Spatially and temporally realistic and dynamic modelling for effects of water, temperature and light on tree population spread

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Abstract

This study suggests a process-based model for the effects of water availability, temperature and light on tree population spread in a Mediterranean environment. The methods include representation of spatial variation in seed availability, topographic attributes, presence of predators and temporal variance through a modelling of changes in temperature and rainfall. The model is developed using fuzzy rules and it provides a prediction of one generation of Aleppo Pine trees. The results show a reasonable agreement between the trees predicted and field observation backed by a visual interpretation of an orthophoto. This research is in progress and in the future we intend to apply the model to six generations of trees between 1949 and 2003. The model will be further developed to represent more processes that affects tree establishment such as tree survival. Efforts will be also given to represent other recruitment factors such as soil properties and parent material.

1. Introduction

The recent rise of spatial ecology emphasizes the critical importance of the spatial context at which ecological processes take place (Levin 1992, Tilman & Kareiva 1997, Silvertown and Antonovics 2001). For example, there has been a recent growing recognition that seed dispersal – one of the most critical processes in plant spatial dynamics (Harper 1977, Schupp & Fuentes 1995, Nathan & Muller-Landau 2000) – should be incorporated in a spatially realistic manner in models of plant population dynamics, because different distributions of dispersal distances can give rise to entirely different dynamics (Levin et al. 2003). Environmental heterogeneity is also of critical importance to plant dynamics, and the study of its pronounced impact goes back to the days of Theophrastus (371-286 BC) (Thanos 1994). Tree population spread processes also occur within large variation in temporal conditions. Temporal variation in climatic characteristics, mainly rainfall and temperature, may cause significant change in the conditions for seed germination. Thus, buried seeds in areas of improved environmental and biotic conditions will not germinate without satisfied amounts of rainfall and suitable surface temperature. It is therefore surprising that plant population models have not incorporated yet spatially and temporally realistic descriptions of key environmental factors that shape seed dispersal and plant recruitment processes. This can be explained by the great complexity of natural habitats, and the difficulty in identifying key

factors and measuring the variation over large spatial and long temporal scales. Recent advances in GIS, geocomputation, remote sensing and field measurements, along with better knowledge on recruitment processes, may allow us to cope with this challenge.

Adult plants produce seeds, with considerable spatiotemporal variation among individuals inhabiting different sites. This generates a non-random spatial structure in the annual (or seasonal) seed output within the population. Seed release is followed by seed dispersal, the major (or only) stage during which individual plants move in space. The process of dispersal is affected by multiple factors (Chambers & MacMahon 1994) that can also vary substantially in space and time (Schupp & Fuentes 1995, Nathan & Muller-Landau 2000). Seed predators can also be affected by environmental heterogeneity and can drastically alter the spatial structure of dispersed seeds (Hulme 1993). Seed dormancy can induce additional component of temporal variation in the availability of seeds for germination (Andersson & Milberg 1998). Spatial patterns of seedlings can be significantly different from those of seeds, because of spatial heterogeneity in the distribution of suitable micro habitats for germination. Similarly, spatial variation in seedling survival, generated for example by differential herbivory, may further alter the pattern of seedlings. Overall, successive stages of early recruitment generally show low concordance (Schupp & Fuentes 1995); hence, modeling plant population dynamics requires detailed descriptions of the spatiotemporal variation in environmental conditions and their effects on different recruitment processes.

This research proposes a spatially and temporally realistic dynamic model to predict long-term tree population spread in a heterogeneous environment. The model is formulated based on mechanistic principles, which describe the conditions during seed dispersal, germination, seedling survival and tree establishment. We applied the model to predict the dynamics of pine population spread during six consecutive decades and evaluated the predictions against field data, using visual interpretation of aerial photography, GPS readings and tree age measurements from annual growth rings.

