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FORUM

The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale

Jean-Paul Metzger (*) and Henri Décamps

Centre d'Écologie des Systèmes Aquatiques Continentaux, UMR C5576, 29, rue Jeanne Marvig, 31055 Toulouse, France.
(*) Present address: *Departamento de Ecologia Geral, Instituto de Biociências, Universidade de São Paulo, CP 11.461, 05508-900, São Paulo, SP, Brazil.*

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Abstract

This paper focuses on the effect of connectivity on biodiversity by proposing a testable hypothesis of a structural connectivity threshold. Evidence of this threshold is supported by percolation theory and by biological models of extinction. Hypothesizing the existence of this connectivity threshold, a conceptual model linking connectivity and biodiversity is presented. We suggested different measurements of connectivity to test the hypothesis of a structural threshold. The identification of this threshold is considered as a practical means to facilitate biological fluxes and optimize species colonization possibilities in designing a policy of conservation biology at the landscape scale.

Keywords: Structural connectivity, percolation, threshold, biodiversity, conservation biology.

Résumé

Ce papier traite des effets de la connectivité sur la biodiversité en proposant une hypothèse testable de l'existence d'un seuil de connectivité structurale. En effet, la théorie de la percolation et des modèles biologiques d'extinction tendent à montrer l'existence d'un tel seuil. En fonction de l'hypothèse soulevée, un modèle conceptuel reliant la connectivité et la biodiversité est proposé. Différentes mesures de connectivité sont présentées afin de tester l'hypothèse du seuil de connectivité structurale. L'identification de ce seuil est considérée comme un moyen de faciliter les flux biologiques et d'optimiser les possibilités de colonisation des espèces dans l'établissement d'une politique de conservation biologique à l'échelle des paysages.

INTRODUCTION

Connectivity characterizes the capacity of a landscape to facilitate or impede movement among resource patches (TAYLOR *et al.*, 1993), and therefore appears as a crucial property for the survival of a metapopulation in a fragmented landscape.

The probability that organisms move between resource patches may be used to measure the connectivity of a species in a given landscape (TAYLOR *et al.,* 1993). However, the measurement of movement probabilities is difficult, expensive and time consuming. Here, we suggest a way to approach landscape connectivity on the basis of an hypothesis that we call the structural connectivity threshold.

Every landscape may be characterized by a degree of structural connectivity for a given habitat (BAUDRY & MERRIAM, 1988). This structural connectivity can be defined and quantified on the basis of interpatch distance, density, complexity, width and quality of corridor networks, density of stepping stones and permeability of landscape matrix ([1]). Specific levels of structural connectivity may or may not satisfy the requirements of a given species depending on the species capacity of movement, demographic potential, minimal area and habitat requirements. In a process of habitat loss, there is a critical threshold where the degree of structural connectivity decreases suddenly and, consequently, the requirements of a large number of species may no longer be satisfied, and extinction rates may increase rapidly (fig. 1). Therefore, conservation of biodiversity, defined here as species diversity, would benefit from an assessment of this threshold by a structural analysis of the landscape.

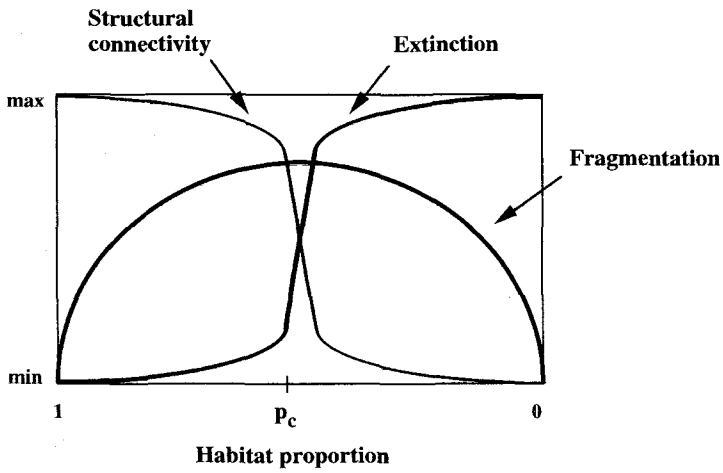

FIG. 1. – Theoretical relations between proportion of habitat, structural connectivity, habitat fragmentation (measured by the proportion of boundaries between habitat and non-habitat units in landscape) and global species extinction. There are critical levels of habitat proportion where fragmentation (*i.e.* local extinction risk) becomes high and connectivity (*i.e.* local colonization probability) becomes low, producing a rapid increase in global species extinction.

