Spatially And Temporally Realistic Modeling For The Effects Of
Water, Light And Temperature On Tree Population Spread

Tal Svoray[1]* and Ran Nathan[2]

[1] Department of Geography and Environmental Development;
Department of Information System Engineering,
Ben-Gurion University of the Negev, Beer-Sheva 84105, Israel.
tsvoray@bgumail.bgu.ac.il
[2] Department of Life Sciences, Ben-Gurion University of the Negev,
Beer-Sheva 84105, Israel.
rnathan@bgumail.bgu.ac.il

Biographies

Tal Svoray is a Lecturer in Geographic Information. His research interests are in remote sensing and GIS modelling of earth surface processes and especially the water-soil-vegetation relationships.
Ran Nathan is a Lecturer in Ecology and Evolution. He is interested in dispersal, migration and other types of organism movements, and especially in their role in shaping the spatial dynamics of plant populations.

Introduction

The recent rise of spatial ecology emphasizes the critical importance of the spatial context at which ecological processes take place (Silvertown and Antonovics 2001). The study of space pronounced impact goes back to the days of Theophrastus (371-286 BC) (Thanos 1994) and it is therefore surprising that plant population models have not incorporated yet spatially 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.

A general process of trees population spread may be described as follows. Adult plants produce seeds, with considerable spatiotemporal variation among individuals inhabiting different sites. This generates a non-random spatial structure in the annual seed output within the population. Seed release is followed by seed dispersal, the 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 (Nathan & Muller-Landau 2000). Spatial patterns of seedlings can be significantly different from those of seeds, because of spatial heterogeneity in the distribution of suitable microsites 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; 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 explicit dynamic model to predict 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 establishment. We applied the model to predict the dynamics of tree population spread during five consecutive decades and evaluated the predictions against extensive field data, using aerial photography and trees age measurements.

Study Area

The Aleppo pine (*Pinus halepensis* Miller) is the most widely distributed pine of the Mediterranean Basin. The species, considered one of the most invasive pines (Rejmánek & Richardson 1996), threatens native biodiversity in various habitats and even causing severe financial losses. Early recruitment processes play a key role in determining Aleppo pine spatial dynamics; 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 (area ~ 4 km^2) holds a native Aleppo pine population that was well isolated for a long time from any neighboring population, with no evidence for any planting, cutting or fire. This population has expanded from 5 trees at the beginning of the 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. To concentrate our efforts on the population of interest, a subset of 0.6 km^2 was selected.

The Model

Assumptions

* Dispersed seeds can germinate only during the winter and spring (between September and May); Seeds that do not survive this term expire and can no longer be considered as candidates. (From Schiller 1979).

* Seeds that germinate and than survive three consecutive years will become trees. (From Nathan et al. 2001).

* Competition with other vegetation formations stems from presence and absence of pine trees. (Nathan et al. 2001).

* Conditions for germination are based on temperature, light conditions and water availability. (Zavala 2000).

- Conditions for seedling survival, are based on distance from the tree as representative of the joint effect of shading and competition on water with adults, sibling competition, and the attraction of seedling herbivores to the vicinity of adult trees. (Nathan et al. 2001).

Spatial variance of environmental controls

The spatial variability that determines the conditions for germination is presented by: water availability through rainfall amounts per pixel (based on the known relationships between tilted and horizontal surface - Sharon 1980) and wetness index (Barling et al.

1994) to determine water flow and accumulation; soil temperature is calculated on a per-pixel basis using the model of Running and Thornton (1996) and light conditions through the crown density of existing pine trees. The climatic data to implement the rainfall and temperature models was purchased for all years between 1945 and today on a weekly basis from the Meteorological Survey of Israel.

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 provides an analytical solution for the distance travelled by an individual seed under any combination of parameter values. In the present application, we divided the 60 ha of the study area into two zones: the dense central stand, for which we applied WINDISPER-E (for trees within a dense forest), and the remaining area outside the stand, for which we applied WINDISPER-L (for trees in open landscapes). The seed output was assumed as 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.

Fuzzy logic

Fuzzy logic was used to evaluate the conditions for germination and independently for seedling survival. In equation 1 (Burrough 1989), MFxi was used to determine the degree of membership of individual environmental factors (Fig. 1) in set a – germinated seeds (or survived seedling respectively).

$$MFxi = \frac{1}{\left(1 + \left\{\frac{(xi - b)}{d}\right\}^2\right)} \qquad (1)$$

where b is the ideal point and d is the widths of the transition zone. Coefficients b and d were defined for each of the factors based on extensive field studies of Schiller (1979) and Nathan et al. 2001. In a similar manner, membership function for seedling survival was determined based on distance from trees. Merging the Mfs was utilized based on equation 2:

$$JMF = ?_1 MFx_1 + ?_2 MFx_2, + \ldots + ?_n MFx_n \qquad (2)$$

where JMF is a joint membership function for all variables and $?_{1\ldots n}$ is weighting factor for each variable.

