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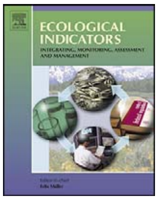

A graph-based approach to investigating the influence of the landscape on population spread processes

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ABSTRACT

Modelling of landscape connectivity is a key point in the study of the movement of populations within a given landscape. For studies focused on the preservation of biodiversity, graph-based methods provide an interesting framework to investigate the landscape influence on population spread processes. Such an approach is described here, based on the mapping of landscape categories in habitat patches, including a diachronic data set describing the population spread within the habitat patches. A minimum planar graph was built by computing spatial distances between all pairs of neighbouring patches. From this structure, two types of analysis are proposed: one focused on the links of the graph and consists in correlating spatial distances and gap indicators computed from the diachronic data. The other was based on the correlations between population data and connectivity metrics at the patch level. As an example, this approach was applied to the spread of the fossorial water vole on the Jura plateau (France), with annual population data covering eleven years from 1989 to 2000. Link analysis allowed to find an optimal set of resistance values used in the least-cost distances computations, and thus to build a relevant graph. From this graph, patch analysis displayed a cyclic correlation between a metric based on potential dispersal flux and the population density, outlining the strong role of landscape connectivity in the population spread. The present study clearly shows that landscape modelling and graph-based approach can produce parameters which are consistent with field observations and thus pave the way to simulating the effect of landscape modification on population dynamics.

1. Introduction

Landscape connectivity is recognised as a key element of biodiversity, expressing the response of organisms to the physical components of landscape (Taylor et al., 2006). As movement is a vital function of most species, ecology pays great attention to the notion of connectivity. Biological invasions (e.g., spread of pest species) may occur as the result of favourable landscape configurations if the diffusion process proves to be landscape-dependent and if the habitat patches are well connected (Minor and Urban, 2008).

Many studies have been undertaken that address the issue of landscape connectivity in the case of spatially explicit habitat (With et al., 1997; Tischendorf and Fahrig, 2000; Urban and Keitt, 2001). The goal is to model functional connectivity by considering the landscape structures and the behavioural responses of a given species (Calabrese and Fagan, 2004; Taylor et al., 2006). Several modelling approaches are available to quantify this potential connectivity, such as the metapopulation incidence function model (Hanski, 1994) and the spatially explicit population model (Conroy et al., 1995). As these models work from a large set of input data, their practical application present challenges that may be overcome by applying graph theoretic approaches (Urban and Keitt, 2001). Numerous studies used this approach most recently to identify the most strategic areas for the preservation of species (Minor and Urban, 2007, 2008; Saura and Pascual-Hortal, 2007; Fall et al., 2007; Galpern et al., 2011).

Different models can be used to represent biological invasions. They include analytical models such as reaction-diffusion equations (Okubo and Levin, 2001; Hastings et al., 2005), which provide efficient expression of the process but restrict the investigation of ecological and landscape factors. In particular, questions about landscape connectivity seem difficult to answer using this type of approach. Biological invasions may be modelled by means of individual-based simulations (e.g., Wadworth et al., 2000), which allow for the use of a stochastic approach with the inclusion of detailed parameters. Although this approach is becoming more practical with the recent increase in computing power, it remains difficult to use for landscape planning at a regional scale. As for

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species/community conservation, the modelling of landscape connectivity to answer questions regarding biological invasions may take advantage of graph-based approaches.

Applying graph-based methods in landscape ecology requires the researcher to first model the landscape structure as a graph. Then, from this representation, patch-based connectivity metrics are used to quantify the importance of each patch in relation to the whole structure (Saura and Pascual-Hortal, 2007). To be validated, the graph and the values provided by these metrics must be compared to empirical data (Urban et al., 2009). Regarding validation, Galpern et al. (2011) have listed several example comparisons according to the nature of the empirical data. Accordingly, the methods that are found valid to correlate presence/absence data or telemetry data with the results provided by connectivity analyses are usually based on distances between the observed individuals and the closest patch on the graph, as in O'Brien et al. (2006) and Minor et al. (2009). These methods cannot be applied in the case of data describing the spread of a species because species spread is a population-level phenomenon that is described by a specific data structure. Mass movements that characterise an invasion are often easier to capture from multi-temporal densities observed at a series of points than through individual trajectories (Hastings et al., 2005). This approach, which is based on diachronic data, explains the need for an adapted statistical procedure.

