



Homogenization in forest performance across an environmental gradient – The interplay between rainfall and topographic aspect



Michael Dorman^{a,*}, Tal Svoray^a, Avi Perevolotsky^b

^a Department of Geography and Environmental Development, Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel

^b Department of Agronomy and Natural Resources, Agricultural Research Organization, Volcani Ctr, Bet Dagan 50250, Israel

ARTICLE INFO

Article history:

Received 25 May 2013

Received in revised form 12 August 2013

Accepted 14 August 2013

Available online 13 September 2013

Keywords:

Aerial photography

Landsat

Tree mortality

Normalized Difference Vegetation Index

(NDVI)

Pinus halepensis

Solar radiation

ABSTRACT

This study aimed to investigate the interaction between local and regional environmental factors that affect forest performance during drought periods. In previous studies, contradictory results regarding the effect of aspect on forests performance, under different settings, were reported. However, each study focused on a different forest ecosystem at a different time frame, making synthesis inadequate. Monoculture planted *Pinus halepensis* forests in Israel, covering a broad climatic gradient (200–850 mm annual rainfall), form a suitable study system to address this question.

We used remote sensing and GIS methods to observe a large number of afforested stands over a wide area at high resolution. Normalized Difference Vegetation Index (NDVI), obtained from Landsat satellite images for 14 years between 1994 and 2011, served as an inclusive measure of forest performance. Data on the examined environmental factors were obtained from spatially interpolated annual rainfall maps and a topographic aspects map. The effects of aspect on NDVI were evaluated separately for three regions along the rainfall gradient: arid (200–350 mm), intermediate (350–500 mm), and humid (500–850 mm).

During the studied period, NDVI declined in the arid region but remained constant in the intermediate and humid regions. NDVI was positively related to annual rainfall in all three regions. The effect of aspect on NDVI was positively associated with rainfall in the arid region, but not in the intermediate and humid regions. In other words, forest performance homogenization across local habitats occurred in the arid region under drought stress. Relatively wet years were characterized by high NDVI values (~ 0.4), with large differences (~ 0.025) between northern and southern aspects, whereas dry years were characterized by low NDVI values (~ 0.3) and small differences (~ 0.01).

The present study supports the concept that under severe drought stress forest performance becomes more homogeneous across local habitats, both temporally (in drought years) and spatially (towards the arid forest boundary). Performance homogenization may occur when low soil water levels are reached, and climatic conditions become the dominant limiting factor. When water availability is high enough, differential performance responses among local habitats are maintained. We evaluated the trends and relations among local and regional environmental factors on performance, and assessed their relative effect sizes. Such an evaluation is essential to link local and global studies aimed at predicting the fate of forests facing global climate change.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Large-scale decline and mortality of forests are occurring with increasing frequency worldwide, and interest in various aspects of this phenomenon is similarly increasing. These aspects range from the physiological mechanisms involved in the process (Anderegg et al., 2012; Choat et al., 2012), to the global carbon budget (Ma et al., 2012) and implications for ecosystem functioning (Anderegg et al., 2013a; Royer et al., 2011). However, one of the

main knowledge gaps in this field concerns the factors determining spatial and temporal patterns of forest mortality, at both regional and local spatial scales (Allen et al., 2010).

On the regional scale, mortality events are often reported from the arid edge of the climatic water-availability gradient (Matyas, 2010; Michaelian et al., 2011; Sanchez-Salguero et al., 2012). However, the effects of local site characteristics, e.g., soil, elevation, topographic aspect, slope and topographic position, in determining forest responses to drought, are not well understood, and contradictory results have been obtained from different studies (see below). Moreover, the interplay between local and regional factors is often ignored, because most studies deal with natural

* Corresponding author. Tel.: +972 86479054.

E-mail address: michael.dorman@mail.huji.ac.il (M. Dorman).

ecosystems in which changes in the forest community occur along regional, i.e., climatic, gradients. This makes comparison between the effects of local-scale factors in different locations inadequate. In the present study, we aimed to investigate quantitatively the interaction between local and regional environmental effects on forest performance during drought, and considered that the most suitable pair of factors for this purpose comprised rainfall gradient (a regional factor) and topographic aspect (a local factor).

Topographic aspect is one of the important local environmental factors affecting vegetation performance (Nevo, 2012; Svoray and Karnieli, 2011; Vicente-Serrano et al., 2012). Aspect affects water availability for plants, since in the northern hemisphere south-facing slopes receive more solar radiation than north-facing ones. This results in more rapid soil moisture loss (Pigott and Pigott, 1993) by means of “direct and indirect influences on solar radiation, surface temperature, evaporation, soil moisture, and precipitation of an area” (Huang and Anderegg, 2012). In water-limited ecosystems this results in higher productivity on northern aspects than on southern aspects (e.g., Coble et al., 2001).

During a drought event the effects of local site quality on forest performance characteristics, such as trunk growth rate and green biomass production or mortality, are not straightforward. In some cases, higher forest mortality rates following drought were observed on southern aspects (Gitlin et al., 2006; Huang and Anderegg, 2012; Worrall et al., 2008). This is intuitively expected, as a consequence of reduced water availability and consequently narrower safety margins to buffer the physiological drought-tolerance limit. In other cases, however, increased mortality was observed on northern aspects (Guarin and Taylor, 2005). This pattern was attributed to higher tree density, which led to more intense competition for water and/or increased probability of insect outbreaks during drought. Finally, in some cases no significant effect of aspect on tree mortality was observed (Brouwers et al., 2013; Martinez-Vilalta and Pinol, 2002; Suarez et al., 2004).

A promising approach to clarifying the contradictions in the patterns of aspect-mortality relations involves taking into account the spatial nonstationarity of this relationship, especially along climatic gradients. In general, it is expected that aspect effect becomes more important as the role of water availability for vegetation development becomes more influential, for instance, in the transition from mesic to xeric environments along an aridity gradient (Sternberg and Shoshany, 2001).

Indeed, the effect of topographic aspect on performance of *Pinus halepensis* was shown to vary according to location along the rainfall gradient. Topographic aspect had a large negative effect – i.e., southern aspects had lower performance – at two arid sites with annual rainfall of 280 and 303 mm (Schiller, 1972), and a minor effect at a more humid site, with 414 mm (Olarieta et al., 2000). At even more humid sites, with 480–740 mm of annual rainfall, the effect was reversed to positive: *P. halepensis* was more abundant on southern aspects, and was gradually replaced by *Quercus ilex*, initially on northern aspects and then also on southern aspects (Zavala et al., 2000). However, an opposite pattern was observed in the temporal domain: Volcani et al. (2005) showed that in Yatir Forest (southern Israel; 236 mm average annual rainfall during 1985–2011) spatial variation in the Normalized Difference Vegetation Index (NDVI) was associated with aspect in a wet year (360 mm), but became insignificant during drought (157 mm). Similarly, in a study of *Pinus sylvestris* forests in an inner-alpine valley Vacchiano et al. (2012) showed that Enhanced Vegetation Index (EVI) values obtained from the Moderate Resolution Imaging Spectroradiometer (MODIS) were not correlated with radiation amount following a drought year, whereas they were correlated in several other years.

The NDVI is the most commonly used remote sensing index in ecological studies (Rouse et al., 1973; Tucker, 1979); in the present

study it served as a measure of forest performance, reflecting the quantity and state of the green biomass (Pettorelli et al., 2005; Wang et al., 2011) in a given location in a given year. The inter-annual variation in NDVI values of *P. halepensis* forests was found to be related to drought intensity in previous studies (Lloret et al., 2007; Vicente-Serrano et al., 2010; Volcani et al., 2005).

P. halepensis grows naturally in the Mediterranean region; its natural distribution is limited by a minimum temperature of -10°C and minimum annual precipitation of 450 mm (Liphschitz and Biger, 2001; Schiller, 2000). Planted forests cover about 8% of the Mediterranean climatic zone in Israel (Osem et al., 2008), and are dominated ($\sim 75\%$) by conifers, of which *P. halepensis* is the most common species (Perevolotsky and Sheffer, 2009). The 25–75% quartile range of planting years in the forests examined in the present study is 1961–1970 (Israel Forest Service GIS layer, 2011), during which *P. halepensis* was planted in a wide range of climatic conditions – from annual rainfall of 850 mm in northern Israel down to 200 mm in the south – which extended beyond the lower limit of precipitation in its natural distribution (Osem et al., 2008). Recently, increased mortality of *P. halepensis* was observed in the planted forests of Israel, following the droughts of 1998–2000 and 2005–2011 (Dorman et al., 2013; Schiller et al., 2005, 2009; Ungar et al., 2013), and similar observations were made elsewhere in the Mediterranean region (Girard et al., 2011, 2012; Sarris et al., 2007; Vicente-Serrano et al., 2010).

