A non-stochastic, physiologically-based model of plant invasion using Ecological Field Theory

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Summary

Invasability is equated with the temporal and spatial distribution of safe seedling recruitment sites within a plant community. Seedlings in the safe sites are then subjected to varying intensities of plant competitive influences from surrounding plants as well as changes in the physical and climatic environments. The magnitude of the competitive influences (stress) and the length of the stress period decide the fate of the seedlings. Ecological field theory (EFT), quantifies plant spatial influences as temporally variable fields about individual plants. The extent of each influence field (domain) is estimated from plant size, and the field intensity is computed as an index using estimates of potential plant growth and actual plant growth for the prevailing climatic and environmental conditions. In this calculation the index increases as combined available resources decrease. Mapping influence fields for a range of climatic conditions (weekly to seasonal) for all plants in the community can be used to define the spatial distribution and dynamics of "safe sites" likely to be available for recruiting plants. Combining this spatial information with seed germination characteristics and environmental conditions gives a numerical model to define the extent and timing of plant recruitment (invasability). The field theory concept necessary to consider invasion is outlined. An application concerns the timing and extent of recruitment of the shrub *Cassia nemophila* into an intact woodland. Cassia is considered to be a "woody weed" in many *Eucalyptus populnea* (poplar box) areas of SW Queensland. The EFT method suggests an approach to answering some of the questions about the impact of global climatic change on plant community dynamics. We argue that to predict community changes requires a combination of physiologically based plant growth models, plant functional attributes, spatial interactions, and changes to the physical and climatic environments. EFT is an attempt to achieve this goal.

Introduction

A major increase in plant populations (an invasion) for particular exotic or native plant species requires a seed source, appropriate climatic/edaphic conditions for germination and safe sites to enable recruitment to occur. Safe sites are considered here as areas in which germination can occur, and where competition from existing plants is insufficient to prevent continued seedling growth following germination. Invasability, the potential of plants to invade an area, can thus be considered as temporal "windows of opportunity" operating against a spatially variable but definable climatic and environmental background. The key considerations then become the spatial definition of safe sites, and their temporal and spatial availability.

Ecological field theory (EFT) (Walker *et al.* 1989) provides a methodology to quantify spatial influences about plants of similar or different size, function and growth form into physiologically based models of plant community dynamics (Wu *et al.* 1985, Sharpe *et al.* 1985, 1986, Penridge and Walker 1986, Walker *et al.* 1986, Penridge *et al.* 1987). Spatial influences are quantified as temporally variable fields about individual plants. The field intensity is calculated from prevailing climatic and environmental variables, and is thus dynamic. By summing together all the fields within a community, areas with low or no plant influences can be identified i.e. a spatial definition of safe sites. The concept applies to all plant communities whether intact or disturbed, native communities or agricultural systems.

The EFT concept differs from conventional competition / recruitment models (see Harper 1977 p 111-113), because competitive interactions (field intensity) are used here to decide the survival and growth of cohorts. Since the calculation of field intensity is physiologically based (plant function and prevailing climate and environmental conditions) the fields are temporally variable and recruitment is non-stochastic.

The EFT methodology has been applied in detail to a semi-arid woodland system as cited above. In this paper the ecological field concept is outlined, the dynamic nature of field intensities illustrated, and the possible application to invasability is explored.

The concept of Ecological fields

The concept of ecological fields is detailed in Walker *et al.* (1989) and can be summarized as follows. Each individual plant (which may be any growth-form) is considered to be surrounded by a circular field of influence which varies through time. The extent of the field is defined as the domain of influence (D) and this is determined by plant size (Figure 1). Wu *et al.* (1985) detail the main considerations in defining the influence domain - root spread, crown spread (light reduction) and litter input (nutrient enrichment) and how these can be mathematically combined into a single value per species or plant functional group (a guild of species which function similarly). In practice the domain is set as a multiple of crown diameter (for a perennial grass a suitable value is 2, for a tree 1.5).

