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Colonization of *Pinus halepensis* in Mediterranean habitats: consequences of afforestation, grazing and fire

Y. Osem · A. Lavi · A. Rosenfeld

Abstract The expansion of *P. halepensis* from plantations into natural sites of high conservation value is becoming a frequent occurrence across the Mediterranean zone of Israel. We studied how colonization of *Pinus halepensis* in natural Mediterranean habitats is related to afforestation, cattle grazing and fire. The study was conducted in a Mediterranean garrigue (Shrubland) located in Ramat Hanadiv Nature Park, southern Mt. Carmel region, Israel. The study area (ca. 350 ha) was divided into cells (100 × 100 m) each of which was categorized with respect to distance from planted pines, grazing (grazed since 1990/ungrazed), fire (burned in 1980/ unburned), and vegetation structure (garrigue, dense garrigue, dense woodland). The location of colonizing pines, typically three m or more in height, was determined using an aerial photograph. Density of colonizing pines decreased linearly with the distance from planted pines within 300 m from planted pines

with a long tail that extended out to ca 1,000 m. Over 90% of the colonizing pines that were found were located within a distance of 300 m (56% of the park area) from planted pines. Colonization was about two times greater under grazing than without grazing. The effects of fire and of the interaction fire × grazing were found insignificant. A separate analysis reveled that colonization was about 2 times larger in patches of sparse woody cover than in those of dense cover. In conclusion, pine colonization was mainly determined by the proximity to seed sources. Additionally, pine colonization was enhanced by cattle grazing probably through reduction of the natural vegetation cover.

Keywords Aleppo pine · Disturbance · Expansion · Garrigue · Invasion · Recruitment

Introduction

Pinus halepensis is the most widespread pine species in the Mediterranean basin. It occurs naturally in southern Europe, North Africa and also in the east Mediterranean (Barbero et al. 1998; Quezel 2000). Native populations of *P. halepensis* in Israel are quite restricted and can be found mainly in the Carmel region or in several other mountainous locations characterized by bright Rendzina soils that developed on soft chalk and marl (Rabinowitch 1985; Schiller 1985). Nevertheless, this species was the most extensively used for afforestation in Israel during the

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twentieth century, and it constitutes as much as 30% of the planted forests that cover about 100,000 ha within the Mediterranean zone of Israel. These forests were planted in a variety of habitat types, some of which are clearly beyond the natural distribution of *P. halepensis,* as recognized today (Liphschitz and Biger 2001). Furthermore, the seed sources that were used for these plantations were mostly exotic, and genetically different from the local, east Mediterranean ecotype (Schiller and Grunwald 1987).

The expansion of *P. halepensis* from plantations into adjacent natural sites some of which are of high conservation importance, is becoming a frequent occurrence in several areas across the Mediterranean zone of Israel (Lavi et al. 2005) and an important environmental issue and source of debate among foresters and nature conservationists. It is quite clear that the pine expansion is related to the extensive use of *P. halepensis* for afforestation, but our understanding of the factors that determine the intensity and dynamics of this process is inadequate. Such knowledge and understanding is important both from the practical viewpoint of predictability, assessment of ecological consequences and management, and regarding more theoretical issues related to succession processes in plant communities.

Pine expansion is presently recognized as a global phenomenon (Richardson and Rejmanek 2004). *Pinus halepensis* and several other pine species are counted among the most invasive species, particularly in the southern hemisphere (Richardson et al. 1994; Rejmanek and Richardson 1996; Richardson and Higgins 1998). Alterations in ecosystem structure and function related to pine colonization were reported by several studies, including: decline in species diversity (Higgins et al. 1999; Richardson and Higgins 1998; Scholes and Nowicki 1998); fuel accumulation and increased fire hazard (Richardson and Higgins 1998); deterioration of water resources (le Maitre et al. 1996; van Wilgen et al. 1996); and changes in soil characteristics (Scholes and Nowicki 1998; Richardson and Higgins 1998; Griffiths et al. 2005). These consequences are particularly important in Mediterranean ecosystems due to their high conservation value.

Colonization by exotic pines has occurred in a number of areas around the world as a consequence of introduction for commercial purposes. For example *P. radiate* in Australia (Baker et al. 2006), *P. nigra* in New Zealand (Buckley et al. 2005), and *P. halepensis* in South Africa (Rouget et al. 2001) and Argentina (Zalba et al. 2008). In such cases pine expansion is generally viewed as a negative process caused by human activities (i.e., invasion). However, the question of whether colonization events that occur within the natural range of a species should be seen as part of the natural dynamics of the ecosystem or as human caused process is more complex. *Pinus halepensis*, for example, has been a native component of Israel's flora for hundreds of thousands of years (Horowitz 1992), long before human impact on the environment became widespread (5,000–6,000 years ago). Changes in the distribution of *P. halepensis*, like other elements of the local flora, have also occurred in past times with relation to climatic variation and anthropogenic activity (Neumann et al. 2009). Studies on the expansion of pine populations from their natural range into adjacent unpopulated sites have yielded various explanations, ranging from global climate change (Kharuk et al. 2005), through local climate variation (League and Veblen 2006; Gray et al. 2006; Dovciak et al. 2005), to more clearly human-related factors such as livestock grazing (Norman and Taylor 2005), abandonment of agricultural land (Prevosto et al. 2003, Neumann et al. 2009), and fire (Pellerin and Lavoie 2003).