([1]) Corridor is a strip of a particular landscape unit (*e.g.* an ecosystem or landuse/cover type) that differs from the adjacent land on both sides (FORMAN, 1995). Stepping stones are ecologically suitable patches where an organism can temporarily stops while moving between habitat patches (modified from FORMAN, 1995). Landscape matrix is the background landscape unit in a mosaic characterized mainly by extensive cover (FORMAN, 1995).

EVIDENCE OF A STRUCTURAL THRESHOLD CONNECTIVITY

A structural connectivity threshold may be assessed first on the basis of the percolation theory (STAUFFER, 1985). According to this theory, rapid changes in size, number and boundary shape (or fractal dimension) of clusters (or habitat patches) occur near a critical probability p_c (or proportion of habitat), where the largest cluster just "percolates", *i.e.* extends from one edge of the map to the other ([2]). The value of p_c for extremely large random maps (with more than 10^9 sites) has been empirically determined to be 0.5928 when clusters are defined only by contacts with the nearest neighbour sites (the four adjacent sites in horizontal and vertical directions), and 0.4072 when the next nearest neighbours (the four diagonal sites) are also taken into account (STAUFFER, 1985). These thresholds have also been confirmed for small maps (with about 10^4 sites) generated by random placement of sites (GARDNER *et al.*, 1987). Important differences in landscape properties occur when maps are generated by random placement of clusters (GUSTAFSON & PARKER, 1992) or by hierarchical structures (LAVOREL *et al.*, 1993), but a critical probability, p_c, is always observed.

If this critical probability coincides with a connectivity threshold (*i.e.* abrupt changes in the capacity of a landscape to facilitate or impede movement), then changes in biological processes have to be expected as suggested by neutral models and biological models of extinction.

Neutral models show that percolation thresholds play a key role in controlling biological fluxes (TURNER *et al.*, 1989; GARDNER *et al.*, 1991). Studying species dispersion, GARDNER *et al.* (1991) concluded that: (1) if the proportion of habitat is above p_c, then landscapes are well connected and no matter how far each species can disperse, all populations (even interior species) will be able to reach a large fraction of available habitat; (2) if the proportion is below p_c, then habitat patches are highly fragmented and a large difference in species abundance and habitat utilization can be produced by small changes in maximum dispersal distance. Species capable of moving greater distances are therefore less affected by local fragmentation. TURNER *et al.* (1989) have shown that the propagation of disturbance was qualitatively different when the proportion of disturbance-susceptible habitat was above p_c. Disturbances occurring only within a habitat (*e.g.* a forest parasite) are favoured by values of p above the percolation threshold. In contrast, disturbances having the capacity of spreading through the matrix or originating in the matrix (*e.g.* invasion of foreign species) are favoured by values of p below the critical threshold. WITH & CRIST (1995), using a simulation model modified from percolation theory, pinpoint critical thresholds of habitat fragmentation at which simulated populations shifted from an initial random pattern of dispersion to an aggregated distribution. These thresholds varied from 20% to 40% of habitat proportion depending on the degree of habitat specialization and the dispersal range of the species. WITH & CRIST's simulation model was empirically verified for two species of grasshopper (*Xanthippus corallipes* and *Psoloessa delicatula*).

([2]) A map is formed by a grid of discrete sites; p is the probability of a site to be considered as an habitat; a cluster is a group of adjacent sites (GARDNER *et al.*, 1987).

Biological models of extinction also indicate the existence of a threshold (McLellan *et al.*, 1986; Franklin & Forman, 1987; Lande, 1987; Naiman *et al.*, 1989; Burkey, 1989; Frankham, 1995; Bascompte & Solé, 1996). A critical range of habitat proportion (or fragmentation level) from which the process of extinction changes rapidly appears in all the proposed models, independently of their limitation and of the chosen parameters. Values of rapid increase (or threshold) in extinction rate vary as a function of biological characteristics of species. In the model of McLellan *et al.* (1986), species with low dispersal abilities and high minimal area requirements show an increase in extinction rate when the proportion of habitat is between 40 and 60% of the landscape. The extinction threshold for species with high demographic potential (*e.g.* high fecundity and survivorship) is about 25 and 50% according to Lande's (1987) metapopulation model. Naiman *et al.* (1989) in a conceptual model propose that biodiversity decreases rapidly when the frequency of ecotones in the landscape increases more than 50%, due to essentially an important increase in interior species extinction. In Burkey's (1989) stochastic model, the probability of extinction varies with different expected growth rates and inter-patch migration rates. In all these cases, there is a critical range of habitat fragmentation where species decline is most rapid. Recently, Frankham (1995) showed that *Drosophila melanogaster, D. virilis* and *Mus musculus* present a threshold relationship between inbreeding and incremental extinction at intermediate levels of inbreeding (*i.e.* at intermediate levels of fragmentation).