In Israel's arid Yatir Forest, the effect of aspect on the NDVI was lower in a drought year than in a wet one (Volcani et al., 2005). In the present study, by focusing on aspect and annual rainfall as examples of local and regional environmental factors, respectively, we aimed to investigate the balance between the two determinants of forest performance. Specifically, we investigated several aspects of the spatio-temporal characteristics of the effects of topographic aspect on forest performance:

1. Spatial scope – What is the spatial scope of the phenomenon (i.e. reduction of aspect effect on performance in drought years)? Is it confined to relatively arid regions or does it occur in more mesic regions as well?
2. Resilience and temporal pattern – How long does the difference in performance between northern and southern aspects remains diminished following drought? Is the previous state recovered after wet year/s?
3. Relationship to climatic condition – How does annual rainfall relate to the difference in performance between northern and southern aspects in a given year? Does the diminished difference among habitats characterize extreme drought years only – i.e., is there a “threshold” rainfall amount? – or does the difference change linearly with the annual rainfall?

2. Materials and methods

2.1. Study area

The study area encompassed all *P. halepensis* forests located in central and northern Israel and aged above 24 years at 1994 (Fig. 1a). The forests extend across a climatic gradient from semi-arid to Mediterranean conditions, i.e., annual rainfall ranging from 200 to 850 mm. The climate in the region is characterized by winter rains occurring mainly during December through March, and a relatively long, dry, hot summer (Osem et al., 2009).

Lahav forest, the second largest forest in the arid part of the study area (200–350 mm), was chosen for tree mortality examination (see Section 2.5). This forest received an average of 280 mm during the period 1985–2011.

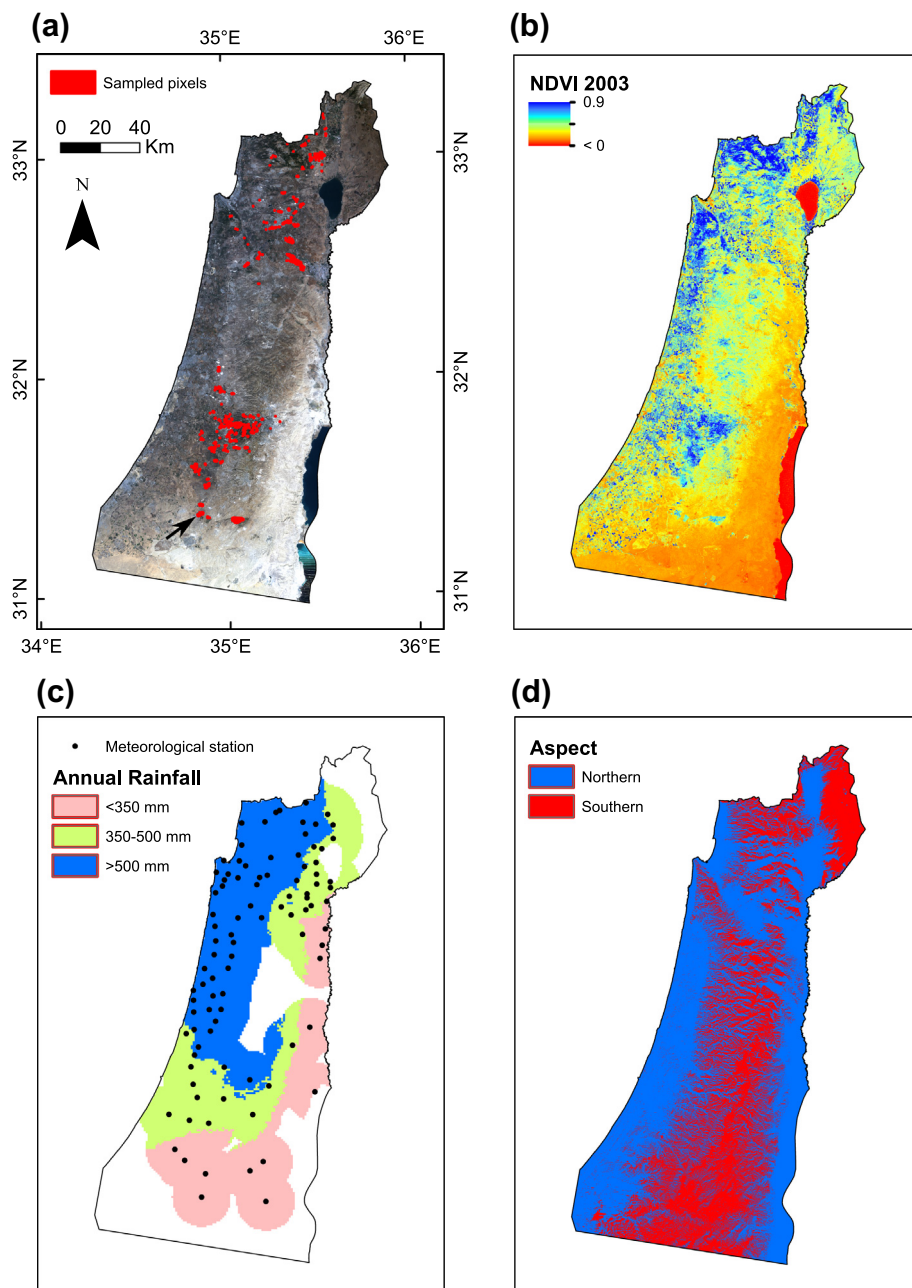


Fig. 1. (a) NDVI sampling locations (4020 pixels, each covering 90×90 m) in planted *P. halepensis* forests in Israel. Symbol size is exaggerated in order to make locations visible. The background is an RGB image prepared from a pair of Landsat-5 satellite images obtained on 11th September 2003. A black arrow marks the location of Lahav forest (see Fig. 5). (b) NDVI image of the studied area, calculated by using a pair of Landsat-5 satellite images obtained on 11th September 2003. NDVI values used in this study were extracted into the 4020 pixels (Fig. 1a) from this image and 13 others, obtained for 14 different years during 1994–2011. (c) Average annual rainfall during 1985–2011, classified into three categories – 200–350, 350–500, and 500–850 mm – and locations of 96 meteorological stations that provide data used in this study. (d) Estimated radiation amount, classified into two categories: above (“southern aspect”) and below/equal to (“northern aspect”) the median encountered among sampling locations. Note that the term “aspect” is not used here in its narrow sense, but as a label for locations differing in their radiation load due to topographic position. Radiation was estimated according to a 25-m DEM layer of Israel. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2. Remote-sensing data

To estimate forest structural responses on a large spatial scale, 26 Landsat-5 TM and two Landsat-7 ETM+ images from the period 1994–2011 were used. Two adjacent Landsat scenes (path 174, rows 37 and 38), both from the same date, were merged to cover the area of interest, yielding a sample of 14 images of the whole study area for years 1994–1995, 1997–2000, 2003–2009, and 2011. The images were selected from a relatively short time window (8th September–16th October) at the end of the dry season,

when there was less than 10% cloud cover over the studied area. This was not found possible in the other four years of the study (1996, 2001, 2002 and 2010). There were two reasons for the choice of this seasonal time window. First, during the dry season there is less variation in water availability for the trees and, therefore, there is less within-season variation in the vegetation activity signal. Second, herbaceous vegetation is completely dry during the summer, therefore a higher proportion of the spectral signal can be attributed to *P. halepensis* trees (Vicente-Serrano et al., 2010).

Images were geometrically corrected in the AutoSync Workstation module of Erdas Imagine 2011 software (ERDAS, Atlanta, GA, USA), by using a 5th-order polynomial geometric model. The images from 2003 were chosen as the reference set for all other images in the series. The Root Mean Square Error (RMSE) was <0.5 pixel length in all cases. Radiometric calibration was based on up-to-date coefficients (Chander et al., 2009). Atmospheric correction was applied with the Dark Object Subtraction 4 method (Song et al., 2001), which was chosen because supplementary atmospheric data, such as Aerosol Optical Depth, were not available for the older images, which necessitated application of an image-based method. Manually prepared cloud masks were used to exclude clouds and cloud shadow areas from the analysis.

