

From microsite selection to population spatial distribution: *Pinus halepensis* colonization in mediterranean-type ecosystems

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Abstract This paper examines the effect of landscape heterogeneity on pine establishment and survival at both juvenile and mature stages. A field survey of seedlings (juvenile stage) was carried out in two sites (Shaharia and Nahal HaHamisha) close to planted forests of *Pinus halepensis* in the dry mediterranean region of Israel. Seedling establishment rate at the microsite level was determined by comparing to the proportions of actual land-cover categories—bare ground, rock, shrub, and tree, using a spectral classification of aerial photographs. The dynamics of tree colonization at one of the sites (Shaharia) during the last 30 years were examined using aerial photographs, GIS tools and generalized linear models, to assess the

effects of distance from planted forest, aspect, slope, and land cover on the density of pine trees, was conducted. Shrub cover was significantly favorable for both juvenile and mature pines at both sites, while the opposite was true for bare ground. Trees had a negative effect at one site. Rock had a positive effect on juveniles in both sites and a negative effect on mature pine distribution, reflecting its facilitative effect in the early stage and constraints for the late stage. A combined land-cover category of shrub+rock in one site, undetectable from aerial photographs, had the strongest effect of both covers on pine establishment. Proximity to the planted forest significantly increased pine density. Facilitation mechanisms provide the necessary mitigation of stresses imposed by irradiance, moisture shortage, and competition from neighboring vegetation on seedling establishment and survival. These mechanisms, combined with the spatial aspect of seed dispersal from planted

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forests, are the key to understanding the multiple-scale dynamics of pine expansion.

Keywords Facilitation · Seedling establishment · Mediterranean community · *Pinus* expansion · Remote sensing · Spatial heterogeneity

Introduction

Recruitment patterns, especially of woody species, are key to understanding biotic and abiotic interactions in mediterranean ecosystems (Matías et al. 2011), as well as other processes in community ecology (Zavala and Zea 2004; Gómez-Aparicio 2008). Shrub encroachment, which has been found to occur world-wide in many ecosystems (Archer et al. 1995; Roques et al. 2001; Wigley et al. 2009), is an example of population development based on recruitment and expansion in natural habitats (Eldridge et al. 2011). Studies of colonization and recruitment of woody plants highlight the role of two limiting factors involved in spatial patterns of recruitment: seed arrival and microsite availability (Eriksson and Ehrlén 1992; Moore and Elmendorf 2006; Dybzinski and Tilman 2012). Even though earlier studies emphasized the need for multi-scale analysis for identifying patterns of colonization, there have been only a few empirical studies of the phenomenon, mainly documenting recruitment of plants in natural habitats and its relation to spatial heterogeneity of land-cover distribution (Gómez-Aparicio 2008; Kramer et al. 2011).

Water availability is a major limiting factor for plant survival during the long, dry, and hot summer of mediterranean ecosystems, and it affects establishment success (Flores and Jurado 2003; Castro et al. 2004; Gómez-Aparicio et al. 2006). Some microsites, for instance underneath shrubs, are also known as safe sites which increase seed survival by improving soil moisture (Gómez-Aparicio et al. 2008; Flores and Jurado 2003; Otto et al. 2010) and increasing nutrient availability (Gómez-Aparicio et al. 2005b) or by protecting from predation (Janzen 1971; Barbera et al. 2006; Glazer 2013). However, the shrubs present an obstacle to the arrival of seeds, mostly of herbaceous plants, and to the development of trees of certain species (Gabay et al. 2012).

The effects of stress gradients on plant–plant interactions were investigated recently in various

ecosystems (Malkinson and Tielbörger 2010; Holmgren et al. 2011). It was hypothesized that under environmental stresses, such as water limitation, interactions between plants shift from competitive to facilitative (Bertness and Callaway 1994; Holmgren et al. 1997; He et al. 2013).

Establishment rate decreases with increasing presence of dense or tall plants (Nathan et al. 2000; Thanos 2000), reflecting the complexity of stress-response interactions—in this case, a trade-off between the effects of lower irradiance levels and improved soil moisture (Becerra and Bustamante 2011; Matías et al. 2011). In heterogeneous habitats and under fluctuating climatic conditions, shrubs provide better microsites for plant survival than trees, even of the same species (Gómez-Aparicio et al. 2005a). This effect is especially significant for a shade-intolerant genus such as *Pinus* (Gómez-Aparicio et al. 2006; Becerra and Bustamante 2011; Holmgren et al. 2011).

Establishment enhancement of seedlings was proposed as an indirect facilitative mechanism of shrubs:

(1) Shrubs reduce the biomass of annual plants and thereby lessen competition for soil moisture and nutrients. This facilitation is mostly significant for competition-sensitive species such as *Fagus sylvatica* (Kunstler et al. 2006). (2) Indirect facilitation through protection from grazing, provided by shrubs in their juvenile stage, has also been reported (Boulant et al. 2008). (3) Under harsh, hot conditions or for drought-sensitive species, light inhibition is a factor that might impair seedling survival (Rodríguez-García et al. 2011). Other environmental factors are known to affect the survival of seedlings, e.g., proximity to rocks or presence of rock fissures can improve soil-moisture and light conditions (Witty et al. 2003; Osem et al. 2011). On the other hand, dense patches of annual plants tend to have a negative effect on seedling survival and development, through competition for soil resources, e.g., moisture and nutrients (Gordon and Rice 1993; Davis et al. 1998). Despite numerous reports on the establishment and survival stages, there is still no comprehensive account of the environmental influences on the juvenile stage. Overall, drought stress is known to be a major limiting factor for survival and development of plants in dry environments, and it is mainly the first-year sprouts that are most vulnerable to dry conditions, which leads to high mortality of juvenile seedlings in mediterranean ecosystems such as pine forests (Gómez et al. 2001; Osem et al. 2013).

