 % of small shrubs and perennial herbs can live for several decades and some even more than a century (Schweingruber and Poschold 2005). Dendrochronological analyses of small plants in arid- to drylands are still rare (but see Brotherson et al. 1984; Patón et al. 1998; Eugenio et al. 2012) and little empirical information on their average age is available.

Most studies on plant-soil relationships have been carried out at short time scales (less than 3 years) as reviewed by Kardol et al. (2013). Long-term studies on

plant dynamics and its relationship with soil development have been usually based on sampling of overall communities along chronosequences (Bolling and Walker 2000; Walker and del Moral 2003; Dana and Mota 2006) whereas individual shifts along ontogenetic gradients within the same community are seldom available (Kardol et al. 2013; but see Pugnaire et al. 1996). Here, we selected a patchy community dominated by the gypsophyte shrub *Ononis tridentata* L. (hereafter *Ononis*) to assess the time this plant requires to create fertility islands below its canopy from unfertile bare gypsum substrates under semiarid Mediterranean climate. *Ononis* is a legume able to recruit on bare gypsum soils and establish mutualistic interactions with N-fixing rhizobial bacteria. We expected that soil chemical fertility and microbial productivity under *Ononis*-dominated plant patches are functions of the nurse age. Based on field observations and previous research on the role of large *Ononis* plants as nurses (Navarro-Cano et al. 2014), we hypothesised that shrubby plant patches rapidly (i.e. in a few decades) increase soil chemical fertility and microbial productivity due to a synergistic effect of the nurse species by augmenting the organic inputs to the soil both directly and indirectly through increasing the abundance of facilitated plant species. We aimed to: i) correlate *Ononis* age with plant growth variables and use them to establish an *Ononis* ontogenetic gradient, ii) quantify soil chemical fertility and microbial productivity shifts along the gradient, and iii) quantitatively separate the direct effects of *Ononis* on soil fertility and productivity and its indirect effects mediated by the facilitation of a plant community below its canopy.

Materials and methods

Study site

We selected one hectare formed by gypsum outcrops in Serra de Crevillent (Alacant, SE Spain; UTM 30 N 689062, 4238201; average 350 m a.s.l., 40 % slope). The climate is semiarid Mediterranean (240 mm mean annual rainfall, 20 °C mean annual temperature) and the soils are Typic Xerorthents (Goberna et al. 2007a). Vegetation is dominated by *Ononis*, the most abundant shrub on gypsum soils in the Iberian Peninsula (Mota et al. 2011), which determines a patch-gap mosaic with an overall 25 % plant cover (Supplementary Information (SI) Fig. S1). The gaps are partially covered by sealing

crusts (Goberna et al. 2007a) and some gypsophytes such as the dwarf shrubs *Helianthemum squamatum* (L.) Dum. Cours. and *Teucrium libanitis* Schreb. The patches promoted by *Ononis* mainly attract non-gypsophyte dwarf-shrubs, perennial grasses and herbs such as *Thymus moroderi* Pau ex Mart., *Brachypodium retusum* (Pers.) Beauv. and *Sedum sediforme* (Jacq.) Pau. *Ononis* seedlings establish in unfertile gaps and modify their fertility subsequently (Navarro-Cano et al. 2014). The gaps have (Mean±SD) TOC, 6.2±2.7 g kg⁻¹, N, 0.7±0.3 g kg⁻¹, P, 0.09±0.04 g kg⁻¹ and K, 3.00±0.73 g kg⁻¹. No significant differences exist between the soil properties below the seedlings (Mean±SD plant height: 10.1±5.8 cm) and their adjacent gaps in the study site, including gravimetric humidity, total organic carbon, macro- and micro-nutrients in the study area (Navarro-Cano et al. 2014).

Ononis age determination and age - size relationship

The shrub *Ononis* has a radial growth, with several stems growing from a tap root at 5–10 cm over the soil surface. Its wood is porous. Stems have circular cross sections in young plants and elliptic, lobed or irregular sections in old plants. Thirty-six *Ononis* plants from the seedling stage up to reproductive adults were selected in the study site. Height, major and minor canopy diameter, and basal circumference of the thickest stem were measured in situ in all plants. For each plant, the thickest stem was transversely cut at the point where the basal circumference was measured and a 5-mm cross section was taken for laboratory processing. Each cross section was polished with increasingly fine sandpaper down to 400 grade. The sections were immersed in 96 % ethanol to strengthen the annual ring contrast (Patón et al. 1998). The number of rings was counted in four perpendicular transects from the pith to the cortex at 40× using a LEICA S8AP0 binocular microscope (SI Fig. S2). Using the whole section of each plant we minimized errors from counting false rings (Schweingruber and Poschlod 2005; Eugenio et al. 2012). Once the age of each plant had been determined, the number of rings was individually regressed against biometric variables (height; mean diameter = major canopy diameter + minor canopy diameter / 2; biovolume = $\pi \times$ major radius \times minor radius \times height; and stem circumference). The equation with best significant fit was chosen to subsequently estimate the age of 50 undisturbed newly selected *Ononis* plants forming the ontogenetic gradient of the

experiment. All regression analyses were carried out with SigmaPlot 11.0 (Systat Software Inc., San Jose, CA, USA).

