

## Chapter 13

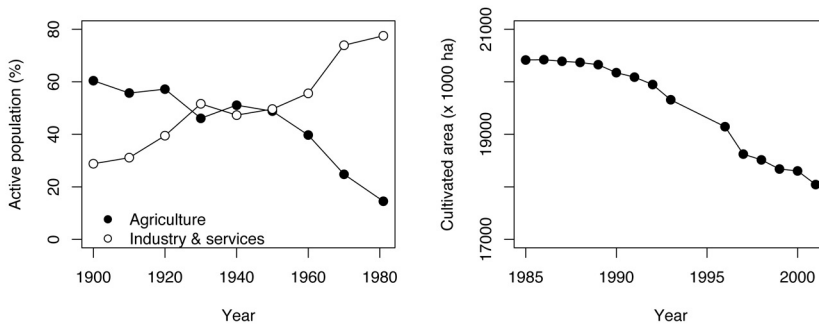
*Old Field Dynamics on the Dry Side of the Mediterranean Basin: Patterns and Processes in Semiarid Southeast Spain*

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Euro-Mediterranean countries have a long history of land use changes and urbanization processes (Antrop 2004). During the past century, with the advent of industrial and tourist development, these countries have experienced an important intensification of land use changes related to the abandonment of rural livelihoods and city sprawl in coastal areas.

On the northern (European) rim of the Mediterranean basin, the socioeconomic changes taking place during this period promoted a dramatic rural exodus, with the consequent abandonment of large cultivated areas (Lepart and Debussche 1992) (figure 13.1). As a result, these previously cultivated areas are now being colonized by natural vegetation, with important implications for processes such as water balance (Bellot et al. 2001), wildfire regime (Pausas 2004) and carbon sequestration (DeGryze et al. 2004). Meanwhile, landscapes on the southern (African) rim of the Mediterranean basin still suffer from overexploitation, especially overgrazing (after clearing), increasing cultivation on pronounced slopes, and associated degradation problems (Le Houérou 1993; Taiqui 1997; Redjali 2004). These contrasting patterns are related to the different socioeconomic, demographic, and political trends occurring between the northern and southern Mediterranean (Puigdefábregas and Mendizabal 1998)

Thus there is some association between land abandonment in mesic Mediterranean ecosystems and overexploitation in drier Mediterranean ecosystems. However, there are also areas in southern Europe (e.g., southeast Spain) that are considered semiarid and are undergoing the process of land abandonment (Bonet et al. 2004; Bonet et al. 2006). In this chapter we will focus on such areas, where studies of vegetation dynamics have been developed only recently (Bonet et al. 2001; Bonet 2004; Bonet and Pausas 2004; Pausas et



**FIGURE 13.1.** (a) Changes in the percentage of active population dedicated to either agriculture or industry and services, during the twentieth century in Spain. From Pausas (2004). (b) Dynamics of the overall cultivated land surface in Spain. Source: Source: Ministerio de Agricultura, Pesca y Alimentación, 2006 and Instituto Nacional de Estadística, 2006, Spain.

al. 2006; Pugnaire et al. 2006). Vegetation dynamics under semiarid conditions differ from that observed in more mesic areas, due to the reduced plant cover that characterizes the former, the differences in the relative importance of interspecific interactions such as facilitation and competition (Bertness and Callaway 1994), and the role that abiotic factors play in the dynamics of plant populations (Escudero et al. 1999). Many studies on secondary succession in both tropical and temperate regions have been carried out in abandoned fields after agricultural use of previously forested lands. Succession in these areas usually leads to the development of forest, although the composition may change from the original forests (Foster et al. 1998; Grau et al. 2003). In the Mediterranean Basin, some studies also indicate a forest development with succession following land abandonment (Housard et al. 1980; Taton and Roche 1994; Debussche et al. 1996, 2001; Debussche and Lepart 1992; Mazzoleni et al. 2004), but under semiarid conditions the forest may not be representative of late stages of succession and is usually not present in remnant vegetation, due to both low water resources and intensive human pressure since the Neolithic period (Badal et al. 1994). In semiarid Spain there is some uncertainty about which vegetation type was present prior to agricultural practices, but many authors suggest that the late-successional communities in these territories are composed of shrublands with a variable tree cover (Bolòs 1967; Rivas-Martínez 1987; Ruiz de la Torre 1990).

For practical reasons, we use a chronosequence approach (i.e., synchronic approach or space-for-time substitution) to infer successional dynamics. Although we recognize that there are some potential problems with using this approach (Pickett 1989), most predictions made with this approach

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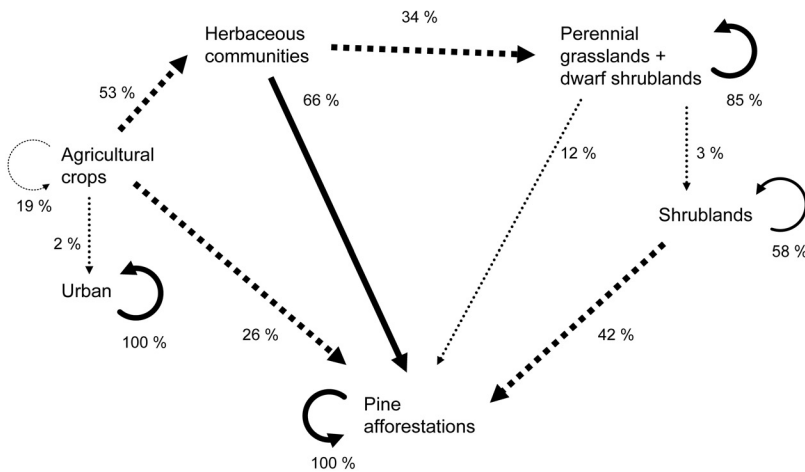
have been validated when revisiting and resampling the studied communities (Debussche et al. 1996; Foster and Tilman 2000). The studies presented here were performed in Alacant Province, southeast Spain. Mean annual temperature is above 18°C and annual rainfall is about 300 mm. Soils are typically developed over marls and calcareous bedrock. Slopes over marls were terraced in the past for cultivation and then abandoned. Hand-built stone terraces permitted cultivation on slopes by preserving soil and maintaining water availability. In some cases, abandoned terraces were afforested with *Pinus halepensis*, and fires affected some of these plantations (Pausas, Bladé et al. 2004; Pausas, Ribeiro, and Vallejo 2004). Natural vegetation surrounding agricultural land 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 the *Pinus halepensis* plantations and with both active and abandoned dry woody crops like almond tree (*Prunus dulcis*), olive tree (*Olea europaea*) and carob tree (*Cerastonia siliqua*). Field abandonment ranges from one to sixty years following the last cultivation, with the main set-aside process taking place from 1946–56 (Bonet et al. 2004).