Pinus halepensis is frequently used in afforestation (Osem et al. 2011) and restoration all over the mediterranean basin (Maestre and Cortina 2004); it functions as a pioneering species, well known for its aggressive colonization capabilities (Higgins and Richardson 1998). In the southern hemisphere (South Africa, Argentina), where *P. halepensis* is not native, it is regarded as an aggressive invasive species (Grotkopp et al. 2002; Richardson and Rejmánek 2004). The high colonizing capability of *P. halepensis* is enhanced by its production of large quantities of seeds with notable dispersal capacity (Nathan and Muller-Landau 2000; Sheffer et al. 2014). The seedlings develop quite rapidly from the early stages to the reproductive stage (10–12 years) (Grotkopp et al. 2002; Keeley 2012).

The spatial pattern of colonizing pine populations is an outcome of the impact of various ecological factors that operate at different stages of pine recruitment: seed production and dispersal, establishment and growth (Nathan and Ne'eman 2004; Steinitz et al. 2011). Earlier studies emphasized colonization close to the seed source, exponentially declining at greater distances (Nathan et al. 2000, 2002; Sheffer et al. 2014). At the landscape scale of pine colonization, there is long-distance dispersal (LDD)—over hundreds of meters and more—which enables rapid spread of the pine population into open landscapes. This LDD has an important role in the development of a new vegetative landscape: a mixed forest of broadleaf and coniferous trees (Zavala et al. 2000; Zavala and Zea 2004; Sheffer 2012).

In Israel, intensive pine planting—mostly of *P. halepensis*—took place from the 1950s to the 1970s; it affected more than 50,000 ha, amounting to about 10 % of the non-desert part of the country (Perevolotsky and Sheffer 2009). Now, a few decades after these afforestation activities, a massive emergence of pine seedlings has been observed in natural habitats throughout the mediterranean region of Israel (Lavi et al. 2005; Osem et al. 2011; Sheffer et al. 2014), which has made it necessary to develop a better understanding of the implications of such massive colonization. This phenomenon has also been reported from various other locations around the mediterranean basin (Sheffer 2012).

Until the mid-1920s, secondary succession processes of mediterranean vegetation had been arrested by intensive human activity—deforestation, grazing, and burning, but in subsequent decades, the situation

was reversed; conservation measures and socio-economic changes led to considerable recovery of forests and woodlands (Naveh and Dan 1973; Blondel and Aronson 1999; Carmel and Kadmon 1999). The successional processes in the mediterranean region of Israel integrate pine colonization and understorey regeneration of broadleaf species within the planted forests (Nathan and Ne'eman 2004; Sheffer et al. 2013). However, it is still difficult to predict whether the combined process will lead to the creation of a mixed forest—a novel pine–oak ecosystem—or to replacement of the coniferous forest by oak-dominated woodland (Zavala et al. 2000; Zavala and Bravo de la Parra 2005; Sheffer 2012).

The use of aerial photographs or satellite images in colonization research provides both spatial and temporal perspectives; combining remote-sensing data with field surveys at various developmental stages enables multi-dimensional analysis of the phenomenon. Some studies focus only at a coarse spatial scale of vegetation dynamics, without distinguishing between developmental stages or between plant life-forms (Kadmon and Harari-Kremer 1999; Fensham and Fairfax 2002). The inherent complexity of biotic and abiotic interactions, which is common in ecological scenarios, has generated a tendency to look for simplified displays of ecological phenomena that treat environmental variables as discrete values. One of the most advantageous features of remote-sensing analysis of natural habitats is the possibility of continuously extracting spatial information, a discipline also known as “ecoinformatics” (Michener and Jones 2012).

In the present study, we took advantage of complete and continuous output of data of land-cover heterogeneity extracted from high-resolution aerial photographs of certain pine colonizing sites. We used these data to analyze growth stages, from the early stage of young seedlings following their survival and through their development to adult trees. Aerial photographs also enabled us to relate seedling development to components of natural land-cover, divided into categories of microsites. We examined, at several different scales, the spatial processes that characterize the dispersion of pine populations into open landscapes. More specifically, we focused on two questions:

- (1) How are pine establishment and seedling survival affected by small-scale ($<0.25 \text{ m}^2$) spatial heterogeneity of natural microsites?

We assumed that some microsites may facilitate pine colonization, whereas others will have a negative effect on seedling survival.

- (2) How does spatial heterogeneity affect pine population distribution in mature stages?

We assumed that the effect of spatially explicit land-cover variables would be similar to that of the microsite categories, but at a larger landscape scale that affects seed dispersal, survival, and plant growth processes.

Methods

Study sites

The research was conducted in two sites—Shaharia and Nahal HaHamisha—that represent the dry mediterranean environment (Fig. 1).

