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Regeneration dynamics of a mixed Mediterranean pine forest in the absence of fire

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ABSTRACT

The aim of this study is to determine the competing regeneration and expansion patterns of two co-occurring pine species (*Pinus brutia*, *Pinus nigra* ssp. *pallasiana*), in a transitional montane Mediterranean zone. We measured the regeneration density of all woody species in 102 randomly located stands along an altitudinal gradient on the island of Lesbos, Greece. Individuals of pines were assigned to different size classes. Topographic factors (altitude, aspect, and soil depth) and light availability (through hemispherical photographs) were measured for each stand. Statistical analyses were applied to explore the effect of each factor on recruitment density of the competing pine species, and to elucidate patterns of interaction. Canopy openness was the most important parameter controlling the recruitment of *P. brutia*, while the regeneration density of *P. nigra* was mainly related to canopy openness and heat load. An idiosyncratic response of the recruitment vigour of the two species was identified along gradients of shade and drought stress. The decline in *P. nigra* recruitment density with drought conditions underlines threats to its population maintenance even in the absence of fire. On the other hand *P. brutia* seems to be a stronger invader in transitional zones. The studied species could be considered typical representatives of the two most widely distributed pine functional types across the Mediterranean basin, and our results agree with the theoretical ability of such species to maintain and expand their populations.

1. Introduction

Across the Mediterranean Basin pines are substantial elements of vegetation (Barbero et al., 1998). According to Keeley and Zedler (1998) pine species can be classified in five major functional types, based upon a suite of traits related to their population dynamics. Two of the most widely distributed Mediterranean pines (*Pinus halepensis* Mill. and *Pinus brutia* Ten.), have fire-related life-history characteristics (Keeley and Zedler, 1998). These species belong to the "R" functional type and present traits such as seed serotiny, short juvenile period, short lifespan and enhanced wind seed-dispersal ability that enables them to deal with "predictable stand-replacing fires". The Mediterranean R-pine functional type (R), is mainly found at relatively low altitudes, and includes light demanding—drought tolerant species, able to exploit disturbed sites created after fire events (Trabaud, 1995; Pausas, 1999a). In mountainous Mediterranean areas, ranging from the western part of Greece to the Taurus Mountain in Turkey, *Pinus nigra* ssp. *pallasiana* is widely abundant and it is usually found at the earlier stages of succession. Nevertheless, it can also be found in pure self-maintained populations, at sites where bioclimatic conditions limit the abundance of more competitive broadleaved taxa (Barbero et al., 1998). It can grow in thermo-Mediterranean to oro-Mediterranean conditions, and it presents an increased ecological plasticity that enables it to compete with evergreen Mediterranean species (Quezel, 1977). Following the pine-species functional classification of Keeley and Zedler (1998), *P. nigra* belongs to the "U" functional group, which contains species found in productive sites with "unpredictable stand-replacing fires". Such species lack serotinous cones, have relative to other pines great shade tolerance and regeneration dependence upon spatial seed dispersal, a slightly longer juvenile phase and a large maximal height.

Higgins and Richardson (1998) simulated the ability of the R and the U functional types to invade discrete ecosystems across a gradient of disturbance regimes. They suggested that the "R-type" is a stronger invader particularly in fire prone environments, although the "U-type" is a more consistent invader in forest stands. Their results are of importance, in the context of climate change related shifts in species topographic ranges (Thuiller et al., 2003), "invasive range expansion" of the established pine populations (Richardson and Higgins, 1998), as well as novel association of species favoured by changes in land use practices (Allen and Breshears, 1998). Both the R (ex. *P. halepensis*—South Africa) and

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the U (ex. *P. nigra*—New Zealand) types have been documented as strong invaders in the southern hemisphere when interacting with the established vegetation (Richardson et al., 1994), but how would such pine types compete each other, for example under a Mediterranean climate ?

The role of fire will probably be more significant compared with the "absolute" drought stress in (especially low altitude) Mediterranean forests under drier future conditions (Fyllas and Troumbis, in press). Indeed, for the northeastern part of the Mediterranean region model simulations have project an increase in the abundance of both the R and U functional type, under enhanced fire frequency, particularly in transitional vegetation zones (Fyllas et al., 2007). Nevertheless, a significant area of forested regions could be expected to develop where species interactions occur in the absence of fire, at least during some transient time periods or due to fire suppression practices. In such cases, drought would be expected to become the most important factor driving vegetation change processes (Allen and Breshears, 1998; Rebetez and Dobbertin, 2004). Thus our study aimed to identify the regeneration dynamics of two typical representative species of the R (*P. brutia*) and the U (*P. nigra*) functional types in the absence of fire, in order to understand the key drivers influencing their landscape patterns of persistence and expansion.