Ontogenetic gradient characterization

We used the mean diameter of *Ononis* to select a size gradient including 50 patches in the study site. The gradient ranged from a seedling with a 1.3 cm mean diameter up to an *Ononis* individual with 236 cm mean diameter, the largest mean diameter found in the study area. The patches did not show any spatial pattern. The age of the plants was estimated using the above-selected equation with best significant fit between the number of rings and the stem circumference, plant height, mean diameter and biovolume. The estimated age was used as a predictor variable in the analyses. The micro-environmental characterization of the gradient was carried out by measuring soil surface temperature, radiation and soil gravimetric humidity from 11 a.m to 12:30 p.m. below the *Ononis* canopy in April 2013, when soil samples were collected. Temperature was measured with a thermometer CRISON 638Pt (Alella, Spain). Radiation was measured with a sensor type SKP 210 (Skye Instruments Ltd., Wales, UK). Gravimetric humidity was measured as described in the following section.

The abundance of facilitated plant species was estimated as the Plant Cover below each *Ononis* canopy in April 2013. Three parallel linear transects were sampled per *Ononis* patch. The transect length was limited to the *Ononis* canopy, thus adjusting the sampling intensity to the patch size. All transects were north-south oriented and distributed as follows within each patch: the first transect crossed the patch through its major diameter, and the other two transects were placed one left and one right of the initial transect at a distance of half the *Ononis* radius. Plant cover was estimated as the percentage of linear transect occupied by facilitated plants summing all three transects per *Ononis* plant. Hence, plant cover provided a standardized estimate of plant abundance below the *Ononis* canopy, which was used as a predictor variable in the analyses.

Soil properties and microbial productivity

Litter and surface soil samples (0–5 cm) were independently collected below the patches shaping the ontogenetic gradient ($N=50$). In both cases, four sub-samples

distributed in the cardinal points of each patch were collected at a distance of the half mean radius, each sub-sample either consisting of all the litter present in a 5×5 cm quadrat or ca. 100 g soil. In all cases, sample collection was performed strictly below the patch canopy, except for the five smallest patches (formed by *Ononis* seedlings) in which sampling was carried out within a 10 cm-radius around each nurse plant. Sub-samples were bulked into single composite samples, thus making one litter sample and one soil sample per patch. Samples were refrigerated and transported to the laboratory. Litter samples were dried in a 65 °C oven for 48 h and weighed to estimate the litter dry weight. Soil samples were sieved through a 1 mm mesh to exclude finely broken litter and avoid an artificial overestimation of organic C and nutrients in the mineral soil. Samples were stored at 4 °C until analysed. Physical and chemical properties were measured using standard procedures. Soil texture was analysed with the Bouyoucos densitometer. Gravimetric humidity content (GH) was calculated as the weight loss after 65 °C oven-drying soil samples. Soil pH and electrical conductivity (EC) were measured in a soil suspension in water (1:2.5 and 1:5 w/v, respectively). Total organic carbon (TOC) and total nitrogen (N) were quantified using a TruSpec Analyser (FLASH EA 1112 Series, LECO Corporation, MI, USA). TOC was quantified after a 55 °C acidic (HCl) treatment of the samples. Other macro- and micro-nutrients were determined by digestion with HNO₃ and H₂O₂, using an Ultraclave microwave digestion system (Milestone S.R.L., Milan, Italy) followed by analysis by ICP (ICAP 6500 ICP Spectrometer, Thermo Fischer Scientific, Waltham, MA, USA). This procedure leads to the digestion and solubilisation of all elemental forms.

We quantified five soil microbial parameters indicative of microbial biomass (microbial biomass carbon), general activity (basal respiration), as well as carbon, phosphorus, and nitrogen cycling (β -glucosidase, alkaline phosphatase and urease activities respectively). All microbial parameters were determined as described in Navarro-Cano et al. (2014), excepting the soil's potential to mineralise organic C, which was estimated through the basal respiration (Nannipieri et al. 1990) as follows: soil samples (1 g) were moistened to 60 % water-holding capacity prior to incubation at 28 °C in 10 cm³ airtight vials. The CO₂ (%) evolved in the vials was measured over 10 days at 2-day intervals by Gas Chromatography (TraceTM Ultra GC equipped with a

Thermal Conductivity Detector, Thermo Scientific) using 220 μl injection volumes. Running was performed for 12 min at 110 °C using helium as carrier gas at 300 KPa. During this period, the samples were kept at 28 °C in a Peltier-controlled module. Basal respiration was calculated as the average C content respired daily per kilogram soil.