Shaharia—designated “SH” below—is located at the south-western corner of the Judean lowland (31°59′ N, 34°83′ W) at an altitude of 230 m above sea level. The climate is dry mediterranean, with average annual rainfall of 400 mm, which occurs mostly during November–February. The site is hilly, with moderate topography and a high cover of dwarf shrubs (batha or phrygana). The dominant shrub is *Sarcopoterium spinosum* (<1 m in height) with the sparse presence of the medium-sized shrub *Rhamnus lycioides* (about 2.5 m in height). The study area is located 50–800 m from a planted forest of *P. halepensis*, planted in 1956. In SH, we examined the link between pine establishment and spatial heterogeneity at two scales—microsite selection of established seedlings (small scale, <0.25 m²) and colonization of the landscape by trees above a height of 1.3 m (large scale, about 2500 m²). The boundary between the two stages (a height of 1.3 m which has been found to correlate with the age of 8 years) is based on the possibility of detecting individual pines from aerial photographs.

Nahal HaHamisha—designated “NH” below—is located in the Judean Hills (35°06′ N, 31°82′ W), west of Jerusalem, at an altitude of 500 m above sea level. The average annual precipitation is 550 mm. The study area is located on a north-facing slope of a dry stream bed. The area is characterized by heterogeneous mediterranean vegetation that ranges from dense to sparse woodland (maquis) with scattered colonizing pine trees. The dominant tree (in many cases growing as a large shrub) in NH is

Quercus calliprinos, accompanied by *Pistacia palaestina*. The study area is located >200 m from a planted forest of *P. halepensis* and *P. brutia*, planted in the 1950s. In NH, we examined the link between pine establishment and spatial heterogeneity at one scale: seedling establishment at the microsite scale of <0.25 m².

Processing and analyzing environmental variables

For both sites, we used digital aerial photographs (Orthophoto, Survey of Israel), with a resolution of (25 × 25) cm² per pixel, taken during July–August 2010. The analysis employed data processing based on the colored layers (Red, Green, and Blue). Two spectral indices were used, enabling us to distinguish between different types/categories of land cover:

$$(1) \text{ Greenness} = \frac{\text{green} - \text{red}}{\text{green} + \text{red}}.$$

This index represents the magnitude of the green color in the aerial photographs, thereby enabling us to distinguish between the categories “shrub,” “tree,” and “bare ground” (which is covered by annual vegetation in winter/spring) (Tucker and Sellers 1986).

$$(2) \text{ Brightness} = \frac{\text{red} + \text{green} + \text{blue}}{3}.$$

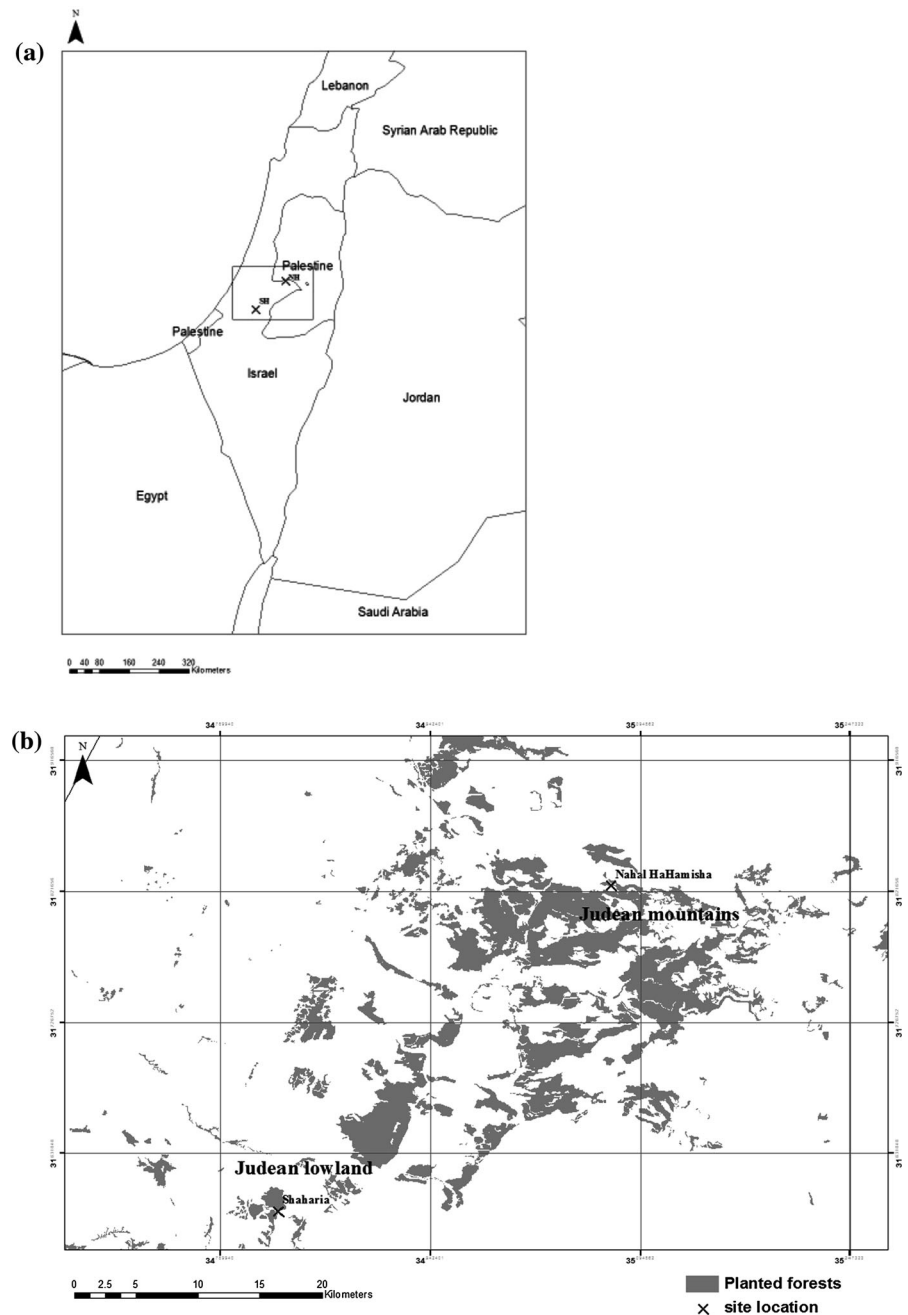
This index represents the magnitude of the white color in the aerial photographs, thereby enabling us to map the distributions of rock and bare ground (Hinkler et al. 2002).