2. Species and study area
The Aleppo pine (*Pinus halepensis* Miller) is the most widely distributed pine of the Mediterranean Basin (Quézel 2000). It is also common in plantations within and outside its natural range, spreading rapidly from plantations to nearby natural habitats (Richardson 2000). The species, considered one of the most invasive pines (Rejmánek & Richardson 1996), threatens native biodiversity in various habitats and even causing severe financial losses, especially across the Southern Hemisphere (Richardson 2000). Early recruitment processes play a key role in determining Aleppo pine spatial dynamics (Nathan and Ne'eman 2003); successful management of natural, planted and invasive populations should therefore be guided by models that incorporate spatial heterogeneity and its effects on early recruitment in a realistic manner.

Mt. Pithulim at the Judean Hills of Israel holds a native Aleppo pine population that was well isolated for a long time from any neighbouring population, with no evidence for any planting, cutting or fire. This population has expanded from five trees at the early 20th century, to the thousands of trees that inhabit the site today. The history of this spatial spread, and of major influencing factors, was reconstructed in exceptionally fine details, providing a detailed long-term perspective into the dynamics of any tree population. The study site on Mt Pithulim and its surroundings covers an area of roughly 4 km^2, which contains several ten thousands pine

trees, including recent plantations. To concentrate our efforts on the population of interest, a subset area of 60 ha (750 x 800 m) was selected. This 60 ha plot was selected to (a) include the core of the old stand and a buffer of at least 150 m around it; (b) to avoid very steep terrain (> 25 degrees) in which fieldwork is extremely difficult; and (c) to represent all the major topographical and edaphic units of the site.

3. The model

Overall

Our model incorporates the spatial and temporal variation of tree recruitment, focusing on factors operating on early stages of seed dispersal and germination. The temporal resolution is a single month for rainfall and temperature and the spatial resolution is a grid cell of 5m X 5m. The model progresses in three steps: (1) evaluation of the conditions for seed survival and germination, on a monthly basis; (2) evaluation of the conditions for seedling-to-adult survival, on a yearly basis; (3) selection of cells that have met a set of expert-defined threshold values for each recruitment factor for each grid cell, followed by selection of cells that have met an expert-defined threshold value for the joint (all factors combined) suitability for each grid cell. The overall conceptual model with its three stages is described in Figure 1:
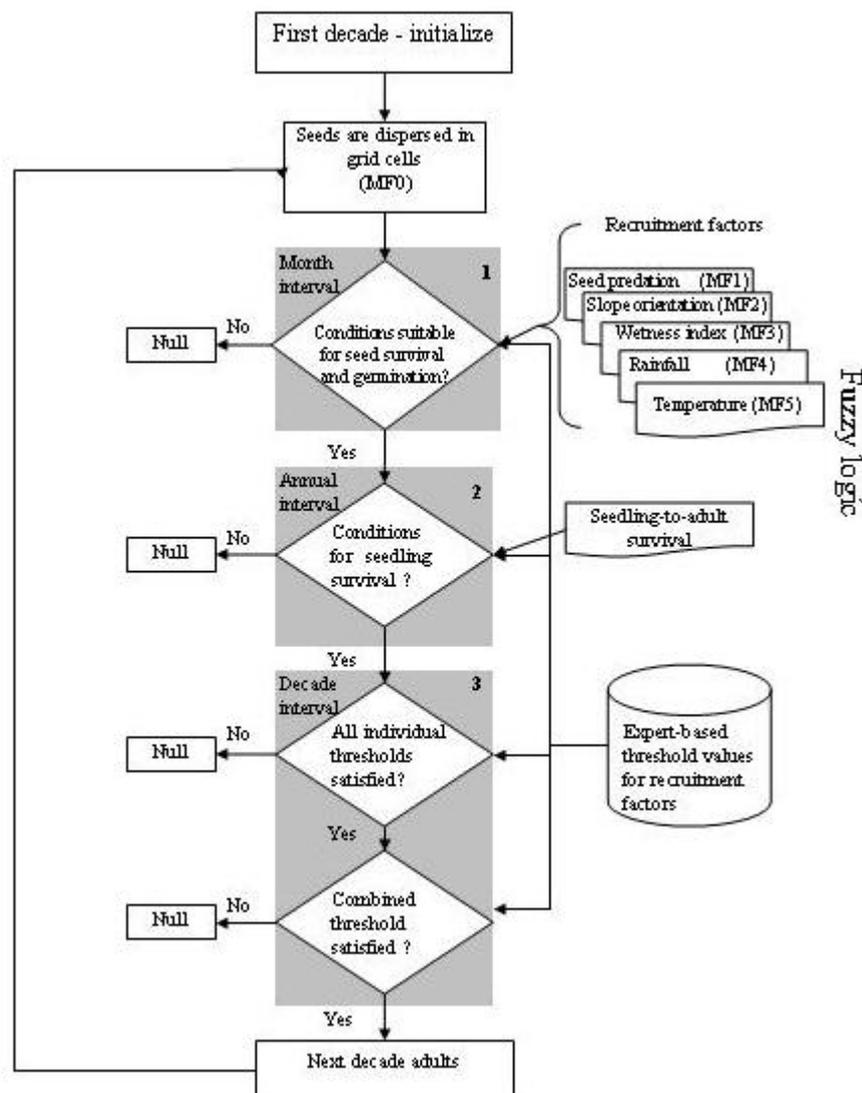
Fig. 1: A conceptual framework for the model developed in the current study.