The present study aimed at understanding human-related factors that influence colonization by *P. halepensis* in Israel. We focused on afforestation, cattle grazing, fire and the resulting changes in vegetation structure, as possible determinants of pine expansion. The distribution of *P. halepensis* has expanded remarkably during the last 60 years as a result of the extensive afforestation efforts that were carried out in Israel. Now, as many of the pine plantations have been reproductive for the last 20–45 years, it is probable that new populations of colonizing pines are strongly associated with these seed sources (Lavi et al. 2005). Spatial patterns of colonization should be expected to represent seed dispersal patterns (Lavi et al. 2005). However, with regard to the wind dispersed *P. halepensis*, these patterns have been shown to be nonlinear (Nathan et al. 2000; Nathan and Ne'eman 2004; Lavi et al. 2005, Williams and Wardle 2005) and may vary strongly in time and space depending on weather regimes and stochastic climatic events (Nathan et al. 2000, 2001). Furthermore, the extent to which colonization is actually determined by seed availability may also be highly variable in time and space (Richardson et al. 1994; Prevosto et al. 2003).

Livestock grazing and fire which are widely recognized as being among the most important human related disturbances, particularly in the Mediterranean basin, may also have multifaceted effects on pine colonization. It is commonly argued, for example, that fire prevention is the main cause for the expansion of pine and also several other woody species in North America (Turner and Krannitz 2001; Brockway et al. 2002; McKay 2000; Norman and Taylor 2005; Coop and Givnish 2007). In contrast, studies in other regions, involving different pine species, have demonstrated that fire may encourage pine regeneration (Ne'eman et al. 2004; Williams and Wardle 2005) and expansion (Turner and Krannitz 2001; Rouget et al. 2001; Pellerin and Lavoie 2003). With regard to *P. halepensis*, fire can result in massive seed release from serotonous cones (Daskalakou and Thanos 1996; Ne'eman et al. 2004), and encourage germination, establishment and growth, through suppression of competition (Daskalakou and Thanos 1996; Ne'eman et al. 2004), and improved nutrient availability (Henig-Server et al. 1996, 2000; Pausas et al. 2003). In contrast, fire may hinder pine colonization by removing facilitating vegetation (Gasque and Garcia-Fayos 2004), impairing seed bed conditions (Kemball et al. 2006) encouraging seed predation (Reed et al. 2005), and burning established pines before they have reached maturity.

The relationships between grazing and pine regeneration and expansion have also been shown to be complex and may exhibit contrasting trends (Darabant et al. 2007; Boulant et al. 2008) depending on grazing regime, herbivore kind, abiotic conditions, and the pine species (Norman and Taylor 2005; Debain et al. 2005; Boulant et al. 2008). Grazing which operates directly on the vegetation structure may influence colonization through various paths including competition and facilitation by the resident vegetation as well as regeneration growth and survival of colonizers.

We studied how the colonization of *P. halepensis* in a Mediterranean garigue is related to the following:

– Distance from pine plantations;
– A wild fire that occurred 28 years ago (1980);
– Cattle grazing during 18 years (since 1990);
– Vegetation structure.

Precise mapping of planted pine groves, the 1980 fire boundaries and 18 years of controlled cattle grazing within the Ramat-Hanadiv Nature Park (southern Mount Carmel region, Israel) provide a unique opportunity to study long-term effects of afforestation, fire and grazing including their interactions on pine expansion in Mediterranean habitats.

Methods

Study site

The study was conducted in the Ramat Hanadiv Nature Park in the southern Mt. Carmel region of Israel. Elevation is 140 m a.s.l. with moderate topography, i.e., slopes ranging from 0 to 10%. The soil is shallow Terra rossa that developed on hard limestone (Cenomanian-Turonian). The climate is Mediterranean: cool rainy winters and hot dry summers, and average annual rainfall of 570 mm that occurs between October and April. The vegetation is categorized as a Mediterranean garrigue, a discontinuous shrubland composed of a mix of short, medium and tall shrubs, dominated by the shrubs *Phillyrea media*, *Pistacia lentiscus*, *Calycotome villosa* and the dwarf shrub *Sarcopoterium spinosum*. The spaces between the shrubs are occupied by rich herbaceous vegetation comprising annual species, hemicryptophytes and geophytes (Hadar et al. 1999). The area has a long history of human impact, including grazing and clearing activities. In 1950 the park area was fenced and grazing was excluded for the following 40 years. Grazing by cattle was reintroduced in 1990, and serves as a means of reducing fire hazard: the herd is brought into the park area as soon the herbaceous dry biomass reaches about 500–600 kg ha^{-1}, approximately 60 days after the first effective rainfall event (late January to mid-February). Grazing intensity ranges from 52 to 130 grazing days ha^{-1} year^{-1} (Gutman et al. 2001). During the last 18 years, i.e., since 1990, some of the park area has been kept ungrazed, to serve as a control (Fig. 1). In May 1980 a wild fire occurred in the park area, and burned as much as 120 ha: one-third of the park's native vegetation area (Dufor-Dror 2001, Fig. 2).

Planted pines

*Pinus halepensis* groves were planted in the Ramat Hanadiv Park, mostly during the 1950s and 1960s

