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The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields

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ABSTRACT

Oldfield succession in Mediterranean ecosystems has been studied extensively in mesic conditions. However, this phenomenon is still poorly understood in semi-arid Mediterranean areas, where reduced plant cover, the importance of facilitation processes and the role of abiotic factors make these environments distinct. We first test whether the carob tree (*Ceratonia siliqua*) generates nucleation patterns in semi-arid oldfields, and to what extent such patterns change with abandonment age. Then we test to what extent nucleation can be explained by the perch effect. And finally, we test whether the nucleated pattern around carob trees is a source of diversity in the oldfields studied. To answer these questions we located oldfields abandoned 25 and 50 years ago (20 in each case) in the Alacant Province (SE Spain, Iberian Peninsula) on the basis of aerial photographs and personal interviews with local landowners and managers. In each oldfield woody plant density and richness were sampled on two microsites: under the carob tree and in the open field. Analysis was performed on all woody plants and by separating the species in two functional groups: fleshy-fruited (with fleshy mesocarp) and non-fleshy-fruited species. The results suggest that woody vegetation colonising abandoned *C. siliqua* fields in SE Spain is not randomly distributed but follows a nucleation pattern with higher plant density under the trees. However, the nucleation pattern is only significant for fleshy-fruited species, suggesting that facilitative interactions alone cannot explain the nucleation pattern and that the perch effect plays an important role. The results also show that the nucleation pattern (total plant density and density of non-fleshy-fruited plants) did not increase with abandonment age, while the perch effect (density of fleshy-fruited plants) did increase significantly. Furthermore, the results also show that the nucleation pattern is not only a loci of high plant density but also a loci of high species richness. Thus we can conclude that the nucleation pattern found in oldfield succession is best explained by the perch effect, while facilitation has a secondary importance. This emphasises the key role that dispersal mode has on the dynamics of vegetation recovery in formerly cropped areas.

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1. Introduction

Given its importance as a global change driver (Houghton et al., 2001), land use change and its ecological aspects are receiving increased interest. In the Mediterranean Basin, the socio-economic changes taking place during the last half of the XX century promoted a dramatic rural exodus, with the consequent abandonment of large cultivated areas (Lepart and Debussche, 1992). As a result, these former cultivated areas are now being colonised by early and late-successional vegetation, a process that has important implications for processes such as water balances (Bellot et al., 2001), wildfire regimes (Pausas, 2004) and carbon sequestration (DeGryze et al., 2004).

Oldfield succession in Mediterranean ecosystems has been studied extensively in mesic conditions (Houssard et al., 1980; Escarré et al., 1983; Peco et al., 1991; Lavorel et al., 1994; Tatoni and Roche, 1994; Tatoni et al., 1994; Montalvo et al., 1995; Debussche et al., 1996; Ne'eman and Izhaki, 1996). However, this phenomenon is still poorly understood in semi-arid Mediterranean areas (e.g. Noy-Meir, 1973; Martínez-Fernández et al., 1995; Margaris et al., 1996; Bonet, 2004; Bonet and Pausas, 2004). Vegetation dynamics after land abandonment under semi-arid conditions differ from that observed in more mesic areas due to the reduced plant cover that characterises the former (Whitford, 2002), the differences in the relative importance of interspecific interactions such as facilitation and competition (Bertness and Callaway, 1994), and the overwhelming role that abiotic factors play on the dynamics of plant populations (Escudero et al., 1999).

Successional processes in formerly cultivated areas are strongly influenced by the nature of the crop that dominated them. In areas formerly planted with tree crops (fruit orchards), it has been suggested that oldfield vegetation is spatially aggregated around the original crop tree (Debussche and Isenmann, 1994). This process has been named 'nucleation' (Yarranton and Morrison, 1974) by analogy with other physical processes, or 'recruitment foci' (McDonnell and Stiles, 1983). This nucleation pattern can be generated by, at least, two different ecological processes: the perch effect and/or the facilitation effect through microenvironmental and resource improvement (Gill and Marks, 1991; Verdú and García-Fayos, 1996).