Soil fertility bioassay

We assessed the correspondence of the *Ononis* ontogenetic gradient to a chemical soil fertility gradient by means of a bioassay with barley (*Hordeum vulgare*) as a phytometer species (see Pugnaire et al. 1996 for a similar procedure). Sieved soil samples collected below the fifty patches were grouped into ten *Ononis* size categories according to the mean diameter ($n=5$ per category), from an average diameter 3.7 cm and 1.5 year-old up to 194 cm and 31.4 year-old (category upgrade every 20 cm diameter approx.). For each category, four pots were filled with soil (85 g per pot) and nine previously soaked (24 h) barley seeds were sowed per pot ($n=36$ seeds per soil category). Pots were incubated in a growth chamber Sanyo MLR-350H (Sanyo, Japan) under a 12-h photoperiod, 85 % relative humidity and cyclic temperature conditions, ranging from 12 °C (dark) to 22 °C (light). The photosynthetically active photon flux density during the light phase was 93 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Each pot was watered twice a week with 10 ml deionised water. Average seedling growth was assessed after 3 weeks by washing the soil and measuring above-ground plant length, above- and belowground biomass and the root-shoot (RS ratio), which is the root biomass divided by the shoot biomass. The biomass measurement was carried out after drying the seedlings in an oven at 65° for 48 h.

Statistical analyses

The evolution of physical and chemical soil properties through the *Ononis* ontogenetic gradient was assessed by linear and non-linear (quadratic, sigmoidal, exponential, power and logarithm) regressions. For each soil property, the model that minimized the residual sum of squares was chosen as the best model (Gotelli and Ellison 2004). Subsequently, the soil variables TOC, N, P, K and GH were reduced by principal component analysis (PCA) to a single variable. This was the first PC, which explained 76 % of the variation, and was

positively correlated with all soil variables (loadings: TOC, 0.48; N, 0.49; P, 0.50; K, 0.39; GH 0.37). Thus, we interpreted this axis as a gradient of increasing chemical fertility (hereafter Soil Fertility). We used the fertility bioassay to evaluate the interpretation of this PC1 as a fertility gradient by performing regressions between the PC1 values (dependent variable) and the three seedling growth measures (length, biomass and RS ratio) as independent variables.

The soil microbial variables, microbial biomass carbon, basal respiration, β -glucosidase, alkaline phosphatase and urease activities were also reduced by principal component analysis (PCA) to a single variable. This was the first PC, which explained 75 % of the variation, and was positively correlated with all soil variables (loadings: microbial biomass carbon, 0.48; basal respiration, 0.21; β -glucosidase, 0.51; alkaline phosphatase, 0.50; urease activity, 0.48). Thus, we interpreted this axis as a gradient of increasing microbial productivity.

Both the effects of *Ononis* Age and the Plant Cover of facilitated plant species on the overall physical-chemical soil properties, as well as the soil microbial activities and biomass were assessed by performing Generalised Linear Models (GLM) with Gaussian error distributions. Firstly, to separate the effects of Age and Plant Cover both were introduced as predictors into the same model with their interaction. GLMs were performed with the R package stats (R Core Team 2013). In order to account for the collinearity between *Ononis* Age and Plant Cover (Pearson, $r=0.54$, $p<0.0001$), we used regression commonality analysis (CA) to decompose regression effects of both predictors. CA separates the explained variance into unique and common (shared) variance (or effects) of predictors, thus quantifying the relative contribution of each predictor to the explained variance of the regression model (Ray-Mukherjee et al. 2014). CAs were carried out with the *yhat* package for R (Nimon et al. 2013). All analyses were performed with R 3.0.2 (R Core Team 2013).

Results

Ononis age determination and age - size relationship

The number of rings in *Ononis* was significantly explained by the stem circumference (Linear regression; $R^2=0.963$; $p<0.0001$), plant height (Exponential; $R^2=0.939$; $p<0.0001$), mean diameter (Linear; $R^2=0.942$;

$p < 0.0001$) and biovolume (Linear; $R^2 = 0.783$; $p < 0.0001$) in the set of 36 plants used to obtain a biometric equation to estimate *Ononis* age. Among all variables, the stem circumference was the variable that best explained the number of rings (Fig. 1). Thus, we used the regression equation between the stem circumference and the number of rings for estimating *Ononis* age in 50 undisturbed plants. The stem circumference of seven *Ononis* individuals fell beyond the range of data used to correlate this variable with the plant's age, and thus their estimated values were the result of extrapolation. All 50 individuals constituted an ontogenetic gradient, with the factor Age ranging from 1 year old in a plant with a height of 1.5 cm up to 38 years old for a plant with a height of 1.24 m, mean diameter of 1.69 m and biovolume of 2.7 m³.

Changes in soil properties along the ontogenetic gradient

Ononis age significantly explained most physical and chemical soil properties. Soil surface temperature and light intensity showed an exponential decay along the ontogenetic gradient ($R^2 = 0.85$ and $p < 0.0001$ for temperature; $R^2 = 0.80$; $p < 0.0001$ for light; SI Fig. S3). Quadratic regression equations gave the best fits for pH ($R^2 = 0.36$; $p < 0.05$) and EC ($R^2 = 0.67$; $p < 0.0001$), whereas sigmoidal models fitted better for litter biomass ($R^2 = 0.65$; $p < 0.0001$; SI Fig. S4), GH ($R^2 = 0.156$; $p < 0.0001$), TOC ($R^2 = 0.55$; $p < 0.0001$) and the macronutrients N ($R^2 = 0.60$; $p < 0.0001$), P ($R^2 = 0.53$;