NDVI was calculated as:

$$NDVI = \frac{\rho_{IR} - \rho_R}{\rho_{IR} + \rho_R} \quad (1)$$

in which ρ_{IR} is the reflectivity in the near-infrared region (Landsat band 4) and ρ_R is the reflectivity in the red region (Landsat band 3) of the electromagnetic spectrum. Image processing, spatial interpolation and statistical analyses were applied by using R software (R Development Core Team, 2012). Atmospheric correction of Landsat images was done with the “landsat” package (Goslee, 2011).

The NDVI data were extracted for 4020 pixels of 90×90 m located in planted forests across Israel (Fig. 1a). NDVI values (Fig. 1b) were extracted into each 90×90 m pixel by averaging pixel values from the overlain nine 30×30 m Landsat pixels, thus reducing the amount of data as well as the effect of geographic registration errors among satellite images. Each pixel was completely within a forest polygon planted with over 80% *P. halepensis* (according to a GIS layer obtained from the Israel Forest Service). Pixels within clouded areas in any of the 14 Landsat images were excluded, i.e., all 4020 pixels were assigned with 14 NDVI values.

2.3. Rainfall data

Annual rainfall maps with 1000-m resolution were produced by applying spatial interpolation to point data from 96 meteorological stations, for 26 rainfall seasons (1985–2011). Two geostatistical interpolation methods were evaluated for this task: Ordinary Kriging and Universal Kriging (Carrera-Hernandez and Gaskin, 2007; Di Piazza et al., 2011; Vicente-Serrano et al., 2003). Universal Kriging was examined with the seven possible combinations of three covariates that were considered to affect average rainfall amount in the studied area: elevation (Goovaerts, 2000), distance from the Mediterranean Sea, and latitude. Thus, eight interpolation procedures were evaluated, and their prediction accuracies were compared by using the mean RMSE obtained from leave-one-out cross validation. Universal Kriging with elevation as a covariate yielded the lowest average RMSE (58.2 mm) among the 26 years, therefore this method was chosen for preparing the rainfall maps. Since interpolation accuracy decreases with distance, only the area within 15 km of the nearest meteorological station was considered for analysis (Fig. 1c). Spatial interpolation of rainfall data was done with the “gstat” package (Pebesma, 2004) in R.

Maps of annual rainfall amount were used for two purposes: (1) to delineate three regions along the rainfall gradient (Fig. 1c); and (2) to extract average annual rainfall time series (Fig. 2c) for each region in order to evaluate the relationship between annual rainfall and aspect effect on NDVI (Table 2, Fig. 3).

2.4. Radiation data

A GIS-based method (Fu and Rich, 2002), implemented in ArcGIS 10.0 software (ESRI, 2012), was used to estimate integrated annual incoming amount of solar radiation over each pixel in a 25-m

resolution Digital Elevation Model (DEM) layer of Israel (Hall and Cleave, 1988). The model calculates an upward-looking hemispherical viewshed based on topography, and then uses it to calculate incoming direct and diffuse radiation from each sky direction, taking into account latitude, date and time. Thus it “accounts for atmospheric effects, site latitude and elevation, steepness (slope) and compass direction (aspect), daily and seasonal shifts of the sun angle, and effects of shadows cast by surrounding topography” (ESRI, 2012). The calculation is repeated for each pixel, producing an annual incoming solar radiation map for the entire studied area.

The 4020 examined pixels were classified as “Southern” or “Northern” aspects, according to whether the radiation amount they receive was above the median encountered among those 4020 pixels, or below/equal to it (Figs. 1c and S1). Thus we use the terms “Northern aspect” and “Southern aspect” not in their narrow sense (slopes facing the north or the south, respectively), but as a label helping the classification of our studied area into two distinct categories differing in their radiation load, while the latter was consistently evaluated based on the surrounding topography for each location.

2.5. Aerial photography

An aerial photograph of Lahav forest was used in order to contrast remote sensing findings with field information on tree mortality. A high resolution (0.25 m) RGB aerial photograph of the forest was obtained in winter 2011/2012. The photograph displays the last of two major forest mortality events that occurred in the arid region during the studied period of 1994–2011 (Shmuel Sprints, Israel Forest Service, personal communication), following the drought of 2005–2011 (Dorman et al., 2013; Ungar et al., 2013). The previous mortality event occurred following the drought of 1998–2000 (Schiller et al., 2005, 2009).

The studied area within Lahav forest (2.72 km²) was selected following the same criteria applied in the regional examination (>80% *P. halepensis* aged above 24 in 1994; see Sections 2.1 and 2.2). Dead trees were identified and marked by manual interpretation of the photograph, where they were clearly distinguishable due to their gray/reddish color, compared to the green living trees (Fig. S1).

The sampled area was covered with a 30-m grid coinciding with the Landsat pixels. Each pixel was classified into northern and southern aspects according to same procedure as in the regional examination (see Section 2.4). The numbers of dead trees and annual NDVI values were also recorded for each pixel. Due to very low cloudiness in Lahav forest during Landsat image acquisition, NDVI values for Lahav forest were available for 17 years (instead of 14 years that were used in the regional examination) – all years between 1994 and 2011 except for 2002 (Fig. S2). Non-forest areas (roads, buildings, etc.) were digitized and pixels where >25% of the area was non-forest were removed from the analysis. For the remaining pixels (92.7%) the number of dead trees per 30 m² was calculated taking into account the proportion of forested area within the pixel.

2.6. Statistical methods

The effects of aspect on NDVI in different years and regions were evaluated by fitting Mixed Effects linear models to the data. Mixed Effects linear models were chosen because they allow incorporation of structures of correlation among observations, in our case – in space (Brown et al., 2011; Zuur et al., 2009). Otherwise, violation of independence among observations would occur (Zuur et al., 2009), because pixels that are close to each other have more similar NDVI values than those further apart. A spherical spatial correlation structure among observations was used (Pinheiro and

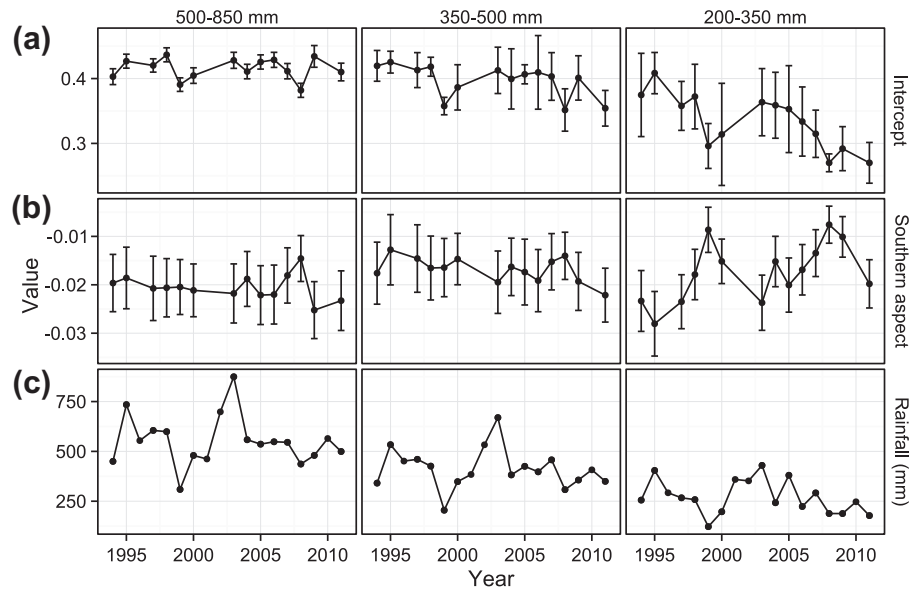


Fig. 2. Coefficients of fixed effects (Table 1) from the Mixed Effects linear models describing mean NDVI in 14 years between 1994–2011 in three climatic regions (humid, intermediate and arid): (a) intercept and (b) aspect (dummy variable for “southern aspect”). Estimates with upper and lower limits of the 95% confidence intervals are shown. (c) Average annual rainfall amount during 1994–2011 for each of the three climatic regions. Note that lines between points do not indicate continuous variation.

Bates, 2000; Zuur et al., 2009), which represented the spatially auto-correlated random effects on NDVI. Effect sizes of the examined factors were assessed according to the fixed effects estimates, with 95% confidence intervals. Mixed Effects models were fitted by using package “nlme” (Pinheiro and Bates, 2000) in R.

The effect of aspect on NDVI was examined by evaluating the model described in

$$NDVI = \beta_0 + \beta_1 * Aspect + \varepsilon \quad (2)$$

in which *NDVI* is the NDVI value of a given (90 × 90)-m pixel, *Aspect* is the dummy variable that represents southern aspects, i.e., the aspect dummy variable had the values of “1” and “0” in southern and northern aspect pixels, respectively, and ε is the error term.