The perch effect refers to the process in which trees remaining from the orchards are used as perches by frugivorous birds (Debussche et al., 1982). These birds swallow fruits from the different shrubs and trees in remnant vegetation patches around the oldfields and defecate and/or regurgitate the seeds while perching in the old crop tree. Thus, seed rain and the resulting seedling recruitment and sapling spatial pattern should be highly patchy and largely restricted to microhabitats beneath trees (Izhaki et al., 1991; Debussche and Lepart, 1992; Herrera et al., 1994; Debussche and Isenmann, 1994; Alcántara et al., 2000). However, high post-dispersal seed predation beneath the woody vegetation (Kollmann, 1995; Hulme, 1998; Rey and Alcántara, 2000) could overwhelm the increased seed rain from the perch effect and have no consequences in the processes leading to final recruitment.

An alternative process for explaining the nucleation pattern is the facilitation effect (*sensu* Connell and Slatyer, 1977). Many studies have reported improvements in soil structure, increases on soil nutrients and microbial activity, and amelioration of harsh microclimatic conditions under woody plants in semi-arid environments, leading to the formation of "resource islands" under the canopy of these plants (Jake and Coughenour, 1990; Verdú and García-Fayos, 1996; Moro et al., 1997; Reynolds et al., 1999). These resource islands are points of high biological activity where facilitative interactions among plant species are dominant (Callaway, 1995; Aguiar and Sala, 1999). Recent studies have emphasised the importance of these interactions in driving plant community structure and dynamics in semi-arid environments (Pugnaire and Luque, 2001; Tewksbury and Lloyd, 2001; Maestre et al., 2003a). In semi-arid oldfields changes in soil and microclimate as described above are also likely to occur around the crop trees, and thus may be responsible for generating the patchy pattern of nucleation.

To our knowledge, none of the studies conducted so far has evaluated the relative importance of the perch and facilitation effects as drivers of vegetation dynamics in formerly cultivated semi-arid areas. In the present paper we first test whether carob trees (*Ceratonia siliqua*, Fabaceae subfamily Caesalpinioideae) generate nucleation patterns in semi-arid oldfields, and to what extent such patterns change with abandonment age. Then we test to what extent nucleation can be explained by the perch effect. If nucleation is observed in fleshy-fruited species only, then it should be caused by the perch effect; otherwise (i.e. if nucleation is observed in both fleshy and non-fleshy-fruited), facilitation (mediated by the improvement in soil conditions and the amelioration of harsh climatic conditions) could be the main driving force in the nucleation. Note that *C. siliqua* does not produce fleshy-fruited bird-dispersed fruits and thus there is no possible confounding between the pure perch effect and the visit of birds attracted by fruits (reward). Furthermore, we studied to what extent the nucleated pattern around *C. siliqua* trees is not only a loci of high plant density but also a source of diversity (diversity loci).

To answer these questions we sampled woody plant density (for both fleshy-fruited and non-fleshy-fruited species) beneath and outside *C. siliqua* trees in semi-arid oldfields abandoned 25 and 50 years ago in the south-eastern Iberian Peninsula. Special emphasis was given to *Rhamnus lycioides* (Rhamnaceae), the most abundant fleshy-fruited species in the study area and common in other Mediterranean semi-arid environments (Tutin et al., 1964–1980). This species is also being increasingly used in the restoration of degraded ecosystems in semi-arid Mediterranean areas (Bonet, 2004; Cortina et al., 2004; Caravaca et al., 2003; Maestre et al., 2003b).

2. Methods

2.1. *Study area*

The study was conducted at the Ventós-Agost Catchment Experimental Station (University of Alacant), in the Municipality of Agost, Alacant Province, SE Spain (38°28′N, 0°37′W, 10–840 m a.s.l.). The catchment area (approx. 1537 ha) is characterised by a semi-arid Mediterranean climate, with a very high interannual variability. Mean annual temperature is 18.2 °C and annual rainfall is 302 mm (Agost Meteorological Station, 1961–1990 period). Soils have developed over marls and calcareous bedrock, and slopes, which are mainly south-facing, vary between 25% and 30%. Natural vegetation is formed by a mosaic of *Stipa tenacissima* steppes, *Brachypodium retusum* grasslands with dwarf shrubs, and shrublands dominated by *Quercus coccifera* and *Erica multiflora* (Bonet et al., 2004). These formations are mixed with *Pinus halepensis* plantations and dry woody crops like almond tree (*Prunus dulcis*), olive tree (*Olea europaea*) and *C. siliqua*. Recently, set-aside processes in the region have extended, and field abandonment ranges from 1 to 60 years following the last cultivation, with the main set-aside process taking place from 1946 to 1956 (Bonet et al., 2004).