The field intensity I (Figure 2) within the domain varies away from the individual plant (the influence surface), and its maximum value for any particular time is a function of the overall environmental conditions for plant growth. Relative leaf growth rates are used to standardize for different growth-forms and plant sizes (growth rates of tree boles are not readily comparable with grass growth). To calculate field intensity, a plant growth index (G) is first calculated as:

$$G = \frac{\text{f actual (H,N,L,T,)}}{\text{f optimal (H,N) f actual (L,T)}}$$

where H = available water, N = available nutrients, L = light, T = temperature
or

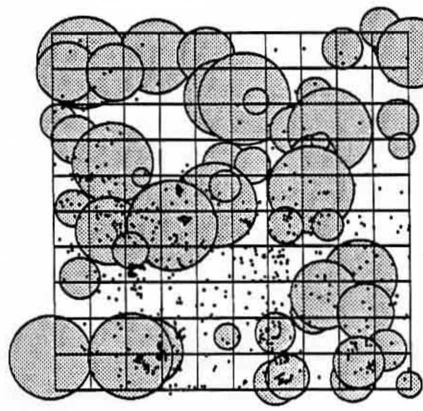

Figure 1 The extent of influence domains for trees (grey) and shrubs (black) within a 50 m x 50 m plot in a *Eucalyptus populnea* woodland. Grass domains are not shown. D is a function of crown diameter per plant. This spatial distribution is used in Figures 4 and 5.

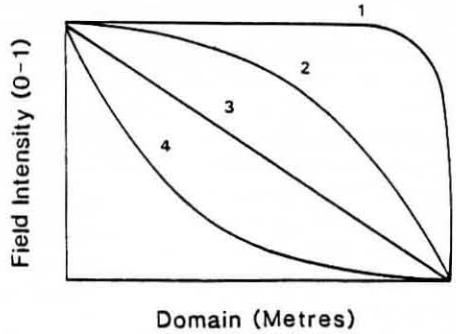

Figure 2 The shape of the intensity/ domain (ID) surface can be varied to simulate different species responses to the fields (#1 represents exclusion within the domain, #4 shows increased tolerance away from the influencing individual).

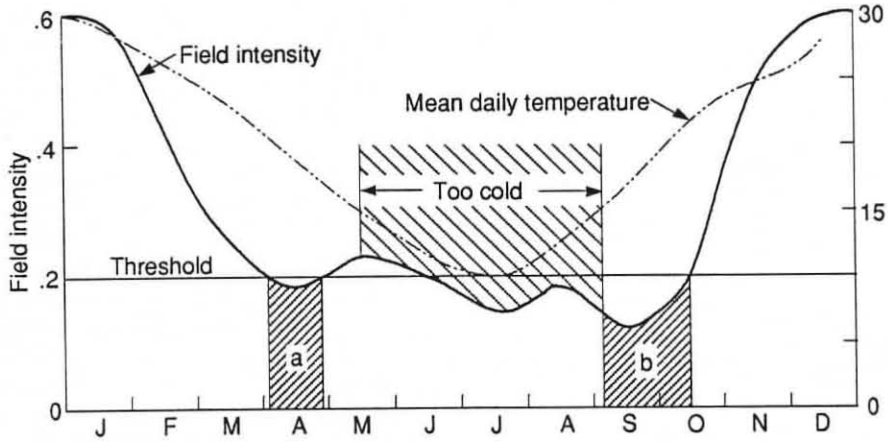

Figure 3 Field intensity is highest in the summer months. Conditions when the temperature is >15°C, and the value for I is <0.2 (threshold) occur in April (a) and September (b). In April favourable conditions do not persist long enough and seedlings perish, in September recruitment occurs.