Fig. 1 Distribution of cattle grazing in Ramat-Hanadiv park since 1990. *Pale green square* Grazed area (since 1990), *violet square* ungrazed area (control), *dark red square* ungrazed area that is not included in the analysis. The white patches represent plantation areas of other tree species (not *P. halepensis*) which were excluded from the analysis. The park area was divided into cells of a 100 m × 100 m grid for the analysis of colonizing pine density
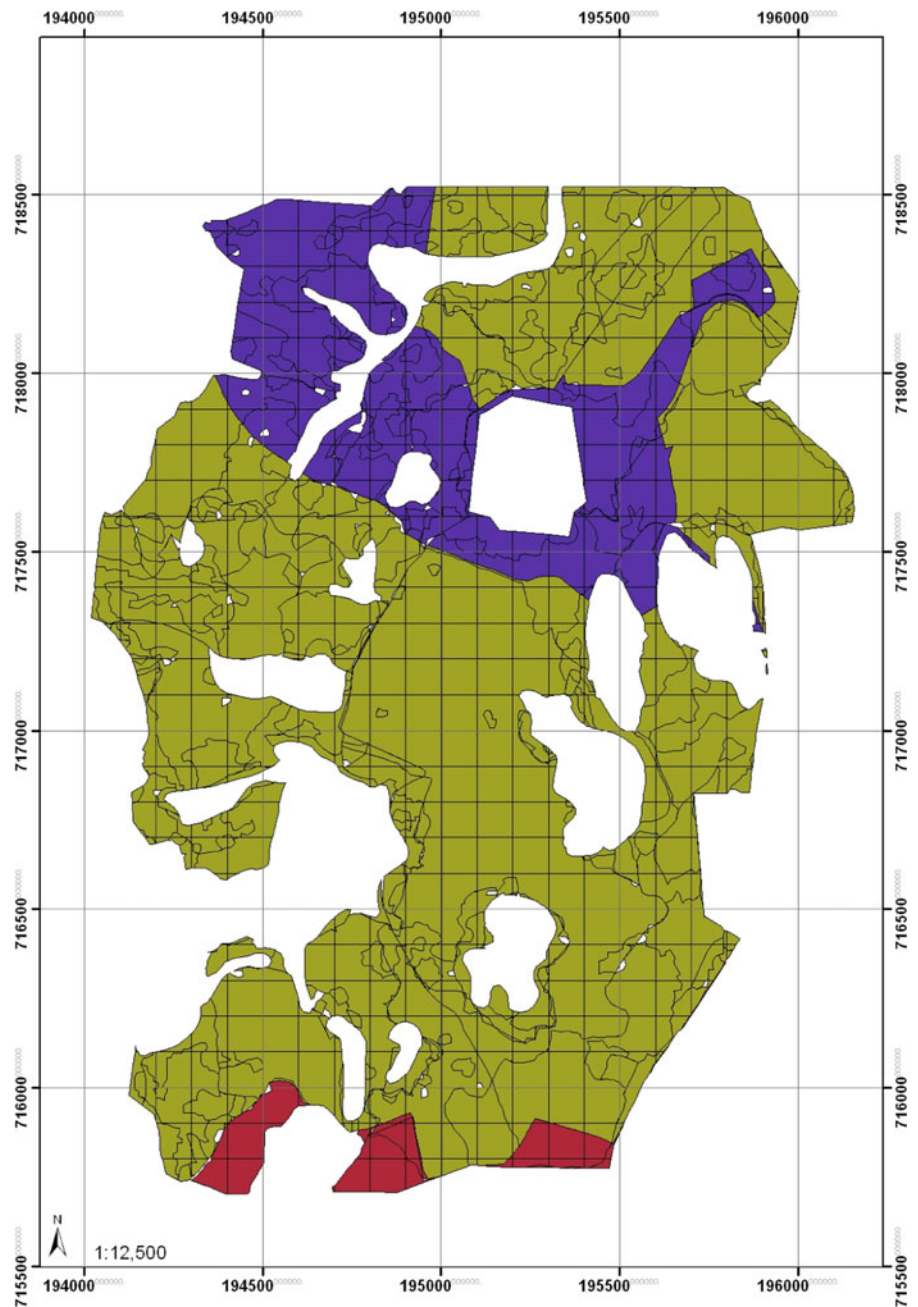
(Schiller 2001). A comprehensive ground survey was conducted in order to identify and map all the planted *P. halepensis* trees within the park area. Identification of planted pines was done by the following steps:

1. Mapped planted groves: Pines that were found within the boundaries of planted groves according to the Park's maps (not including regenerating

pines within the groves) were all classified as planted and their position was marked by GPS.

2. Unmapped planted groves: Pines within several unmapped small planted groves were also classified as planted according to information provided by the park managers and several other criteria i.e. position of grove (along a trail), spatial distribution of trees (clear straight

Fig. 2 Distribution of areas burned in Ramat-Hanadiv Park during the 1980 fire. *Light brown square* Burned area (1980), *light green square* unburned area
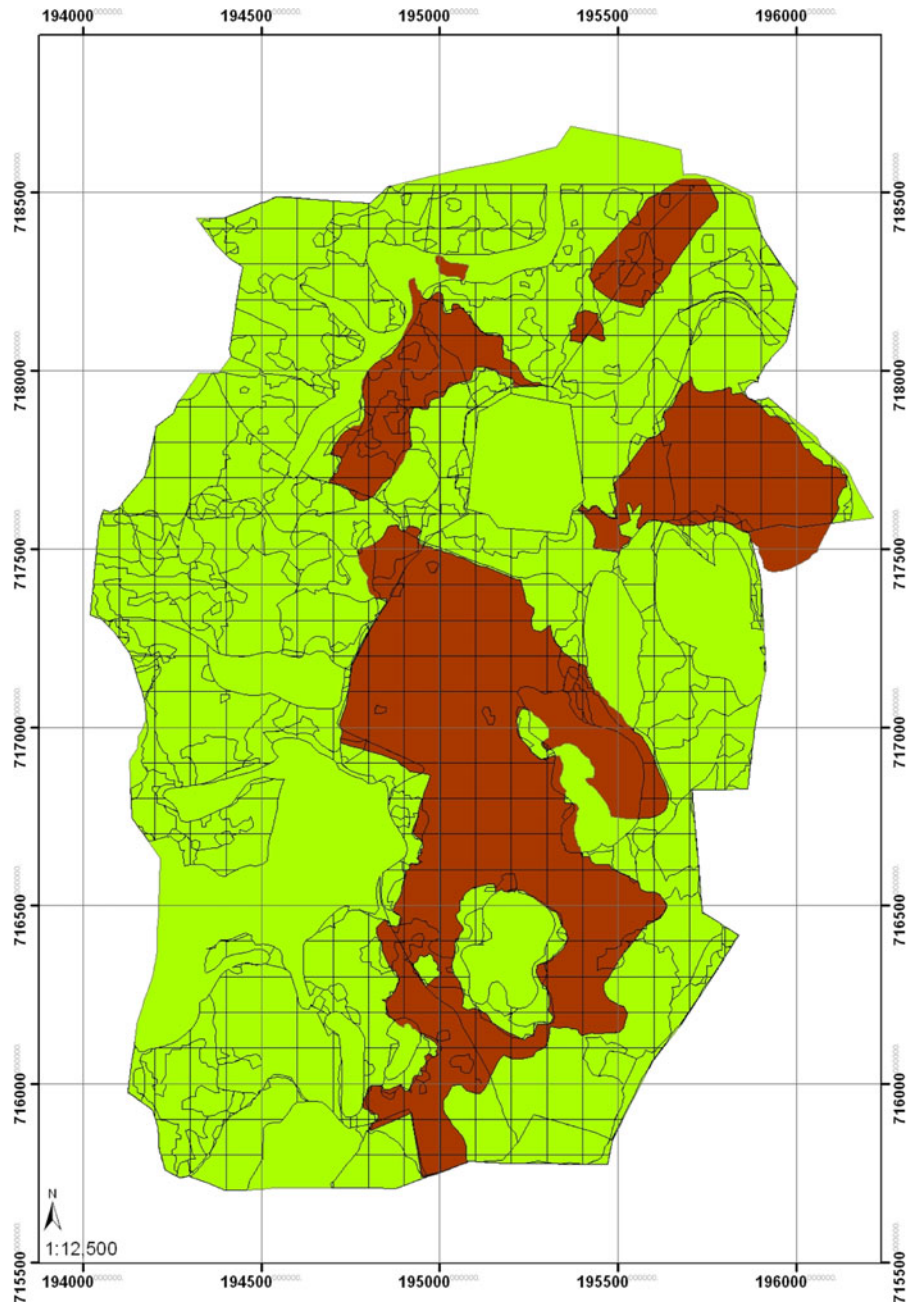
lines, uniform spaces) and age distribution (even aged).