2.2. *Sampling*

In 1999 we located all the oldfields containing a *C. siliqua* tree in our study area using available digital cartography (Bonet et al., 2004). Most fields in the area were relatively small and had one or very few *C. siliqua* trees, sometimes in combination with cereal crops. We first preselected the fields that had a single tree (Plate 1). From all these sites, we randomly selected oldfields that had been abandoned 25 and 50 years ago (20 oldfields in each case), on the basis of aerial photographs and personal interviews with local landowners and managers (Bonet and Pausas, 2004). Abandonment is defined here as the cessation of ploughing and sowing.

The selected oldfields were sampled during the springs of 1999 and 2000. The area of each oldfield and the projected canopy area of each associated *C. siliqua* tree was measured. All the woody species present underneath the canopy of the *C. siliqua* trees (hereafter named Tree microsite) and outside this canopy (hereafter named Field microsite) were counted. Species were divided in two types: fleshy-fruited (with fleshy mesocarp) and non-fleshy-fruited. From these data, we obtained plant density data by dividing the total number of individuals by the projected area of the *C. siliqua* tree (Tree microsite) and by the area of the oldfield (Field microsite). Species richness and species density (number of species per area) were also obtained for both microsites.

Plate 1 – Oldfields with single carob trees (*C. siliqua*) abandoned 25 years ago in the study area (Alacant, SE Spain).

2.3. *Data analysis*

The effect of microsite and abandonment age on plant density, species richness and species density were tested by two-way ANOVA. Prior to these analyses, the plant density data were root-transformed, and the species density data were log-transformed. For species richness, the Poisson error distribution was assumed in a GLM model (Margules et al., 1987; Pausas, 1994; Pausas et al., 2003). Separate analyses were conducted for all the species pooled, for fleshy-fruited species, for non-fleshy-fruited species and for *R. lycioides*.

3. Results

A total of 31 woody species were found in the 40 oldfields studied; nine of them were fleshy-fruited (Table 1). Woody plant density (individuals·m^{-2}) was significantly higher in the Tree than in the Field microsite (3.26 ± 1.6 vs. 1.93 ± 1.3 individuals·m^{-2}, respectively), but the effect of abandonment age and the interaction were not significant (Table 2). However, if only the fleshy-fruited species are considered, the significance and the explained variance increased (Table 2). Fleshy-fruited species density was substantially higher (ca. 25 times) in the Tree than in the Field microsite (1.183 ± 0.89 vs. 0.046 ± 0.03), and these differences were especially pronounced in the 50-year oldfields (both the abandonment age and the interaction were significant, Table 2 and Fig. 1). The same pattern was observed for the density of *R. lycioides* (Tables 1 and 2). The density of non-fleshy-fruited woody species was similar in the two microsites (ca. 1.98 ± 1.4 individuals·m^{-2}), but decreased with abandonment age ($P < 0.025$, Table 2).

Total woody species richness was higher in the Field than in the Tree microsite (Table 3), but this difference was likely due to the fact that the field area (163 ± 197 m^2) is much higher (on average ca. seven times) than the area under the tree (24.4 ± 11.8 m^2). Despite these large differences in area size between microsites, the number of fleshy-fruited species was significantly higher in the Tree microsite compared to the Field. For all species groups (total, fleshy and non-fleshy), species density (number of species m^{-2}) was significantly higher in the Tree microsite (Table 3). Non-fleshy-fruited species richness tended to decrease with abandonment age, while fleshy-fruited species increased or remained constant with age (Table 3).