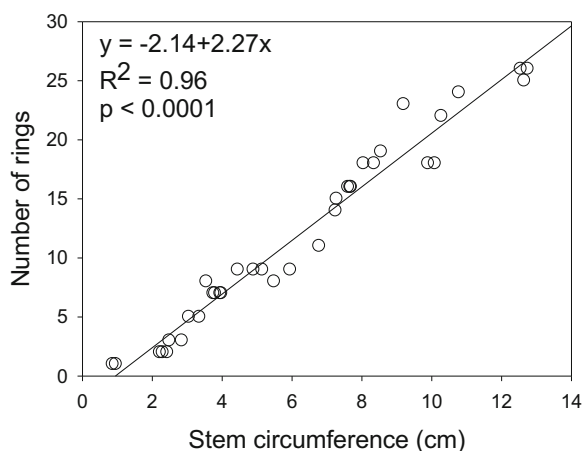


Fig. 1 Linear regression between the stem circumference and the number of rings of 36 *Ononis* plants. The regression equation, explained variance and significance of the F-test are shown

$p < 0.0001$) and K ($R^2 = 0.12$; $p < 0.06$). The improvement of soil properties ranged from two-fold (K) up to six-fold (TOC) from *Ononis* seedlings to around 20-year-old *Ononis* age, when the curve tended to saturate (Fig. 2). Most micro-nutrients behaved similarly or even slightly decreased in patches beyond 30 year-old (SI Fig. S5). The percentages of sand, silt and clay remained constant along the ontogenetic gradient, overall averaging (mean ± 95 % CI) 61.3 ± 2.0 , 25.4 ± 2.4 and 13.4 ± 1.1 , respectively.

Most microbial parameters quantified increased significantly with *Ononis* age. Specifically, microbial biomass C, urease, phosphatase and β -glucosidase activities rose throughout the gradient by roughly 4.5-fold, four-fold, 16-fold and 17-fold, respectively (SI Fig. S7). The microbial respiration was the only productivity parameter that significantly grew during the first 25 years of the gradient and slightly started to drop after that time. Likewise, the first PC that resulted from a PCA including the mentioned variables, which we interpreted as an increasing gradient of Microbial Productivity, was highly correlated to *Ononis* age through a quadratic regression model (Fig. 3).

Soil fertility bioassay

The fertility bioassay showed that all the barley above-ground seedling length, biomass and root-shoot ratios were functions of the first principal component of the PCA carried out using TOC, N, P, K and GH. Quadratic curves gave the best fits in all the cases, although with similar results to linear and sigmoidal models. Above-ground length was positively correlated with PC1 (Fig. 4), seedlings planted into soil collected under the biggest patches being 43 % larger than those planted into soil from the smallest patches (Fig. 4). Seedling biomass rose 42 % along PC1 (SI Fig. S6), whereas the RS ratio showed a negative relationship with PC1 (SI Fig. S5). This supported our interpretation of PC1 as a gradient of increasing chemical fertility.

Relative contribution of *Ononis* and facilitated plant species to changes in soil productivity

The plant cover of facilitated species significantly increased along the ontogenetic gradient (Fig. 5). Within the first 10 years of *Ononis* growth, the plant cover of facilitated species rose up to 35 %, and this value was maintained in the subsequent 28 years (Fig. 5).

