The dynamics of invasion as a function of landscape connectivity

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Summary In this paper we investigate the role that landscape connectivity plays in facilitating plant invasions. Our goal was to describe the effect of local and long-distance dispersal on population spread at the landscape scale. For this we used a graph theory framework, and described the spatial spread of a plant invader in terms of a network. Our network description captured both the phase change (described by percolation models) and increased spread rate resulting from long distance dispersal. The difference in dispersal potentials is presented as a possible explanation for the lag phase (i.e. the initial population growth phase, during which population numbers remain relatively constant prior to rapid spread in the landscape) seen in some invaders and we suggest that locally dispersed plants will be more sensitive to this phenomenon than plants that have long distance dispersal mechanisms.

Keywords Graph networks, landscape modelling, percolation, plant invasions.

INTRODUCTION

If we are to better understand and predict the ingress of invasive plants into natural communities we need to have general rules of invasion. However, the interactions of plants and their environment is complex, and simple rules are hard to find (Brown *et al*. 2002). In this paper we focus on the role that landscape connectivity plays in facilitating plant invasions.

The spread of a plant across a landscape is a function of the dispersal mechanism of the plant and the geographic distribution of suitable habitat in the landscape. The plant will spread, or traverse, across the landscape if the patches of suitable environment are connected by the dispersal mechanism of the plant.

One method of investigating how the connectedness of a landscape influences spread is the use of percolation theory (for a good review of complex spatial ecological interactions, including percolation theory, see Green and Sadedin 2005)). Percolation models have the defining feature that the point at which the landscape is traversable occurs abruptly as the amount of suitable habitat increases. This phase change can be visualised if we imagine a square grid of white tiles where we randomly change white tiles to black. As the number of black tiles increases, the isolated black tiles begin to form into patches, and each additional black tile connects patches together until the grid changes from being black tiles surrounded by white tiles to being white tiles surrounded by black. At this point each black tile is connected to every other black tile in a large interconnected patch. Percolation models link the extent of spread of an invasive organism with the level of landscape connectivity and thus with habitat fragmentation (With 2002). The models also show that plants with long-distance dispersal are better able to spread in a more fragmented landscape. However, a limitation of percolation models is that they are confined to simulating the effect of local connections. One common feature of plant dispersal that is not easily incorporated into percolation theory is the effect of rare long distance dispersal.

The effect of long-distance dispersal is predicted by the theory of nascent foci (Moody and Mack 1988). Nascent foci refer to the spread of plant populations from new growth patches. Plants that propagate by short distance seed dispersal tend to grow in patches. A long distance dispersal event increases the growth rate, as it allows growth to occur away from the patch.

A type of model that can incorporate long distance dispersal within a percolation type framework is a network model. A network node describes a plant invasion as the movement of a plant between connected patches of landscape, expressing the dynamics of invasion in terms of a 2D graph where the landscape patches are nodes and the dispersal events are the connections linking the nodes.

In this paper we construct a network model of plant invasion and test the effect of long distance dispersal on the onset of a connected landscape.

MATERIALS AND METHODS

The spatial model of plant invasion is a two dimensional grid of cells, each of which can contain a plant. The plant can spread throughout the matrix if it is connected to an empty cell that is suitable for its establishment. The cells are connected by local links to their immediate neighbours and also by wider connections to cells chosen randomly from the rest of the matrix, representing long distance dispersal. The connections to other cells are made when a cell becomes occupied. The patterns of these connections are analysed when the simulation stops in order to calculate the extent and speed of invasion.

The computer program, written in JAVA, is based on a simple cellular automaton model. The habitat space is described by a matrix of 64 × 64 cells. Each cell of the matrix holds two Boolean values, occupancy and suitability. The landscape structure is defined by the fraction of the landscape that is suitable. This ranges from 10% to 100% in the experiments. The distribution of suitable cells in the matrix is random. Each cell also contains a list of other cells that it is linked to. We compared the invasion pattern of a hypothetical plant that has only local dispersal (each cell is connected to its four immediate neighbours) with one that has approximately 13% of its seed more widely dispersed (where a cell is connected with an other cell chosen at random from the complete matrix).