4. Discussion

In the oldfields studied, woody species density was substantially higher beneath *C. siliqua* trees than in the open field; that is, woody species colonisation of abandoned *C. siliqua*

Table 1 – List of woody species observed in the oldfields studied (fleshy-fruited and non-fleshy-fruited species) with their abundance (mean number of individuals) in each microsite (*N* = 20): outside the canopy in the field terrace (Field) and beneath the carob tree canopy (Tree), for both the 25 and 50 years old oldfields

Species name (Family)	Field		Tree	
	25	50	25	50
Non-fleshy-fruited species				
Fumana ericoides + *F. thymifolia* (Cistaceae)	40.2	55.1	2.7	2.3
Thymus vulgaris (Lamiaceae)	22.4	36.1	3.2	5.2
Anthyllis cytisoides + *A. terniflora* (Fabaceae)	21.4	23.5	7.9	3.9
Helianthemum violaceum (Cistaceae)	18.5	21.0	8.1	3.5
Teucrium homotrichum + *T. murcicum* (Lamiaceae)	4.8	23.5	2.2	8.7
Coronilla minima ssp. *lotoides* (Fabaceae)	3.6	29.0	0.85	3.5
Phagnalon saxatile + *P. rupestre* (Asteraceae)	15.4	9.4	5.7	1.1
Helianthemum syriacum (Cistaceae)	10.9	13.3	1.5	1.3
Sideritis leucantha (Lamiaceae)	8.3	8.3	3.0	1.2
Globularia alypum (Plantaginaceae)	0.35	16.8	0.05	2.5
Helichrysum stoechas (Asteraceae)	5.2	9.7	0.6	0.6
Dorycnium pentaphyllum (Fabaceae)	3.8	2.3	0.85	0.5
Haplophyllum linifolium ssp. rosmarinifolium (Rutaceae)	0	5.4	0.05	1.1
Bupleurum fruticescens (Apiaceae)	0.6	3.5	0.25	1.1
Cheirolophus intybaceus (Asteraceae)	0	3.8	0	0.75
Thymelaea hirsuta (Thymelaeaceae)	2.8	0.35	0.8	0
Ruta angustifolia (Rutaceae)	0	1.2	0	1.4
E. multiflora (Ericaceae)	0.1	0.65	0.3	0
Fleshy-fruited species				
R. lycioides (Rhamnaceae)	0.9	2.1	8.9	44.15
Asparagus horridus (Liliaceae)	2.7	4.5	1.6	5.7
Juniperus oxycedrus (Cupressaceae)	0.1	0.7	0.2	0.4
Ephedra fragilis (Ephedraceae)	0	0.2	0.15	1
Osyris lanceolata (Santalaceae)	0.1	0.1	0.15	0.65
P. lentiscus (Anacardiaceae)	0	0	0	0.35
O. europaea var. sylvestris (Oleaceae)	0	0	0.1	0.25
Arbutus unedo (Ericaceae)	0	0	0	0.1
Rhamnus alaternus (Rhamnaceae)	0	0	0	0.05

Species are sorted by their mean abundance. Nomenclature following Mateo and Crespo (2001) for species, and The Angiosperm Phylogeny Group (Bremer et al., 1998) for family names. Some closely related species were aggregated to avoid some uncertainties in the plots that the individuals were poorly developed.

Table 2 – Mean density of woody plants (individuals·m^{-2}) and two-way ANOVA for total, fleshy-fruited and non-fleshy-fruited species and for *R. lycioides* in relation with the different microsite (Tree vs. Field, M) and abandonment age (25 vs. 50 years, A)

	Plant density (individuals m^{-2})				ANOVA						
	Field		Tree		Microsite (M)		Abandonment age (A)		M × A		
	25	50	25	50	$F_{1,76}$	P	$F_{1,76}$	P	$F_{1,76}$	P	R^2
Total species	2.10	1.75	3.12	3.40	19.4	< 0.0001	0.02	0.87	1.38	0.24	0.215
Fleshy-fruited species	0.045	0.048	0.56	1.80	200.4	< 0.0001	37.9	< 0.0001	35.9	< 0.0001	0.783
Non-fleshy-fruited species	2.06	1.71	2.56	1.60	0.01	0.815	5.2	< 0.025	1.18	0.28	0.078
R. lycioides	0.010	0.012	0.456	1.485	217.6	< 0.0001	35.0	< 0.0001	30.5	< 0.0001	0.788