The model described by Eq. (2) for NDVI data of each of the 14 years was evaluated separately for each of three regions: arid, 200–350 mm; intermediate, 350–500 mm; and humid, 500–850 mm. Note that “arid”, “intermediate” and “humid” do not refer to climatic regions; they are labels to enable easier reference to relative position along the rainfall gradient. An estimate and a 95% confidence interval for the intercept (β_0 in Eq. (2)) and aspect effect (β_1 in Eq. (2)) were obtained from each of the 42 (i.e., 14 years × 3 regions) models (Fig. 2 and 3, Table 1). The coefficients with 95% confidence intervals were not standardized, and therefore were interpreted at their original scale (Schielzeth, 2010). In other words, β_0 estimates express NDVI values at northern aspects; β_1 estimates express the NDVI reduction in southern aspects compared to northern aspects. The 42 models were then used to show predicted NDVI values in northern and southern aspects in the three regions, during the examined time period (Fig. 4).

The effect of aspect on the frequency of dead trees, in Lahav forest, was evaluated using a Poisson Generalized Linear Model (GLM). The independent variable was the aspect dummy variable (southern vs. northern); the dependent variable was dead trees count; the sampling units were the 2440 30-m² cells. Since overdispersion was detected, the standard errors were corrected using a quasi-GLM model (Zuur et al., 2009, p. 226).

3. Results

The results of fitting the models (Eq. (2)) are summarized in Table 1. The estimates of intercept and aspect effects, for each climatic zone, are also plotted in Fig. 2a and 2b, respectively. The use of a Mixed Effects linear model, instead of a linear model, was favorable, according to the Akaike Information Criterion (AIC; Akaike, 1974; Zuur et al., 2009). Values of the AIC for the Mixed Effects linear models (Column “AIC” in Table 1) were better than those for the analogous linear models (Column “AIC (linear)” in Table 1) in all 42 cases, with differences ranging between 687 and 2165 AIC units.

Estimates for the intercept show differing temporal trends among the three climatic regions (Fig. 2a). The range of intercept estimates values observed over time increased with progress from the humid region (500–850 mm), through the intermediate region (350–500 mm), and towards the arid region (200–350 mm). Ranges of intercept estimates in the three respective regions were 0.38–0.44 (average = 0.42), 0.35–0.43 (average = 0.40), and 0.27–0.41 (average = 0.33). In the intermediate region, and even more so in the arid region, the final (2011) intercept estimate was significantly lower than the initial (1994) estimate, according to confidence intervals (Fig. 2a), which suggests that the NDVI declines in these two regions were moderate and steep, respectively. Linear regressions of intercept estimates as functions of time (year) were used to examine this trend. In the humid and intermediate regions no significant temporal decline of the intercept estimate was observed (slope = −0.0001, $p > 0.1$; and slope = −0.0023, $p > 0.05$, respectively). In the arid region, however, the intercept estimate declined significantly ($p < 0.01$) by 0.0057 NDVI units per year. This apparent divergence among climatic regions, in forest stand performance following the two drought periods of 1998–2000 and 2005–2011 was discussed elsewhere (Dorman et al., 2013) and will not be further addressed here.

Estimates of aspect effects were negative across all regions and years, and always differed significantly from zero, according to confidence intervals (Fig. 2b). This means that lower NDVI values were observed on southern aspects (Fig. 1c), as could be expected. Aspect effect estimates were lower than intercept estimates by an order of magnitude (Fig. 2 and 4) and ranged from −0.025 to

Table 1

Estimates and standard errors (SE) for the fixed effects of Mixed Effects linear models. Each row corresponds to one of the 42 evaluated models that describe NDVI as a function of aspect in three regions (humid, intermediate and arid) and in 14 years (1994–1995, 1997–2000, 2003–2009, and 2011). *P*-values are not shown since they were <0.001 in all cases. The AIC value of each model is presented under “AIC”. For comparison purposes, AIC values of the analogous linear models (i.e., ordinary linear regression) based on the same data, are presented under “AIC (linear)”.

Region	Year	Intercept		Aspect (southern)		AIC	AIC (linear)
		Estimate	SE	Estimate	SE		
Humid	1994	0.40	0.006	−0.020	0.003	−6105	−4052
Humid	1995	0.43	0.005	−0.019	0.003	−5866	−4344
Humid	1997	0.42	0.005	−0.021	0.003	−5731	−4150
Humid	1998	0.44	0.006	−0.021	0.003	−6061	−4290
Humid	1999	0.39	0.005	−0.020	0.003	−6273	−4507
Humid	2000	0.40	0.006	−0.021	0.003	−6399	−4436
Humid	2003	0.43	0.006	−0.022	0.003	−5999	−3851
Humid	2004	0.41	0.006	−0.019	0.003	−6269	−4165
Humid	2005	0.43	0.006	−0.022	0.003	−6027	−4257
Humid	2006	0.43	0.006	−0.022	0.003	−6012	−4286
Humid	2007	0.41	0.006	−0.018	0.003	−6236	−4368
Humid	2008	0.38	0.006	−0.015	0.002	−6896	−4754
Humid	2009	0.43	0.009	−0.025	0.003	−6076	−3960
Humid	2011	0.41	0.007	−0.023	0.003	−5953	−3814
Intermediate	1994	0.42	0.012	−0.018	0.003	−4353	−2546
Intermediate	1995	0.43	0.009	−0.013	0.004	−4089	−2760
Intermediate	1997	0.41	0.014	−0.015	0.004	−4144	−2740
Intermediate	1998	0.42	0.007	−0.017	0.003	−4312	−3168
Intermediate	1999	0.36	0.007	−0.016	0.003	−4534	−3308
Intermediate	2000	0.39	0.018	−0.015	0.003	−4773	−2608
Intermediate	2003	0.41	0.018	−0.019	0.003	−4329	−2590
Intermediate	2004	0.40	0.024	−0.016	0.003	−4510	−2714
Intermediate	2005	0.41	0.008	−0.017	0.003	−4250	−2839
Intermediate	2006	0.41	0.029	−0.019	0.003	−4318	−2853
Intermediate	2007	0.40	0.019	−0.015	0.003	−4560	−2744
Intermediate	2008	0.35	0.017	−0.014	0.002	−4971	−3097
Intermediate	2009	0.40	0.017	−0.019	0.003	−4497	−2871
Intermediate	2011	0.35	0.014	−0.022	0.003	−4676	−2924
Arid	1994	0.37	0.033	−0.023	0.003	−3642	−2830
Arid	1995	0.41	0.016	−0.028	0.003	−3529	−2842
Arid	1997	0.36	0.019	−0.023	0.003	−3890	−3152
Arid	1998	0.37	0.025	−0.018	0.003	−4027	−3175
Arid	1999	0.30	0.018	−0.009	0.002	−4249	−3253
Arid	2000	0.31	0.040	−0.015	0.002	−4252	−2695
Arid	2003	0.36	0.026	−0.024	0.003	−3823	−2702
Arid	2004	0.36	0.026	−0.015	0.003	−3998	−2980
Arid	2005	0.35	0.034	−0.020	0.003	−3858	−2819
Arid	2006	0.33	0.027	−0.017	0.003	−4000	−3041
Arid	2007	0.31	0.019	−0.013	0.002	−4145	−3123
Arid	2008	0.27	0.007	−0.008	0.002	−4621	−3607
Arid	2009	0.29	0.017	−0.010	0.002	−4421	−3166
Arid	2011	0.27	0.016	−0.020	0.003	−4066	−3103

Table 2

Estimates, standard errors (SE), *p*-values and adjusted R^2 values for linear regression models describing the relationships depicted in Fig. 3, i.e., of the intercept and aspect effects as functions of rainfall amount.

