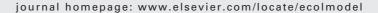
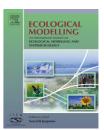


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Cost distance defined by a topological function of landscape

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ABSTRACT

Distance is a basic concept in the domain of animal species motion. Cost distances, rather than Euclidian distances, are more and more used in order to have a more realistic measure, on the basis of resistance values assigned to each landscape class. We propose here a method to compute resistance values by using topological functions of landscape, i.e. by taking account of the proximity of habitat/non-habitat edges, with continuous functions. An example is given when comparing cost distances and the propagation of water vole in the massif of Jura (France). The comparison with usual cost distances gives information about the ecological assumptions. The results show also that the statistical behaviour of the distances depending of the parameters of the functions allows to precise the influence of edges in terms of spatial range.

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1. Introduction

Distance is a basic concept inherent to any geographical space. This notion is a key factor in population ecology and especially in animal movement analysis. In the well-known theory of "isolation by distance" (Wright, 1943), it is considered a central factor playing of role on species invasions or species extinctions. According to this theory, the genetic difference between populations increases with geographical distance when considering a spatial scale higher than the average dispersal distance of the species. The relationship between genetic distance and geographical distance (Rousset, 1997, 2000) is then a proxy used to infer the individual movement ability of a given species (Arter, 1990; Michels et al., 2001; Arnaud, 2003; Coulon et al., 2004; Berthier et al., 2005; Broquet et al., 2006). In landscape ecology, spatial distance is of a primary importance in the concepts of connectivity and fragmentation (Forman

and Godron, 1986; Forman, 1995). Distance is also explicitly included in the formulation of some landscape metrics such as the proximity index proposed by Gustafson and Parker (1994) and in the use of graph theory applied to the spatial relations between landscape patches (Urban and Keitt, 2000; Bunn et al., 2000). The application of diffusion-reaction models in the context of population movements (Turchin, 1998; Okubo and Levin, 2001) requires the use of the distance between places and a central point (as a "release point"). All these examples of analysis based on the notion of spatial distance show the great importance of its measurement.

Euclidian distance, "as the crow flies" when applied to the flat space of maps, is the simplest measure of a distance. However its use assumes a neutral spatial framework, which is not very realistic when representing effective spatial accessibility. In the context of animal population movements, the assumption of a homogeneous space where all places are

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equally accessible is rarely justified (Matthiopoulos, 2003): the habitat of the studied species, the configuration of habitat patches, resources, corridors or displacement constraints lead to a very heterogeneous space and finally challenges the relevance of Euclidian distance. Following these observations, several authors have shown the interest of least-cost distances (or cost distances) that take into account the spatial heterogeneity. These distances are computed from raster data only (for example from a given cell to a target cell) and allow to allot a movement resistance value to each landscape class called a "friction". Cost distances are sometimes called "effective distances" (Ferreras, 2001), in contrast to the Euclidian distance.

The use of cost distance computations is more and more popular in ecology (Knaapen et al., 1992; Yu, 1996; Pain et al., 2000; Bunn et al., 2000; Halpin and Bunn, 2000; Ray et al., 2002; Chardon et al., 2003; Adriaensen et al., 2003; Ray and Burgman, 2006), since they are implemented in several GIS softwares (ESRI, 1996, 2001; Eastman, 1998; Ray, 2005). The choice of the resistance values assigned to each landscape class is usually based on a specific knowledge of the mobility behaviour of the studied population. A resistance of 1 is quite often assigned to the habitat class and to the displacement corridors; a higher level is given to the other classes in relation to their degree of "hostility" (presence of potential predators) or their ability to limit the movements (physical barriers, lack of resources).

Verbeylen et al. (2003) have shown a simple method to determine an optimal combination of resistance values when using the cost distance in prediction model of species abundance. However, the assignment of uniform resistance values to all landscape classes implicitly means that a given landcover class involves a uniform displacement behaviour. This is in contradiction with the well-known "edge effect" in ecology (see for example Paton, 1994; Reese and Ratti, 1988; Fagan, 1999). Following this effect, the proximity to different landcover classes can lead to a modification of this behaviour for several reasons: change of accessibility to resources, increase of predator risk, and so on. For example, for a species subject to predators living outside its habitat, the land-cover class defining this habitat does not necessarily correspond to a uniform context of mobility, because of the varying ability of predators to reach these areas. In an ecological context where the main moving factor of a given species is the accessibility to resources, the inhospitable land cover classes may be partially crossed by the individuals, provided they remain near the boundary, because in this case their resources remain accessible.

In consequence, we argue that proximity to the limit between hospitable and inhospitable areas can play a great role in the permeability of landscape to animal movements. However, the classical approach of cost distances does not take this phenomenon of progressive permeability into account: it simply replicates the discrete structure of land cover classes in the spatial distribution of resistance values. The aim of the present paper is to show that a specific method of allocation of resistance can be implemented in order to improve the relevance of cost distance when the limits between certain land cover classes play an effective ecological role.

Starting from a simplified landscape divided into two classes – habitat (H) non-habitat or inhospitable (NH) – a method is proposed to assign variable resistance values to

each class. Such values are defined by a function of the position in relation to the boundary between H and NH and by applying what we call "a topological function of landscape". An additional class designated "neutral class" or N is added to include areas which are not under the influence of the previous boundary. After the presentation of the data set and the used method (2) we will show the results obtained in the context of the spread of a rodent population in a part of the Jura massif (France) (3).

2. Materials and methods

2.1. Research context and data set

In the Jura massif, the grasslands are regularly swarming with a rodent species, the common vole (Arvicola terrestris). The spread of the vole populations makes a travelling wave with a period of about 5 years (Giraudoux et al., 1997). This travelling wave ruins the grasslands (Quéré et al., 1999) and promotes the transmission of diseases (Delattre et al., 1998). Furthermore, the use of pesticide leads to many environmental consequences especially by hitting vole predators (Delattre et al., 2000). In this context, biologists and geographers seek to understand the role of landscape structures on the vole spread. As several epicentre zones have been identified (Duhamel et al., 2000), we focus here on the "plateau of Nozeroy", a zone influenced by a single epicentre in order to analyze the spread phenomenon without interferences.

This zone is a plateau of approximately 200 km² composed of a matrix of grassland surrounded by large forests of conifers, which may be considered as almost impassable barriers for vole populations (Fig. 1). Different spatial configurations of grasslands are present in the plateau: certain parts contain very large and continuous grassland patches (openfield) whereas other parts can be considered as bocage structures, i.e. fragmented by hedges and some linear forest elements. The relief is rather homogeneous, at an altitude ranging between 700 and 900 m and without significant topographic accidents.

Starting on April 2002, estimations of A. terrestris density were done every 6 months in a set of cells of observation in a regular grid of $1\,\mathrm{km^2}$. One cell out of two was analyzed, giving a total of 92 sites of observation. For each site, the density was estimated on the basis of vole tumuli count along two 250 m diagonal segments (Fig. 2a). Using this count, a surface index, expressed as a percentage, was calculated as described in Giraudoux et al. (1995); a resulting value of 0 means the absence of vole and a value of 100 means a maximal vole density.

This paper analyzes the initial phase of the invasion of the plateau by the A. terrestris. At the start of the observation (April 2002), the high densities are located in a very small area in the north of the zone. The unique site of observation with the maximal value of 100 is considered here as the local epicentre of the diffusion (Fig. 2b). The challenge is to explain the spatial distribution of densities at the next date of observation (September 2002) through a function of spatial distance from the epicentre. As different types of spatial distance may be used (Euclidian distance, cost-distances), the resulting spa-

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