#### Patterns in Semiarid Old Field Dynamics

Patterns in old field dynamics in the semiarid areas are determined by landscape dynamics, plant cover and composition, and species richness.

#### *Landscape Dynamics*

During the second half of the twentieth century, the vegetation changes resulting from both the abandonment of various dry crops and the plantations of Aleppo pine on other old fields transformed the landscape pathways in the Agost-Ventós catchment (Alacant). The analysis of trends in land cover categories using GIS, aerial digitized photographs (from 1946 and 1999), and field work surveys (Bonet et al. 2001, 2004) allows us to understand the dynamic patterns, by counting the transition cases between land cover classes on a sequence of land cover maps in the study area (figure 13.2). These values, expressed as percentages of occupied land area, indicate the land cover changes that occurred during the last decades. Land cover categories are defined by landscape structures: urban, agricultural crops, herbaceous communities, perennial grasslands, and dwarf shrublands, including alpha grass (*Stipa tenacissima*) steppes, shrublands, and pine plantations (figure 13.2).



**FIGURE 13.2.** Observed transitions in land cover changes in a semiarid agricultural landscape (Agost-Ventós catchment, Alicante) between 1946 and 1999. Diagram shows the pathways of landscape change, estimated using aerial photographs and GIS analysis (Bonet et al., 2004). Perennial grasslands and shrublands include agricultural land outside the terrace cropping area.

Natural processes of land cover change represent 98% of the changes in recent abandoned crops (i.e., only 2% of the observed transitions were from dry crops to urban land). These land cover changes are derived from two different processes: natural vegetation recovery (as a result of autogenic vegetation dynamics dominated by old field succession) or human afforestation (pine plantations). Some afforestation has been performed in all the land cover classes (shrubland, grassland, or herbaceous). Note that natural vegetation recovery (i.e., by means of old field succession) does not include the woodland land cover category under the semiarid conditions studied.

The rate of land cover change was higher during the first period in the land abandonment sequence. The initial transitions were observed to follow a pathway from dry crops to herbaceous communities, perennial grasslands plus dwarf shrub communities, and shrublands. This landscape pattern is consistent with the one described in semiarid old field succession (Bonet 2004) and is similar to other semiarid areas (Alados, Pueyo et al. 2004). Herbaceous communities showed no permanence in the landscape between the coupled 1946–99 land cover maps, while perennial grasslands presented the higher rate of permanence (85% of observed transitions) along the abandonment pathway (from abandoned crops to shrublands). The case of permanence of perennial grasslands (such as *Stipa tenacissima* or *Brachypodium retusum* formations) is an example of community stability with slow species

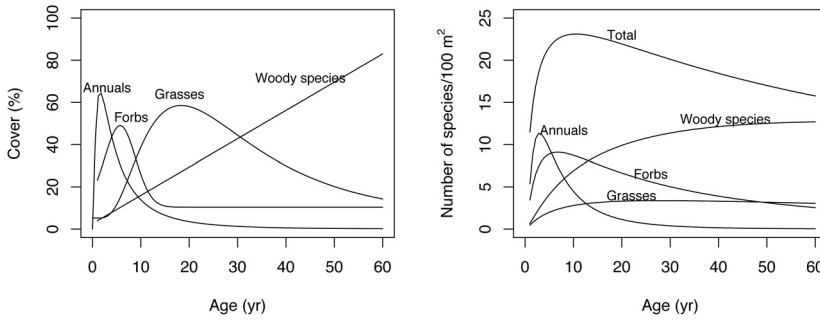
turnover, thus indicating that the dynamics of this vegetation is not necessarily progressive.

The main landscape changes between 1946 and 1999 were due to afforestation in old fields and affected all abandonment stages (figure 13.2). Plantations of Aleppo pine began in the study area around 1946 and increased between 1956 and 1974 over recently abandoned crops (Bonet et al. 2004). The afforestation pathway was especially relevant in herbaceous communities (66% of the observed transitions) and shrublands (42%).

### *Plant Cover and Composition*

We studied a sixty-year chronosequence of old fields formerly planted with tree crops (fruit orchards) and that were not afforested (Bonet and Pausas 2004). In this chronosequence, a total of 222 plant species were recorded in 96 plots (100 m<sup>2</sup>). Plant cover ranged from 45.5% to 100% and was not dependent on abandonment age ( $p = 0.419$ ); high cover values were found at any time following abandonment. However, the cover of each life form showed a significant and different pattern along the abandonment age gradient, and there was a clear tendency in the order of dominance of the different life forms (figure 13.3a). Annuals, forbs, and grasses showed a skewed pattern, while woody species showed a linear trend. Annuals were the first species to cover the old fields, reaching high cover values in the first five years after abandonment (mean of ca. 60%, but up to 100% in some cases). However, they were almost absent approximately twelve years after abandonment. Perennial forbs also reached a maximum during the first ten years, while perennial grasses peaked at ten to twenty-five years after abandonment. Woody species showed a significant monotonic increase throughout the time span studied (sixty years) (figure 13.3). The number of life forms decreased with abandonment age, from four co-occurring during the first twenty years, to two life forms, and finally (at ~ sixty years) the vegetation was practically dominated by one life form (woody species), although one grass species (*Brachypodium retusum*) persisted (with low cover) on the sixty-year-old plots.