RESULTS AND DISCUSSION

Extent of invasion Our model suggests that invasive plants that lack long distance dispersal mechanisms will only invade landscapes where at least half of the landscape is suitable (Figure 1). Furthermore, invasion exhibits the previously identified phase change of the landscape becoming abruptly traversable as the amount of suitable habitat exceeds 50%. Where there is long distance dispersal the landscape is traversable at a lower value and the phase change in ability of the landscape to be traversed is less apparent (Figure 1).

These results suggest that plants that are predominately locally dispersed will be more sensitive to habitat fragmentation than those with long distance dispersal mechanisms. The results also indicate that a small change in the availability of suitable habitat could result in a rapid change in the extent of the spread of the invader. This could be a possible explanation for the lag phase seen in some invader species. If this is a possible contributory mechanism for the lag phase then we predict that locally dispersed plants will demonstrate lags more often than long distance dispersers.

Rate of invasion Figure 2 shows that the invasion rate of the plant with long distance dispersal is much greater than the locally dispersed plant above the percolation threshold (approximately 60% of habitat is suitable). The invasion rate for locally dispersed plants at the percolation point is lowest because of the convoluted traversal path dictated by the spatial complexity of the linked landscape. Above this point the increase in habitable landscape allows for smoother and quicker traversal paths. Below this value neither type of plant traverses across the complete landscape.

The difference in spread rate above the percolation point could be explained by the occurrence of nascent foci. With the local disperser, the patch size increases at the edges as any new growth can only occur into an

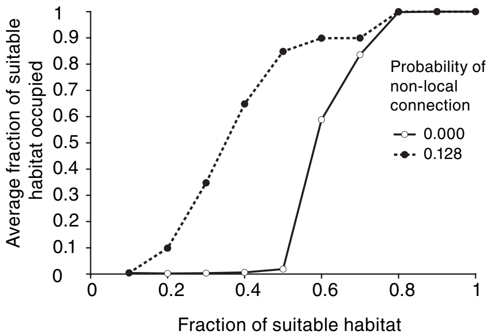

Figure 1. The fraction of suitable cells occupied at the end of a simulation for a series of levels of suitable habitat. The solid line is where there is only local dispersal and the dashed line is where 12.8% of the seeds have long distance dispersal. Each point is the average of 20 replicate runs.

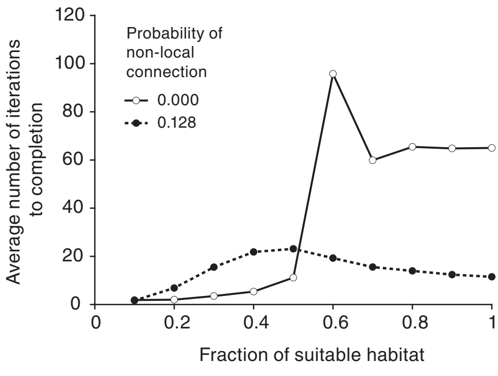

Figure 2. The number of iterations that the simulation takes to cover the fraction of suitable cells occupied at the end of a simulation (see Figure 1) for a series of levels of suitable habitat. The solid line is where there is only local dispersal and the dashed line is where 12.8% of the seeds have long distance dispersal. Each point is the average of 20 replicate runs.

unoccupied area that can be reached by short distance seed dispersal. The growth of a patch is therefore constrained by the growth rate of the plant and the total available area that the seed dispersal can reach. When the patches are small, the relative area of the growing edge (the surface area) is large. As the patch increases in size, the size of the edges with respect to the bulk of the patch area is smaller. One large patch will grow more slowly than several small patches of the same area. A long distance dispersal event will create a new patch. The new patch or nascent focus increases the growth rate of the total population and in turn becomes a potential source of new dispersal events. This too produces an exponential increase in the growth of the population.

Long distance dispersal is increasingly recognised as a driver of invasion spread speeds (Nathan 2005) and it has been suggested that some features of long distance dispersal vectors, such as frugivores and wind, can be targeted for management (Gosper *et al.* 2005, Buckley *et al.* 2005, 2006). We highlight here that the interaction between landscape structure and long distance dispersal is important for predicting and managing invasions. Lag phases and sudden rapid spread are both predicted by this model. We expect that modelling approaches combining landscape heterogeneity with long distance dispersal will provide valuable tools for understanding and prioritising invasive species management at a landscape scale.

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