Four different land-cover categories were defined: bare ground, rock, shrub, and tree. In NH, we added another category—shade—which included aerial photograph patches that were obscured because of the topography and incident angle of solar radiation.

We randomly selected 10–15 sample units from each land-cover category (>50 pixels), selected on the aerial photographs in SH and located in the field in NH, for creating threshold values of the spectral indices. Differences in thresholds between sites corresponded to differences in light levels, topography, and vegetation densities. Table 1 in Online resource presents the spectral thresholds for the various land-cover categories in each of the sites.

All spectral and spatial processing in this study was done with ArcGIS software, Version 10.1 (ESRI Inc., Redlands, CA, USA).

Fig. 1 **a** Map of Israel and the adjacent regions; **b** Site locations (X) in the mediterranean region of Israel. *Gray patches* represent the planted conifer forests in the area



Spatial distribution of land-cover categories

We randomly selected 10–15 sample units from each land-cover category (>50 pixels), for creating threshold values of the spectral indices.

A spot or a patch of pixels with a uniform category property was united and defined as a unit. Several

spatial corrections were applied to the processed classified maps:

- The division of land cover in the NH study area into categories was corrected according to the topography of the dry stream slopes (originally cells of 25×25 cm). In SH, the effect of topography on cell size was negligible.

Table 1 The set of best Poisson generalized linear models describing pine counts as a function of environmental variables in Shaharia

Aspect (south or flat)	Distance	Bare ground	Rock	Slope	R^2	AIC	Weight
	−0.705	−0.730	−0.286	−0.092	0.560	490.39	0.395
	−0.722	−0.692	−0.256		0.557	490.90	0.306
−0.135	−0.714	−0.713	−0.281	−0.115	0.561	491.89	0.186
0.022	−0.720	−0.696	−0.258		0.557	492.89	0.113

Standardized estimates, R^2 , AIC, and akaike weights are shown for each model

- units $<0.5 \text{ m}^2$ were classified as “null” (no data) because this size was found to be the minimal size at which objects could be identified and verified.
- units $<3 \text{ m}^2$ in the tree category were transferred to the shrub category; small trees and shrubs were included in the same category because their impact on the colonization process is similar.
- In NH, sample units defined as shade were considered “null.”
- Units that fitted more than one category were reclassified as “null.”
- “Null” units with adjacent units of a given category on all sides were reclassified as belonging to the adjacent category.
- When ground verifying at the SH site, we found that a significant fraction of the shrub land-cover category was superimposed on hard rock (mostly caliche). Therefore, following a field survey, the shrub category was split into two categories—shrubs and shrub+rock. A field survey determined that the spatial distribution of the shrub+rock category was uncorrelated with other variables, i.e., it was randomly distributed within the shrub category. Therefore, we randomly selected a number of shrub pixels corresponding to the proportion of the study area occupied by the shrub+rock fraction—5.12 % of the total area (about 10 % of shrub category) and reclassified them as shrub+rock.
- Verification of the classification was conducted differently for each of the sites:
SH: 50 points in each category were chosen randomly and examined visually in the original photograph; shrub+rock category was included in the shrub category.
NH: 10–40 points in each category were chosen and identified by observation through binoculars from a fixed point in the field and then compared with the digital classification.

The accuracy of the classification was calculated as the proportion of correct points out of the total number of points.

The spatial distribution of land-cover units was extracted from the classified map at both scales: the *microsite scale*, that corresponds to a shrub, tree, rock, or a patch of bare ground, of minimal size (0.5×0.5) m^2 , that could potentially become a suitable microsite for seedling establishment, and afterward summed for the *landscape scale*, that corresponds to spatially explicit pine distribution in cells of (0.5×0.5) m^2 .

Mapping pine trees

In SH

All pine trees above a height of 1.3 m in the study area were mapped using recent digital photographs combined with past black and white aerial photographs, taken in 1986 and 2007. The mapping was verified in the field by randomly selecting trees, both from the photographs and in the field, with a mobile GIS–GPS system. The accuracy of the mapping was determined as 92 % for the pine trees; most of the error represented omission of trees below 3 m in height.

In NH

All pine trees in the study area were mapped with the help of a visual survey. Only trees taller than approximately 1–1.5 m, i.e., the average height of pines emerging from the native vegetation and therefore easily recognized and identified, were mapped.

After mapping the pines, we divided the tree category into two sub-categories: tree, comprising native trees and big shrubs that were not pine, such as *R. lycioides* in SH, or *Q. calliprinos* or *P. palaestina* in NH, and pine trees.