Plant composition, summarized as an ordination axis, clearly changed with abandonment age ( $R^2 = 0.83$ ;  $p < 0.0001$ ). The variability in vegetation composition along the chronosequence was mainly explained by differences in previous crop type (figure 13.4a; table 13.1). Slope was also seen to be a significant factor. Although slope is correlated with abandonment age (fields located on sites with difficult conditions for farming were the first to be abandoned), it had a significant effect on cover even when age was considered (i.e., as covariate) (table 13.1). Vegetation composition variability was higher

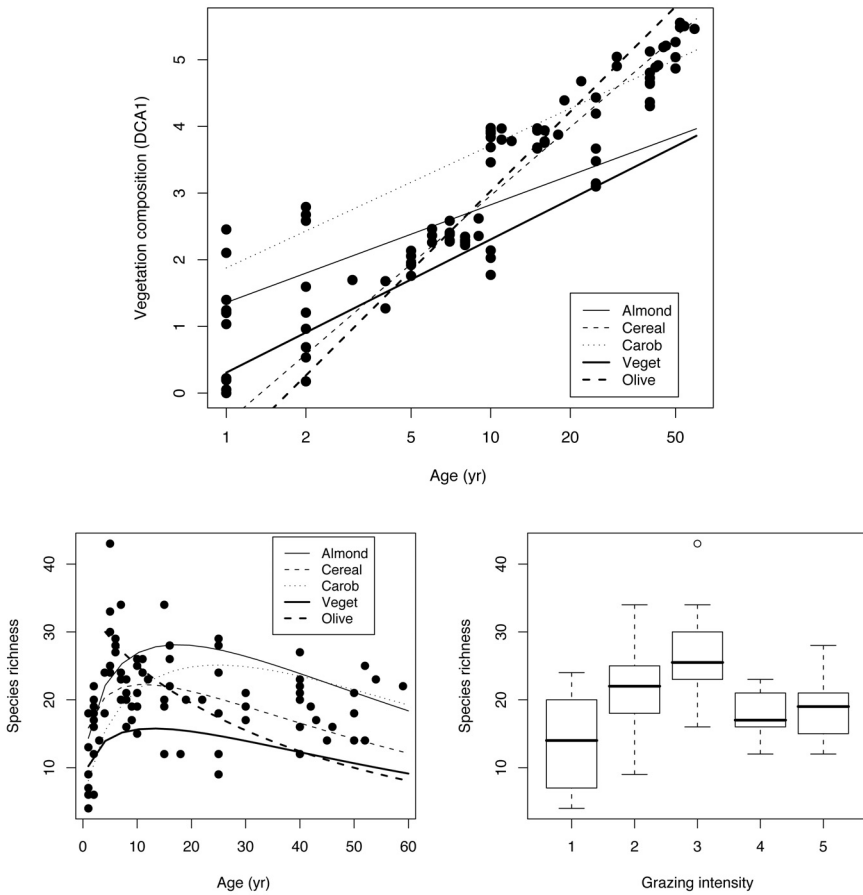


**FIGURE 13.3.** Changes in (a) plant cover and (b) species richness for the different life forms along a chronosequence in Alacant, SE Spain. Fitted lines were all significant ( $p < .0001$ ). Elaborated from data in Bonet and Pausas 2004.

during the first postabandonment years and tended to converge with time since abandonment (figure 13.4a).

### *Species Richness*

Species richness per plot ( $100 \text{ m}^2$ ) ranged from four to thirty-four, and there was a significant nonlinear relationship with abandonment age ( $R^2 = 0.36$ ;  $p < 0.0001$ ; figure 13.3b) (Bonet and Pausas 2004). Thus, species richness follows a hump-shaped curve as described for richness in relation to environmental variables and productivity (see Pausas and Austin 2001). Species richness also showed different patterns for the various life forms (figure 13.3b), and the order along the age gradient was similar to cover; the main difference was that there were few species of perennial grasses with high cover. This different richness pattern for each functional group results from differences in colonization capacity and persistence. For example, most annual plants or short-lived perennials are either present in the fields as weeds during cropping or find shelter in the active field margins; thus, they can increase in number and cover quickly after abandonment. However, these species may be displaced when resources are taken over by long-lived perennial plants. The results suggest that, under semiarid conditions, total species richness shows a peak in the early stages of the chronosequence. This pattern may be attributable both to the importance of immigration processes during the early stages of succession and the dominance of extinction processes after approximately fifteen years since abandonment. Nevertheless, the species richness pattern and life form replacement during semiarid old field succession can also vary with the precipitation gradient (Otto et al. 2006). The most out-



**FIGURE 13.4.** Variability in the relation between vegetation composition (expressed as a vegetation ordination axis, DCA1) and abandonment age (logarithmic scale) can be explained by differences in the previous crop type (a). Variability in the relationship between species richness and abandonment age can be explained both by the different, previous crop type (b) and by the grazing intensity (c). See statistics in table 1. Previous crop types are: almond trees, cereals, carob trees, vegetable fields, and olive trees. Explained deviance = (a) 93.7%; (b) 58.2%; (c) 31.1%; and 66%, for (b) and (c) together, i.e., the model with age, previous crop type, and grazing intensity.

standing differences in life form richness and cover are shown by annual plants, whose patterns showed a strong dependence on water availability.

Species richness variability throughout the chronosequence can be explained by previous crop type and grazing intensity (figures 13.4b and 13.4c; table 13.1). Old almond orchards have the highest richness while old

TABLE 13.1

*Effect of factors explaining the variability in the vegetation composition and species richness in the studied oldfields.*

	Vegetation composition		Species richness	
	<i>F</i>	<i>p</i>	Chi sq.	<i>P</i>
Previous use	11.426	<.00001	41.302	<.00001
Slope	5.1378	.02573	10.781	.001
Altitude	1.7888	ns	.0	ns
Grazing intensity	1.7996	ns	44.269	<.00001

Note: Vegetation composition is inferred as an ordination axis (see Fig. 4), and tested with ANOVA using the *F*-test; Species richness is tested with a GLM (Poisson error distribution) and the significance evaluated using the Chi-squared test. Logarithm of age used as covariable in all cases.

vegetable fields have the lowest richness. Grazing intensity explains a significant ( $p=0.001$ ) part of the variability in richness even when age and previous use are included in the model, suggesting that the factors are independent. Species richness in relation to grazing intensity shows a humped pattern with highest richness at intermediate levels of grazing (figure 13.4c), as has been suggested for different disturbance types (Huston 1979). Grazing promotes the coexistence of different functional groups (McIntyre et al. 1995), altering the inhibition pathway and favoring species richness (Noy-Meir 1998). Furthermore, increased dispersal by the grazers (Malo and Suárez 1995a, 1995b) could also promote richness. Other authors found differential effects on diversity in other Spanish semiarid old field communities depending on the stage of development of the vegetation and the environmental conditions (Alados, Elaich et al. 2004a; Alados et al. 2005). However, experimental trials in semiarid environments in the United States showed no relevant effects of moderate grazing on plant diversity along old field successions (Coffin et al. 1998). Thus the effect of grazing on semiarid old field richness deserves further study.

