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Old nurses always die: impacts of nurse age on local plant richness

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Abstract Palatable exotic shrubs plantation in heavily degraded rangeland has been massively managed in arid and semi-arid Algeria. An associated effect observed to these managements is an increase of plant richness in these plantations due to positive interactions involving nurse species that ameliorate stressful environmental conditions. Our objective was to assess the importance and impact of nurse age on the recovery of herbaceous plant species richness. The impact of the shrub presence on the spatial repartition of herbaceous plant richness was quantified, and we tested whether it remains constant with nurse growth and ageing. Using cumulative species richness on radial transects from the nurse centre to nurse external canopy we described the spatial patterns of plant species richness around different *Atriplex canescens* from saplings to senescent individuals. Resulting cumulative radial species curves were modelled using linear and non-linear models and tested against null models. Nurse volumes and overall plot species richness exhibited a sigmoid shape from 2 to 15 years. The best-fitted models of the radial cumulative species richness changed with the nurse age. In young life stages, a strong positive effect under the shrub was detected. At intermediate life stages, the richness in the subcanopy was significantly impoverished whereas cumulative richness sharply grew under the shrub external canopy. At senescent life stage, cumulative species richness did not indicate a remaining effect of the shrub. An improved description of planted

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shrubs nurse effect consequences on plot richness is provided and suggests that late plantation opening to stock can concur to the maximization of species richness in afforested plots.

Keywords *Atriplex canescens* allometry · Curve fitting · Desertification · Facilitation · Nurse effect · Null models · Steppic ecosystems

Introduction

In the Alfa grass steppe in semi-arid Algeria, over-grazing of low-productivity dry lands and recurrent dry years have led to the extension of degraded land with very low vegetation cover, up to the complete disappearance of perennials in some areas (UNEP 1999). A survey of the 27 million-ha territory of the Algerian Forests General Direction (DGF 2009) concluded that 5.8 % of the area suffered from desertification, 10 % classified as highly sensitive to desertification, and 41 % sensitive. Mean vegetation cover has fallen from 30 % at the end of the 1970s to 15 % in 2013, whereas the fodder production had been divided by five (Hirche et al. 2013). General consequences went from destruction of plant communities to soil erosion, with socio-economic issues affecting local populations (Mainguet 1990).

To reduce the degradation and increase plant biomass of semi-arid habitats, plantations have been established by several countries in North Africa, Asia, America, the Middle East and Oceania, especially in the case of very advanced degradation (Mulas and Mulas 2007). In Algeria, *Atriplex canescens* (Pursh) Nutt., native from North America, was chosen and massively planted since 1994 in heavily degraded zones. This exotic species is particularly resistant to drought summer and to cold winter temperatures, and provides high quality forage that bridges the food deficit of livestock during winter (Shoop et al. 1985). The plantation of this shrub induced local modifications at soil and vegetation scales. Previous works in the same area described a rise of plant richness and an increased plant cover in plantations compared with unmanaged areas (Amghar et al. 2012). At the plant scale, visual observations of spontaneous vegetation patches around planted shrubs have led to infer a non-random spatial pattern, as has been largely

documented in similar semi-arid environments (e.g. Alfa steppe in Southeastern Spain: Maestre and Cortina 2005; Pugnaire 2010), underlining the key role of facilitation (positive interaction) in stressed ecosystems.

Positive interactions (Clements et al. 1926; Callaway and Walker 1997; Tewskbury and Lloyd 2001) are widely recognized as an important process influencing spatial and temporal vegetation patterns, especially in stressed habitats (Abdallah et al. 2008; Jeddi and Chaieb 2010). For example, a plant species might protect another one directly from extremes of climate or indirectly from the impacts of herbivores or potential competitors (Callaway 1995). This nurse species might provide additional resources through canopy leaching, microbial enhancement, mycorrhizal networks and hydraulic lift that enhance the performance of other plants. Facilitation not only increases individual plant performance but also often plays an important role in improving conditions of growth for new species, increasing biological diversity, and thus impacts plant community composition (Tirado and Pugnaire 2003; Brooker et al. 2008; Gomez-Aparicio 2009). Facilitation is being increasingly discussed as an ecological mechanism useful for developing vegetation restoration tools in severe and highly disturbed environments (see reviews by Young et al. 2005; Padilla and Pugnaire 2006; Halpern et al. 2007; Brooker et al. 2008).

These positive interactions appear when a nurse species provides (i) buffered conditions for light and temperature and (ii) better conditions for moisture, soil nutrients and sediment fixation (Whitford 2002). The facilitated species gains a better potential to establishment, survival, growth and thus reproduction (Rousset and Lepart 2000; Tewskbury and Lloyd 2001). Although several studies address the role of the ontogeny of the facilitated species on plant–plant interactions (Miriti 2006; Le Roux et al. 2013; Soliveres and Maestre 2014a, b), and as emphasized by Armas and Pugnaire (2005) "…few studies addressed the long-term effects of the nurse plant by continuing to monitor success beyond the seedling stage", few authors have investigated the role of nurse sizes.