Assumptions

Six assumptions are made regarding the processes that dictate tree population spread:

Seed dispersal

* Seed dispersal can be simulated from data on a few physical and biological factors, as implemented in the dispersal simulator WINDISPER (see below).

Seed survival and germination
* Seed survival increases with distance from adult trees due to the attraction of seed predators to the vicinity of adult trees (Nathan and Ne'eman 2003).
* Seeds can germinate only during the winter and spring (between November and April inclusive); Seeds that did not germinate do not survive for the next year (Izhaki et al. 2000).
* Seed germination is primarily affected by surface temperature and water availability (Thanos 1994).

Establishment
* Seedling survival increases with distance from adult trees due to shading, competition for water with adults, sibling competition and the attraction of seedling herbivores to the vicinity of adult trees (Nathan et al. 2000).
* Tree mortality occurs mostly during early establishment processes (Nathan and Muller-Landau 2000); hence individuals that survive the seed and seedling stages will become adults (Nathan and Ne'eman 2003).

Seeds dispersal model
Seed dispersal was simulated using the mechanistic simulator WINDISPER (Nathan et al. 2001). WINDISPER assumes a lognormal distribution of horizontal windspeed, and normal distribution of vertical windspeed (truncated to exclude net upward movements), height of seed release and seed terminal velocity. The model assumes a logarithmic vertical profile of the horizontal windspeed. It has been tested against extensive seed trap data for a native Aleppo pine population on Mt. Carmel (Israel) and on our study site, showing close agreement between predictions and observations. As with these previous applications of this simulator, we assumed here that the seed output is a linear function of the tree canopy projection, and the distance travelled by each individual seed was calculated after random selection of parameter values, based on their measured empirical distribution.

Spatial and temporal variation of recruitment factors
Spatial variation in soil water content is strongly dependent on topographic conditions through surface and subsurface runoff convergence and dispersion. Field observations had shown that lower areas in the catchment are moister due to the accumulated water reaching these plots through upper and lower runoff flows (Beven and Kirkby 1979). Among the key topographic parameters affecting surface hydrology, the local slope and the catchment area determine the hydraulic gradient and the potential water flux to a given area (Barling et al. 1994). Following Beven and Kirkby (1979) and Burrough et al. (1992), we used these two parameters in conjunction as a wetness index (Equation 1) to represent areas of dry and wet conditions.