Microsite selection survey

In summer 2011, we randomly selected seedlings between 2 and 8 years old. We randomized steps and direction in searching for the nearby seedlings, 78 seedlings in SH and 100 seedlings in NH. For each seedling, whorls—which indicate seedling age (Sheffer et al. 2014)—were counted. We compared the distribution of seedlings among different microsites (designated “Observed”) with the relative sizes of the land-cover categories occupied by these microsites (designated “Expected”) in both sites.

The microsite analysis was based on three assumptions:

- (1) Two-year-old and older seedlings were considered successfully established.
- (2) The microsite underneath the seedling had not changed since the germination stage.
- (3) Over time, there was an equal probability for a seed to reach any location (microsite) in the study area.

We tested the assumption that the distribution of established seedlings was random (H_0) against the alternative assumption of microsite preference (H_1) by applying the Chi-square (χ^2) test.

Analysis of pine tree colonization in SH

The relationships between tree density and environmental variables were examined by applying poisson generalized linear models (GLM), since the outcome variable represents counts. The sample size was 300 cells of $(50 \times 50) \text{ m}^2$ covering the study area (Fig. 2). Grid data may contain spatial dependence due to spatial autocorrelation and may violate the assumption that the observations are independent. Therefore, we tested the possibility for spatial autocorrelation in pine density by Moran’s I test. Since neither positive nor negative autocorrelation was found (Moran’s $I = 0.42$), the GLM analysis was valid at the current scale.

The effects of euclidean distance from the planted forest, aspect, slope, and cover of bare ground and rock on the pine tree counts per cell were determined. Shrub cover was not used as an independent variable since it was strongly (negatively) correlated with bare ground cover (Pearson’s correlation coefficient = -0.90 , $p < 0.001$). Cover of large shrubs and trees (mostly

R. lycioides) was negligible; therefore, this variable was also excluded from the model.

The Euclidean distance of the center of each cell from the edge of the planted forest was mapped manually using the digital aerial photographs. For the land-cover variables, we used processed data from the classified digital photographs. The area of each layer within each cell was summed as an independent variable. About 10 % of the shrub category was estimated as shrub+rock, and therefore, in a simplified assumption of random distribution, we transferred 10 % of shrub category in each cell to Rock category. The land-cover-type values could range from no cover to full cover, i.e., 0–100 %. The topographic variables—slope and aspect—were determined from a geographic contour layer at a resolution of 5 m. The contour layer was converted to a DEM layer, at a resolution of 1 m per pixel. The slope was calculated as the average angle of the cell. The aspect was a dummy variable representing two categories: cells with more than 50 % pixels with a north-facing aspect and >5 % slope were considered “North-facing”; the rest were considered “south-facing or flat.”

The 32 GLMs with all possible combinations of the five independent variables were confronted with the data in a *model selection* procedure (Johnson and Omland 2004). The models were ranked according to the akaike information criterion (AIC), which was calculated as

$$\text{AIC} = 2k - 2\ln(L),$$

where L is the maximized value of the likelihood function for the model and k is the number of estimated parameters in the model.

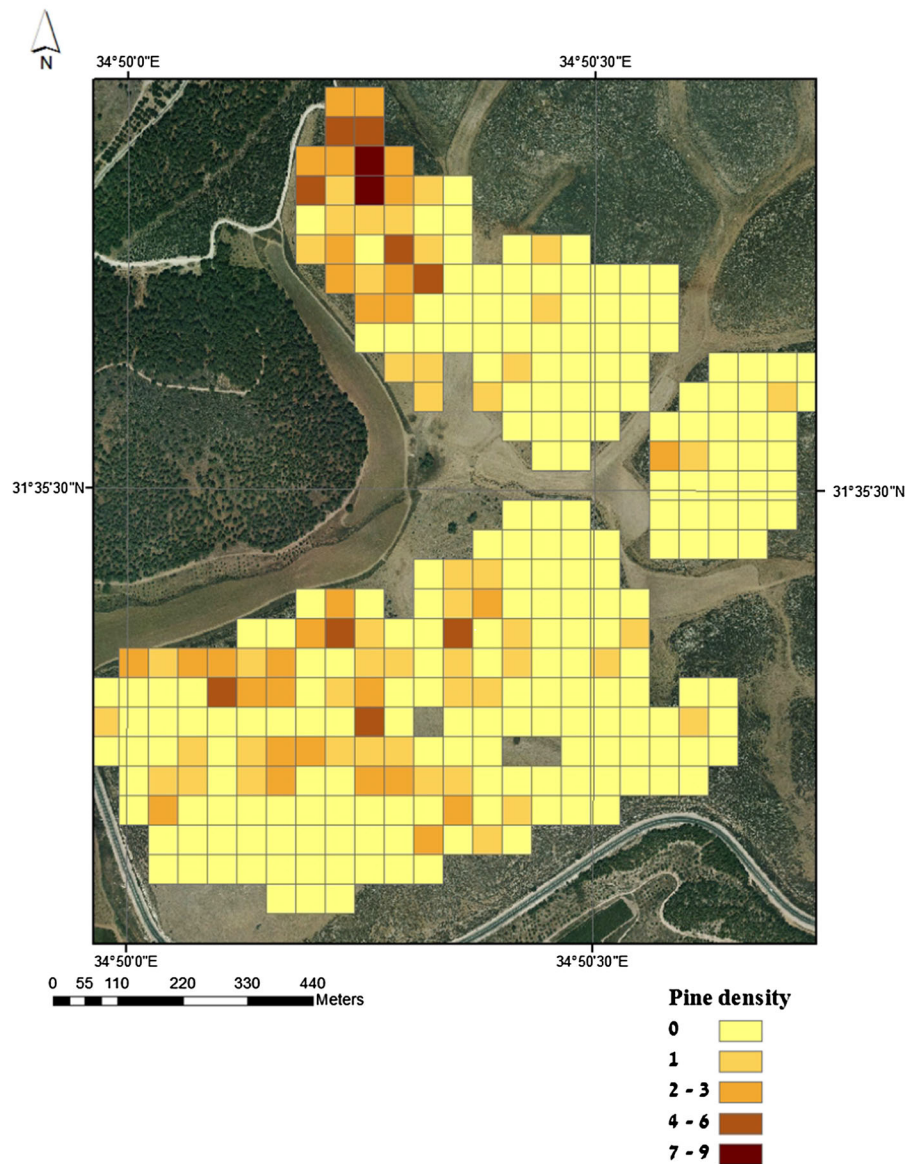
Akaike weights, derived from the AIC, represent the relative likelihood of the models given the data. Size and direction of effect for each independent variable were expressed by the respective standardized parameter estimates from the best model(s). Model selection was done in R (R Core Team, 2015) using the MuMIn package (Barton 2014).