fields in semi-arid conditions was not randomly distributed but instead followed a nucleation pattern. The fact that this pattern was highly significant for fleshy-fruited species alone, and not for the remaining species (Table 2), suggests that facilitative interactions only cannot explain it, and that increased seed rain due to the perch effect should be invoked. For instance, the density of *R. lycioides*, a bird-dispersed species (Jordano and Herrera, 1981; Jordano, 1987), showed a clear nucleation pattern (Table 3). Similar patterns have found for other species of the same genus, such as *R. alaternus* (Gulias et al., 2004) and *R. ludovici-salvatoris* (Traveset et al., 2003), in Mediterranean shrublands. Likewise, nucleation patterns around orchard trees have been observed for other fleshy-fruited bird-dispersed Mediterranean species such as *Pistacia lentiscus* and *Daphne gnidium* in areas formerly cropped with *C. siliqua* and *O. europaea*, respectively (Verdú and García-Fayos, 1996, 1998). To what extent, the nucleation pattern in each of the above cases is due to the perch effect or to facilitation mediated by improved environmental conditions under the canopy of shrubs and/or trees is difficult to know, and perhaps both processes may be relevant in the recruitment of Mediterranean fleshy-fruited species (Gulias et al., 2004). Furthermore, in the case of *O. europaea*, bird perching may be due to the vertical structure but also to the attraction by the fleshy fruits of this species. Our results suggest that the perch effect may be more relevant than the facilitation effect in driving the dynamics of oldfield vegetation in semi-arid environments, at least during the time frame evaluated here. This does not minimise the importance of facilitation as a driver of vegetation dynamics in these and other environments, but rather emphasises the overwhelming role that dispersal mode has on the dynamics of vegetation recovery in formerly cropped areas (Bonet and Pausas, 2004). Future experiments on seed rain

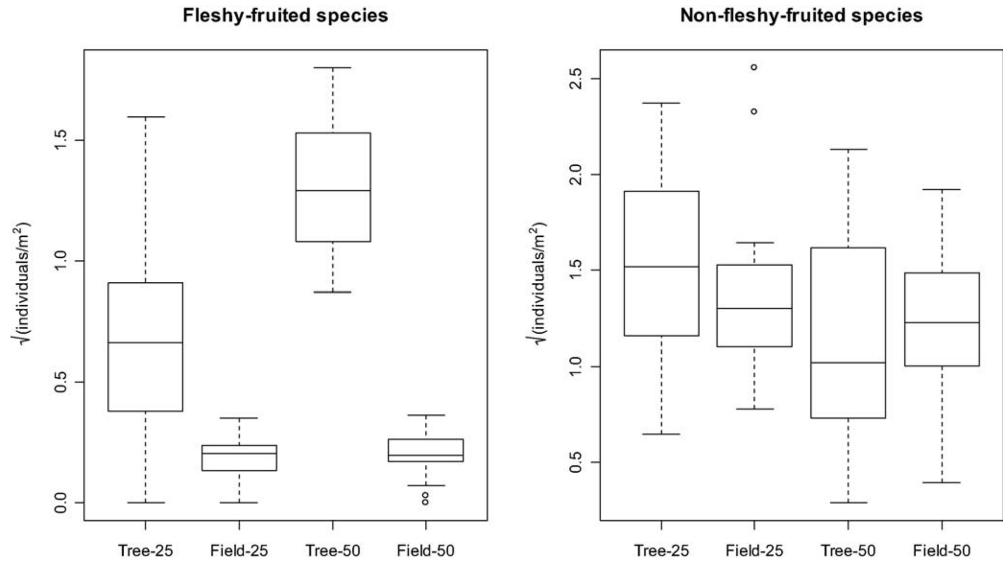

Fig. 1 – Median (horizontal line), first and third quantiles (box) and extreme values on woody plant density (expressed as the square root of the number of individuals m^{-2}) of fleshy-fruited species (left) and non-fleshy-fruited species (right) observed on the two microsites (Tree, beneath *C. siliqua* trees, and Field, outside the tree) for 25 and 50 years old oldfields. See Table 3 for the statistical analyses of these data.