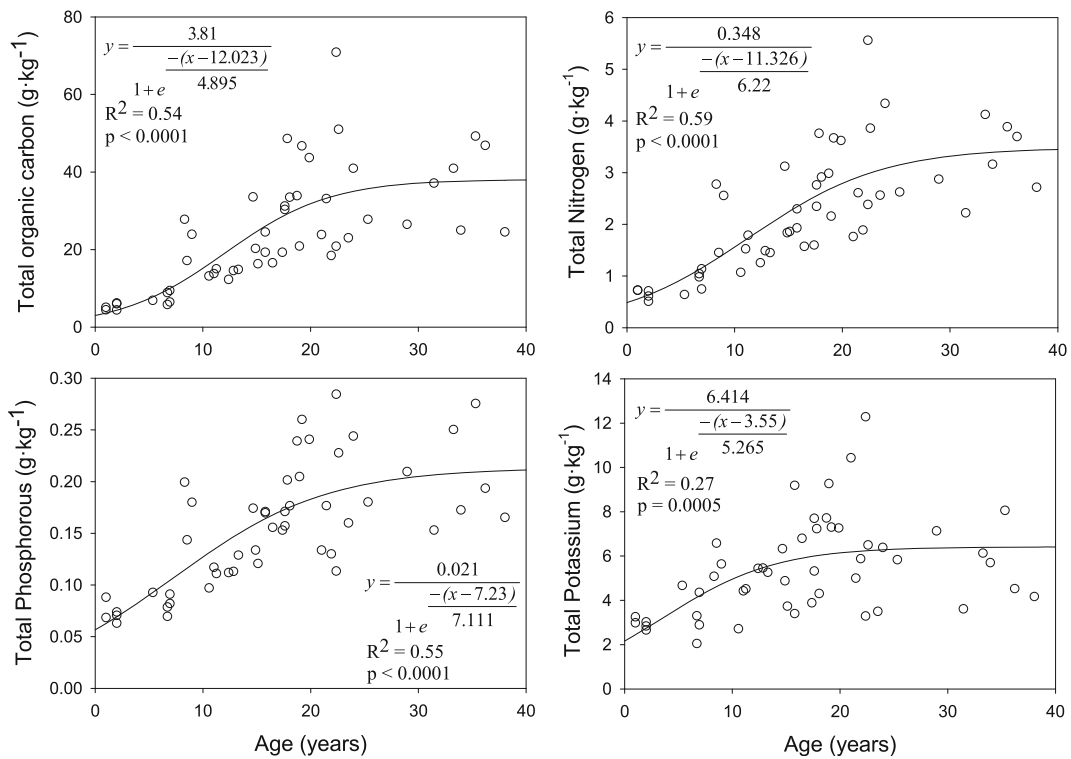


Fig. 2 Regression models showing the best fit (minimum residual sum of squares) shaping the effect of *Ononis* Age on the total organic carbon, total nitrogen, total phosphorus (sigmoidal fit) and

total potassium (quadratic fit). The regression equation, explained variance and significance of the F-test are shown. Data are given on an oven-dried weight basis

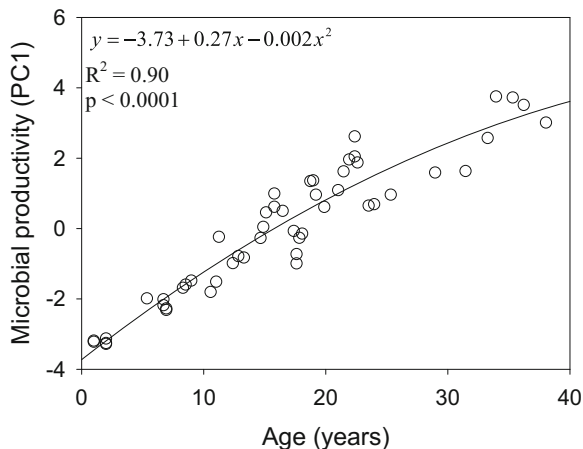


Fig. 3 Regression model showing the quadratic fit of *Ononis* Age on the soil microbial productivity, defined as the first principal component of the PCA used to reduce microbial respiration, microbial biomass C, urease, phosphatase and β -glucosidase activities to a single component. The regression equation, explained variance and significance of the F-test are shown

The GLM performed using Age and Plant Cover as predictors of Soil Fertility within a single model showed a positive effect of both variables on the dependent variable, whereas their interaction had a significant negative effect (Tables 1 and 2). The model explained 58.4 % of the variance. To interpret the effect of the interaction Age \times Plant Cover, the variable Age was discretized into three intervals determining three plant age categories, namely i) young *Ononis* individuals (1–12 years), ii) adults (13–25 years) and iii) mature plants (26–38 years). The effect of Plant Cover on Soil Fertility is compared for the three Age categories in Fig. 6. This figure shows that the positive effect of Plant Cover on Soil Fertility was significant in young *Ononis* plants, and gradually weakened through the ontogenetic gradient until it disappeared. The commonality model (CA) indicated that *Ononis* Age was the largest contributor to the explained variance of Soil Fertility (49.3 % out of the overall 58.4 %: 21.9 % of unique variance and 27.4 % of common variance) (Table 3). The Plant Cover of facilitated plant species contributed to 31.5 % of the

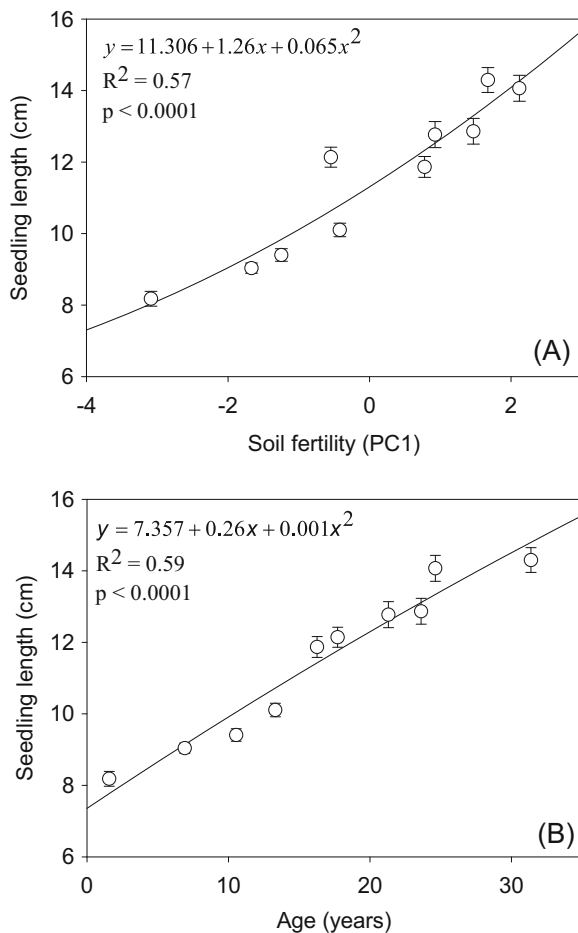


Fig. 4 Regression models showing the quadratic fits of the above-ground barley seedling length as a function of the increasing chemical fertility determined by the *Ononis* ontogenetic gradient **a** and the above-ground barley seedling length as a function of the estimated *Ononis* age below which the soil samples used in the fertility bioassay were collected. The regression equations, explained variance and significance of the F-test are shown. Each point is the average \pm SE of 36 seedlings after 3 weeks in a growth chamber

explained variance (9.1 % of unique variance and 22.4 % of common variance (Table 3). Finally, the interaction Age \times Plant cover explained 34.2 % of the variance (4.5 % of unique and 29.6 % of common variance).