3. Unidentified trees: Several other single pines that were suspected as being planted due to their location near other planted nonnative tree species, were ether classified as unidentified and taken out of the analysis or classified as planted if their age was 35 year. or more (clearly above the

maximum age found within colonizing pines that were surveyed).

The planted groves in Ramat hanadiv are mainly concentrated in the north-eastern part of the park (981 trees), but two small groves are located outside the park, one (34 trees) near the northern park boundary and the other (42 trees) near its southern boundary
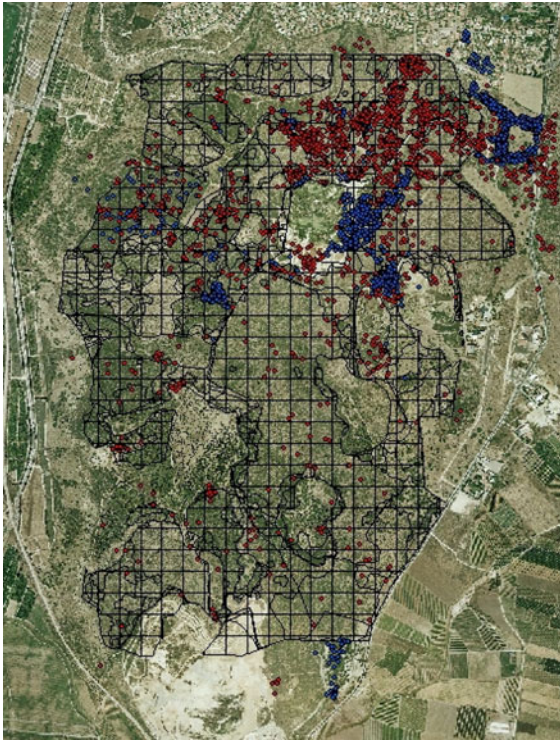
Fig. 3 The distribution of *P. halepensis* trees in Ramat-Hanadiv Park 2007. *Blue diamond* Planted pines, *red diamond* colonizing pines. The park area was divided into cells of a 100 m × 100 m grid. Cells (100 m × 100 m) that were not homogeneous with respect to grazing, fire, or vegetation form were further divided

(Fig. 3). Another group of pines (123 trees) was planted in 1978 and is located near the center of the park area. Several additional scattered planted pines were found, aged between 35 and 60 year. All the planted trees were mapped using a GPS devise and GIS (Fig. 3).

Position of colonizing pines

The position of colonizing pines was determined using an aerial photograph with (25 × 25)-cm resolution, taken in July 2007 with an RMK-TOP system. The photograph was analyzed and pines that colonized the park area were located by visual scanning, and a ground survey was conducted to verify that analysis. Various areas in the park representing various vegetation structures were examined in the ground survey. Pines located by the aerial photograph were typically 3 m or more in height (110 out of 111

individuals). Another 40 pines, all shorter than three m, that were found by the ground survey could not be found by means of the aerial photograph. Thus, the results of this study refer to colonizing pines which exceeded 3 m in height; these colonizers were mapped (Fig. 3). The average age of 50 randomly selected colonizing pines of around 3 m height (±0.5 m) was found to be 14.68 ± 0.84 year. Therefore, the aerial photograph provides information on the distribution of pines that have colonized within the park area prior to ca. 1994. The total number of colonizing pines (including pines shorter than 3 m) may be appreciably larger.

Analysis of wind direction

Seed dispersal by *P. halepensis* is usually associated with events of high temperature and low relative air humidity (hereafter "sharav"), i.e., temperature >30°C; relative humidity <25% (Nathan et al. 1999), therefore we analyzed the distribution of wind directions in the park area during such events, over a 6-year period (2003–2008). This was done by collecting records of the wind direction at maximal speed on an hourly basis. The data set included more than 50,000 hourly records.