Results

Land-cover classification and microsite preference

The accuracy of the land-cover classification was 94 % in SH and 85 % in NH. Detailed maps of land-

Fig. 2 Pine density in the Poisson generalized linear models grid, each cell of $(50 \times 50) \text{ m}^2$, superimposed on an aerial photograph of Shaharia (“SH”). Darker shades of brown represent increasing tree density, from no trees (pine density = 0) to nine trees per plot (maximal value)



cover classification for both sites are presented in online resource (Figs. 1, 2, 3). The shrub+rock category was extracted randomly in a non-spatial method from shrub category in SH (as described earlier) and therefore is missing from the land-cover map. Figure 3 presents the spatial division of the land-cover categories, including the separation between shrub and shrub+rock in SH. It can be seen that the dominant category in both sites was shrub, but in NH, a larger area was covered with trees and pines, and bare ground covered 15 % less of the total land-cover area than in SH.

Microhabitat preference for pine establishment is presented in Fig. 4a for SH and in Fig. 4b for NH. In both sites, there is a statistically significant higher proportion of pine establishment within patches of shrub and rock (Chi-square (χ^2): $n = 78$, $df = 6$, $p < 0.001$ in SH; $n = 79$, $df = 4$, $p < 0.05$ in NH). It appears that in SH, there was a preference for pine establishment in shrub and rock, and an even stronger preference for the combined category, shrub+rock. Pine establishment under tree in NH was low even though trees accounted for a large proportion of the land cover. Pine establishment on bare ground

Fig. 3 Spatial distribution of land-cover categories expressed as percentages of total area. **a** Shaharia site (“SH”) as *black* columns, including division of Shrub into shrub and shrub+rock; **b** Nahal HaHamisha site (“NH”) as *empty* columns

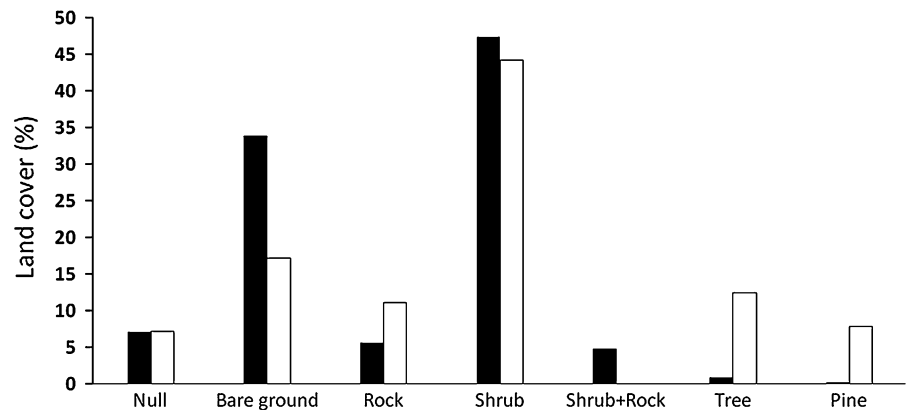
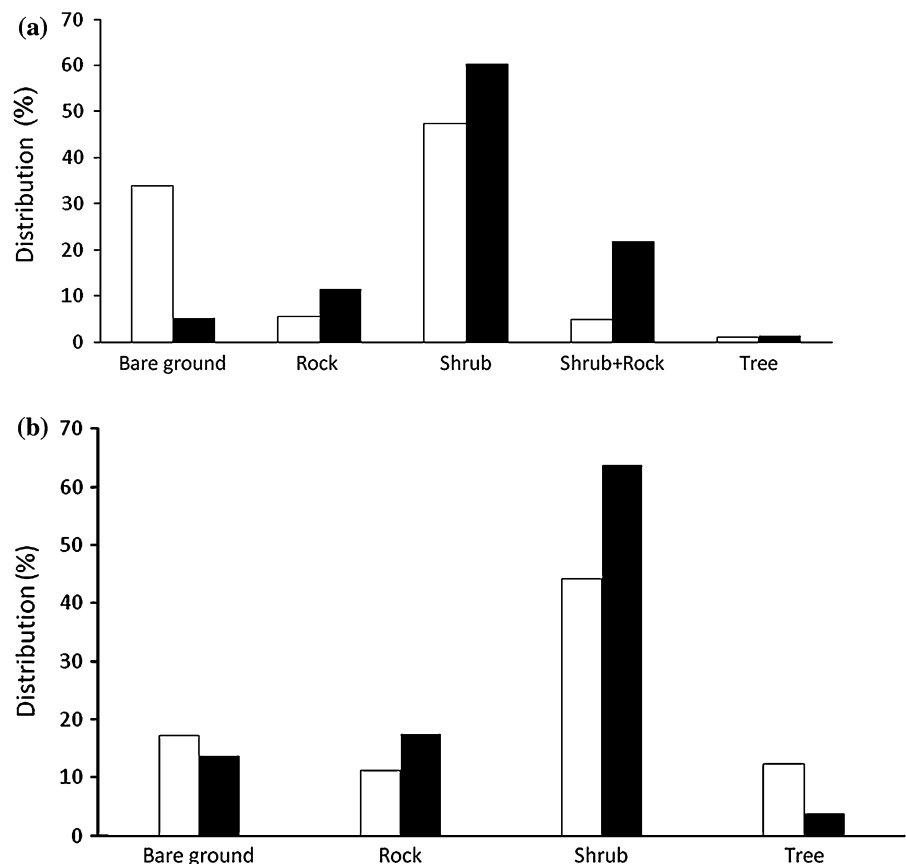