A second GLM showed a positive effect of Age and Plant Cover of facilitated species on Microbial Productivity, whereas their interaction had a marginally significant negative effect (Table 2). The model explained 90.5 % of the variance. Overall, the relative contribution of *Ononis* Age to the shift of Microbial Productivity along the ontogenetic gradient was vastly greater than

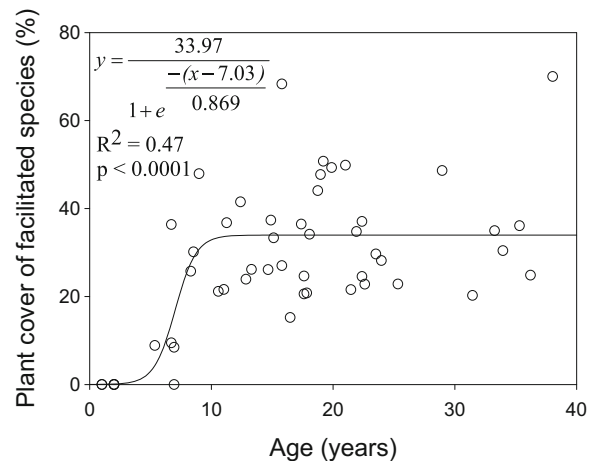


Fig. 5 Sigmoidal regression between *Ononis* Age and Plant Cover of facilitated species. The regression equation, explained variance and significance of the F-test are shown

that of Plant Cover (Table 4). Age explained 89.9 % out of a total 90.4 % (29.7 % of unique variance and 59.1 % of common variance), whereas Plant Cover explained 34.6 % (1.6 % of unique variance and 33 % of common variance).

Discussion

The nurse shrub *Ononis* induced rapid soil fertility and microbial productivity shifts along a 40 years ontogenetic gradient. Soil changes under severe stress conditions were especially fast during the first 20 years, the magnitude of these shifts lessening progressively beyond that age. We have shown that these changes are not only due to the direct effect of *Ononis* but also, although in a minor proportion, to the indirect effect of the facilitated plant community thriving under its canopy. As far as we are aware, this is the first time that the

Table 1 Generalised linear model showing the effects of *Ononis* Age and the abundance of facilitated plant species (Plant Cover) on the Soil Fertility, which was the first principal component of the PCA used to reduce the soil variables Gravimetric humidity, Total Organic Carbon and the macronutrients Total Nitrogen, Phosphorous and Potassium to a single component

	Estimate	SE	t-value	P
Intercept	-3.47	0.514	-6.755	< 0.0001
Age	0.176	0.036	4.920	< 0.0001
Plant Cover	0.063	0.02	3.177	0.0027
Age \times Plant Cover	-0.002	0.001	-2.241	0.0299

Table 2 Generalised linear model showing the effects of *Ononis* Age and the abundance of facilitated plant species (Plant Cover) on the Soil Microbial Productivity, which was the first principal component of the PCA used to reduce the microbial basal respiration, the microbial biomass carbon and the urease, phosphatase and β-glucosidase microbial activities to a single component

	Estimate	SE	t-value	P
Intercept	-3.633	0.244	-14.886	< 0.0001
Age	0.203	0.017	11.965	< 0.0001
Plant cover	0.026	0.009	2.773	0.008
Age × Plant cover	-0.001	0.001	-1.924	0.061

relative effects of the nurse species and its facilitated understory on soil fertility and microbial productivity are quantified and dated.

Ononis substantially increased the soil fertility on barren gypsum soils under semiarid conditions in only two decades. As an illustration, total organic carbon increased six-fold (from ca. 5 to ca. 30 g·kg⁻¹), and a similar evolution applied to main macro-nutrients. This is particularly remarkable in these areas submitted to a double abiotic stress, that is, water limitation and soil toxicity (Parsons 1976). Most micronutrients showed, however, a slight tendency to decrease beyond 30 years likely because of *Ononis* aging. In the field, fallen branches leading to sparser canopies can be commonly observed in the oldest individuals, and this might reduce organic inputs and increase nutrient runoff. We can unequivocally identify *Ononis* as the initial promoter of soil fertility since this species is an early colonizer

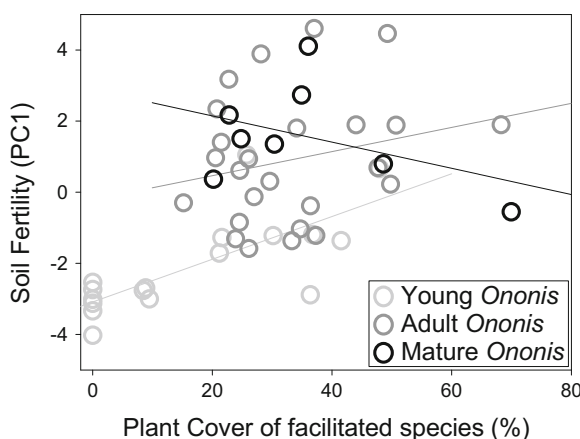


Fig. 6 Shifts in the effects of Plant cover of facilitated species on Soil fertility through three *Ononis* age categories: Young (0–12 year-old; n=17), Adult (13–25 year-old; n=25); Mature (26–38 year-old; n=8). The linear relationship was only significant for young plants ($R^2=0.57$; $p<0.001$)