Table 3 – Mean species richness and density (number of species·m^{-2}) and two-way ANOVA for total, fleshy-fruited and non-fleshy-fruited species ($N = 20$) in relation with the different microsite (Tree vs. Field, M) and abandonment age (25 vs. 50 years, A)

	Field		Tree		ANOVA P-values		
	25	50	25	50	Microsite	Age	M × A
Number of species							
Total species	12.15	14.65	9.05	9.90	< 0.0001	0.027	0.469
Fleshy-fruited species	1.45	2.00	1.85	3.30	0.009	0.002	0.42
Non-fleshy-fruited species	10.70	12.65	7.20	6.60	< 0.0001	0.32	0.09
Species density (# m^{-2})							
Total species	0.16	0.10	0.65	0.40	< 0.0001	0.0005	0.339
Fleshy-fruited species	0.02	0.014	0.11	0.12	< 0.0001	0.453	0.137
Non-fleshy-fruited species	0.15	0.08	0.53	0.28	< 0.0001	0.00017	0.80

For species richness data, a Poisson analysis is used; species density data were log-transformed.

would be needed for a better quantification of the role of seed dispersal.

It is interesting to mention that the nucleation pattern (total plant density and non-fleshy-fruited plant density) did not increase with abandonment age, while the perch effect (fleshy-fruited plant density) did (Table 2). Both fleshy-fruited plant density and *R. lycioides* density were higher beneath *C. siliqua* trees than in the field, and the magnitude of these differences were larger in 50-year-old fields than in 25-year-old fields (significant interactions in Table 2). This result suggests that the perch effect increases in importance along succession. This trend can be explained by the higher seed rain due to the longer time since abandonment (Debussche and Isenmann, 1994). Furthermore, there may also be a positive feedback in which fleshy-fruited species establish and produce fruits below the perch tree, and these additional fruits attract more birds (Sargent, 1990), further increasing the seed rain under the *C. siliqua* tree canopy.

The microsite beneath the *C. siliqua* tree represents a “diversity loci” in semi-arid oldfields, as described for other woody species in desert shrublands (Tewksbury and Lloyd, 2001) and semi-arid steppes (Maestre and Cortina, 2005). That is, in our conditions, bird-mediated seed rain of fleshy-fruited species generates a high spatial variability in both plant density and diversity, and this variability is dependent on the vertical vegetation structures remaining from the abandoned orchard. In fact, it has been recognised that after tree crop abandonment in Mediterranean landscapes, vegetation does not follow the traditional path from “early-successional” species to “late-successional” species; rather, the so-called “late-successional” species may appear early after abandonment (Ne’eman and Izhaki, 1996; Bonet, 2004; Bonet and Pausas, 2004). This early appearance of “late-successional” species is due to the perch effect.

These results may have important implications in the management of semi-arid Mediterranean ecosystems. The long-time human pressure (e.g. grazing, wood harvesting, massive cultivation and terracing and then massive abandonment) in these systems has degraded many of the semi-arid landscapes of the Mediterranean Basin (Jauffret and Lavorel, 2003; Maestre and Cortina, 2004a; Bonet et al., in press). Currently, there is strong social pressure to restore or accelerating natural processes of regeneration in these landscapes (Pausas et al., 2004; Vallejo et al., 2006). The limited success of conventional restoration activities in semi-arid Mediterranean areas (see Maestre and Cortina, 2004b for a discussion), emphasises the need of incorporating ecosystems-specific structural and functional processes into their active management. The fact that the perch effect provides important seed rain for regeneration and for increasing diversity in a variety of environments opens up the possibility of using artificial perching sites for accelerating landscape regeneration. This technique has been applied mainly under tropical conditions (McDonnell, 1986; Holl, 1998) and, to our knowledge, has not been experimentally tested under semi-arid conditions. Further experimental studies are thus needed to evaluate the suitability of this technique for Mediterranean semi-arid landscapes.

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