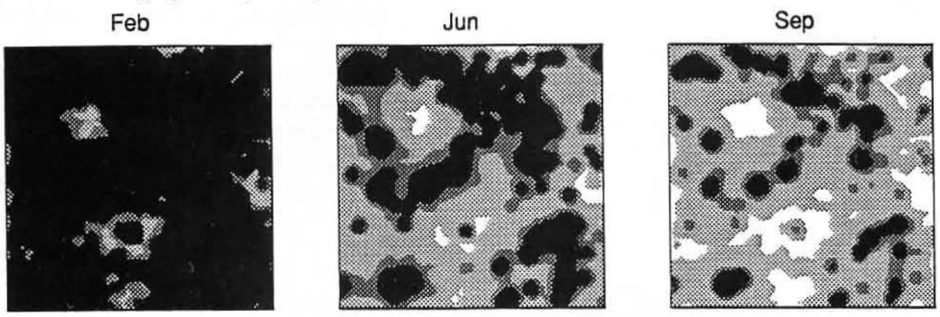

Figure 4 Field intensity about trees and shrubs were calculated at monthly intervals. Sites where recruitment is unlikely are shown in black and grey.

$$G = \frac{\text{ARGR (actual relative growth rate)}}{\text{PRGR (potential relative growth rate)}}$$

Since I (field intensity) is considered to be low under conditions of abundant resource availability, I is related to G as:

$$I = (1 - G)$$

Any plant growth model which combines available resources into a single index can be used to calculate actual and potential leaf area growth rates. The growth model developed as part of the EFT project is described by Sharpe *et al.* (1986).

The shape of the influence surface can be varied to provide a range of possible plant functional responses to fields (exclusion through to facilitation Figure 2). For simplicity a linear decline in field strength away from a plant is used and where overlap occurs between fields, field strengths are additive. (This is a simplification of EFT as outlined in Walker *et al.* 1989).

Survival (S) of an individual is determined on a species basis by:

(*a*) a field intensity threshold (based on the species growth response to water, light, nutrients and temperature) above which the seedling is under stress. In the example (Figure 3) this is set at 0.2 (scale 0 - 1)

(*b*) the length of time the seedling can withstand the stress. In the example the seedling dies if the threshold value persists for four weeks.

Plant functional attributes (germination characteristics, responses to light, water, nutrients, salinity etc) are entered into a look-up table. Here the intent is to present a simple illustration of EFT and we do not deal with the broad issue of how to define plant functional types (see Wu *et al.* 1986, Walker *et al.* 1989).

An illustration of the invasion of a woody weed into a woodland.

The illustration attempts to predict the spatial extent and magnitude of the recruitment of *Cassia nemophila* into a poplar box woodland at Wycanna in South West Queensland. This *Cassia* species is considered to be a "woody weed" in large areas of poplar box lands (Beeston *et al.* 1980). The two rules applied are -

1. *Cassia* seed germinates when the mean daily temperature is above 15°C;
2. *Cassia* seedlings die if moisture in the top 2-5 cm of soil drops below permanent wilting point at any time during the first four weeks of germination (high water stress after germination).

A hypothetical situation to illustrate application of these simple rules is given in Figure 3. Figure 3 shows the weekly variation in field intensity and mean daily temperature. The field intensity (I) threshold is set at 0.2 (on a scale 0 - 1) and the time when the mean daily temperature drops below 15°C is shown. Field intensity is generally high during the summer months and drops below the threshold at times during spring, winter and autumn. The temporal "recruitment windows of opportunity" - *a* and *b*, for *Cassia nemophila* recruitment are indicated. Above the stress threshold value, the shrub seedlings are under stress, and can survive in this high stress condition for 4 weeks. Thus in this illustration, germination event (*a*) fails to recruit new plants whereas event (*b*) results in successful recruitment.

The identification of the spatial location and magnitude of *Cassia* recruitment is illustrated in Figure 4 and Figure 5. Here the field intensities (I) within a 50 x 50 m poplar box woodland plot were calculated at monthly intervals. The spatial locations of plants and the climatic data are for a woodland plot located at Wycanna (28°58'S, 149°50'E) in South West Queensland. The process is in two parts.