The main difference between the pattern observed in our study area and classic replacement patterns suggested for mesic Mediterranean ecosystems (Houssard et al. 1980; Escarré et al. 1983) has to do with the time lag in which these changes occur. In our case, about 45% of total woody species richness is reached ten years after abandonment, while in mesic Mediterranean conditions (southern France), woody species reached less than 20% of their total richness at this time (Escarré et al. 1983). This pattern could be partially attributed to an early colonization of some shrub species (e.g., *Rhamnus lycioides*) through the facilitation of bird-dispersed seeds by cultivated trees acting as perches.

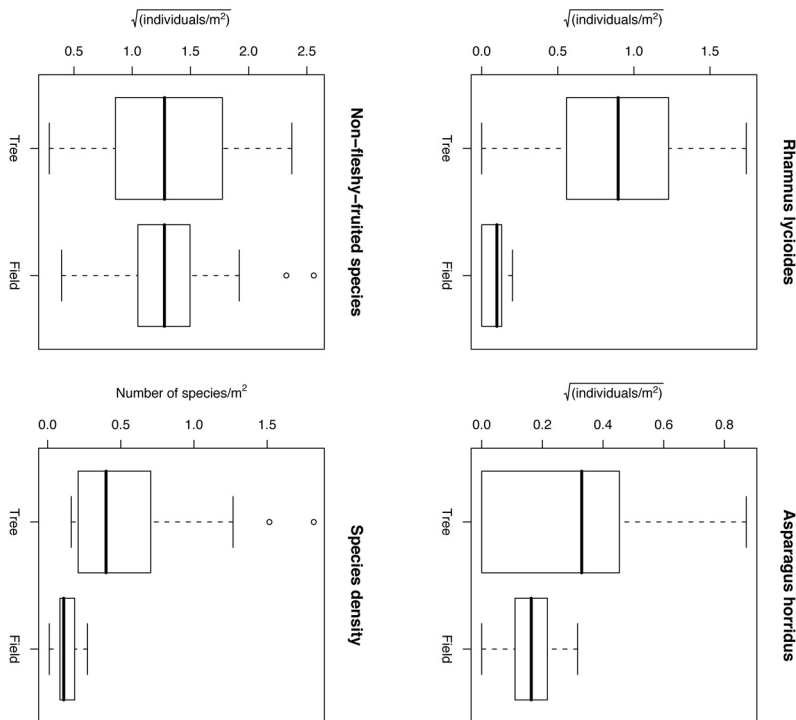


### Processes Driving Semiarid Old Field Dynamics

In areas formerly planted with tree crops (fruit orchards), it has been suggested that old field vegetation is spatially aggregated around the original crop tree (Debussche and Isenmann 1994). This process has been named “nucleation” (Yarranton and Morrison 1974) through 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). 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). 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 in soil nutrients and microbial activity, and amelioration of harsh microclimatic conditions under woody plants in semiarid environments (Jake and Coughenour 1990; Verdú and García-Fayos 1996; Moro et al. 1997; Reynolds et al. 1999). In semiarid old fields changes in soil and microclimate as described earlier are also likely to occur around the crop trees, and thus may be responsible for generating the patchy pattern of nucleation, where population dynamics could also be governed by species-specific environmental triggers (Pugnaire et al. 2006).

Nucleation patterns in old field succession have been found for several Mediterranean species, such as *Rhamnus alaternus* (Gulias et al. 2004), *R. ludovici-salvatoris* (Traveset et al. 2003), and *Pistacia lentiscus* and *Daphne gnidium* (Verdú and García-Fayos, 1996, 1998). However, to what extent the pattern is due to the perch effect or to the facilitation effect through microenvironmental and resource improvement has seldom been tested (Pausas et al. 2006). Comparing plant density beneath carob trees (*Cerastion siliqua*) and in the surrounding fields, we observe that fleshy-fruited, bird-dispersed species (e.g., *Rhamnus lycioides*, *Asparagus horridus*) are more abundant beneath the trees than in the open field, while nonfleshy-fruited species do not show any differential density pattern (figure 13.5). As a consequence, species density is higher beneath the trees (figure 13.5). These results cannot be explained by facilitative interactions only; increased seed rain due to the perch



**FIGURE 13.5.** Perch effect: plant density of two fleshy-fruited species, (a) *Rhamnus lycioides*, and (b) *Asparagus horridus*; and of all the nonfleshy-fruited species; plus (d) the species density observed on two microsites: tree (beneath *Ceratonia siliqua*) and field. Density of both fleshy-fruited species and species density were significantly different ( $p < .0001$ ) between the two microsites; density of nonfleshy-fruited species did not differ between microsites. Box plots indicate median (horizontal line), first and third quartiles (lower and upper sides of the box), 95% confidence intervals (vertical lines), and extreme values (dots)... Elaborated from data in Pausas et al. (2006).

effect should also be invoked. This emphasizes the overwhelming role that dispersal mode has on the dynamics of vegetation recovery in formerly cropped areas under a dry climate (Bonet and Pausas 2004; Pausas et al. 2006; Pugnaire et al. 2006). This does not mean that microenvironmental and resource improvement under trees does not play a role, but that its importance in the colonization process may be secondary.