Table 3 Commonality matrix separating the relative importance of *Ononis* Age and the abundance of facilitated plant species (Plant Cover) on the Soil Fertility. Commonality coefficients, both unique and common, along with % total contribution of each predictor variable or sets of predictor variables to the regression effect, are shown

Factor	Coefficient	%Total
Unique to age	0.2188	37.45
Unique to plant cover	0.0912	15.61
Unique to age × Plant cover	0.0454	7.77
Common to age and plant cover	-0.0675	-11.55
Common to age and age × Plant cover	0.0050	0.86
Common to plant cover and age × Plant cover	-0.0451	-7.72
Common to age, plant cover and age × Plant cover	0.3364	57.57
Total	0.5842	100.00

of bare unfertile micro-sites (Navarro-Cano et al. 2014). The temporal pattern of organic matter (OM) enrichment observed is similar to classical examples from humid or sub-humid climates with high primary productivity (reviewed by Walker and del Moral 2003). Chronosequences from North American and Norwegian glacial moraines, and temperate and subarctic floodplains showed a three- to five-fold OM increase in 50 years. Several studies performed in drylands that did not report soil enrichment after several decades explicitly avoided collecting samples below the canopy of plant patches. For instance, Bolling and Walker

Table 4 Commonality matrix separating the relative importance of *Ononis* Age and the abundance of facilitated plant species (Plant Cover) on the Microbial Productivity. Commonality coefficients, both unique and common, along with % total contribution of each predictor variable or sets of predictor variables to the regression effect are shown

Factor	Coefficient	% Total
Unique to age	0.2972	32.85
Unique to plant cover	0.0160	1.76
Unique to age × Plant cover	0.0077	0.85
Common to age and plant cover	-0.0123	-1.37
Common to age and age × Plant cover	0.2536	28.04
Common to plant cover and age × Plant cover	-0.0076	-0.84
Common to age, plant cover and age × Plant cover	0.3500	38.70
Total	0.9045	100.00

(2000) did not find an increase in fertility (<2.5 % OM) based on a 88-year chronosequence in abandoned roads in the Mojave Desert. Dana and Mota (2006) found a low fertility enrichment rate (from 0.5 to 1.4 % OM) along two 70-year chronosequences in semiarid gypsum soils recolonized by dwarf shrubby vegetation in quarries from SE Spain. Bonet (2004), who surveyed a >32-year chronosequence of secondary succession in abandoned fields in semiarid SE Spain, did not find any relationships between time since abandonment and either soil moisture, organic carbon or total nitrogen. On the contrary, those surveys that accounted for the patchiness of drylands found results comparable to ours. Pugnaire et al. (1996) measured three-fold organic C and N rises, and a two-fold P increase below the canopy of the nurse legume *Retama sphaerocarpa* in semiarid alluvial deposits from SE Spain. Similar to our case, they reported a significant soil fertility development in soils below plants older than ca. 16 years old, along a size gradient estimated to roughly correspond to 6–47 year-old individuals. Other rapid soil fertility enrichment was described by Wezel et al. (2000) below sparse shrubs in several Sahelian fallow fields (from 1 to >10 years after cutting and left in fallow). They found organic carbon and total nitrogen enrichment ratios from 1.3 up to 1.7 in patches compared to gaps. Unfortunately, the nurse species in the surveys by Pugnaire et al. (1996) and Wezel et al. (2000) have the ability to resprout, what makes difficult a precise dating of the patch. This is not the case of *Ononis* (Guerrero-Campo et al. 2006). Separation and quantification of the indirect role of the symbiont N-fixers on the positive effect of the legumes *Ononis* or *Retama* (among others) on soil properties in a temporal sequence would need specific testing.

Our results show a synergistic effect of the nurse plant and its facilitated plant community in the rapid accretion of soil productivity that we detected under harsh abiotic conditions. As soon as it established *Ononis* started ameliorating the micro-environmental conditions. In 10 years after establishment, we detected roughly 28 % temperature decrease, 83 % light intensity decrease and 100 % soil gravimetric humidity increase (SI Fig. S3). These micro-environmental shifts rapidly promoted soil fertility and microbial productivity, while facilitating the rapid growth of a plant community composed by species that are functionally complementary to *Ononis* (Navarro-Cano et al. 2014). Here, by using a bioassay under controlled environmental conditions we confirmed that changes in soil properties along the ontogenetic gradient were associated with an increased