Experimental design

We studied the variation in the density of colonizing pines with respect to distance from planted trees, grazing since 1990 (grazed vs. ungrazed), the 1980 fire event (burned vs. unburned), and vegetation structure. For vegetation structure we used a qualitative vegetation survey conducted by Lahav (1997, Fig. 4), and concentrated on the three most abundant vegetation forms, i.e., Garrigue (moderate woody cover, ca. 70%, typically dominated by the shrubs: *Phillyrea media* ca. 25% of total woody cover, *Pistacia lentiscus* ca. 35%, *Calycotome villosa* ca. 15% and the dwarf shrub *Sarcopoterium spinosum* ca. 15%), dense garrigue (woody cover ca. 95%, *Phillyrea media* ca. 6% of total woody cover, *Pistacia lentiscus* ca. 40%, *Calycotome villosa* ca. 20%, *Rhamnus lycioides* ca. 7% and *Sarcopoterium spinosum* ca. 7%), and dense woodland (taller woody cover including *Quercus calliprinos* trees), out of 11 vegetation forms that were categorized in the survey. The variations in vegetation structure are considered to represent varied combinations of site

conditions, land use, and disturbance history. We focused on pine colonization in areas of natural vegetation (excluding planted groves) on moderate slopes (ca. 0–10%) with Terra-rossa soils. Small patches of other soil types, i.e., Rendzinza and alluvial soils, and steeper slopes were excluded.

The park area was divided into cells measuring 100 m × 100 m, each of which was categorized with respect to grazing, fire, and vegetation structure by means of GIS. A cell that was not homogeneous with respect to each of these three factors was further divided, and this process resulted in the definition of 1,684 cells ranging from few square meters up to 1 ha in size. We then excluded cells smaller than 100 m^2, and measured the average distance of the center of each of the remaining 1,400 cells from the closest 5, 10, 20, and 40 planted *P. halepensis* trees, and calculated the density of colonizing pines within each of these cells. The total area covered by the cells that were included in the analysis amounts to 352 ha.

Statistical analysis

We used Moran's I Index for spatial autocorrelation to determine weather the distribution of colonizing pines was dispersed (negative autocorrelation), clustered (positive autocorrelation) or random (the null hypothesis). In order to investigate the relationship between density of colonizing pines (hereinafter: colonization density) and distance from planted pines we pooled cells according to a 25-m interval (average distance from planted pines), and applied regression analysis of colonization density vs. the average distance from the cell center of the closest 5, 10, 20 and 40 planted pines. We calculated the average distance firstly by including the closest pines regardless of their direction from the cell (hereinafter: all-round planted pines), and secondly by including only those located east and south-east (67°–135°) of the cell (hereinafter: eastern-southeastern planted pines). We selected this azimuth range following analysis of wind direction records during 6 years, which showed that east and south-east winds accounted for 45–54% of all winds during sharav events (Table 1). We used GLM analyses in order to determine the effects of grazing and fire on the density of colonizing pines, and applied these analyses within various ranges of distance from planted pines: 0–100; 0–200; 0–300; and 300–1,050 m. We used the distance from planted

pines as a covariate (ANCOVA) within the ranges within which colonization density and distance were found to be linearly related, i.e., 0–200 and 0–300 m. Separate GLM analyses served to determine the effect of vegetation structure on pine density, with distance from planted pines used as a covariate in the same way. We used separate analyses because of the possibility that vegetation structure might have been influenced by grazing and fire.

Results

Relationship between plantations and colonization

Altogether, 1,448 colonizing *P. halepensis* were found within 352.28 ha (area of natural vegetation) of the park area (Table 2). An analysis of spatial autocorrelation revealed that the distribution of colonizing pines was clustered (i.e. positive autocorrelation, Moran's I Index = 0.202, Z = 44.34, $P < 0.0001$). Among the various regressions applied in order to test the relationship between colonization density and distance from planted pines, the best explanations were achieved by using the average distance from the closest 10 planted pines (hereinafter: distance from planted pines) with a root-root transformation (sqrt x, sqrt y) and to a lesser extent a log–log transformation (inverse power law model) (Table 3, Fig. 5). A stronger relationship was found by plotting colonization density against distance from all-round 10 closest planted pines (Table 3) than by plotting it against eastern-southeastern 10 closest planted pines (Table 4). Colonization density decreased sharply and linearly with the distance from planted pines within 300 m from planted pines (Table 3) with a long tail that extended out to ca. 1,000 m (Fig. 5). As much as 40% of the colonizing pines that were found in the park area were located within an average distance of 100 m from the closest 10 planted trees, which covered 17% of the park area, and over 90% within 300 m, which covered 56% of the park area (Table 2).

Effects of cattle grazing and fire on colonization

The effects of grazing and fire were analyzed within four different ranges of average distance from planted