### Semi-arid Old Field Restoration

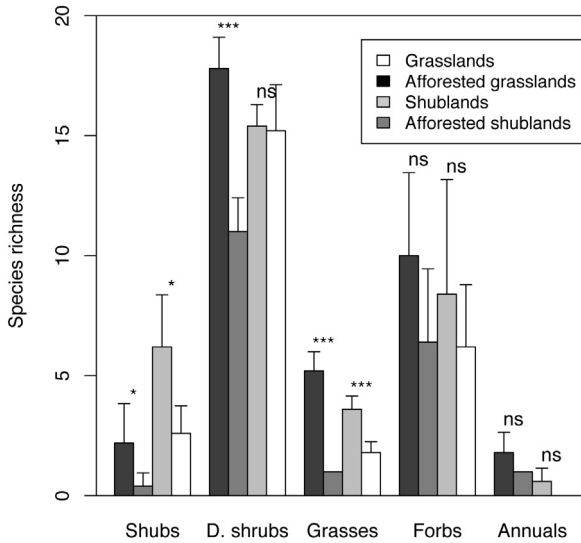
We will now explore the traditional and more contemporary approaches to old field restoration in semi-arid Spain.

### *Traditional Old Field Restoration: Pine Afforestation*

Conifers, mostly pines, have long been used for reforestation in Mediterranean countries. For instance, the proportion of area reforested with conifers (compared to total area reforested) during the last decades was ca. 90%, 94%, 47%, 55%, 86%, and 71% in Spain, Turkey, Algeria, Morocco, Portugal, Greece and Tunisia, respectively (Pausas, Bladé et al. 2004). In the case of semiarid areas of the Mediterranean Basin, including semiarid Spain, *Pinus halepensis* has been the preferred species for afforestation projects in old fields (Valle and Bocio 1996; Cortina et al. 2004). This pine species shows a high relative survivorship in stressed environments (Vilagrosa et al. 1997; Calamassi et al. 2001). Currently, these Aleppo pine plantations constitute the dominant forest land cover (more than 90% of the forested area) in Alicante Province, southeast Spain. The objectives of these plantations were mainly to increase forest productivity, and also to protect watersheds and provide employment in rural areas. The traditional strategy for reforesting in the Mediterranean was to first introduce a fast-growing pioneer species such as pine (Ceballos 1938), under the assumption that this species would facilitate the introduction (either artificial or natural) of late-successional hardwoods. Nevertheless, this latter step was seldom applied because of the costly silvicultural postplantation operations required and the current disturbance regime. Furthermore, the facilitation effect of *P. halepensis* has been questioned (Maestre et al. 2003) and, in fact, in some cases pine plantations may have negative consequences on both the natural vegetation dynamics and in different ecosystem processes (Maestre and Cortina 2004; Chirino et al. 2006). For instance, both the afforested shrublands and the afforested grasslands showed lower species richness than the original shrublands and grasslands, for total species and for most life forms (figure 13.6). In addition, extensive pine plantations resulted in large and homogeneous areas covered with flammable, even-aged pines, interconnected through other old fields dominated by flammable shrublands. This landscape structure and composition with high fire hazard facilitated the spread of large fires during the last decades (Pausas and Vallejo 1999; Pausas 2004; Pausas, Ribeiro, and Vallejo 2004). Thus, although traditional pine plantations have partially achieved some of their initial objectives in some areas, there is a need to be critical and to revise the massive afforestation strategy.

### *Current Tendencies: Toward Restoring Biodiversity*

Although increased forest production may still be an objective, current forest restoration actions in the Mediterranean area have new aims directed toward



**FIGURE 13.6.** Species richness (mean and standard deviation, in 100 m<sup>2</sup>). Statistical comparisons are between natural and afforested communities. Elaborated from data in Chirino et al. (2006). ANOVA (\* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ )

compliance with international obligations (e.g., Convention on Biodiversity, Convention to Combat Desertification, Convention on Climate Change), namely, to increase carbon fixation, to enhance biodiversity and rural development, and to reduce the fire and erosion risk. Moreover, most of the semi-arid agricultural set-aside land is privately owned. Recent European Union and national policies encourage land abandonment in less productive and marginal lands, thus providing subsidies to farmers to promote and maintain ecosystem services and natural capital in abandoned lands. Considering that the soil erosion risk on old, abandoned, terraced lands is small and shows lower rates than in other land cover types (Cerdà 1978), the restoration and conservation of biodiversity could be the main restoration management target in old field ecosystems (Bonet 2004).

The conflict between pine plantations and preexisting grassland and shrubland conservation is a common topic in Mediterranean semi-arid ecosystem management (Esteve et al. 1990). It is now clear that neither plant richness nor many ecosystem functions are improved by pine afforestations and that semi-arid grasslands and shrublands are the habitat for rare and protected fauna at the European scale (Tellería et al. 1988; Yanes 1994). Thus, in many cases, afforestation is unnecessary or even detrimental. Currently, efforts are directed toward developing restoration techniques for a diversity of Mediterranean shrubland species, especially resprouting species that confer

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high resilience to fire (Vilagrosa et al. 2003; Pausas, Bladé et al. 2004; Vallejo et al. 2006). Many of these resprouting shrubs are considered “late-successional species.” However, we have shown that in many Mediterranean old fields the colonization of woody species may start very early in old woody crops, thanks to both the role of trees as perch sites for frugivorous birds (the perch effect) (Pausas et al. 2006) and to the improved microsite conditions for germination and survival (Verdú and García-Fayos 1996). Thus, the use of artificial perches (e.g., dead trees, artificial woody structures) in old fields could accelerate colonization rates (bird-mediated restoration). As attractive as this technique is for promoting succession, it has seldom been applied in Mediterranean ecosystems, and most examples come from elsewhere (e.g., McClanahan and Wolfe 1993). In this context, removal of old or dead trees after abandonment or fire (e.g., burned pine plantations) should be discouraged. Furthermore, the strong relationship between oaks and their dispersal vector (Bossena 1979) merits a deep exploration in light of Mediterranean landscapes reforestation.