AN HYPOTHETICAL MODEL OF BIODIVERSITY LOSS

According to these previous models, single populations present different thresholds of connectivity according to their biological requirements. When the structural connectivity threshold is exceeded, disturbance propagation is increased in the matrix (Turner, 1989; Turner *et al.*, 1989), recolonisation rate is locally reduced (Verboom & Lankester, 1991; Villard *et al.*, 1992) and population connectivity thresholds are exceeded for a large number of species. This supports the hypothesis that a decrease in structural connectivity is at the origin of an increase in extinction rate. Therefore, a model can be developed to link habitat loss and biodiversity by accounting for differences in the structural connectivity threshold (fig. 2). In this hypothetical model, biodiversity varies in a four step pattern. In a first step, a low degree of habitat loss creates new habitats for edge species and globally the biodiversity increases (B1>Bo, step I). The fragments are still well connected and the majority of species occur as a single population. As the proportion of habitat decreases, fragmentation increases and the structural connectivity declines. A metapopulation structure may appear, with local extinction/recolonisation dynamics. Generalists and boundary species disseminate, while species more sensitive to fragmentation become extinct (change from B_1 to B_c in phase II, fig. 2). When the habitat proportion exceeds a critical value (p_c), the fragmentation level reaches a maximum and the connectivity threshold is surpassed (fig. 1). For a great number of species, habitat connectivity becomes too low for recolonization of empty patches to occur and local extinction tends to exceed recolonization. Therefore, biodiversity at a regional level decreases suddenly (change from B_c to B_2 in phase III). For lower proportions of habitat, patches become totally isolated, and a metapopulation

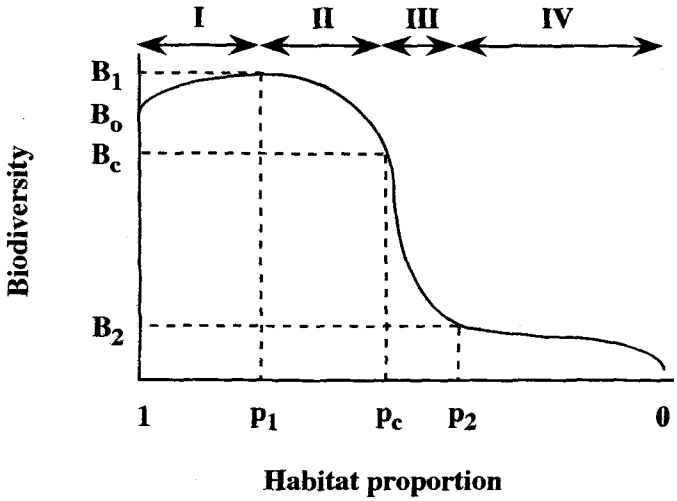

FIG. 2. – Conceptual model linking biodiversity to habitat proportion. This model hypothesizes the existence of a transition phase where abrupt decrease in structural connectivity occurring for a critical proportion of habitat, p_c, leads to an important decline in biodiversity.

structure or dynamics no longer exists (OPDAM *et al.*, 1993). Biodiversity remains low and only generalist and boundary species persist.

STRUCTURAL CONNECTIVITY MEASUREMENTS

The level of a connectivity threshold will vary among habitats and landscapes. Given the diversity of habitat structures and proportions, repeatable measurements of connectivity are needed to perform comparisons.

Percolation thresholds are easily measured and may be considered as a first estimate of structural connectivity thresholds. However, the relationship between percolation and connectivity is not always pertinent. Some landscapes (*e.g.* strongly compacted) are connected but do not percolate (fig. 3A), other landscapes (*e.g.* with linear structures) percolate but are not connected (fig. 3B). Actually, the concept of connectivity is far more complex than the concept of percolation. Factors that determine structural connectivity are not included in the measurement of percolation, *e.g.* the complexity of the corridor networks or the permeability of the matrix.