Region	Intercept – rainfall relation (Fig. 3a)				Aspect effect – rainfall relation (Fig. 3b)			
	Estimate	SE	<i>p</i> -value	Adj. R^2	Estimate	SE	<i>p</i> -value	Adj. R^2
Humid	7.59×10^{-5}	2.71×10^{-5}	0.0162	0.34	-1.29×10^{-6}	5.46×10^{-6}	0.8180	−0.08
Intermediate	1.48×10^{-4}	5.02×10^{-5}	0.0121	0.37	1.61×10^{-7}	6.72×10^{-6}	0.9810	−0.08
Arid	3.40×10^{-4}	9.23×10^{-5}	0.0031	0.49	-4.92×10^{-5}	1.35×10^{-5}	0.0033	0.49

−0.015 (average = −0.021), −0.022 to −0.013 (average = −0.017), and −0.028 to −0.008 (average = −0.017), in the humid, intermediate and arid regions, respectively. Again, the range of observed values was widest in the arid region, suggesting that variation among northern and southern aspects was also highest in this region. Negative correlations were found between the estimates of intercept and aspect, among years, in the humid (Pearson's correlation coefficient (*P*) = −0.61, *p* < 0.05) and arid (*P* = −0.77, *p* < 0.01) regions, but not in the intermediate region (*P* = 0.15, *p* > 0.1). It is apparent that in the arid region, temporal changes in aspect effect estimates

mirrored those of the intercept (compare panels “a” and “b” for the “200–350 mm” region in Fig. 2). However, according to linear regression, the aspect estimate in the arid region did not change significantly with time (slope = 0.00058, *p* > 0.05), unlike the decreasing intercept estimate in that region. In other words, it seems that in the arid region temporal fluctuations in NDVI were accompanied by fluctuations in the effect of aspect, whereas the former (but not the latter) also persistently decreased with advancing time. Also in the intermediate and humid regions, no significant changes in the aspect estimate over time were observed

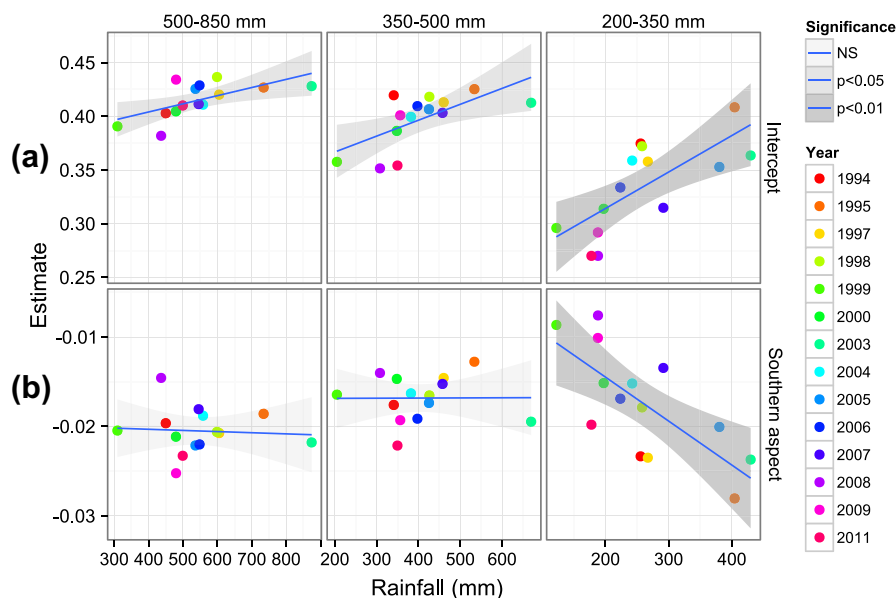


Fig. 3. (a) Intercept and (b) aspect effect estimates (Table 1; Fig. 2a and b) as functions of annual rainfall (Fig. 2c) among years, in three examined regions. The predicted linear regression line of the estimate as a function of rainfall (Table 2) is shown in blue, with the 95% confidence interval surrounding the line shaded in gray. Transparency of the confidence interval band corresponds to significance of the linear regression slope. Note that the ranges of x-axis values are not the same among panels. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

(slope = -0.00024 , $p > 0.05$ and slope = -0.0001 , $p > 0.1$, respectively).

The relationships between the estimates of the intercept (Fig. 2a) and aspect (Fig. 2b) effects of a certain year with annual rainfall of that year (Fig. 2c) are shown in Fig. 3, and the statistics of these relationships are summarized in Table 2. The intercept estimates had a significant positive relationship with annual rainfall (Fig. 3a, Table 2) in all three regions, which means that the temporal fluctuations of NDVI (Fig. 2a) coincided with those of annual rainfall (Fig. 2c). The estimates of aspect effect, however, were not significantly correlated with rainfall in the humid and intermediate regions (Fig. 3b, Table 2). Only in the arid region was a significant negative relationship, which appears to be linear, found between rainfall and the effect of aspect on NDVI (Fig. 3b, Table 2). In other words, no “threshold” amount of rainfall was identified that would prompt NDVI homogenization among northern and southern aspects. Instead, a gradual reduc-

tion of the aspect effect was observed among years with decreasing annual rainfall. It appears that, in the arid region, relatively wet years were characterized by high NDVI values (~ 0.4) and large differences (~ 0.025) between northern and southern aspects. Relatively dry years, however, were characterized by low NDVI values (~ 0.3) and small differences (~ 0.01) between northern and southern aspects.

A total of 4220 dead trees were identified on the aerial photograph within the 2.72 km² sampled in Lahav forest (Fig. 5). Based on an estimate of trees density in 2011 in each of the forest polygons (Shmuel Sprints, Israel Forest Service, personal communication), this translates to $\sim 3.5\%$ mortality. However, the frequency of dead trees was more than three times higher on the southern aspects compared to the northern aspects (2.50 and 0.68 trees per 30 m² pixel, on average, respectively; Figs. 5, 6 and S1). The difference among aspects was statistically significant according to a GLM of dead trees count as a function of aspect ($p < 0.001$). The

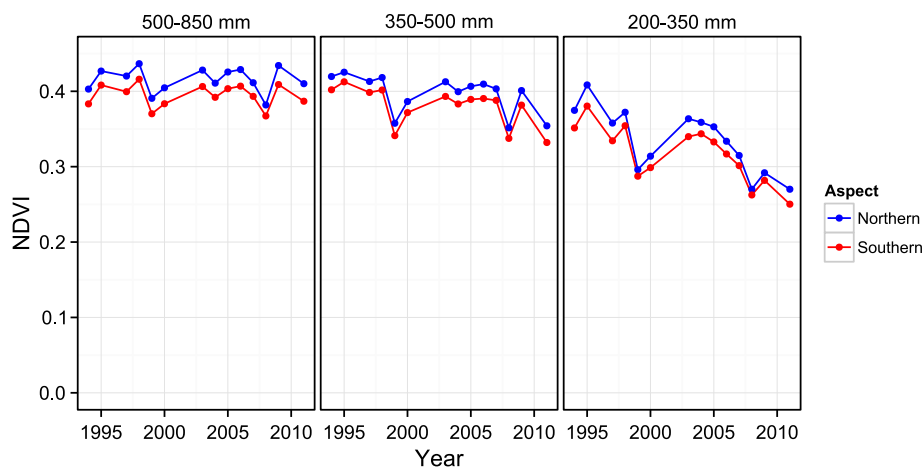


Fig. 4. Predicted NDVI values in 14 years during 1994–2011, based on the 42 Mixed Effects linear models described in Table 1. Note that lines between points do not indicate continuous variation, and also that differences between northern and southern aspect locations were significant in all cases (according to confidence intervals, Table 1 and Fig. 2b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

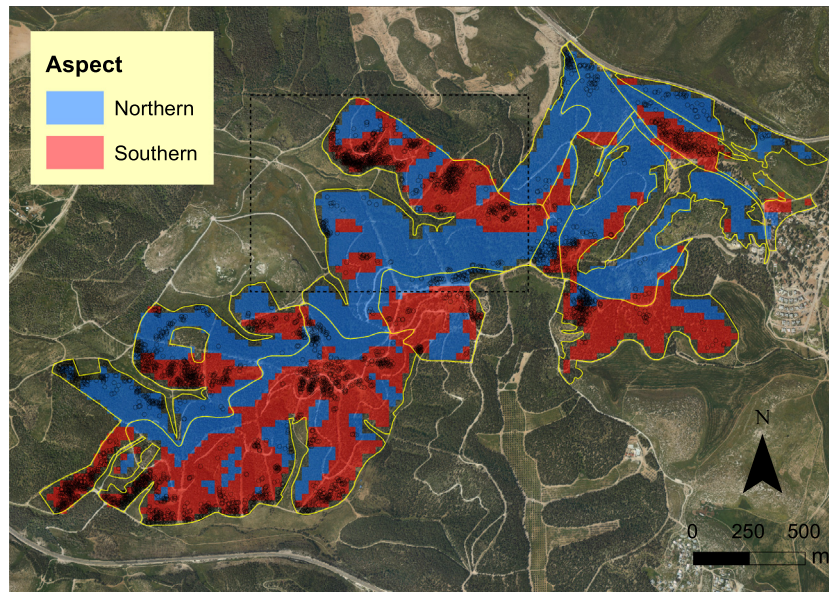


Fig. 5. Trees mortality in Lahav forest following the 2005–2011 drought. Black circles mark the locations of dead trees, manually identified on an aerial photograph from winter 2011/2012. Semi-transparent blue and red colors mark northern and southern aspects, respectively. See Fig. S1 for a zoom-in view and ground photographs of the area marked by a black dashed rectangle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