$$WI = Ln\left[\frac{As}{\tan \boldsymbol{b}}\right] \qquad (1)$$

where As is the specific catchment area (the upslope contributing area) and β is slope angle of the surface. The parameter As was calculated using ArcGIS 8.2 flow accumulation algorithm, while the local slope (degrees) was calculated using the ERDAS Imagine Terrain Analysis algorithm. Solar radiation depends on the local slope orientation thus affects evapotranspiration rates and water loss (deficit). Consequently, south-facing slopes are less humid than slopes oriented to the north, east or west (Kutiel 1992).

Monthly statistics of surface temperature and rainfall are from measurements taken at Israel Meteorological Service (IMS) station at Beir-Jimal, 16 km west of the study site, between 1945 and 2003. High temporal variance exists in both rainfall (ranging between 1.5 and 460 mm per month) and temperature (ranging between maximum temperature of 12 and 34^{0}C).

The biotic conditions for seed predation and seedling survival are based on the distance from the trees that was set for the nearest neighbour pixel of each tree. Thus, cells that are already occupied by trees will not allow the development of a new tree and the adjacent pixels are of less favourite conditions from more distant cells. Consequently, the second neighbourhood and onward provide the best conditions for seed and seedling survival.

Fuzzy model
Fuzzy logic is used here to assess the suitability of grid cells for tree establishment. Several membership functions (table 1) are used to determine the degree of membership of each individual recruitment factor to the set A which represents a group with sufficient conditions for the establishment of a new Aleppo pine tree.

Attribute	Type	id	MF type	MF	Weights ?
Available seeds	Biotic	MF0	Linear	$\beta\text{-}x/\beta\text{-}\alpha$	0.25
Seed predation	Biotic	MF1	S^{+}	$1-(x-\gamma/\gamma-\alpha)^{2}$	0.25
Slope orientation	Topography	MF2	Linear	$\beta\text{-}x/\beta\text{-}\alpha$	0.0625
Wetness index	Topography	MF3	Linear	$\beta\text{-}x/\beta\text{-}\alpha$	0.0625
Temperature	Climate	MF4	Combined linear and S^{+}	$1-(x-\gamma/\gamma-\alpha)^{2}$; $\beta\text{-}x/\beta\text{-}\alpha$	0.0625
Rainfall	Climate	MF5	S^{+}	$1-(x-\gamma/\gamma-\alpha)^{2}$	0.0625
Seedling mortality	Biotic	MF6	S^{+}	$1-(x-\gamma/\gamma-\alpha)^{2}$	0.25

Table 1: A Summary of the membership functions used in our model. β is defined as the maximum point; α is the minimum point and x is the grid cell value. ? are the weights while $0 < ? < 1$ and $\Sigma\ ? = 1$. S^{+} is S-shape membership function with a right open shoulder often used in fuzzy logic with the equation described in table 1.

The weights are determined based on our understanding of the processes that dictate the tree population spread: seed dispersal, survival and germination and tree establishment. The weights are of equal importance for each process and thus, MF0, MF1 and MF6 that represent processes

1, 2 and 4 respectively are set to a weight value of 0.25. Process 3 of seed germination is represented here by the combined effect of wetness index, slope orientation, rainfall and temperature. The factors that affect this process (MF2-MF5) were also assumed to have equal importance and therefore, their weights are set to 0.0625.

To perform step 1 in the overall model (Fig. 1), the membership functions are joint (JMF) on a monthly basis using equation 2 and the weights ($?_{1..6}$) detailed in table 1.

$$JMF \text{ (month)} = ?_0 MF0 + ?_1 MF1, + \ldots + ?_5 MF5 \tag{2}$$

This JMF model is well-known as the convex combination JMF where the membership of a cell in the new fuzzy set A is determined based on the weighted sum of the membership functions MF0…MF5.