In steppic ecosystems, several studies have reported the key role of dominant species on ecosystem functioning (Aronson et al. 1993). These species (especially during dry season) represent micro-island for soil fertility (Schlesinger et al. 1996a, b). For

example, *Stipa tenacissima* generates tussocks with organic matter and fine sediment content higher compared to bare soil (Aidoud et al. 1999), higher moisture and humidity. These patches of monospecific vegetation induce a protection against sediment erosion (Puigdefabregas and Sanchez 1996; Cerdà 1997) and thus represent a protection for new species establishment. Nevertheless, few studies have focused on the effect of nurse age (from its establishment to its senescence) on species richness and composition.

Classical methods to investigate facilitation strength are based on a comparison of target species performances beneath nurse species with adjacent open areas, using removal procedure or existing open patches (Michalet 2006). This type of dichotomous design has spawned a wealth of results (e.g. Soliveres and Maestre 2014a, b), but such method is inadequate for assessing the effects of the nurse species on the entire community scale since it compares only two contrasting situations and not intermediary ones. The effectiveness of the protection under a nurse species is likely to depend on its canopy structure. Changing environmental and climate conditions in and around the subcanopy were suggested by Drezner (2006). This author demonstrated that *Carnegiea gigantea,* a beneficiary species, was significantly clustered within the inner 10 % of the area beneath the nurse canopies. Therefore, fine and spatially continuous association pattern monitoring lacks to better detect the dynamics of plant-nurse interactions and effect at the entire community level.

Lastly, the age or ontogenic development of nurse species should also be considered in plant interactions studies. Ontogenetic changes that target species experience throughout their life cycle can strongly modulate the intensity of interactions and facilitation/competition shifts (e.g. Morris and Wood 1989; Shumway 2000; Armas and Pugnaire 2005; Le Roux et al. 2013; Navarro-Cano et al. 2015). Nevertheless, to our knowledge, the effect of the age of nurse species on the outcome of plant–plant interactions had been poorly studied and only concern interaction studies at the whole community scale (Pugnaire et al. 1996; Navarro-Cano et al. 2015) and not at the nurse plant scale.

In this study, we investigated the effect of a potential nurse species (*Atriplex canescens*) on semi-arid vegetation richness using 15-year growth sequence reconstruction (namely 2, 5, 10 and 15 years). We aimed at describing the plant species richness patterns as influenced by the shrub (i.e. in the subcanopy and the

outskirts), hypothesizing that (i) the shrub positively impacts plant richness relative to its own size and that (ii) the magnitude of this positive effect varies with nurse plant age.

Materials and methods

Regional context

Steppes of the tussock grass (*Stipa tenacissima L.)* are typical arid and semi-arid vegetation formations of the Mediterranean basin. Their economic uses (mainly grazing for decades) have led to their historical development at the expense of original *Pinus halepensis* and *Quercus ilex* forests (Rivas-Martínez 1987; Aidoud 1989; Le Houérou 2001). These formations are nowadays threatened by overgrazing, leading to desertification.

In heavily degraded steppes (vegetation cover weaker than 15 % and sometimes reduced to zero), massive plantations of an exotic species *Atriplex canescens* have been managed. This technique leads within a few years (2–5 years) to an increase in species richness and pastoral value (Amghar et al. 2012).

Site selection

The study was located in Ain Chouhada, 87 km south west from the town of Djelfa, Algeria [34°14′39″N, 2°31′41″E, 1225 m asl, mean annual precipitation 337 mm (ONM 2011)]. Mean annual temperature is 20.1 °C, with monthly minima and maxima, respectively, of 4.6 and 25.5 °C (1971–2007 averages). Soils are classified as calcimagnesic, and the landscape is predominantly quaternary sandy to sandy loamy on slightly undulating haut plateaux to 3 % slope (Pouget 1980).

A 749 ha plantation of *Atriplex canescens*, managed by the High Commission for Steppe Development, was used as study site. This plantation was divided in subunits ranging from 10 to 200 ha, which were planted from 1996 to 2009.

Atriplex plants were obtained from seeds germinated in a greenhouse. After 1 year of development, plants were transplanted in the field and monthly watered with 10 L of water during 6 months.

These plantations are usually rented for fodder to livestock owners 4–5 years after plantation. At Ain

Chouhada site, a local priority given to protection of the nearby village against sand deposits led to the interdiction of domestic grazing on the whole site since first planting in 1996. These local conditions offered an opportunity to study ungrazed plantations up to 15-year old.