Orthophotos

Twenty-four historical panchromatic air photos ranging from the year 1944 to 2000 were purchased. An additional color air photo from 1996 was retrieved from Advanced Digital Mapping, including an orthophoto and a DEM at 0.25 m horizontal resolution. Seven photos were selected from the years 1949, 1956, 1963, 1974, 1986, 1993 and 2000, thus covering one photo per decade since the 40th. The photos were scanned and the images were rectified using the

Orthobase Pro tool of the ERDAS IMAGINE. The spatial resolution of the orthophotos is 0.43 m with 13 GCPs and total RMS error of less than 0.6 m.

Fieldwork

A reconstruction of the history of pine expansion within the 0.6 km^2 plot involves field mapping of all individual Aleppo pine trees that currently occupy this site. An intensive fieldwork, assisted by GPS unit, has yielded mapping of ~ 1500 trees, estimated as the entire population. This map is combined with visual interpretation of air photos and age determination by annual growth rings, to reconstruct the history of pine expansion in the site from 1945 till today. For each individual tree, we estimated the years of: germination; establishment; and death (0 = still alive). In addition, diameter at breath height (DBH, [cm]), basal area, crown projection area [m^2] and height [m] were measured.

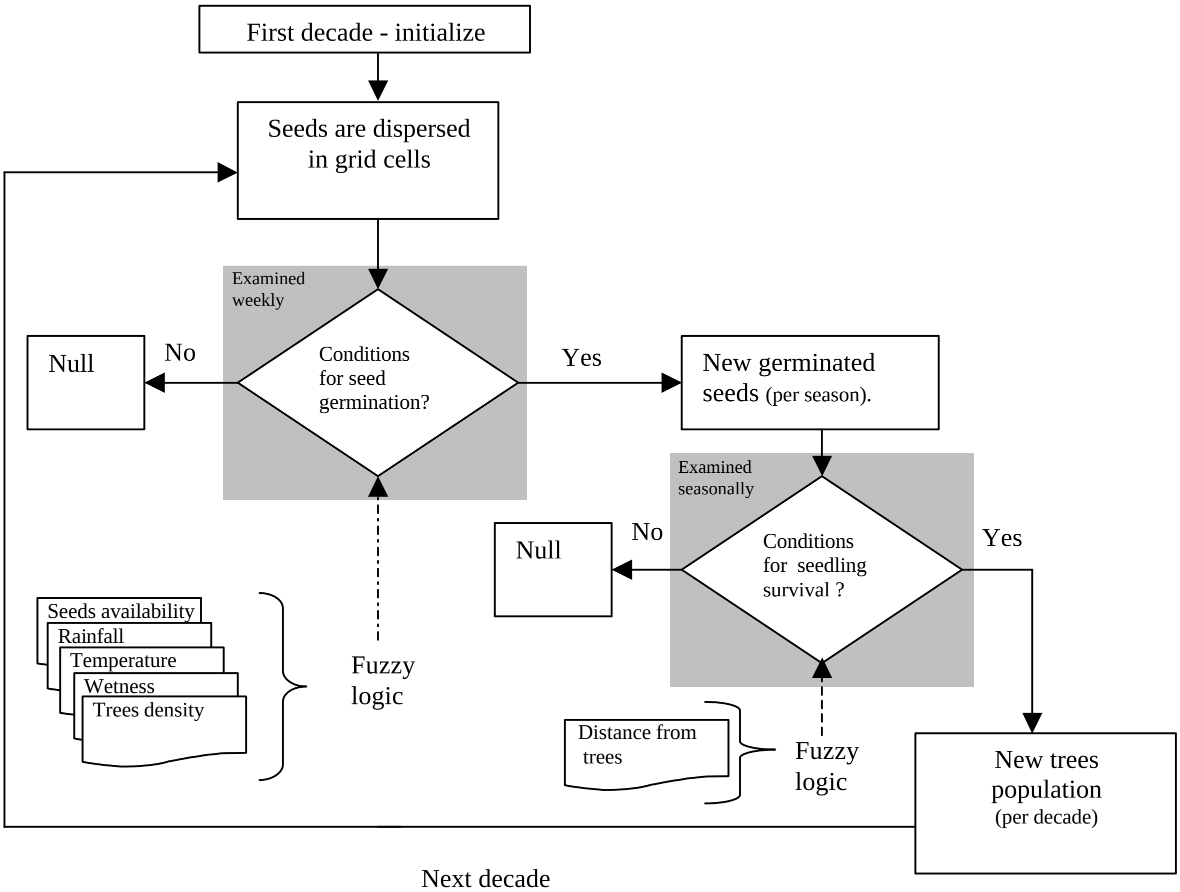

Fig. 1: The spatio-temporal model developed in the current study. In general, conditions for seed germination are examined on a weekly basis in each cell. Then, at the end of every season, cells of satisfactory conditions are being marked. Later, conditions for seedling survival are tested for "germinated cells" and if satisfactory, the presence of a new tree is recoded. The sum of the new trees per decade is then tested against validation data.

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