This approach could be very useful to represent complexities in tree population spread processes. For example: incases that MF2 is low due to south-facing slope location, MF3 can compensate with high membership value due to footslope location. However, in cases that no seeds reach their destination to a given cell, and consequently MF0 is equal to zero, other MF values may falsely compensate and the cell might be attributed to the set A although good conditions with no seeds will not allow germination. To overcome this problem we added to the model a rule that adjusts the entire JMF (month) to zero when MF0 is equal to zero.

To implement step 2 with an annual analysis that includes a consideration of mortality of seedlings, we used equation 3.

$$JMF(\text{Year}) = \frac{\sum JMF_{Nov} + \ldots + JMF_{April}}{6} + \lambda_6 MF6 \tag{3}$$

The sum of monthly JMFs is divided by the number of months and thus the annual joint membership function of the recruit factors is the average monthly JMF. This step is done to normalise the data and thus the total JMF for the last step (decade JMF) will also sum to one in the best-case-scenario.

In next step (3), to represent the spatio-temporal conditions for each decade we use equation 4:

$$JMF \text{ (Decade)} = \Sigma JMF_{1\ldots10} \tag{4}$$

Step three of the model is finalised through two tests that determine which of the cells are expected to be covered by a tree in the next generation. This is done using simulated threshold values that represents degrees of membership from which the establishment of a tree is expected (defuzzification). The threshold values are determined based on mechanistic

assumptions that are used to populate equations 2, 3 and 4. The tests include threshold values for the suitability of the final JMF and for the suitability of each of the recruitment factors separately. The map prediction data is validated against visual interpretation of historical air photos and tree rings measurements.

Fieldwork – model validation
For the first generation (1949-1956) we have gathered a database of 64 trees that represent half of the entire population at this year. The data was gathered using a field survey assisted by DGPS readings and measurement of tree rings. The database is verified against visual interpretation of an orthophoto that was produced from an airphoto that was acquired at 1956. The airphoto was scanned and the image was rectified using the *Orthobase Pro* tool of the ERDAS IMAGINE. An additional colour air photo from 1996 was retrieved from Advanced Digital Mapping, including an orthophoto and a DEM at 0.25 m horizontal resolution. The spatial resolution of the orthophoto is 0.43 m with 13 GCPs and total RMS error of less than 0.6 m. Additional database of ~ 20 trees that their age was determined using the tree ring methodology will be used also to validated the tree establishment predictions on a multi-temporal basis. For each individual tree, we also estimated in the field the diameter at breath height (DBH, [cm]), basal area, crown projection area [m^2] and height [m].

4. Results
The results show relatively good agreement between observed Aleppo pine tree population of 1956 and the potential conditions of the modelled cells, i.e., grades of the total joint membership function (figure 2).
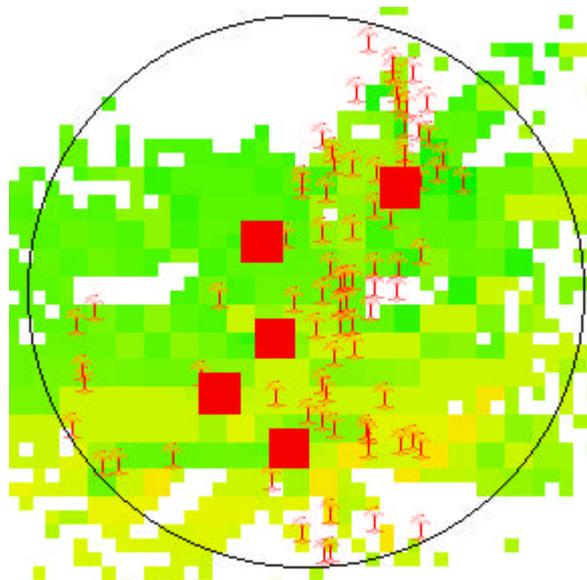
Fig. 2: A map of the spatial distribution of the second generation of trees at 1956 within a radius of one hundred meters from the centre of the first generation population. The background is a map of the total JMF (decade) grades where reddish colours represent lower membership grades and greenish colours represent higher membership grades.