Additionally, the relationship between grazing intensity and species richness (figure 13.4c) indicates that moderate grazing could promote the coexistence of different species and functional types (Lavorel et al. 1994), altering the inhibition pathway of *Brachypodium retusum* and favoring the annual species pool, and thus increasing species richness. These systems could be subjected to small-scale disturbance grazing by livestock (sheep) and wild herbivores (rabbits). Though the effect of this kind of grazing has usually been described in terms of defoliation and seeds consumption, ectozoochorous and endozoochorous dispersal would also be favored (Malo and Suárez 1995a, 1995b).

Traditional restoration plans in Mediterranean ecosystems have not considered the role of fauna. However, there is increasing evidence of the strong role of plant-animal interactions in driving succession and shaping biodiversity, and these interactions (perching, grazing, dispersal, pollination, etc.) should be encouraged for quick and cost-efficient restoration actions. Certainly, further research is needed for promoting plant-animal interactions as a restoration goal under Mediterranean conditions, but the current build up of information suggests that there is a lot to learn in this direction.

## Conclusion

Semiarid old field succession in southeast Spain is characterized by an early postabandonment peak in plant species richness. This pattern may be attributable to the high turnover rate (due to immigration and extinction processes) during the early stages of succession, which promotes the

coexistence of several life forms. Even so, the general trend toward replacing annual and biennial species with perennial forbs, grasses, and woody plants is also well apparent. This early-peak richness pattern could also be partially attributed to an early colonization of some so-called late-successional shrub species through the facilitation of bird-dispersed seeds by remnant cultivated trees acting as perches. Previous land use has been shown to be very important for understanding the variability of plant composition and richness in semiarid old fields, and the different disturbance regimes should be considered for understanding the mechanisms driving patterns through old field succession.

From our observations of old field dynamics in semiarid Spain we can suggest the following restoration priorities:

- Although soil conservation is generally assured in terraced old fields, care should be taken in some soil types where terraces are in a degradation process that promotes erosion. In such cases, soil conservation should be the priority of any restoration action.
- Ecosystem resilience should be improved with respect to human and nonhuman disturbances, that is, to ensure the regeneration capacity after fire and other disturbances (Vallejo et al. 2006).
- Biodiversity should be encouraged by: (a) promoting the reintroduction of key species that have disappeared because of past land uses, and (b) promoting animal-plant interactions for quick and cost-efficient restoration actions.

## REFERENCES

- Alados, C. L., A. Elaich, V. P. Papanastasis, H. Ozbek, T. Navarro, H. Freitas, M. Vrahnakis, D. Larrossi, and B. Cabezudo. 2004. Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. *Ecological Modelling* 180:523–35.
- Alados, C. L., Y. Pueyo, O. Barrantes, J. Escos, L. Giner, and A. B. Robles. 2004. Variations in landscape patterns and vegetation cover between 1957 and 1994 in a semiarid Mediterranean ecosystem. *Landscape Ecology* 19:543–59.
- Alados, C. L., Y. Pueyo, D. Navas, B. Cabezudo, A. Gonzalez, and D. C. Freeman. 2005. Fractal analysis of plant spatial patterns: A monitoring tool for vegetation transition shifts. *Biodiversity and Conservation* 14:1453–68.
- Alcántara, J. M., P. J. Rey, F. Valera, A. M. Sánchez-Lafuente. 2000. Factors shaping the seedfall pattern of a bird-dispersed plant. *Ecology* 81:1937–50.
- Antrop, M. 2004. Landscape change and the urbanization process in Europe. *Landscape and Urban Planning* 67:9–26.
- Badal, E., J. Bernabeu, and J. L. Vernet. 1994. Vegetation changes and human action from the Neolithic to the Bronze Age (7000–4000 B.P.) in Alicante, Spain, based on charcoal analysis. *Vegetation History and Archaeobotany* 3:155–66.

## 13. Old Field Dynamics on the Dry Side of the Mediterranean Basin 261

- Bellot J., A. Bonet, J. R. Sanchez, and E. Chirino. 2001. Likely effects of land use changes on the runoff and aquifer recharge in a semiarid landscape using a hydrological model. *Landscape and Urban Planning* 778:1–13.
- Bertness, M. D. and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecology and Evolution* 9:191–93.
- Bolòs, O. 1967. Comunidades vegetales de las comarcas próximas al litoral situadas entre los ríos Llobregat y Segura. *Memorias de la Real Academia de Ciencias y Artes de Barcelona* 38(1).
- Bonet, A. 2004. Secondary succession on semi-arid Mediterranean old-fields in south-eastern Spain: Insights for conservation and restoration of degraded lands. *Journal of Arid Environments* 56:213–33.
- Bonet, A., J. Bellot, D. Eisenhuth, J. Peña, J. R. Sánchez, and C. J. Tejada. 2006. Some evidence of landscape change, water usage and management system co-dynamics in south-eastern Spain, In *Water management in arid and semi-arid regions: Interdisciplinary perspectives*, ed. P. Koundouri, K. Karousakis, D. Assimacopoulos, P. Jeffrey, and M. A. Lange, 226–51. Edward Elgar, Aldershot, UK.
- Bonet A., J. Bellot, and J. Peña. 2004. Landscape dynamics in a semiarid Mediterranean catchment (SE Spain). In *Recent dynamics of Mediterranean vegetation and landscape*, ed. S. Mazzoleni, G. di Pasquale, M. Mulligan, P. di Martino, and F. Rego, 47–56. John Wiley and Sons, London, U.K.
- Bonet, A., and J. G. Pausas. 2004. Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. *Plant Ecology* 174:257–70.
- Bonet A., J. Peña, J. Bellot, M. Cremades, and J. R. Sánchez. 2001. Changing vegetation structure and landscape patterns in semi-arid Spain. In *Ecosystems and sustainable development 3.*, ed. Y. Villacampa Esteve, C. A. Brebbia, and J.-L. Uso, 377–86. Wit Press, Boston.
- Bossena, I. 1979. Jays and oaks: An eco-ethological study of a symbiosis. *Behaviour* 70:1–117.
- Calamassi, R., M. F. Gianni Della Rocca, M. Falusi, E. Paoletti, and S. Strati. 2001. Resistance to water stress in seedlings of eight European provenances of *Pinus halepensis* Mill. *Annals of Forest Science* 58:663–72.
- Ceballos L. 1938. *Plan general para la restauración forestal de España*. ICONA, Madrid.
- Cerdà, A. 1978. Soil erosion after land abandonment in a semiarid environment of South-eastern Spain. *Arid Soil Research and Rehabilitation* 11:163–76.
- Chirino E., A. Bonet, J. Bellot, and J. R. Sánchez. 2006. Effects of 30-year-old Aleppo pine plantations on runoff, soil erosion, and plant diversity in a semi-arid landscape in south eastern Spain. *Catena* 65:19–29.
- Coffin D. P., W. A. Laycock, and W. K. Lauenroth. 1998. Disturbance intensity and above and belowground herbivory effects on long-term (14 y) recovery of a semiarid grassland. *Plant Ecology* 139:221–33.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–44.
- Cortina, J., J. Bellot, A. Vilagrosa, R. Caturla, F. T. Maestre, E. Rubio, J. M. Martínez and A. Bonet. 2004. Restauración en semiárido. In *Avances en el Estudio de la Gestión del Monte Mediterráneo*, ed. R. Vallejo and J. A. Alloza, 345–406. Fundación CEAM, Valencia.
- Debussche, M., G. Debussche, and J. Lepart. 2001. Changes in the vegetation of *Quercus*