Atriplex shrubs selection

To describe the effect of the planted shrubs on the presence of other plant species, we used a space for time substitution approach (Pickett 1989) and built a chronosequence with plots of 2-, 5-, 10- and 15-year old. We hereafter name plot a homogeneous unit in which shrubs were planted within a month. Ages of Atriplex were chosen according to the following criteria: (i) the youngest had to be old enough to avoid lasting effect of sapling watering, i.e. having endured one dry season, (ii) the oldest was constrained by plantation chronology and (iii) the two intermediate ages were spaced as evenly as possible between the youngest and the older one.

Within the plantation, we randomly selected three plots for each chosen age class, with a distance from 700 to 1200 m between plots (obtaining a total of 12 plots). In each plot, we randomly selected one shrub. Starting from this plant 19 other shrubs were chosen, evenly spaced by a distance of 20 m on a square grid following plantation lines to avoid autocorrelation. On each of these 20 shrubs, five morphological measures were performed (height and horizontal length of canopy projection in the four cardinal directions). Means and standard errors of these five parameters were then computed for each plot. Three individual among the 20 shrubs were chosen conditionally to each of their morphological values lying within plot mean $\pm$ 1 standard error for the five parameters altogether. If more than three shrubs were filling the conditions, then three were randomly chosen among them. We actually have selected 36 Atriplex shrubs (4 age classes $\times$ 3 plots for each age class $\times$ 3 shrubs in each plot). Shrub volumes were estimated using an ellipsoidal approximation using the following formula, h and r_i being the shrub height and the four transect lengths, respectively.

$$v = \sum_{i=1}^{4} \frac{\pi.h.r_i}{6}$$

Assessment of shrub impact on the spatial structure of plant richness

To assess the impact of shrubs on seed plant species richness patterns, we designed a sampling protocol proportional to the size of the nurse plants. For each of the 36 shrubs, we drew 4 transects from the shrub centre in the four cardinal directions (namely, 144 radial transects). For each transect, we doubled the canopy radius length and divided the obtained length in 60 evenly spaced contact points. We obtained 30 points in the subcanopy and 30 points in outskirts of the shrub. On each contact point, we used a vertical rod and noted each plant species contacted by the rod, Atriplex excluded. If a species had two or more contacts with the rod, it was only noted once per contact point.

This design allowed us to compute and graph the relative species richness accumulation curve (hereafter RSRAC), expressing as the ratio of cumulated plant richness to the total plant richness of transect along the 60 contact points.

This RSRAC curve has the following properties:

- It starts at 0 (or the ratio of the number of species met at the centre of the nurse/total transect richness) and ends at 1.
- It has an horizontal length equal to twice the nurse shrub radius (i.e. is horizontally centred on the plant border).
- It never decreases, being a cumulative curve.

  The main assumption of the modelling approach is extrapolated from the body of knowledge on the species-area curve (reviewed in Scheiner 2003): instead of plotting the richness against area, richness is here plotted against the distance to shrub centre. In species-area curves, the slope of the curve is interpreted as beta diversity and the intercept as alpha diversity. We interpret the RSRAC slope variation as an indicator of the nurse impact on the surrounding plant richness: the more sloppy the curve is at a point, the more species are accumulating at this point, be it in, near or far from the shrub, irrespective of the actual shrub size, our design being isometric.

We also computed the distance at which half the transect richness is reached, thereafter PC50 %. Plant community Euclidean dissimilarity was also computed using a matrix of the 108 plant species met in the

144 transects and tested to evaluate the differences between age classes.

Radial species richness accumulation curves modelling

Models tested

In order to assess the impact of the shrubs on the species richness, we evaluated the shape of the RSRAC using linear and non-linear models. The set of models (Fig. 1) against which the RSRAC were tested was (Scheiner 2003; Paine et al. 2012) as follows, "x" being the distance to the nurse centre:

– Linear model in which the slope [parameter a in formula (1)] is constant along the transect. Linearity is assumed to indicate the absence of a shrub effect on plant richness.

$$\frac{SR}{SRmax} = ax + b \tag{1}$$

– Logistic model in which the slope hits a maximum at an inflexion point [x_{mid} in formula (2)]. This point can be interpreted as the distance at which positive effects of shrub on plant richness are balanced by negative effect of surrounding environment. The parameter Scal is related to the steepness of the slope.

$$\frac{SR}{SRmax} = \frac{1}{1 + e^{\left(\frac{x_{mid} - X}{scal}\right)}} \tag{2}$$

– Negative exponential model in which the slope decreases along the transect, thus a positive shrub (nurse) effect on richness weakening with distance.

$$\frac{SR}{SRmax} = a - (1 - e^{-cx}) \tag{3}$$

– Exponential model, in which the slope increases along the transect, indicating a decreasing (while moving away from the nurse) negative effect of the shrub on richness.

$$\frac{SR}{SRmax} = M_0 e^{rx} \tag{4}$$

Models were extracted from Pinheiro and Bates (2000), Tjorve (2003), Dengler (2009) and Paine et al. (2012).