1. In Figure 4 the high intensity fields (shown as black and grey) indicate for the months of February, June and September the areas where successful recruitment is unlikely. The white areas indicate the sites where *Cassia* recruitment is possible.
2. The recruitment sites for *Cassia* are shown more clearly in Figure 5 in which the temperature and field intensity constraints are applied (mean daily temperature > 15°C, I < 0.2), and the extent of recruitment shown in black. Recruitment occurred in April, but seedlings have virtually all died by August. Recruitment again occurs in September, and although losses are indicated, some plants successfully recruit.

In this case a small "invasion" has occurred. But, slightly different conditions, particularly following the April germination could result in a major "invasion". The model can be modified to produce such scenarios since this requires only the modification of the functional attributes and the climatic / environmental conditions.

Discussion

The purpose of this paper has been to present the idea of applying EFT to plant invasions, rather than present validation studies. Validation of any ecological concept is usually difficult, for EFT some attempts are described in Walker *et al.* (loc. cit). The importance of exploring new ideas to model plant community behaviour is heightened by the pressing need to predict plant community responses to disturbances, especially in native grazing lands, and possible responses to global climatic changes. Even minor changes to seasonal rainfall patterns could result in invasions of undesirable species. The question is how to predict such invasions. Stochastic methods generally lack any mechanism and depend on observations which may no longer apply in a changed situation. An alternative non-stochastic approach presented here uses an environmentally-driven physiologically-based method, and characteristics of the plant species to decide recruitment. This approach has several attractions despite the apparent complexity.

The central thesis on which this application of Ecological Field Theory is based, is that