This paper deals with the application of graph-based methods used in landscape connectivity modelling to cases of biological invasion described by diachronic data. From the landscape graph, two successive stages are proposed: (1) a link analysis, in which several metrics defining the spatial distances are compared and selected according to their fit with indicators of synchrony; (2) a patch analysis, in which patch-level connectivity metrics are linked to the local kinetics observed in habitat patches on a timeline. The spread of the fossorial water vole (*Arvicola terrestris*) in the plateau of Jura (France) serves as an example for this presentation.

2. Methods

2.1. Data preparation and methodological choices

2.1.1. Identification of habitat patches

The application of graph-based methods to the study of landscape connectivity can start from a raster map in which the habitat of the species under study and all of the elements assumed relevant to a particular behaviour are defined in categories. The first step in creating a category consists of defining the habitat patches, which will be the nodes of the graph. In general, it is simply a matter of identifying clusters of adjacent pixels belonging to the habitat category. However, the habitat patches do not correspond to all the areas classified as habitat if one assumes that a patch has to include a core area separated from the matrix by an edge zone, according to the species needs. As proposed by Vogt et al. (2007a, 2007b), pre-processing of the landscape map using a morphological spatial pattern analysis (MSPA) allows one to distinguish between the habitat patches and other favourable areas containing no core. The morphological categories provided by this method have to be re-classified according to the ecological assumptions linked to the focal species (see, for example, Vogt et al., 2009). This pre-processing produces a map defining a habitat patch category.

To integrate a diachronic analysis within the graph structure, the habitat patches have to be associated with multi-temporal data describing the presence or the density of the species. This step involves data preparation, which varies according to the context of the analysis and the nature of the data collected for the spatial entities. In this paper, we do not develop the different possibilities. We remain in the generic framework where a large number of the habitat patches (but not necessarily all of them) are associated with density data acquired at different dates.

2.1.2. Spatial metrics selection

All the habitat patches will be considered nodes, preferably defined as two-dimensional entities rather than points. Depending on how the links are defined between these nodes, several types of spatial graphs may be built from the same set of habitat patches (Galpern et al., 2011; Dale and Fortin, 2010; Fall et al., 2007). A first basic parameter of the links is the spatial metric used to measure the distance between patches, usually edge-to-edge in the case of two-dimensional nodes. One has to choose between (i) Euclidean distance, a spatial metric resulting from a binary definition of landscape (habitat versus non habitat), which may be sufficient in certain cases (Galpern et al., 2011) but which more often limits the investigations of species-landscape interactions and (ii) least-cost distance, also known as effective distance, which allows for the inclusion landscape heterogeneity in spatial metrics by attributing a resistance value to each landscape category (Ray et al., 2002; Adriaensen et al., 2003).

2.1.3. Graph selection

In most of the recent studies, the links of the landscape graph are defined as the pairs of patches separated by a distance that is less than the species-specific maximal distance of dispersion. However, before this thresholding procedure, one must choose the graph topology. Two main topological possibilities are available: (i) the complete graph, potentially including all the links, (ii) the minimum planar graph (MPG), i.e., a subsection of the complete graph in which a link cannot cross another link (Fall et al., 2007). The complete graph is more often used because the MPG is considered a simplification of the complete graph (Galpern et al., 2011). Nonetheless, this simplification does not affect certain connectivity metrics derived from the graphs. For example, patch-level metrics including a distance-decay effect, such as the F metric (see Section 2.2), yield similar values when intra-patch distances are taken into account and when computations are based on a shortest path algorithm.

When analysing the influence of a landscape on population spread and including data in the graph structure, the choice of the topology has to take into account other aspects regarding the context of the analysis:

1) The use of the complete graph can lead to spatial autocorrelation when an analysis involves the paths linking the patches. By taking into account every pair of patches within the limit of the maximal distance threshold, the complete graph is likely to overlay several paths, resulting in over-representation of some of the landscape elements. This spatial autocorrelation, due to the graph topology, is different than the autocorrelation naturally induced by the spread phenomenon.
2) When the dispersal range of the species under study is short compared to the distance between patches, and when patch density is relatively high, it is likely that spread will occur from a patch to its nearest neighbours.
3) The density of the data describing the spread process may influence the analysis design. With sparse data, i.e., if only a few patches are documented in the study area, a majority of links will resist analysis because they will connect to at least one undocumented patch. In this case, the complete graph is the only possible option because it contains all the links connecting two documented patches, which may constitute the key elements to be analysed. Conversely, a high density of documented patches makes the analysis of the MPG possible.