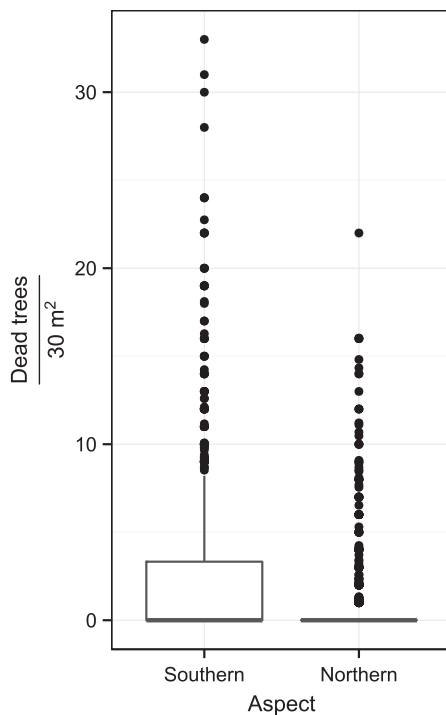


Fig. 6. Box and whiskers plot of dead trees count, among 30 m² pixels on southern and northern aspects in Lahav forest (Fig. 5). The upper and lower “hinges” correspond to the 25% and 75% quartiles. The upper whiskers extend from the hinge to the highest value that is within 1.5 of the 25–75% inter-quartile range. Data beyond the end of the whiskers are outliers and plotted as points.

concentration of dead trees on southern aspects was also evident from ground-view (Fig. S1).

4. Discussion

In the arid region, the effect of aspect was relatively stable in the long term, but was characterized by temporary deviations

whose magnitude was proportional to the annual rainfall amount (Fig. 3b). The average effect of aspect in the arid region was -0.017 , meaning that, within a forest, when moving from northern to southern aspects, NDVI decreased, on average, by 0.017 units, which is $\sim 5\%$ of the average NDVI in that region. However, the effect of aspect was not constant in time; it was related to the varying annual rainfall. Dry years were characterized by a significant weakening of the aspect effect, down to -0.008 ($\sim 2\%$ of the average NDVI), while wet years were characterized by a significant increase, to as much as -0.028 ($\sim 8\%$ of the average NDVI; Fig. 2b).

It may be assumed that during drought years, soil water availability becomes so limiting that the advantage of northern aspects is annulled. In other words, possibly because of very low levels of physiological activity (Schiller and Atzmon, 2009) throughout the forest in drought years, trees in all local habitats are affected. This may be manifested in reduced needle production, i.e., shorter and fewer needles, and/or defoliation (Baquedano and Castillo, 2006; Borghetti et al., 1998; Korner et al., 2005), resulting in uniformly low NDVI values across diverse habitats. In wet years, however, the advantage of the northern aspects may be realized. In such years the soil water content may be high enough to allow, for example, prolonged physiological activity on the northern aspects in spring and early summer (Klein et al., 2005; Schiller and Cohen, 1995). The contrast between northern and southern aspects will then appear, because cessation of physiological activity is reached faster in the latter.

An analogous hypothesis was suggested to explain why forest mortality patterns differed among different temporal phases of a drought event. Mortality was hypothesized to be higher in locations with high tree density, where competition for soil water is more intense, in the earlier phases of a mortality event (Negron and Wilson, 2003), and more homogeneous among differing density levels in the later phases of that event (Floyd et al., 2009; Ganev and Vojta, 2011). It was hypothesized that, in the case of an extreme drought, density dependence might operate in the earlier phases of mortality events, when trees in less competitive environments could obtain sufficient moisture, whereas those faced with competition could not. Later, under persistent drought stress, density dependence might be masked because the environmental

conditions would be so stressful that competition was no longer important, and mortality would occur at all density levels (Floyd et al., 2009; Ganey and Vojta, 2011).

The low responsiveness of the aspect effect to annual rainfall in the intermediate and humid regions (Table 2, Fig. 3b) might be attributed to the less extreme limitation on tree performance in those regions than in the arid region. Examination of the x-axis in Fig. 3 shows that in the intermediate and humid regions annual rainfall levels during the 14 examined years were only once lower than 300 and 400 mm, respectively, whereas in the arid region 11 out of the examined 14 years received less than 300 mm of rainfall. In contrast to this obvious difference in rainfall regimes, the performance difference among regions was not very high at the beginning of the studied period. In 1994–1995, average estimated NDVI values were 0.42, 0.43 and 0.39 in the humid, intermediate and arid regions, respectively (Fig. 2a). Thus, fluctuations in the performance difference between northern and southern aspects (Fig. 2b), and the accompanying decline in the performance “base level” (Fig. 2a) in the arid region, may both be viewed as manifestations of the decline exhibited by *P. halepensis* forests in the arid region during the examined 18-year period of 1994–2011 (Dorman et al., 2013).

It may be hypothesized that, in the arid region, damage caused to the forest under very low water availability was causing homogenization of performance in drought years, possibly because of low needle production in all habitats. Irreversible damage that led to mortality through, e.g., defoliation and depletion of carbon-reserves (Galiano et al., 2011; Sanchez-Salguero et al., 2012), or through accumulated hydraulic damage (Anderegg et al., 2013b), could have reduced potential productivity in subsequent years. In contrast, in the intermediate and humid regions, invariable differences between northern and southern aspects (Fig. 2b) and stable performance “base levels” (Fig. 2a) were observed. These two patterns may express the preservation of high enough soil water levels to maintain a persistent advantage of improved local habitats and to avoid irreversible drought damage, respectively.

The abovementioned two hypotheses, regarding variation in aspect effect in the temporal and spatial domains, are analogous. Performance homogenization among local habitats occurred in the arid region during drought, supposedly when very low levels of soil water availability were reached, and regional climatic conditions became the dominant limiting factor. However, performance differences among local habitats were maintained in all years in the intermediate and humid regions, and in the arid region in wet years only, since water availability was high enough to allow differential performance responses among local habitats.

In light of the proposed explanation, higher sensitivity to drought, i.e., a higher ratio between performance figures during normal vs. drought periods, may be expected in locally improved habitats (Fig. 4). In agreement with the latter, Knutson and Pyke (2008), in southern Oregon, USA, reported a significant negative association between growth rates in wet and dry years ratio, on the one hand, and radiation amount, on the other hand, in both *Pinus ponderosa* and *Juniperus occidentalis*. However, they regarded the finding as contradictory to the expectation that locations with increased radiation stress would be more sensitive to climatic changes. In the present study we observed the opposite: inferior local habitats, such as southern aspects, might exhibit lower drought sensitivity of performance traits such as NDVI. This is because drought impact becomes the major limiting factor, and homogenization of performance occurs across all habitats. Contrariwise, during wet years the potential for advantageous performance is exploited in the improved habitats. However, from the demographic point of view indeed the opposite pattern of sensitivity was observed: mortality was higher in the inferior habitats (Huang and Anderegg, 2012) in a representative forest within the

arid region. It appears that although improved habitats exhibit relatively steeper performance declines following drought, inferior habitats nevertheless fall to lower absolute performance levels (Figs. 4 and S2), and thus may be the first in which trees exceed critical physiological thresholds and mortality occurs (Figs. 5 and S1).

The difference in performance between northern and southern aspects was significant in all cases, in addition to significant temporal fluctuations caused by rainfall variation in the arid region (Fig. 2b). However, these fluctuations were quite small, compared with the “background” long-term changes of average forest performance (Figs. 2a and 4). For example, the average rate of performance decline in the arid region (-0.0057 NDVI units year $^{-1}$) was only one third of the average difference in performance between northern and southern aspects (0.017 NDVI units). Thus, during this 18-year study period, the performance “base level” in the arid region forests declined by a value six times the average performance difference between northern and southern aspects. This simple calculation demonstrates the importance of providing effect size information, i.e., the mean value with its confidence interval (Cohen, 1994; Nakagawa and Cuthill, 2007). The latter enables evaluation of the relative importance of the studied environmental effect in the context of other effects that characterize the studied system. In that respect the present study adds to the previous study focusing only on effect significance (Volcani et al., 2005).