Null models approach

We used a null-model approach to test non-randomness in the radial accumulation of species around the shrub, implying that non-random processes affect species in the subcanopy and the outskirts of the shrub. The vegetation in the plots at the time of the plantation
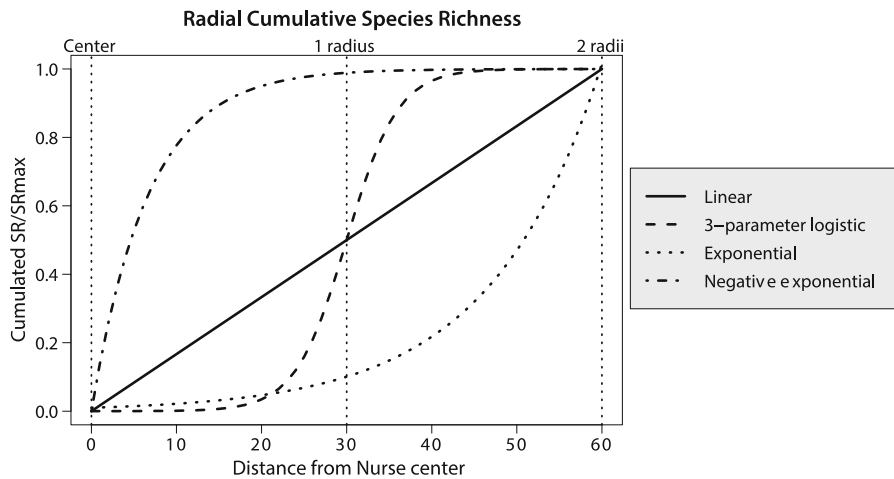

Fig. 1 Idealized shapes of the four linear and non-linear models used for fitting radial species richness accumulation curves. Parameters used are for linear $a = 0.015$ and $b = 0$, for 3-parameter logistic Max $= 1$, $X_{mid} = 30$ and Scal $= 3$, for exponential $M_0 = 0.01$ and $r = 0.077$, for negative exponential $c = 0.15$. Note that *horizontal axis* is labelled with lecture point numbers, maxing at 60

was null or nearly so. We thus assumed that deviation from random patterns of richness accumulation around the shrubs was to be linked with its presence. We assessed the nurse effect magnitude change by comparing the shape of models and their parameters for each age class of nurse plant.

According to Gotelli and Colwell (2001), we followed the three steps for a null-model analysis in community ecology: first for the observed data, we computed the RSRAC and tested regressions for each nurse age class (3 plots × 3 shrubs × 4 directions = 36 transects each of 60 lecture points) using the four reference models (Eqs. 1–4). We retained the best model by using R^2 and Akaike information criterion (AIC) as estimates of the goodness-of-fit of regressions, and we calculated the observed parameters of the best model.

We then generated 1000 null communities per transect with random permutations of the observed data matrix by maintaining the total species occurrence fixed. We thus reshuffled species along the radial transect. For each randomization, we recomputed the RSRAC and tested regressions to calculate the expected parameters of the models.

Lastly, we compared the observed parameters with the distribution of expected parameters to assign a probability value to the observed patterns. If the observed parameters fell within the 5th to 95th percentiles of the expected parameters distribution, the null hypothesis (i.e. absence of observed RSRAC deviation from random community) could not be rejected. Otherwise, we concluded that species in the subcanopy and/or the outskirts of the shrub plant were affected by a non-random process.

All statistical analyses and calculations for null models were performed with R software (R-core-Team 2015) and stats package.

Model fitting and parameters estimation were made using functions implemented in R software (Pinheiro and Bates 2000; R-Core-Team 2015). Parameters tested for each model were a and b for linear model; X_{mid} and Scal for the logistic model; M_0 and r for the exponential model and c for the negative exponential; R^2 was tested for all four models.

Pastoral values around shrubs

The pastoral value around each shrub was estimated by multiplying each species occurrence (the number of

contact points on which they were met, giving a maximum of 4 radii × 60 points = 240 occurrences) by its specific quality index as proposed by CRBT (1978). The shrub itself was not taken into account for the calculation.