Fig. 4 Microsite selection by pine seedlings. Comparison between total areas of respective land-cover categories, expressed as percentages of total area and represented by empty columns, and establishment percentage in the microsite of each respective category as represented by *black* columns. **a** Shaharia site (“SH”). **b** Nahal HaHamisha site (“NH”). The effect of microsite was statistically significant in both sites (SH: $n = 78$, 6 *df*, $p < 0.001$; NH: $n = 79$, 4 *df*, $p < 0.05$) with a preference for shrub



microsites was much lower than their proportional land-cover area in both of the sites.

Analysis of pine tree colonization in Shaharia

A set of four “best” generalized linear models (out of 32 examined models) describing pine tree colonization

had cumulative support approaching 100 % (Table 1). The model set revealed strong negative effects of distance from forest border and bare ground cover on established pine counts. Rock cover had a weaker negative effect, while topographic variables (slope and aspect) were relatively unimportant based on their presence in only two out of four models (each) and their

small effect sizes. Overall, 56 % of variation was explained by any one of the four models. The effects of distance from forest border, bare ground, and rock were negative, meaning that higher establishment took place closer to the forest border, in locations with lower bare ground cover and lower rock cover.

Discussion

Colonizing populations provide an opportunity to analyze dispersal patterns, seedling survival, and plant growth rates associated with landscape heterogeneity. In the present case, we focused on two scales—the *microsite scale* for investigating pine establishment (recruitment patch) and *landscape scale* for the development of young and mature trees—in order to understand population dynamics and development in newly colonized fields.

Pinus halepensis seedling survival—a microsite-scale perspective

The establishment of *P. halepensis* seedlings at both sites was significantly related to specific microsite categories, namely shrub and rock (and also shrub+rock in SH). In both sites, bare ground microsites were unfavorable for pine germination and early establishment, most probably due to stress factors such as competition with annual plants, grazing, or harsh conditions in the dry season. These observations are consistent with earlier studies (Gómez-Aparicio et al. 2008). In our present study, dwarf shrubs, mainly *S. spinosum*, functioned as nurse plants or safe sites for *P. halepensis* seedlings, probably by mitigating the rapid soil desiccation and seed/seedling predation (Barbera et al. 2006; Glazer 2013). The enhancement of *P. halepensis* seedling survival by shrubs in the drier conditions of SH compared to those of NH is consistent with earlier findings of increased plant–plant facilitation under increasing stress (He et al. 2013). Thus, *S. spinosum* shrubs can be regarded as nuclei of colonization, as suggested by Yarranton and Morrison (1974).

On bare ground covered with herbaceous vegetation, *P. halepensis* seedlings were exposed to high irradiation, competition with herbaceous vegetation for soil moisture (Gordon and Rice 1993; Davis et al. 1998; Kunstler et al. 2006), and post-dispersal seed

predation (Glazer 2013). The advantage of shrub+rock over bare ground was slightly stronger in SH than in NH, probably because of the lower precipitation level in SH, which may lead to severe water limitation. The consistent findings in different sites highlight the significant effect of water limitation on plant–plant interactions in dry environments such as the eastern mediterranean (Flores and Jurado 2003; Gómez-Aparicio et al. 2005a).

Cover of rock or shrub+rock in SH also facilitated the early stage of seedling development in rock fissures most likely because of the better soil-moisture conditions in the fissures. However, a landscape-scale analysis indicated that rocks eventually tended to become limiting microsites for root development in the later growing stages. In SH, shrub+rock appeared to be the microsite category with the strongest facilitation. Since the shrub+rock is an undetectable spatial category, we conducted a field survey based on the assumption of random distribution of rocks under shrubs. Alternative spatial distribution (e.g., cluster, uniform) of rocks under shrubs may yield different results. This category is actually a combination of two favored categories, each of which contributes to improving seedling survival by enhancing above- and below-ground soil-moisture conditions, reducing competition and providing safety from predators. Thus, seedlings that happen to germinate in rock fissures have a lower probability of completing full development to mature trees, because of the physical limitation on root-system development; on the other hand, those growing next to a rock may enjoy a favored microsite due to water accumulation in cracks (Jones and Graham 1993) and improved light conditions (Witty et al. 2003; Osem et al. 2011), such that growth under a shrub and next to a rock benefits from a double-facilitative effect.