We suggest that structural connectivity includes three components which must be evaluated separately. A first component is the continuity in the spatial arrangement of habitat areas that can be quantified by a percolation measurement. For this measurement not to be biased by the presence of narrow corridors (fig. 3B), we suggest that it be measured only for interior habitats. There is also a need to measure various degrees of percolation, not only percolating and non-percolating states. These degrees of percolation may be approached by the number of dilations necessary for percolation to appear, as explained in the examples of figure 4. This measurement, that we name "interior habitat percolation degree" (IHP), is useful to distinguish different degrees of connectivity when applied to very fragmented

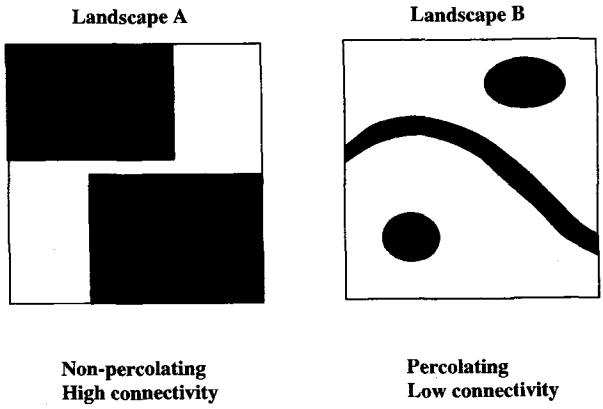

FIG. 3. – Two examples of landscapes where percolation states do not coincide with connectivity degree. Habitat is represented in black.

landscapes, where the proportion of habitats are clearly below percolation threshold ($p < 0.40$).

A second component of structural connectivity is the complexity and the quality of corridor and stepping stone networks (BUREL, 1989; BUREL & BAUDRY, 1989; HENEIN & MERRIAM, 1990; BUREL, 1992; FAHRIG & MERRIAM, 1994). Corridors and stepping stones are usually recognized as playing a key role in facilitating biological fluxes (WEGNER & MERRIAM, 1979; MERRIAM & LANOUE, 1990; SAUNDERS & HOBBS, 1991; SOULE & GILPIN, 1991), in reducing extinction risks (FAHRIG & MERRIAM, 1985; LEFKOVITCH & FAHRIG, 1985; BURKEY, 1989), and in supplying refuges against disturbances (SAUNDERS *et al.*, 1991; LYNCH & SAUNDERS, 1991). Thus, corridors and stepping stones are essential components of the connectivity. Methods for the measurement of these structures rely on the frequencies of various types of hedgerow intersections, the mesh size of hedgerow networks, and the density of corridors and stepping stones in the landscape (FORMAN & BAUDRY, 1984; BAUDRY, 1984; BAUDRY & MERRIAM, 1988; OPDAM, 1988). Such measurements are suitable for landscapes which are highly fragmented or composed of linear habitats (*e.g.* hedgerows, gallery forests).

The third component of structural connectivity is the permeability of the inter-habitat matrix which also controls biological fluxes of some species (WHITCOMB *et al.*, 1976; PREVETT, 1991; DATE *et al.*, 1991; GUEVARA *et al.*, 1992; GUEVARA & LABORDE, 1993). Although KOZOVA *et al.* (1986) and SOULE & GILPIN (1991) give some indications, no measure of permeability has been established formally. Permeability may be measured on the basis of functional distances. In a raster Geographic Information System, it is possible to code every pixel from the image according to its distance (di) to the nearest habitat pixel (fig. 5). The permeability of the inter-habitat units is represented by a coefficient of resistivity (Ri). A unit with low permeability (resistant to organism movement) will be given a high Ri coefficient. On the contrary, a very permeable inter-habitat unit will be given a low Ri coefficient. The resistivity coefficients may be computed empirically or from measurements of species habitat suitability for the different inter-habitat units. The degree of permeability (PMi) is then obtained by multiplying, for each pixel i, the