Fig. 4 Distribution of vegetation forms based on a vegetation survey by Lahav (1997). *Olive green square* Dense Woodland, *green square* dense garrigue, *light blue square* garrigue
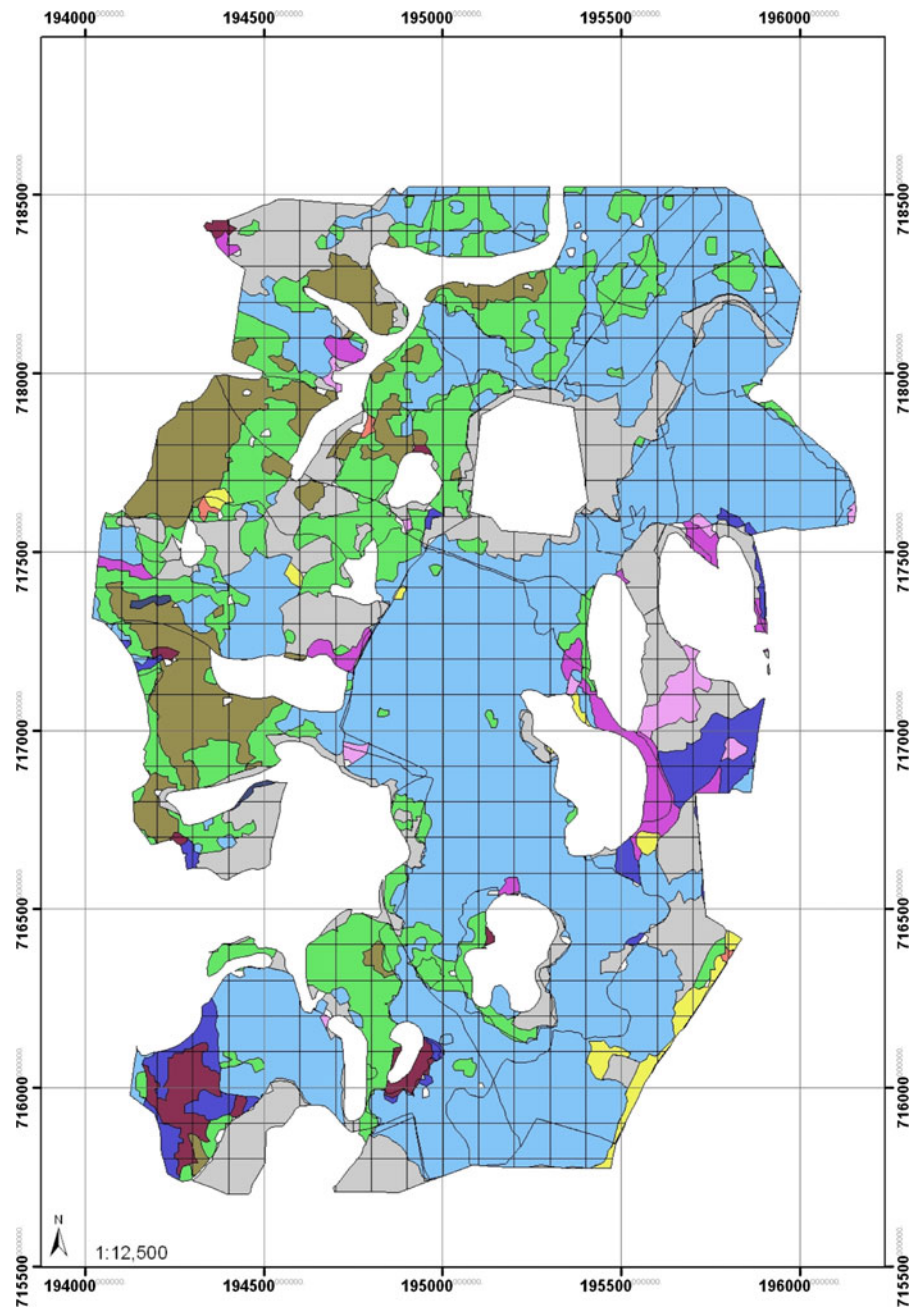
Table 1 Proportions of wind directions during "sharav" events (temperature ≥ 30°C; RH ≤ 15, 20 and 25%) in Ramat-Hanadiv

RH (%)	N	North (%)	North east (%)	East (%)	South east (%)	South (%)	South west (%)	West (%)	North west (%)
≤15	161	9	3	28	26	4	16	8	6
≤20	273	13	4	30	19	5	12	9	9
≤25	363	12	6	29	16	6	11	7	13

The proportions were calculated based on hourly data over 6 years of wind direction at maximal speed. Hourly maximal speed of eastern-southeastern winds during sharav events ranged between 1.5 and 6.7 m s^{-1}

Table 2 Numbers of colonizing pines in various ranges of distance from planted pines

Range of average distance from 10 closest planted pine trees (m)	Number of colonizing pines	Area (ha)	Proportion out of total number of colonizing pines in the analyzed park area	Proportion of total analyzed park area	Average density of colonizing pines (ha^{-1})
0–100	580	58.49	0.40	0.17	9.92
0–200	1,134	139.05	0.78	0.39	8.16
0–300	1,322	198.33	0.91	0.56	6.67
0–1,050	1,448	352.28	1.00	1.00	4.11

Table 3 Regression analyses on the relationship between density of colonizing pines and average distance from all-round planted pines

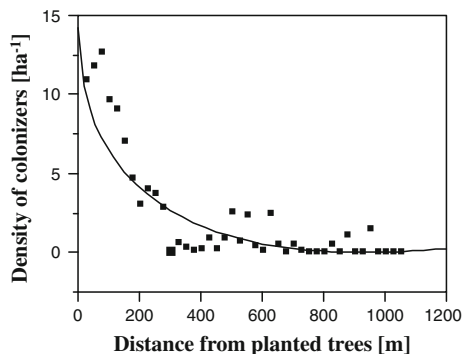| Number of closest planted pines for calculation of average distance	Range of distance from planted pines (m)	Model	R^2	N	P
5	950	$(y)^{-2} = a + b\,(x)^{-2}$	0.73	38	<0.0001
5	950	$\log(y) = a + b\,\log(x)$	0.48	31	<0.0001
5	350	$(y) = a + b\,(x)$	0.75	14	<0.0001
10	1,050	$(y)^{-2} = a + b\,(x)^{-2}$	0.73	42	<0.0001
10	1,050	$\log(y) = a + b\,\log(x)$	0.46	32	<0.0001
10	350	$(y) = a + b\,(x)$	0.92	14	<0.0001
20	1,125	$(y)^{-2} = a + b\,(x)^{-2}$	0.60	45	<0.0001
20	1,125	$\log(y) = a + b\,\log(x)$	0.38	35	<0.0001
40	1,200	$(y)^{-2} = a + b\,(x)^{-2}$	0.51	48	<0.0001
40	1,200	$\log(y) = a + b\,\log(x)$	0.24	38	0.0025

Fig. 5 The relationship between density of colonizing pines and average distance from closest 10 planted pines located all-round the cell

trees: 0–100, 0–200, 0–300, and 300–1,050 m. Although the portion of variance explained by the GLM models was relatively low, the effect of cattle grazing on colonization density was found significant within all three shorter ranges (Table 5): within 0–100, 0–200, and 0–300 m, respectively, from planted pines, colonization density was 2.3, 2.4 and

1.8 times larger under grazing than without grazing (Fig. 6). The effects of fire and of the interaction fire × grazing were found insignificant (Table 5). In addition, no significant effects of grazing and fire on colonization density were found within the longer range of 300–1,050 m from planted pines.