Results

Atriplex sizes and vegetation properties

Height and biovolume estimated for each age class of shrub showed an increase between 5 and 10 years. Within each age class, transect lengths were not significantly different with respect to orientation (Kruskal–Wallis test, $p = 0.203$, Chi-squared = 4.60, df = 3), whereas the ratio height: mean radius decreased with life stage (Kruskal–Wallis test, $p < 0.001$, Chi-squared = 112.6, df = 3) (Table 1). Species richness met around the shrubs increased with shrub age peaking at 10 years (Table 2) and decreased at 15 years. PC50 % was significantly different between age classes, with the 2- and 5-year age classes reaching half of the richness within the canopy, whereas 10- and 15-year classes present a PC50 % near the canopy border (Table 2). A list of the species met with occurrence in each age class is detailed in supplementary information, Table S1. Dissimilarity between floristic composition met around the shrubs shows (Table 3) consistently a minimum within each age class, thus reflecting an internal similarity within age classes, and a maximal distance between the oldest age class and the age classes 5 and 10 years. This pattern is observed with the overall plant list and for perennials, but appears to be slightly different for therophytes: whereas the minimal dissimilarity was within age class, the maximum distance was between 5- and 10-year age classes. Vegetation pastoral value under and around the shrubs was significantly different between age classes, reaching a maximum at 10 years, a minimum at 15 years and intermediate values at 2 and 5 years (Table 3).

Radial species richness accumulation curves

RSRAC shape changed with growth and ageing of shrubs: exponential (2 years) then sigmoid (5 and 10 years) and linear (15 years). Higher R^2 values stood between 0.736 and 0.573 (Table 4). R^2 and AIC

Table 1 Biometrical parameters for the 4 *Atriplex canescens* age classes ($n = 9$ for each class)

Age class (years) (cm)	Biovolume (L)	Height (cm)	Mean transect length
2	310.8[b] (168.6)	72.6[b] (11.2)	43.1[b] (11.1)
5	343.1[b] (85.0)	69.3[b] (15.0)	48.5[b] (4.9)
10	2128.6[a] (446.5)	110.1[a] (9.9)	95.6[a] (8.7)
15	3457.4[a] (1765.1)	111.4[a] (16.1)	118.8[a] (23.2)

Standard deviations are in brackets

Superscripts indicate statistical differences from a Kruskal–Wallis rank sum test with Bonferroni correction at a level of 0.05

Table 2 Plant richness for the 4 *Atriplex canescens* age classes ($n = 9$ for each class), point at which half of the total transect plant richness is reached (max = 60, $n = 36$ for each age class) and pastoral values for each shrub

Age class (years)	Therophyte richness	Perennial richness	Overall richness	PC50 %	Pastoral value
2	6.3[b] (2.2)	3.3[a] (2.2)	9.7[b] (3.5)	12.7[b] (9.6)	710.9[bc] (444 .1)
5	6.0[b] (2.7)	3.3[a] (1.0)	9.3[b] (3.1)	14.7[b] (10.9)	961.3[ab] (263.8)
10	12.0[a] (2.2)	5.0[a] (2.6)	17.1[a] (3.4)	26.4[a] (10.9)	1090.3[a] (490.0)
15	8.0[b] (2.5)	4.2[a] (3.0)	12.2[b] (4.6)	26.8[a] (12.8)	505.9[c] (208.1)

Standard deviations are in brackets

Superscripts indicate statistical differences from a Kruskal–Wallis rank sum test with Bonferroni correction at a level of 0.05

criteria of goodness-of-fit were congruent at 2 (exponential model) and 15 years (linear model). AIC and R^2 results were slightly non-congruent as the lower AIC was reached by negative exponential model at 5 years and logistic model at 10 years, and best R^2 by logistic model at 5 years and linear model at 10 years. In both cases, values of R^2 and AIC, respectively, were similar for both models. As R^2 was recognized as "an inadequate measure for non-linear models" (Spiess and Neumeier 2010), we granted priority to AIC in comparisons between AIC and R^2 results.

Parameters tested by null models were

– At 2 years (Fig. 2a), R^2 and c parameters for negative exponential model were significantly higher than expected by chance (EBC), respectively, $p < 0.001$ and $p < 0.01$. Negative exponential model thus best described RSRAC shape at sapling life stage.
– At 5 years (Fig. 2b), results were mixed between negative exponential model (R^2 higher than EBC, $p < 0.01$, c parameter lower than EBC, $p < 0.01$) and logistic model (not significantly different than EBC for R^2, highly significant higher than EBC for the parameter X_{mid} ($p < 0.001$). On the basis of AIC, the best-fitted model was the negative exponential.

– At 10 years (Fig. 2c), the logistic model exhibited the lowest AIC, associated with a highly significant higher than EBC value of the parameter X_{mid} ($p < 0.001$). The linear model had the highest R^2 value (higher than EBC, $p < 0.001$), with both parameters a and b significantly lower than EBC ($p < 0.001$). The AIC indicated a logistic model with the parameter X_{mid} fixed at 27.71, i.e. an inflexion point nearly at the shrub periphery.
– At 15 years (Fig. 2d), linear model was the best fitted, with the lowest AIC.
– The sequence of best-fitted models observed from the sapling stage to the senescent shrub was thus as follows: negative exponential at 2 years, negative exponential at 5 years, logistic at 10 years and linear at 15 years.