- pubescens* woodland after cessation of coppicing and grazing. *Journal of Vegetation Science* 12:81–92.
- Debussche, M., J. Escarré, and J. Lepart. 1982. Ornitochory and plant succession in Mediterranean orchards. *Vegetatio* 48:255–66.
- Debussche, M., J. Escarré, J. Lepart, C. Houssard, and S. Lavorel. 1996. Changes in Mediterranean plant succession: Old-fields revisited. *Journal of Vegetation Science* 7:519–26.
- Debussche, M., and P. Isenmann. 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* 69:414–26.
- Debussche M., and J. Lepart. 1992. Establishment of woody plants in Mediterranean old fields: Opportunity in space and time. *Landscape Ecology* 6:133–45.
- DeGryze S., J. Six, K. Paustian, S. J. Morris, E. A. Paul, and R. Merckx. 2004. Soil organic carbon pool changes following land-use conversions. *Global Change Biology* 10:1120–32.
- Escarré, J., C. Houssard, M. Debussche, and J. Lepart. 1983. Évolution de la végétation et du sol après abandon cultural en région méditerranéenne: Étude de successions dans les garrigues du Montpellierais (France). *Acta OEcologica*, 4:221–39.
- Escudero, A., R. C. Somolinos, J. M. Olano, and A. Rubio. 1999. Factors controlling the establishment of *Helianthemum squamatum*, an endemic gypsophile of semi-arid Spain. *Journal of Ecology* 87:290–302.
- Esteve, M. A., D. Ferrer, L. Ramírez-Díaz, J. F. Calvo, M. L. Suárez-Alonso, and M. R. Vidal-Abarca. 1990. Restauración de la vegetación en ecosistemas áridos y semiáridos: Algunas reflexiones ecológicas. *Ecología. Fuera de Serie*, 1:497–510.
- Foster, B. L. and D. Tilman. 2000. Dynamic and static views of succession: Testing the descriptive power of the chronosequence approach. *Plant Ecology* 146:1–10.
- Foster, D., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: Regional forest dynamics in central New England. *Ecosystems* 1:96–119.
- Gill, D. S., and P. L. Marks. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecological Monographs* 61:183–205.
- Grau H. R., T. M. Aide, J. K. Zimmerman, J. R. Thomlinson, E. Helmer, and X. Zou. 2003. The ecological consequences of socioeconomic and land use changes in post agriculture Puerto Rico. *BioScience* 53:1159–68.
- Gulias, J., A. Traveset, N. Riera, M. Mus. 2004. Critical stages in the recruitment process of *Rhamnus alaternus* L. *Annals of Botany* 93:723–31.
- Herrera, C. M., P. Jordano, L. López-Soria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: Bridging frugivore activity and seedling establishment. *Ecological Monographs* 64:315–44.
- Houssard, C. J., J. Escarre, and F. Romane. 1980. Development of species diversity in some Mediterranean plant communities. *Vegetatio* 43:59–72.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* 113:81–101.
- Izhaki, I., P. B. Walton, U. N. Safriel. 1991. Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *Journal of Ecology* 79:575–90.
- Jake W. F., and M. B. Coughenour. 1990. Savanna tree influence on understorey vegetation and soil nutrients in north-western Kenya. *Journal of Vegetation Science* 1:325–34.
- Lavorel, S., J. Lepart, M. Debussche, J. D. Lebreton, and J. L. Beffy. 1994. Small scale disturbances and the maintenance of species diversity in Mediterranean old fields. *Oikos* 70:455–73.