Effect of vegetation structure on colonization

We also analyzed pine colonization with respect to vegetation structure, and found that, within the distance ranges 0–200 and 0–300 m, colonization density was significantly larger, by 2.1 and 1.9 times, respectively, in the garrigue than in the dense-woodland patches (Fig. 7).

Discussion

Our results showed a clear positive relationship between pine colonization and proximity to planted pines, i.e., seed sources. The observed pattern was

Table 4 Regression analyses on the relationship between density of colonizing pines and average distance from eastern-southeastern planted pines
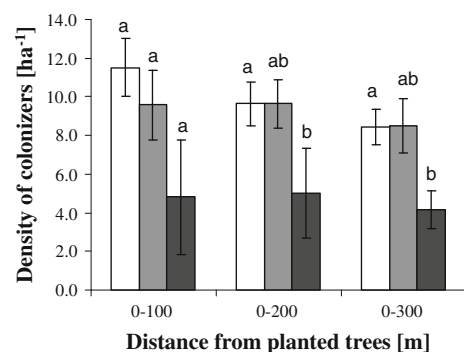
Number of closest planted pines for calculation of average distance	Range of distance from planted pines (m)	Model	R^2	N	P
10	1,200	$(y)^{-2} = a + b\,(x)^{-2}$	0.68	47	<0.0001
10	1,200	$\log(y) = a + b\,\log(x)$	0.50	25	<0.0001
10	350	$(y) = a + b\,(x)$	0.68	13	<0.0001

Table 5 GLM analyses of the effects of average distance from closest 10 planted pines (Distance), Grazing (grazed, ungrazed) and Fire (burned, unburned) on pine colonization in different ranges from planted pines

Range of average distances from closest 10 planted pine trees (m)	Model R^2	Model DF	Factor	F	P
0–100	0.04	734	Distance	–	–
			Grazing	7.64	0.006
			Fire	0.057	0.81
			Grazing × fire	0.049	0.82
0–200	0.04	558	Distance	3.56	0.05
			Grazing	14.26	0.0002
			Fire	0.009	0.92
			Grazing × fire	0.04	0.89
0–300	0.04	264	Distance	20.33	<0.0001
			Grazing	13.82	0.0002
			Fire	0.076	0.78
			Grazing × fire	1.30	0.84
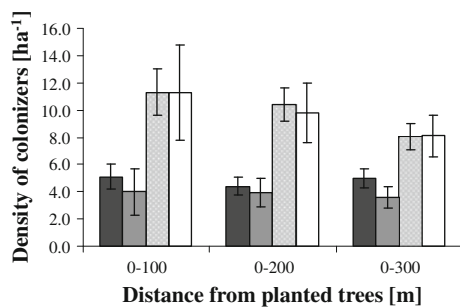
Fig. 6 Density of colonizing pines as affected by grazing (since 1990) and fire (in 1980). *Open square* Grazed-unburned, *square with dots* grazed-burned, *gray square* ungrazed-unburned, *black square* ungrazed-burned

Fig. 7 Density of colonizing pines as affected by vegetation form. *Black square* Dense woodland, *gray square* dense garrigue, *open square* garrigue. *Different letters* above columns indicate significant differences within each distance range

typical of wind-dispersed plant species (Nathan et al. 2000, 2001). This pattern has already been discussed quite extensively in previous work on *P. halepensis* (Nathan et al. 2000; Nathan and Ne'eman 2004; Lavi et al. 2005). However, the recruitment curve that was determined in the present study extended over a wider range than those reported by Nathan et al. (2000) and Lavi et al. (2005): the linear decline that

occurred within a range of ∼300 m from seed source in the present study was found within a range of only ∼30 m in the previous studies. This difference may be related to the fact that in the present study, young colonizing pines were not included in the survey (i.e., we included only trees of 3 m or more in height). The spatial distribution of young seedlings may be more

tightly related to the distance from seed sources and realized at shorter ranges than that of mature colonizers. Furthermore, in the previous studies it was shown that the spatial distribution of pine recruits was clearly related to seed dispersal by eastern winds, which are associated with sharav events. In the present study, however, the spatial arrangement of colonizing pines was better explained by the distance from all-round pines rather than by that from eastern-southeastern planted pines, i.e., seed sources located east and south-east from the measured plot. This was in spite of the fact that eastern and south-eastern winds were associated with sharav events in Ramat-Hanadiv.

It may be inferred that the planted pines in Ramat-Hanadiv were the major seed source for pine recruitment, within the park area, and, therefore the main cause of "colonization pressure". This pressure was specifically high within 300 m of planted pines, which defines 56% of the park's area and encompasses more than 90% of colonizing pines. Nevertheless, the importance of distant (300–1,000 m) colonizing pines as future seed sources for expansion (i.e. saltation dispersal) should not be overlooked (Nathan et al. 2001; Lavi et al. 2005). Many such pines have already reached their reproductive phase.