The results are examined within a radius of one hundred meters from the centre of the first

generation – the five trees - since this distance was found as most effective for predicting seed dispersal with WINDISPER (Nathan et al. 2001). Figures 3 illustrates the seed dispersal membership values of the cells surrounding the first generation and thus it represents the effective range of short-distance seed dispersal from the five trees of the first generation. The use of a limit of one hundred meters excludes from the analysis trees that could be established as an outcome of ling-distance dispersal. This population, although there is an evidence for its existence in 1956, is beyond the scope of this paper and will be discussed elsewhere.
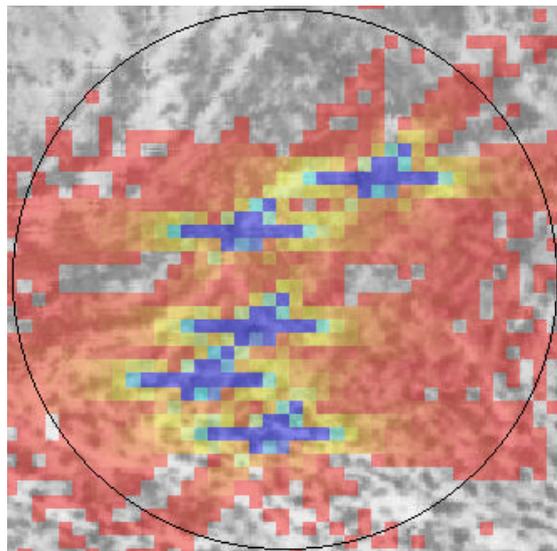
Fig. 3: A map of the membership grades of seed dispersal where bluish colours represent higher values and reddish colours represent lower values. The background is a panchromatic orthophoto acquired at 1956.

In general, figure 2 shows that only fourteen of the eighty-nine trees are located on cells with extremely low potential for tree evolution (represented by white cells). Many of the other trees, located in the northern part of the study area were developed on cells with higher potential values while up to twenty trees, located in the southern part of the studied area, were developed on cells with lower potential.

A quantitative analysis of the results in figure 2 requires to test how many trees did and how many trees didn't actually established in cells of high and low potential. The decision of what are "high" and "low" potential cells was done based on a threshold value that was set for the total JMF grades. Arbitrarily we have decided that 0.59 is the threshold value from which cells will be considered as cells of high potential. Table 2 shows the presence and absence of trees in the two groups of cells:

	High potential cells	Low potential cells
Presence of trees	51	28
Absence of trees	541	692

Table 2: A summary of the four categories that represent the presence and absence of trees within cells of high and low potential.

A chi-square test (df=3; *P*<0.0001) had shown that the number of trees that were observed in cells of high potential is significantly higher that the number of trees observed in cells of low potential. Similarly, cells with low potential had shown significantly higher number of cells characterized by absence of trees than the absence of trees observed in cells of high potential.

5. Conclusions

We had shown in this work that a mechanistic model that represents realistically spatial and temporal variation in water conditions, temperature and seed and seedling predation provides relatively good predictions of tree population spread for one generation between 1949 and 1956, in the heterogeneous Mediterranean environment of Mount Pitulim, Israel. Our proposed model provides good agreement between cells of high potential and actual tree observations. Likewise, cells of low potential had shown significantly more cases of absence of trees than cases of presence. Furthermore, cells of zero potential were populated by trees in very rare cases that were observed mainly in the margins of the studied area. These cases were attributed to long distance seed dispersal processes that were excluded from the current analysis. Further application of the model framework suggested here to more generations in the study area and to other sites populated by Aleppo pine trees will help to improve our understanding of processes of tree population spread.

6. References

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