Discussion

The use of *Atriplex canescens* shrub to compensate for fodder lack in Algerian degraded steppe is recognized as an efficient tool to ameliorate degraded rangeland and thus local conditions for plant development (Amghar et al. 2012). In the present study, two hypotheses were tested: (i) the shrub positively

Table 3 Euclidean distances (dissimilarity) between plant species met around the 4 *Atriplex canescens* age classes ($n = 9$ for each class) for overall species list, therophytes and perennials (in and between classes)

Overall species composition dissimilarity

	2	5	10	15
2	0.42[d] (0.18)			
5	0.50[c] (0.07)	0.37[e] (0.16)		
10	0.54[b] (0.08)	0.54[b] (0.09)	0.42[d] (0.18)	
15	0.54[b] (0.09)	0.58[a] (0.08)	0.57[a] (0.08)	0.38[e] (0.15)

Therophytes species composition dissimilarity

	2	5	10	15
2	0.44[ef] (0.20)			
5	0.58[bc] (0.13)	0.41[f] (0.18)		
10	0.57[bc] (0.12)	0.62[a] (0.12)	0.47[de] (0.22)	
15	0.53[cd] (0.13)	0.58[ab] (0.11)	0.55[ab] (0.09)	0.36[g] (0.19)

Perennials species composition dissimilarity

	2	5	10	15
2	0.41[de] (0.17)			
5	0.45[de] (0.08)	0.34[f] (0.16)		
10	0.50[c] (0.08)	0.45[d] (0.09)	0.49[e] (0.17)	
15	0.54[bc] (0.12)	0.58[a] (0.09)	0.59[b] (0.11)	0.41[de] (0.14)

Standard deviations are in brackets

Superscripts indicate statistical differences from a Kruskal–Wallis rank sum test at a level of 0.05

impacts plant richness relative to its own size and (ii) the magnitude of this positive effect varies with nurse plant age.

Life stages encompassed in the study

The study site is composed of several ungrazed plantation of *Atriplex canescens* and some of them can be considered as the oldest ones in Algeria by the time of the study. We based our assertion that the 15-year-old stage was representative of a senescent life stage considering (i) the lack of difference in biovolume between 10 and 15 years, (ii) the visual observation of numerous gaps in 15-year-old *Atriplex* canopies and (iii) the strong lignification of these shrubs. To our knowledge, no study has been published on life stages of this American species in the North African area.

Effects of *Atriplex* on plant richness

The design used to assess the impact of *Atriplex* on local vegetation highlights the increase of plant species whatever the age of the plantation. Plantation of *Atriplex* always increased plant richness in the steppe compared to degraded steppes before plantation where plot richness was near or equal to 0 due to desertification processes. *Atriplex* acts thus as an effective nurse species in these habitats both at the plant scale and the community scale. Bellingham et al. (2001) showed that development of vegetation on previously denuded or bare substrate led to a soil nutrients increase. In a similar steppe context, in Tunisia, Jeddi et al. (2009) found a nutrient enrichment under three nurse species. A mechanism often presented as confounding nurse effect is the development of nurse plants in nutrient-rich patches, leading to an enhancement in local richness causally unrelated to the nurse presence. Our study site, where *Atriplex* were planted on a rectangular grid, and our random protocol for *Atriplex* choice allow us to reject this mechanism, even if we can not reject an impact of an initial soil enrichment during sapling plantation. The small volume of the culture bags in which the sapling are transplanted (less than 1 L.) leads us to consider this effect as small if not negligible once the shrub has reached its adult life stage.

The overall impact of the shrub on surrounding plant richness is not constant along time. After 10 years, results show a decrease of this variable. In Southern USA, its area of origin, maximum estimated longevity of *A. canescens* is reported to be of 29 years (Goldberg and Turner 1986). Our study thus encompasses half the maximum longevity of the shrubs. Shrubs were showing a strong trunk lignification at the age of 15 years and discontinuities in canopy allowing light to reach the ground under the shrub (data not shown), leading to the modification of local conditions (i.e. increase of temperature). We thus consider that the 15-year age class is representative of a mature to senescent shrub and is the age limit to the beneficial effect recorded.