At this point it should be asked: to what extent is pine colonization determined solely by seed flow or limited also by safe-site availability? Safe sites are points in time and space at which a set of the diverse conditions necessary for recruitment occurs. As seed flow determines the level of "colonization pressure" the availability of safe sites may determine the level of "resistance to colonization" (Manning et al. 2004, 2005). Safe-site availability may be strongly influenced by disturbances as well as by management actions (Manning et al. 2004, 2005). In the present study we chose to focus on grazing and fire as key management and/or disturbance factors.

The density of colonizing pines was about twice as great in grazed areas than in ungrazed ones. Since *P. halepensis* is a wind-dispersed species that lacks means to assist epizoochory by large herbivores, it may be assumed that the direct effect of cattle grazing on seed flow was minor. In contrast, cattle grazing may have had quite significant consequences with regard to safe-site availability, because of its effects on variable factors such as vegetation structure, granivore activity, and seed-bed conditions. According to Lavi et al.

(2005) significant seed dispersal by *P. halepensis* starts by the age of approximately 20 year. It is, therefore, reasonable to assume that colonization pressure arising from pines planted during 1950–1960 began as early as 25–35 years ago, i.e., around 1980, whereas grazing was reintroduced into the park area less than 20 years ago, i.e., after 1990. Furthermore, according to the average age found for pines of 3 m height, i.e. 14 year, the majority of colonizing pines which could be identified by the aerial photograph have probably established in the park area prior to the reintroduction of grazing. Thus, the observed positive effect of grazing on pine colonization was probably mainly related to removal of competing vegetation and encouragement of pines that established themselves prior to the introduction of grazing (Seymour 2008). On the other hand, it is still possible that the influence of grazing was also related to early pine recruitment stages, i.e. better seed survival (Smit et al. 2001; Shibata et al. 2008) and improved conditions for germination and establishment conditions (Darabant et al. 2007), that occurred during the early 1990's shortly after the reintroduction of grazing. The winter of 1992, for example, was extremely rainy and could have supported a significant pine establishment episode. Several recent studies conducted in the Mediterranean region (Darabant et al. 2007; Boulant et al. 2008) and elsewhere (Vittoz et al. 2008) have revealed varied trends with regard to the influence of grazing on pine colonization. It is quite reasonable to consider that the effect of grazing on *P. halepensis* colonization may vary in accordance with changes in factors such as grazing regime and habitat condition (Debain et al. 2005).

The effect of the fire that occurred in the park 28 years ago on pine colonization was not evident in the present study. This finding conflicts with the results of a study in Argentina that found a clear positive effect of fire on *P. halepensis* invasion into natural vegetation sites (Zalba et al. 2008). Differences in post-fire pine colonization/regeneration may result from variations in the level of propagule pressure that occurs shortly after the fire. This would be determined, to a large extent, by the population of mature pine trees, i.e. those carrying seeds, that actually burned and released their seeds from serotonous cones during the fire event. With regard to colonization resistance, fire can create a window of opportunity for pine recruitment, through removal of

vegetation cover (Pausas et al. 2003; Zalba et al. 2008), and creation of suitable conditions for early establishment in the ash layer (Henig-Server et al. 1996, 2000; Pausas et al. 2003). Nevertheless, in contrast to continuous cattle grazing, which continuously removes the herbaceous vegetation cover, as well as reducing woody cover to some extent, a fire event can have a positive effect on the herbaceous vegetation, through the one-time removal of woody vegetation cover. Herbaceous species, mainly grasses, have been shown to compete strongly with pines during early recruitment of the latter (Schiller 1979). Thus, the lack of a clear effect of the 1980 fire on pine colonization in the Ramat-Hanadiv Park may be attributed to prevalence of low propagule pressure shortly after the fire event, i.e., not many mature pines burned, and relatively high resistance to colonization generated by fast recovery of the herbaceous vegetation during the first few years after the fire.

Our present results showed that pine colonization was lower in plots with dense woody vegetation cover, i.e., dense woodland. This finding matches previous results that showed better regeneration of *P. halepensis* under conditions of open vegetation structure with high light availability (Schiller 1979; Prevosto and Ripert 2008) and supports the hypothesis that developed undisturbed vegetation structures should exhibit higher resistance to pine colonization. Thus, the removal of vegetation cover by means of grazing, cutting or fire might result in increased pine colonization. Within this context, it is noteworthy that the consequences of a fire event occurring within the park area which is, at present, populated by mature colonizing pines may be quite different from those of the 1980 fire event. This would be due to the possible combination of intense propagule pressure, caused by seed release from burned pines, and low resistance because of vegetation removal, both of which occurring shortly after the fire event.

As the conditions offered in Ramat-hanadiv provide a unique opportunity to examine the ways by which afforestation, fire and grazing interact in determining pine expansion the possible influences of several other variables must not be overlooked. For example, a comprehensive study on the variability in post fire regeneration of *P. halepensis* has highlighted the importance of several other human related factors such as the existence of terraces and the handling of

burned material, as well as nonhuman related factors such as topography and rainfall (Pausas et al. 2004).

Conclusions

In light of our findings, we propose the following:

1. Colonization pressure in the Ramat-Hanadiv Park, and probably in other similar areas in Israel, is predicted to increase, in the short term, i.e., up to about 30 year, because of the increased population of seed-dispersing pines that resulted from colonization. Prediction of colonization pressure over a longer time range—ca. 40 year and more—is more complicated, because aging and mortality in mature forests that were planted during the 1950s and 1960s may become increasingly important.

2. In areas where vegetation cover is still developing, the predicted increase in colonization pressure may be counterbalanced by increased resistance to colonization. Well developed vegetation belts, a few hundred meters wide, around plantations, which can be promoted through grazing exclusion, for example, might possibly serve to hinder undesired pine colonization. These belts could be maintained by periodical removal of colonizing pines.

3. Special attention should be given to scenarios of simultaneous increase in pressure and decrease in resistance, such as might occur shortly after fire events.

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