Establishment levels under trees differed between the sites, mostly because of the varied spatial distribution of this land-cover category. In SH, trees occupy a much smaller area than in NH, most likely because of lower precipitation in SH, which limits tree development (Sternberg and Shoshany 2001a). Therefore, the sparse patches of trees in SH have a minor impact on the establishment of pine seedlings. However, establishment under trees in NH is relatively low, even though trees are abundant there. Shade levels created by mature *Quercus calliprinos* or *Pistacia* spp., the dominant species in the site, are most probably too

oppressive for pine seedlings, which are considered shade-intolerant (Zavala et al. 2000). Mature trees can also compete with the young seedlings for water (Zavala and Zea 2004). This finding of intolerance to high shade levels is consistent with other findings from trade-off analyses of plant interactions and dynamics (Holmgren et al. 2011).

The Shrub land-cover category, which occupies more than 50 and 40 % of the open landscape in SH and NH, respectively, is the only land-cover category that facilitates pine seedling colonization and development. Therefore, it can be considered a successional agent in the development of pine populations (Gómez-Aparicio et al. 2008; Flores and Jurado 2003).

Pinus halepensis population growth—intermediate landscape scale

The use of intermediate landscape scales (hundreds of meters) for spatial analysis of the development of colonizing *P. halepensis* populations provides a complementary insight into pine colonization and seedling establishment. Whereas the microsite survey focused on the survival of juvenile seedlings in each land-cover category, Generalized Linear Models revealed the spatial patterns of land-cover and seed source effects on population structure.

In both studied forests, a significant number of mature pines were found at distances of hundreds of meters from the forest border; this represents an intermediate-distance dispersal (Waitz 2013). We suggest that this scale, which also comprises spatial information on land-cover heterogeneity and topography, indicates an important regional-scale effect on the vegetative formation dynamics and implies the creation of a new vegetative formation through pine colonization: an association between broadleaf shrubland and pine forest (Sheffer 2012). A GIS simulation indicated that over a few decades the relative abundance of pines is expected to increase and create an open forest in the drier site and full canopy cover in 50–60 years in wetter habitats (Waitz 2013).

The significant effect of the land-cover categories, bare ground and rock, on pine colonization is indicative of the harsh climatic conditions under which this process occurs—high irradiation exposure, declining availability of soil moisture during the prolonged dry summer and autumn, and limited underground space for root systems. Although topographic aspect had a

relatively minor independent effect on pine establishment, it is well known that shrub cover (and accordingly also bare ground cover) is affected by topographic aspect in mediterranean ecosystems. A northern aspect is known to provide a favorable habitat (Sternberg and Shoshany 2001b; Bellot et al. 2004; Soliveres et al. 2010) because of reduced irradiation and improved moisture conditions. On the southern aspects, however, high irradiation leads to lower cover of woody vegetation and, consequently, supports for higher cover of herbaceous plants that compete with young pine seedlings for soil moisture. These interactions highlight the creation of a landscape pattern in the intermediate range of several hundred meters away from the planted forest border. Within this range, dense populations of colonizing *P. halepensis* seedlings are common on north-facing slopes; they are associated with shrubs, which facilitate the pine colonizing process.

Introduction of pines into the native landscape has become an integral part of the current successional process of woody vegetation in the mediterranean region, following the late development of broadleaf species (Bonet and Pausas 2004). The spatial pattern of colonization by pines—establishment in microsites, which serve as recruitment/germination patches, under shrubs and next to rocks—accompanied by other, broadleaf species such as *Q. calliprinos*, *Pistacia palaestina*, or *Rhamnus lycioides* has led to the creation of a new mosaic landscape: mixed forest in the mesic region (Nahal HaHamisha—NH) and open park forest in the dry region (Shaharia—SH).

All in all, we see how the heterogeneous mediterranean landscape affects the successional pathway by differentially facilitating colonization by pine trees dispersed from forest patches (planted or natural). Some land-cover units enhance colonization, whereas others impede it; some microsites facilitate the process whereas others obstruct it. The overall outcome is the establishment of patches of colonizing pines within an already heterogeneous landscape, thus restoring the original mixed pine/oak climax that has been modified by humans over millennia of anthropogenic disturbances (Baruch 1990; Perevolotsky and Seligman 1998).

Conclusions

Colonization of open landscapes by *P. halepensis* is determined mostly by the distribution of distinct

habitats within this landscape. We propose a spatial differentiation of dry mediterranean habitats into different microsites that differ in the support they provide for colonizing pines (limit or enhance juvenile stages, i.e., seed survival and post-emergence survival of seedlings). The landscape level may also be considered a mosaic of land-cover units that determine the presence of the late growth stage of pine trees. Safe sites such as shrubs have a positive effect on seedling survival and growth and constitute the major facilitating land-cover for pine colonization, while other land-cover types function as restraining factors by limiting establishment or survival of the early stage or limiting growth of the late stage. Thus, a multi-scale observation reveals some of the complexity of pine colonization in the heterogeneous environment of mediterranean landscapes. Colonization by pine trees dispersed from forest patches is strongly related to both spatial heterogeneity of the land-cover structure and to dispersal patterns. Further pine colonization may be enhanced due to encroaching shrubs, which act as a major facilitating agent for colonization. These spatial processes also imply the existence of successional processes at the landscape level that may restore the extinct climax vegetation of the mediterranean landscape.

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