Relation of nurse size to nurse effect strength

Nurse size has been recognized as an important factor for the strength of positive effects (Callaway and Walker 1997; Tewskbury and Lloyd 2001; Martinez

Table 4 Results of linear and non-linear modelling for each age class ($n = 36$ with 9 shrubs × 4 radii per age class)

Age classes (years)	2	5	10	15
Linear				
AIC	−259.17	−878.92	−1311.21	**10.62**
R^2	0.464	0.579$^{>>>}$	**0.736**$^{>>>}$	**0.596**
a	0.012	0.013$^{<<<}$	0.017$^{<<<}$	0.017$^{<<<}$
b	0.36$^{<}$	0.29$^{<<<}$	0.018$^{<<<}$	0.002$^{<<<}$
3-parameter logistic				
AIC	−448.29	−1066.09	**−1324.82**	29.44
R^2	0.511	**0.611**	0.733	0.583
X_{mid}	12.47$^{>}$	15.25$^{>>>}$	27.71$^{>>>}$	29.11$^{>>>}$
Scal	11.86	12.15$^{>}$	11.14	11.68
Exponential				
AIC	−98.83	−634.62	−948.62	200.85
R^2	0.399	0.502$^{>>>}$	0.663$^{>>>}$	0.531$^{>}$
M_O	0.448$^{<}$	0.398$^{<<<}$	0.200$^{>>>}$	0.184$^{<<<}$
R	0.0151$^{>}$	0.0173$^{>>>}$	0.029$^{>>>}$	0.030$^{>>>}$
Negative exponential				
AIC	**−505.34**	**−1082.02**	−854.03	260.70
R^2	**0.573**$^{>>>}$	0.539$^{\gg}$	0.577$^{\gg}$	0.439$^{\ll}$
c	0.059$^{\gg}$	0.051$^{\gg}$	0.030$^{\gg}$	0.028$^{>>>}$

Superscripts indicate significances extracted from null models: >: less than 5 % of simulated values greater than observed; ≫: less than 1 % of simulated values greater than observed; >>>: less than 0.1 % of simulated values greater than observed. <: less than 5 % of simulated values smaller than observed; ≪: less than 1 % of simulated values smaller than observed; <<< less than 0.1 % of simulated values smaller than observed

Lower values for Akaike Information Criterion and R^2 for each age class are bolded

and Garcia-Franco 2004). For example, Callaway and Walker (1997) suggested theoretically that the increasing benefactor size could lead to higher strength of facilitation in stressful environment. The field study of Martinez and Garcia-Franco (2004) also demonstrated that the individual number of beneficiary species (*Trachypogon plumosus* and *Schizachyrium scoparium*) increased with the benefactor size (*Chamaecrista chamaecristoides*), except for the largest benefactors in a mobile dune system in central Gulf of Mexico. Nevertheless in extremely severe environment, it has been suggested that the positive effects of the benefactors decrease with their size probably because they are less successful at ameliorating biotic conditions and promoting the survival of beneficiary species (Kitzberger et al. 2000) due to very low biomasses of nurse species (see theoretical model developed by Michalet et al. 2006). Our results, if they do not allow us to test the strength of the one-to-one species interaction, indicates that the impact of the nurse is sequential: in the two first age classes, the slope of the RSRAC is maximized under the shrub; this maximum is reached at the shrub canopy border at

10 years with a logistic model. At 15 years, the nurse effect has vanished, as the best fit is a linear model with constant slope. The shift between a negative exponential model at 5 and 10 years (decreasing slope) and a logistic one at 10 years can be interpreted as the appearance of less favourable environments at the centre of the shrub and the migration of optimal environments towards the periphery of the shrub. To summarize, the point where the RSRAC slope is maximized migrates towards the periphery of the shrub faster than the shrub itself grows. The highly significant higher than EBC value for parameter X_{mid} in 10-year logistic model indicates a strong impact of the nurse on this distance of inflexion point to nurse centre, drawing it towards the nurse border. This effect disappears at 15 years.