The study area on the island of Lesbos was situated on an altitudinal gradient, where populations of the R (*P. brutia)* and the U (*P. nigra*) functional types are both established, thus providing an excellent model for understanding the interaction between these two groups. We thus explored the regeneration dynamics of these two species at a transitional Mediterranean zone, by censuring their recruitment vigour in natural stands where fire has been excluded for at least 50 years (Lesbos local forest authority). Soil depth, aspect, slope and altitude as well as light availability at the forest floor (analysis of fisheye photographs (Whitmore et al., 1993)) were measured for each plot, with the effect of the topographic profile (mainly as an index of potential drought pressure) approximated using estimates of incoming solar radiation (McCune and Keon, 2002). We hypothesised that there would be a differential response of regeneration vigour between the two pine species along the micrometeorological gradient existing in the study area.

2. Materials and methods

2.1. Study area

The study was conducted along an altitudinal gradient ranging from approximately 600 to 800 m a.s.l. on the mountain of Parakila-Anemotia (39°12′N, 26°05′E) located in the central part of the island of Lesbos, North Eastern Aegean, Greece. The climate of the study area is classified as accentuated thermomediterranean (Tselepidakis and Theoharatos, 1989) based on the Gaussen's index, with 14.7 °C annual mean temperature and 500 mm total annual precipitation for the last 4 (available) years, measured at an altitude of 307 m above sea level (Autohazard Pro, http://geo-fire1.aegean.gr/autohazard//lesvos.asp). Soils are classified as Cambisols (Jones et al., 2005) formed on pyroclastics (Kosmas et al., 2000).

P. brutia and *P. nigra* ssp. *pallasiana* are the two dominant forest tree species of the region, covering an area of 500 ha (Aravanopoulos and Panetsos, 1998). Isolated individuals of *Juniperus oxycedrus* L., *Quercus coccifera* L., *Q. pubescens* Wild., *Phillyrea latifolia* L., *Olea europea* L., *Arbutus unedo* L. and *A. andrachne* L. also occur, mainly in shrub form at the forest floor, and do not generally contribute to the canopy profile. On northern mesic sites, *P. nigra* forms pure stands from an altitude of 650 m. *P. brutia* is more drought-tolerant than *P. nigra*, and thus can be found in greater abundance in drier, southern-oriented sites.

2.2. Field measurements

One hundred and two randomly located stands were sampled in square plots of 100 m^2 (10 m × 10 m) along the altitudinal gradient of this natural forest. A quasi-random (in terms of location) and systematic (in terms of altitude) plot deployment was followed. Our unique "rule" when allocating the sample plots was to balance our sample regarding altitude and orientation and avoid the edge effects from the road (50 m transverse distance). We obtained 31 plots at altitudes less than 650 m, 33 between 650 and 700 m, and 38 plots above 700 m. Twenty-five plots faced northwards, 26 eastwards, 27 southwards and 24 westwards. Stands having a recent surface fire event were excluded, on the basis of field indicators (for example abundance of *Cistus* spp. or remaining burnt material and fire scars on the trunks). The measured stands had not been burned at least during the last 50 years (Lesbos local forest authority).

In each plot we measured diameter at breast height (*dbh*) and height (with a clinometer) of all living woody stems greater than 1.3 m high. For individuals shorter than 1.3 m, only height was measured. In the centre of each plot hemispherical photographs were taken, with a Nikon Coolpix 5400 with fisheye adaptor (FC-E9), mounted on a tripod, placed 1 m above the forest floor. The camera was always levelled and its top side was oriented northward. All pictures were taken under overcast conditions, early in the morning and before sunrise during the spring and summer months of 2006, with a fixed aperture (f = 7.9) and were slightly underexposed (2/3 f-stops) (Hale and Edwards, 2002). The slope and orientation of each plot were recorded; we avoided steep slopes (>30°) in order to exclude their effect on canopy related variables (Walter and Torquebiau, 2000). Soil depth was calculated with an iron stick as the average value from five random points within the plot.

2.3. Data analysis

Recorded individuals of both pine species were categorized to four size classes based on their height, *viz.* seedlings (0.01–0.10 m), small saplings (0.11–0.50 m), saplings (0.50–1.00 m) and canopy trees (>1.00 m). Note that the camera was set at 1 m above the ground, and thus only individuals in the "canopy class" contributed to the canopy closure measurements. Plots were further classified based on the canopy dominance type, which was defined by the abundance of established mature individuals taller than 2 m. Three dominance classes were identified; *P. brutia* or *P. nigra* dominated stands, and mixed plots. In mixed plots we either observed an invasion of *P. brutia* in mature *P. nigra* stands, or a substantial regeneration of *P. nigra* in *P. brutia* dominated stands.

The photographs were analyzed by three researchers independently (in order to avoid threshold subjectivity), using the HemiView ver. 2.1 software (Delta-T Devices Ltd.). From the variety of outputs provided by HemiView, the visible sky and leaf area index (LAI) parameters were used. Visible sky ranged from 0 (completely closed canopy) to 1 (completely open). When multiplied by 100 this value expressed a measure of canopy openness (CO) (Montgomery, 2004).

Aspect and slope for each stand were integrated into a parameter designated the "heat load" (McCune and Keon, 2002). In our study, heat load (HL) provides a unitless measure of the potential drought pressure on each plot, based on its topographic profile (orientation and slope). The term "potential" is used to distinguish heat load from actual drought stress, as meteorological