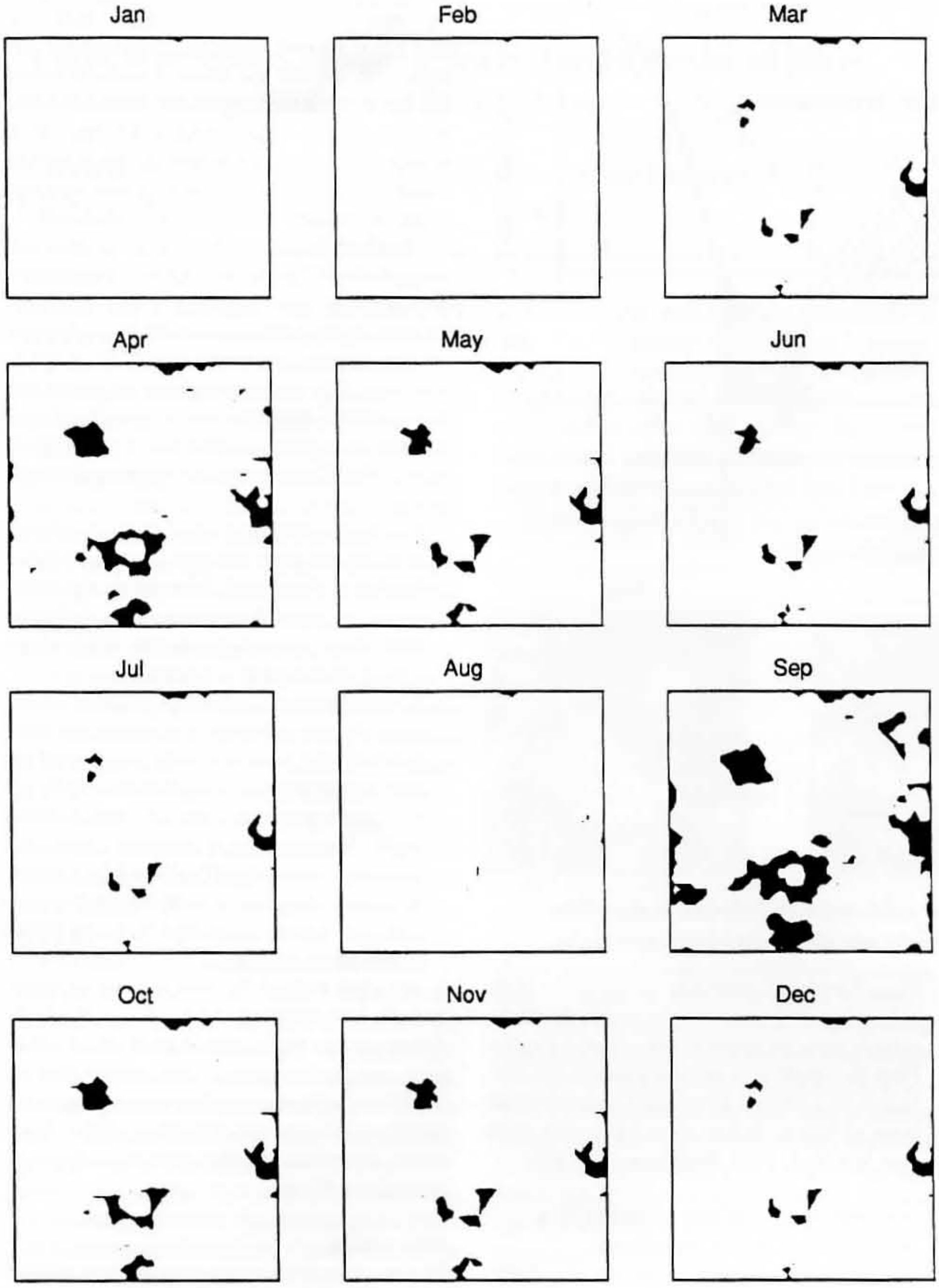

Figure 5 The spatial extent of *Cassia* recruitment into a woodland at monthly intervals during a year. The seedlings that recruited in April died, some survived after germinating in September.

climatic or physical stress will result in resetting the field strengths, and depending on the phenology of the available plant species, new species mixes will result. The actual changes in community composition are deemed to be primarily driven by competitive interactions and this represents the response mechanism to change. Clearly this thesis will not hold for all systems, but may be generally true for semi-arid systems which occupy a significant proportion of terrestrial ecosystems. The idea that competitive interactions drive succession is not new, indeed it is one of the first concepts developed in plant ecology (see for example the work of Cowles 1899, Clements 1916). However, the tendency has been to be contented with descriptions of change or consider recruitment and death as stochastic events. EFT offers a possible beginning to introduce some mechanisms into community responses to stress.

Some problems as well as advantages are apparent in the concept. A possible problem is obtaining field data about spatial arrangements and sizes of plants necessary as input into EFT. These data are tedious to obtain, and very few studies exist at the community level which track plant spatial locations through time. A way around this input problem is to simulate likely spatial distributions and mixes of plants. Such a procedure is described by Penridge *et al.* (1987) and Wu *et al.* (1987). This procedure enables various scenarios to be tested as small plots. Plot size for the EFT version described can be a limitation since it is a function of computer power and tends to be limited to about 5000 individuals. This limitation can be overcome by considering for example grasses as leaf areas per m^2 rather than as individuals. Presently studies are in progress to investigate the use of thermal and multispectral imagery at pixel sizes of 5 x 5 m up to 1 x 1 km as input for applications at regional scales (Jupp *et al.* 1990).

The major advantage of the EFT approach is that it is possible to include changes to the overall environment or spatially variable resources into the model. These aspects are considered in the RESCOMP model described by Penridge *et al.* (1987). An example of the consequences of changing environmental conditions has been described by Braunack and Walker (1985). They examined the impact of domestic animal grazing on soil structure, and demonstrated that grazing resulted in lower water infiltration rates, and hence less available water. Changes to the water balance can be included in the resource part of the calculation of field strength. An ability to consider changes to the overall resource seems vital to any plant community dynamics model and is included in the EFT concept.

The EFT idea is in its infancy, but seems to have the right ingredients to define outcomes in terms of population changes which depend on changes to resources and spatial interactions.

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