To explain these patterns, we cannot exclude the existence of a remnant seed bank in the soil at the moment of plantation and thus can interpret the development of species richness during the ageing of the plantation as the result of both seed trapping and direct and indirect facilitation for seeds germination and development. The changing shape of SRAC is in
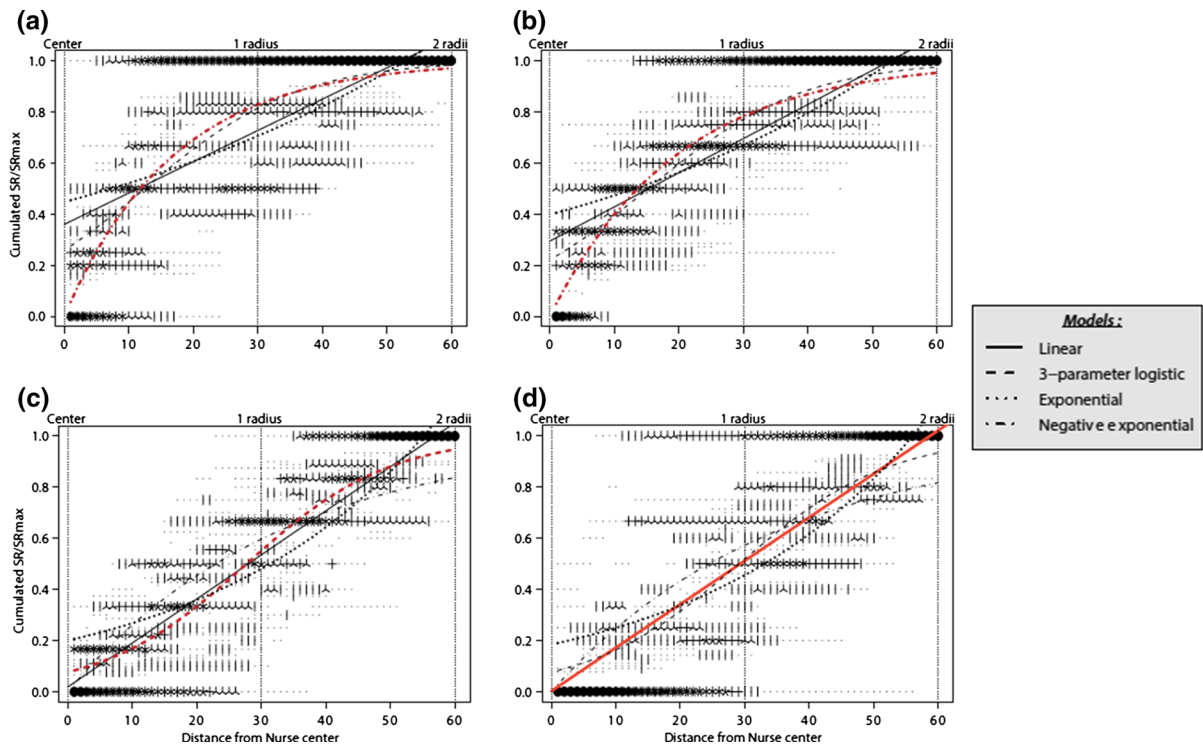
Fig. 2 Cumulative species richness accumulation curves for **a** 2 years, **b** 5 years, **c** 10 years and **d** 15 years. For each age class, n = 2160 (9 shrubs × 4 radii × 60 sampling points). Overlapping points are represented by *rays* around the point, the number of rays equals the number of overlapping points. Linear and non-linear models are plotted, the model with the lower AIC is plotted in *red*, or *bold* in printed version. Note that *horizontal axis is labelled to include the 60 lecture point numbers (See Materials and Methods section)*. (Color figure online)

line with results reported by Facelli and Brock (2000) on the changes occurring during and after *Acacia papyrocarpa* growth in South Australia. This study underlined the changes in vegetation composition between the understory of a nurse tree, gaps and understory of a dead nurse tree. The high dispersion of the points on Fig. 2 is nevertheless representative of a high variation in the field around an individual shrub. This variation might be linked to the transect orientations, which was visually important.

We described here the sequence of the impact of the shrub on the vegetation richness in and around its understory, and provided descriptive elements on the weakening of the positive effects of the nurse on global richness under and around it after 10 years.

Application to the plantation management

As pointed out by Brooker et al. (2008), there is an increasing need for the development of novel,

inexpensive and efficient restoration techniques for preserving ecosystem function and services in these highly degraded areas (e.g. Ormerod et al. 2003; Hobbs et al. 2006). Strategies to combat erosion and soil loss in Algeria were mainly (i) massive *Pinus halepensis* plantations (the so-called green belt in the 1970s, with 270,000 ha planted with a very low average success) and (ii) later sand dune fixation using psammophytes (*Tamarix gallica* and *Retama retam*). These methods were technically and financially heavy to implement and brought mixed results.

Management decisions to open plantations to livestock are actually based on the overall vegetation cover. This descriptor is massively influenced by the shrubs development, not much taking into account the plant community of the plantation as a whole. Recognizing the role of nurse species in plant richness patterns and quantifying it along the shrub life stages can thus be of help as decision tool for plantation managers if they were to integrate plant richness in

their priorities. To struggle against desertification, nurse effects have commonly been involved in restoration techniques by planting local or exotic shrub species and were thus of help in improving environmental conditions, ecosystem properties and services such as animal forage providing (Gomez-Aparicio 2009; Padilla and Pugnaire 2006). Our results demonstrate that, in the case of *Atriplex canescens* and for a duration of 15 years, the nurse effect as it can be detected by the null-model analysis of richness patterns around the shrubs is not constant during the shrub life, and that it vanishes at 15 years. We further point to a significant difference between the age classes encompassed in our study, with a maximal pastoral value reached at 10 years. This duration is to be compared with the usual exclosure period during which plantations are protected for grazing, namely 3 to 5 years. This duration does not appear as sufficient to take advantage of the nurse potential of *Atriplex*. Plantations opening to livestock after 10 years would yield more plant species thanks to *Atriplex* presence, and an additional increase in pastoral value. Our study indicates indeed that, taking only into account the plant species richness, there is no further benefit to expect in the five following years.

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