plant length and biomass of the phytometer species. Furthermore, under the same experimental conditions we detected decreasing root-shoot ratios with *Ononis* age indicating a reduction in the abiotic stress that induces a smaller root system in favour of the above-ground organs (Gedroc et al. 1996; Lloret et al. 1999). Hortal et al. (2013) also found increasing levels of soil microbial activity along three size classes in *Retama sphaerocarpa*. In our study system, the nurse plant *Ononis* alone was responsible for 37.5 % of the explained variance for the Soil Fertility, whereas the facilitated plants per se accounted for 15.6 % of the variance. The remaining variance was due to the common effects of both predictors. Hence, *Ononis* contributed to soil fertility both directly and indirectly through facilitation. *Ononis* was also the main promoter of soil microbial productivity, and in this case the direct effect of the facilitated community below its canopy seemed to be less relevant. A manipulative experiment to monitor two sets of nurse plants (one excluding facilitated species and an unaltered control) since the establishment stage would allow validating our results. Functional complementarity between the nurse species and its understory in traits such as rooting depth or spread has been posed as a fundamental mechanism that avoids niche overlap, and thus maximizes facilitation (Gómez-Aparicio 2009; Verdú et al. 2012). In addition, the coexistence of functionally dissimilar species is known to enhance plant biomass and abundance through alleviating competition (Callaway 1994; Cadotte et al. 2008). This might therefore augment the supply of organic inputs to the soil (Spehn et al. 2000) and increase the abundance of soil microbes, meso- and macro-fauna (Milcu et al. 2013).

We measured a significant build-up of the litter layer, whose biomass exponentially increased in the first decade reaching up to $600 \text{ g} \cdot \text{m}^{-2}$ in the last stage of the ontogenetic gradient. This was a mixed leaf litter (nurse + facilitated plants) which was dominated by *Ononis* senesced leaves and branches (field observation), likely due to its major biovolume and summer deciduous character. *Ononis* leaves are succulent (76 ± 1 % water per leaf), a character determining faster decomposition rates than those of species with higher leaf toughness (Gallardo and Merino 1993). We did not quantify root or mycorrhizal exudation. Therefore, we cannot estimate the relative contribution of exudates and leaf litter from *Ononis* to the organic enrichment of the soil surface, since this would require an ad hoc experiment. Nevertheless, this species has a low root density and although

we did not measure it in this survey, its fine roots are very rare in the first 20 cm-depth (De Baets et al. 2007). On the contrary, most of the plants facilitated by *Ononis* are dwarf shrubs, perennial grasses and herbs (Navarro-Cano et al. 2014), whose root system is mainly concentrated within the upper 20 cm (Guerrero-Campo 1998; De Baets et al. 2007). Apart from direct organic inputs from the plant biomass, other mechanisms have been suggested to underlie soil fertility increase underneath plant patches in drylands. Wezel et al. (2000) interpreted contrasting soil enrichment ability among Sahelian plant species as an effect, among other factors, of their sand and dust trapping ability, which related to their aboveground canopy structure. Burke et al. (1999) attributed the formation of fertile islands in Colorado to the nurse plant ability to shape micro-hillocks beneath its canopy by soil surface elevation and physical redistribution of soil materials. In our study area, we did not observe evident micro-reliefs below *Ononis*, where in the other hand plant litter from the patch canopy was remarkable (Fig. S4) and so aerial trapping or redistribution by surface runoff were likely not remarkable. Anyway, further quantification of the origin of the soil nutrient enrichment discerning fallen litter vs dust entrapment would be necessary to confirm our observations.

The age range covered by our ontogenetic gradient proved suitable to detect individual effects on soil productivity in the studied area. As no other studies have determined the age of *Ononis* we cannot assess whether our range is frequent in other gypsum areas dominated by this species. Schweingruber and Poschold (2005) found that less than 100 out of 834 perennial plants in Central Europe were more than 20 years old. In abiotically stressful environments there are no references compiling the proportion of short perennial plants that can live for several decades. Nevertheless, some works indicate that the life span of many dwarf shrubs surpasses 20 years old. This is the case of typical nurse species such as *Rosmarinus officinalis*, *Cistus monspeliensis*, *Hormatophylla spinosa*, *Ononis fruticosa* and *Linum suffruticosum* in Mediterranean drylands (up to 20–56 years old; Roy and Sonié 1992; Lloret et al. 2003; Gazol and Camarero 2012) or *Lepidium subulatum* in semiarid gypsum soils (up to 26 years old; Eugenio et al. 2012). Linking medium life-span species with nursing ability and promotion of fertility islands may play an essential role in the small-scale spatial heterogeneity of soil properties in drylands. This approach could have also applications in

restoration programs. Selection of nurse shrubs with fertility-triggering traits might be introduced as a tool for restoring degraded ecosystems under dry conditions (Padilla and Pugnaire 2006). Previous assessment of local age-productivity or age-fertility relationships would allow also a better and rapid prediction of time rate for aim compliance (Siles et al. 2008), something usually stated in the theory of restoration but factually missing in many restoration programs.

Conclusions

Our study suggests that plant age determination can help in quantifying the recovery rates of barren soils mediated by plant facilitation. We show that a single nurse shrub can induce a significant soil development under harsh conditions in just two decades. Our study adds a temporal component to those surveys that encourage the selection and plantation of nurse shrubs so as to configure restoration programs in drylands (Castro et al. 2002; Barberá et al. 2006; Padilla et al. 2009; Cortina et al. 2011).

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