In summary, the present findings support the concept that under severe drought forest performance becomes more homogeneous across local habitats, both temporally (in drought years) and spatially (towards the arid forest boundary). In these settings, the role of climate as a limiting factor to performance increases, whereas the roles of local factors, such as topographic aspect, become masked. It was also demonstrated that the local differences in performance between locally improved and locally inferior locations remained well conserved in the long term, even while the region suffered from regional performance reduction resulting from recurrent drought. The ability to observe a homogeneous forest ecosystem, in terms of species composition and structure, with high resolution over a wide area, was made possible by using remote sensing. Such an examination enabled a detailed evaluation of the trends and relationships among local and regional environmental factors, as they affect performance, as well as assessment of the relative importance of their effects. In addition to the basic ecological insight, such an evaluation is essential for relating local and global studies that aim at predicting the fate of forests in face of global climate change.

Acknowledgements

We thank Israel Tauber, Ronen Talmor, Efrat Sheffer and Shmuel Sprintsins for providing GIS layers of the planted forests, and the Israeli Forest Service (KKL) for permission to use these data. We thank Talia Horovitz and the Israel Meteorological Service for providing the rainfall data. This study was supported by a grant from the Chief Scientist of the Israeli Ministry of Agriculture and Rural Development, and the Jewish National Fund. We thank two anonymous reviewers for useful comments on a previous version of the manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2013.08.026>.

References

- Akaike, H., 1974. A new look at the statistical model identification. In: IEEE Trans. Auto. Cont. AC19, pp. 716–723.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684.
- Anderegg, W.R.L., Berry, J.A., Smith, D.D., Sperry, J.S., Anderegg, L.D.L., Field, C.B., 2012. The roles of hydraulic and carbon stress in a widespread climate-induced forest die-off. *Proc. Natl. Acad. Sci. USA* 109, 233–237.
- Anderegg, W.R.L., Kane, J.M., Anderegg, L.D.L., 2013a. Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3, 30–36.
- Anderegg, W.R.L., Plavcova, L., Anderegg, L.D.L., Hacke, U.G., Berry, J.A., Field, C.B., 2013b. Drought's legacy: multiyear hydraulic deterioration underlies widespread aspen forest die-off and portends increased future risk. *Global Change Biol.* 19, 1188–1196.
- Baquedano, F.J., Castillo, F.J., 2006. Comparative ecophysiological effects of drought on seedlings of the Mediterranean water-saver *Pinus halepensis* and water-spenders *Quercus coccifera* and *Quercus ilex*. *Trees – Struct. Funct.* 20, 689–700.
- Borghetti, M., Cinnirella, S., Magnani, F., Saracino, A., 1998. Impact of long-term drought on xylem embolism and growth in *Pinus halepensis* Mill. *Trees* (Berlin) 12, 187–195.
- Brouwers, N.C., Mercer, J., Lyons, T., Poot, P., Veneklaas, E., Hardy, G., 2013. Climate and landscape drivers of tree decline in a Mediterranean ecoregion. *Ecol. Evol.* 3, 67–79.
- Brown, C.J., Schoeman, D.S., Sydesman, W.J., Brander, K., Buckley, L.B., Burrows, M., Duarte, C.M., Moore, P.J., Pandolfi, J.M., Poloczanska, E., Venables, W., Richardson, A.J., 2011. Quantitative approaches in climate change ecology. *Global Change Biol.* 17, 3697–3713.
- Carrera-Hernandez, J.J., Gaskin, S.J., 2007. Spatio-temporal analysis of daily precipitation and temperature in the Basin of Mexico. *J. Hydrol.* 336, 231–249.
- Chander, G., Markham, B.L., Helder, D.L., 2009. Summary of current radiometric calibration coefficients for Landsat MSS, TM, ETM+, and EO-1 ALI sensors. *Rem. Sens. Environ.* 113, 893–903.
- Choat, B., Jansen, S., Brodribb, T.J., Cochard, H., Delzon, S., Bhaskar, R., Bucci, S.J., Feild, T.S., Gleason, S.M., Hacke, U.G., Jacobsen, A.L., Lens, F., Maherali, H., Martinez-Vilalta, J., Mayr, S., Mencuccini, M., Mitchell, P.J., Nardini, A., Pittermann, J., Pratt, R.B., Sperry, J.S., Westoby, M., Wright, I.J., Zanne, A.E., 2012. Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755.
- Coble, D.W., Milner, K.S., Marshall, J.D., 2001. Above- and below-ground production of trees and other vegetation on contrasting aspects in western Montana: a case study. *For. Ecol. Manage.* 142, 231–241.
- Cohen, J., 1994. The Earth is round (p -less-than.05). *Am. Psychol.* 49, 997–1003.
- Di Piazza, A., Lo Conti, F., Noto, L.V., Viola, F., La Loggia, G., 2011. Comparative analysis of different techniques for spatial interpolation of rainfall data to create a serially complete monthly time series of precipitation for Sicily, Italy. *Int. J. Appl. Earth Obs. Geoinf.* 13, 396–408.
- Dorman, M., Svoray, T., Perevolotsky, A., Sarris, D., 2013. Forest performance during two consecutive drought periods: diverging long-term trends and short-term responses along a climatic gradient. *Forest Ecol. Manage.* 310, 1–9.
- ESRI Inc., 2012. ArcMap Version 10.0 (Redlands, CA: ESRI).
- Floyd, M.L., Clifford, M., Cobb, N.S., Hanna, D., Delph, R., Ford, P., Turner, D., 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern pinon-juniper woodlands. *Ecol. Appl.* 19, 1223–1230.
- Fu, P.D., Rich, P.M., 2002. A geometric solar radiation model with applications in agriculture and forestry. *Comput. Electron. Agric.* 37, 25–35.
- Galiano, L., Martinez-Vilalta, J., Lloret, F., 2011. Carbon reserves and canopy defoliation determine the recovery of Scots pine 4 yr after a drought episode. *New Phytol.* 190, 750–759.
- Ganey, J.L., Vojta, S.C., 2011. Tree mortality in drought-stressed mixed-conifer and ponderosa pine forests, Arizona, USA. *For. Ecol. Manage.* 261, 162–168.
- Girard, F., Vennetier, M., Ouarmim, S., Caraglio, Y., Misson, L., 2011. Polycyclism, a fundamental tree growth process, decline with recent climate change: the example of *Pinus halepensis* Mill. in Mediterranean France. *Trees – Struct. Funct.* 25, 311–322.
- Girard, F., Vennetier, M., Guibal, F., Corona, C., Ouarmim, S., Herrero, A., 2012. *Pinus halepensis* Mill. crown development and fruiting declined with repeated drought in Mediterranean France. *Eur. J. For. Res.* 131, 919–931.
- Gitlin, A.R., Shultz, C.M., Bowler, M.A., Stumpf, S., Paxton, K.L., Kennedy, K., Munoz, A., Bailey, J.K., Whitham, T.G., 2006. Mortality gradients within and among dominant plant populations as barometers of ecosystem change during extreme drought. *Conserv. Biol.* 20, 1477–1486.
- Goovaerts, P., 2000. Geostatistical approaches for incorporating elevation into the spatial interpolation of rainfall. *J. Hydrol.* 228, 113–129.
- Goslee, S.C., 2011. Analyzing remote sensing data in R: the landsat Package. *J. Stat. Softw.* 43, 1–25.
- Guarin, A., Taylor, A.H., 2005. Drought triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *For. Ecol. Manage.* 218, 229–244.
- Hall, J.K., Cleave, R.L., 1988. The DTM project. *Geol. Surv. Isr.* 6, 1–7.
- Huang, C.-Y., Anderegg, W.R.L., 2012. Large drought-induced aboveground live biomass losses in southern Rocky Mountain aspen forests. *Global Change Biol.* 18, 1016–1027.
- Klein, T., Hemming, D., Lin, T.B., Grunzweig, J.M., Maseyk, K., Rotenberg, E., Yakir, D., 2005. Association between tree-ring and needle delta C-13 and leaf gas exchange in *Pinus halepensis* under semi-arid conditions. *Oecologia* 144, 45–54.
- Knutson, K.C., Pyke, D.A., 2008. Western juniper and ponderosa pine ecotonal climate-growth relationships across landscape gradients in southern Oregon. *Can. J. For. Res.* – Rev. Can. Rech. For. 38, 3021–3032.
- Korner, C., Sarris, D., Christodoulakis, D., 2005. Long-term increase in climatic dryness in the East-Mediterranean as evidenced for the island of Samos. *Reg. Environ. Change* 5, 27–36.
- Lipshitz, N., Bigger, G., 2001. Past distribution of Aleppo pine (*Pinus halepensis*) in the mountains of Israel (Palestine). *Holocene* 11, 427–436.
- Lloret, F., Lobo, A., Estevan, H., Maisongrande, P., Vayreda, J., Terradas, J., 2007. Woody plant richness and NDVI response to drought events in Catalanian (northeastern Spain) forests. *Ecology* 88, 2270–2279.
- Ma, Z., Peng, C., Zhu, Q., Chen, H., Yu, G., Li, W., Zhou, X., Wang, W., Zhang, W., 2012. Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proc. Natl. Acad. Sci. USA* 109, 24232427.
- Martinez-Vilalta, J., Pinol, J., 2002. Drought – induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *For. Ecol. Manage.* 161, 247.
- Matyas, C., 2010. Forecasts needed for retreating forests. *Nature* 464, 1271.
- Michaelian, M., Hogg, E.H., Hall, R.J., Arsenaault, E., 2011. Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biol.* 17, 2084–2094.
- Nakagawa, S., Cuthill, I.C., 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* 82, 591–605.
- Negron, J.F., Wilson, J.L., 2003. Attributes associated with probability of infestation by the pinon IPS, IPS confusus (Coleoptera: Scolytidae), in pinon pine, *Pinus edulis*. *West. N. Am. Nat.* 63, 440–451.
- Nevo, E., 2012. "Evolution Canyon", a potential microscale monitor of global warming across life. *Proc. Natl. Acad. Sci. USA* 109, 2960–2965.
- Olarieta, J.R., Uson, A., Rodriguez, R., Rosa, M., Blanco, R., Antunez, M., 2000. Land requirements for *Pinus halepensis* Mill. growth in a plantation in Huesca, Spain. *Soil Use Manage.* 16, 88–92.
- Osem, Y., Ginsberg, P., Tauber, I., Atzmon, N., Perevolotsky, A., 2008. Sustainable management of Mediterranean planted coniferous forests: an Israeli definition. *J. For.* 106, 38–46.
- Osem, Y., Zangy, E., Bney-Moshe, E., Moshe, Y., Karni, N., Nisan, Y., 2009. The potential of transforming simple structured pine plantations into mixed Mediterranean forests through natural regeneration along a rainfall gradient. *For. Ecol. Manage.* 259, 14–23.
- Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. *Comput. Geosci.* 30, 683–691.
- Perevolotsky, A., Sheffer, E., 2009. Forest management in Israel – the ecological alternative. *Isr. J. Plant Sci.* 57, 35–48.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20, 503–510.
- Pigott, C.D., Pigott, S., 1993. Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. *J. Ecol.* 81, 557–566.
- Pinheiro, J.C., Bates, D.M., 2000. Mixed-Effects Models in S and S-PLUS. Springer Verlag, New York.
- R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, <<http://www.R-project.org/>>.
- Rouse, J.W., Haas, R.H., Schell, J.A., Deering, D.W., 1973. Monitoring vegetation systems in the Great Plains with ERTS. In: 3rd ERTS Symposium, NASA SP-351 I, pp. 309–317.
- Royer, P.D., Cobb, N.S., Clifford, M.J., Huang, C.-Y., Breshears, D.D., Adams, H.D., Camilo Villegas, J., 2011. Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: primary and secondary ecological implications. *J. Ecol.* 99, 714–723.
- Sanchez-Salguero, R., Navarro-Cerrillo, R.M., Swetnam, T.W., Zavala, M.A., 2012. Is drought the main decline factor at the rear edge of Europe? The case of southern Iberian pine plantations. *For. Ecol. Manage.* 271, 158–169.
- Sarris, D., Christodoulakis, D., Korner, C., 2007. Recent decline in precipitation and tree growth in the eastern Mediterranean. *Global Change Biol.* 13, 1187–1200.
- Schielzeth, H., 2010. Simple means to improve the interpretability of regression coefficients. *Meth. Ecol. Evol.* 1, 103–113.
- Schiller, G., 1972. Ecological Factors Affecting the Growth of Aleppo Pine in the Southern Judean Hills, Agricultural Research Organization, Forest Division, Ilanot, Leaflet No. 44 (in Hebrew).
- Schiller, G., 2000. Ecophysiology of *Pinus halepensis* Mill. and *P-brutia* Ten. In: Ne'eman, G.T.L. (Ed.), Ecology, Biogeography and Management of *Pinus Halepensis* and *P. Brutia* Forest Ecosystems in the Mediterranean Basin. Backhuys Publishers, Leiden, The Netherlands, pp. 51–65.
- Schiller, G., Atzmon, N., 2009. Performance of Aleppo pine (*Pinus halepensis*) provenances grown at the edge of the Negev desert: a review. *J. Arid Environ.* 73, 1051–1057.
- Schiller, G., Cohen, Y., 1995. Water regime of a pine forest under a Mediterranean climate. *Agric. For. Meteorol.* 74, 181–193.