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- Le Houérou, H. N. 1993. Land degradation in Mediterranean Europe : Can agroforestry be a part of the solution? A prospective review. *Agroforestry Systems* 21:43–61.
- Lepart, J., and M. Debussche. 1992. Human impact on landscape patterning: Mediterranean examples. In *Landscape boundaries: Consequences for biotic diversity and ecological flows*, ed. A. J. Handsen and F. di Castri, 76–106. Springer, New York.
- Maestre, F. T., and J. Cortina. 2004. Are *Pinus halepensis* plantations useful as a restoration tool in semiarid Mediterranean areas? *Forest Ecology and Management* 198:303–17.
- Maestre F. T., J. Cortina, S. Bautista, and J. Bellot. 2003. Does *Pinus halepensis* facilitate the establishment of shrubs in Mediterranean semi-arid afforestations? *Forest Ecology and Management* 176:147–60.
- Malo, J. E., and F. Suárez. 1995a. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. *Oecologia* 104:246–55.
- . 1995b. Establishment of pasture species on cattle dung: The role of endozoochorous seeds. *Journal of Vegetation Science* 6:169–74.
- Mazzoleni, S., G. di Pasquale, M. Mulligan, P. di Martino, and F. Rego, eds. 2004. *Recent dynamics of Mediterranean vegetation and landscape*. John Wiley and Sons, London, U.K.
- McClanahan T. R., and R. W. Wolfe. 1993. Accelerating forest succession in a fragmented landscape: The role of birds and perches. *Conservation Biology* 7:279–88.
- McDonnell, M. J., and E. W. Stiles. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109–16.
- McIntyre, S., S. Lavorel, and R. M. Tremont. 1995. Plant life-history attributes: Their relationship to disturbance response in herbaceous vegetation. *Journal of Ecology* 83:31–44.
- Moro, M. J., F. I. Pugnaire, P. Haase, and J. Puigdefábregas. 1997. Effect of the canopy of *Retama sphaerocarpa* on its understorey in a semiarid environment. *Functional Ecology* 11:425–31.
- Noy-Meir, I. 1998. Effects of grazing on Mediterranean grasslands: The community level. In *Ecological basis of livestock grazing in Mediterranean ecosystems. Proceedings of the International Workshop held in Thessaloniki (Greece) on October 23–25, 1997*, ed. V. P. Papanastasis and D. Peter, 27–39. European Commission for Science, Research and Development. Brussels, Belgium.
- Otto, R., B. O. Krüsi, C. A. Burga, and J. M. Fernández-Palacios. 2006. Old-field succession along a precipitation gradient in the semi-arid coastal region of Tenerife. *Journal of Arid Environments* 65:156–78.
- Pausas, J. G. 2004. Changes in fire and climate in the eastern Iberian Peninsula (Mediterranean basin). *Climatic Change* 63:337–50.
- Pausas, J. G., C. Bladé, A. Valdecantos, J. P. Seva, D. Fuentes, J. A. Alloza, A. Vilagrosa, S. Bautista, J. Cortina, and R. Vallejo. 2004. Pines and oaks in the restoration of Mediterranean landscapes in Spain: New perspectives for an old practice—a review. *Plant Ecology* 171:209–20.
- Pausas J. G., A. Bonet, F. T. Maestre, and A. Climent. 2006. The role of the perch effect on the nucleation process in Mediterranean semi-arid oldfields. *Acta Oecologica* 29:346–52.
- Pausas, J. G., E. Ribeiro, and R. Vallejo. 2004. Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. *Forest Ecology and Management* 203:251–59.

- Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. In *Long-term studies in ecology: Approaches and alternative*, ed. G. E. Likens, 110–35. Springer-Verlag, New York.
- Pugnaire, F. I., M. T. Luque, C. Armas, and L. Gutiérrez. 2006. Colonization processes in semi-arid Mediterranean old-fields. *Journal of Arid Environments* 65:591–603.
- Puigdefábregas, J., and T. Mendizabal. 1998. Perspectives on desertification: Western Mediterranean. *Journal of Arid Environments* 39:209–24.
- Redjali, M. 2004. Forest cover changes in the Maghreb countries with special reference to Morocco. In *Recent dynamics of Mediterranean vegetation and landscape*, ed. S. Mazzoleni, G. di Pasquale, M. Mulligan, P. di Martino, and F. Rego, 23–32. John Wiley and Sons, London, U.K.
- Reynolds, J. F., R. A. Virginia, P. R. Kemp, A. G. De Soyza, and D. C. Tremmel. 1999. Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecological Monographs* 69:69–106.
- Rivas-Martínez, S. 1987. *Memoria del mapa de series de vegetación de España*. ICONA, Madrid.
- Ruiz de la Torre, J. 1990. *Mapa Forestal de España*. Memoria General. Ministerio de Agricultura y Pesca. ICONA, Madrid.
- Taiqui, L., 1997. La dégradation écologique au Rif marocain: Nécessités d'une nouvelle approche. *Mediterranea. Serie de estudios biológicos* 16:5–17.
- Tatoni, T., and P. Roche. 1994. Comparison of old-field and forest revegetation dynamics in Provence. *Journal of Vegetation Science* 5:295–302.
- Tellería, J. L., F. Suárez, and T. Santos. 1988. Bird communities of the Iberian shrub steppes. *Holarctic Ecology* 11:171–77.
- Traveset, A., J. Gullás, N. Riera, M. Mus. 2003. Transition probabilities from pollination to establishment in a rare shrub species (*Rhamnus ludovici-salvatoris*) in two habitats. *Journal of Ecology* 91:427–37.
- Valle, F., and I. Bocio. 1996. Restauración de la vegetación en el sureste de la Península Ibérica. *Cuadernos de la SECF* 3:109–22.
- Vallejo, R., J. Aronson, J. G. Pausas, and J. Cortina. 2006. Mediterranean woodlands. In *Restoration ecology: The new frontier*, ed. J. van Andel and J. Aronson, 193–207. Blackwell Science. Oxford, UK.
- Verdú, M., and P. García-Fayos. 1996. Nucleation processes in a Mediterranean bird-dispersed plant. *Functional Ecology* 10:275–80.
- . 1998. Old-field colonization by *Daphne gnidium*: Seedling distribution and spatial dependence at different scales. *Journal of Vegetation Science* 9:713–18.
- Vilagrosa, A., J. Cortina, E. Gil-Pelegrín, and J. Bellot. 2003. Suitability of drought-preconditioning techniques in Mediterranean climate. *Restoration Ecology* 11:208–16.
- Vilagrosa, A., J. P. Seva, A. Valdecantos, J. Cortina, J. A. Alloza, I. Serrasolsas, V. Diego, M. Abril, A. Ferran, J. Bellot et al. 1997. Plantaciones para la restauración forestal en la Comunidad Valenciana. In *Avances en el Estudio de la Gestión del Monte Mediterráneo*, ed. R. Vallejo and J. A. Alloza, 435–546. Fundación CEAM, Valencia.
- Yanes, M. 1994. The importance of land management in the conservation of birds associated with the Spanish steppes. In *Nature conservation and pastoralism in Europe*, ed. E. M. Bignal, D. I. McCracken, and D. J. Curtis, 34–40. Joint Nature Conservation Committee, Peterborough, U.K.
- Yarranton, G. A., and R. G. Morrison. 1974. Spatial dynamics of a primary succession: Nucleation. *Journal of Ecology* 62:417–28.