- Schiller, G., Ungar, E.D., Genizi, A., 2005. Is tree fate written in its tree rings? Characterization of trees in Kramim forest following the 1998/99 dry winter. *Yaar*, 18–25 (in Hebrew).
- Schiller, G., Ungar, E.D., Cohen, S., Moshe, Y., Atzmon, N., 2009. Aspect effect on transpiration of *Pinus halepensis* in Yatir forest. *Yaar* 11, 14–19 (in Hebrew).
- Song, C., Woodcock, C.E., Seto, K.C., Lenney, M.P., Macomber, S.A., 2001. Classification and change detection using Landsat TM data: when and how to correct atmospheric effects? *Rem. Sens. Environ.* 75, 230–244.
- Sternberg, M., Shoshany, M., 2001. Influence of slope aspect on Mediterranean woody formations: comparison of a semiarid and an arid site in Israel. *Ecol. Res.* 16, 335–345.
- Suarez, M.L., Ghermandi, L., Kitzberger, T., 2004. Factors predisposing episodic drought-induced tree mortality in *Nothofagus* – site, climatic sensitivity and growth trends. *J. Ecol.* 92, 954–966.
- Svoray, T., Karnieli, A., 2011. Rainfall, topography and primary production relationships in a semiarid ecosystem. *Ecohydrology* 4, 56–66.
- Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Rem. Sens. Environ.* 8, 127–150.
- Ungar, E.D., Rotenberg, E., Raz-Yaseef, N., Cohen, S., Yakir, D., Schiller, G., 2013. Transpiration and annual water balance of Aleppo pine in a semiarid region: implications for forest management. *For. Ecol. Manage.* 298, 39–51.
- Vacchiano, G., Garbarino, M., Borgogno Mondino, E., Motta, R., 2012. Evidences of drought stress as a predisposing factor to Scots pine decline in Valle d'Aosta (Italy). *Eur. J. For. Res.* 131, 989–1000.
- Vicente-Serrano, S.M., Saz-Sanchez, M.A., Cuadrat, J.M., 2003. Comparative analysis of interpolation methods in the middle Ebro Valley (Spain): application to annual precipitation and temperature. *Clim. Res.* 24, 161–180.
- Vicente-Serrano, S.M., Lasanta, T., Gracia, C., 2010. Aridification determines changes in forest growth in *Pinus halepensis* forests under semiarid Mediterranean climate conditions. *Agric. For. Meteorol.* 150, 614–628.
- Vicente-Serrano, S.M., Zouber, A., Lasanta, T., Pueyo, Y., 2012. Dryness is accelerating degradation of vulnerable shrublands in semiarid Mediterranean environments. *Ecol. Monogr.* 82, 407–428.
- Volcani, A., Karnieli, A., Svoray, T., 2005. The use of remote sensing and GIS for spatio-temporal analysis of the physiological state of a semi-arid forest with respect to drought years. *For. Ecol. Manage.* 215, 239–250.
- Wang, X., Piao, S., Ciais, P., Li, J., Friedlingstein, P., Koven, C., Chen, A., 2011. Spring temperature change and its implication in the change of vegetation growth in North America from 1982 to 2006. *Proc. Natl. Acad. Sci. USA* 108, 1240–1245.
- Worrall, J.J., Egeland, L., Eager, T., Mask, R.A., Johnson, E.W., Kemp, P.A., Shepperd, W.D., 2008. Rapid mortality of *Populus tremuloides* in southwestern Colorado, USA. *For. Ecol. Manage.* 255, 686–696.
- Zavala, M.A., Espelta, J.M., Retana, J., 2000. Constraints and trade-offs in Mediterranean plant communities: the case of holm oak-Aleppo pine forests. *Bot. Rev.* 66, 119–149.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer-Verlag, New-York.