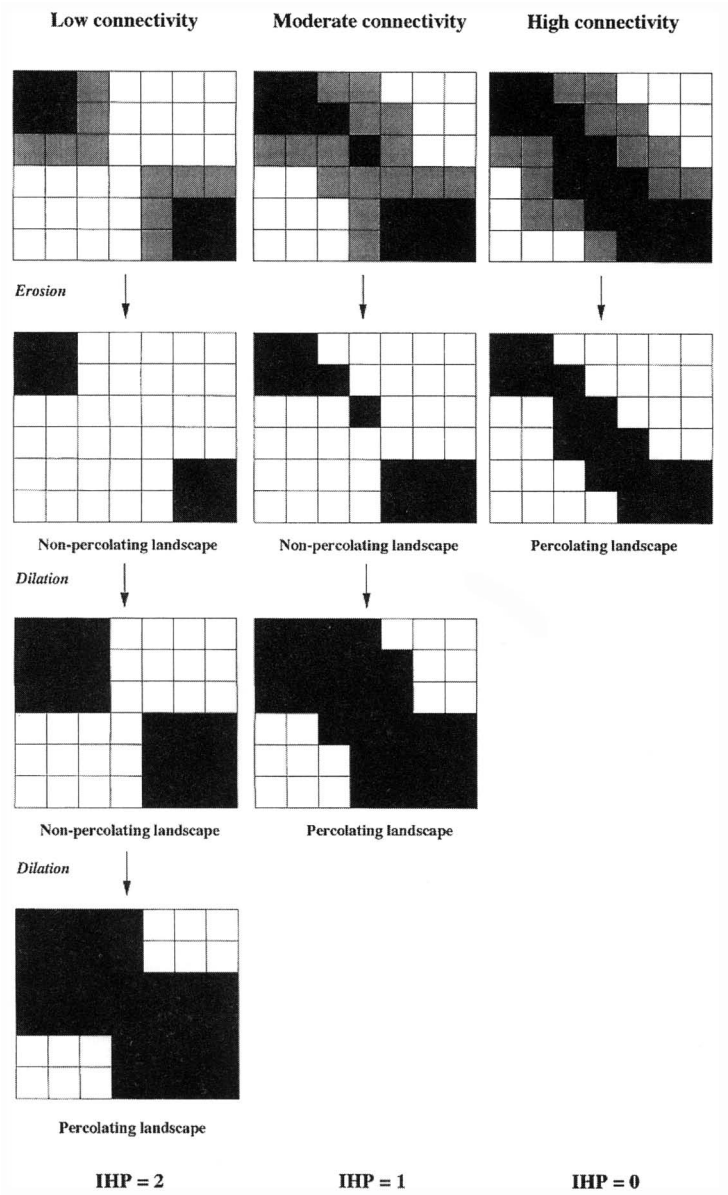

FIG. 4. – Examples of "interior habitat percolation degree" (IHP) measure for three landscapes with high, moderate and low connectivity degrees. Erosion and dilation are basic mathematical morphology transformations (SERRA, 1982). For these examples, the transformations have been done with a moving window of 3 by 3 pixels. Therefore, the initial erosion allows to isolate interior habitat pixels. The connectivity (IHP) is then measured by the number of dilations necessary to obtain a percolation of interior habitat. The greater this number, the less connected is the habitat.
Legend: ■: interior habitat; ▒: boundary habitat.

isolation distances by the resistivity coefficients (PMi=di.Ri). The more PMi is, less permeable is the pixel *i* (fig. 5).

The values of these three components of structural connectivity will vary according to some choices, like landscape grain size, boundary and corridor width definitions, habitat and non-habitat distinction. These initial conditions must be defined in accordance with the biological characteristics of the species considered (*e.g.* habitat requirement, capacity of movement). For example, a very demanding species (*e.g.* an interior species) with low capacity of movement will respond to landscape in a fine grain scale while a less demanding species with high capacity of movement will respond in a coarse grain scale. Landscape studies must be performed at scales appropriate to the species of interest (GARDNER *et al.*, 1991).

The three components of structural connectivity are complementary and enable evaluation of the various aspects of structural connectivity. However, IHP is the most general measure that can be applied to every type of landscape. This index could be initially used to stratify landscapes into areas of different degrees of connectivity.

HYPOTHESIS TESTING

The effect of connectivity on biodiversity needs further investigation. A possible way to test the hypothesis of structural connectivity thresholds would be to evaluate the biological diversity of similar habitats from landscapes having different habitat proportions and, for each proportion, different degrees of connectivity. This would give the degree of linkage between specific diversity and connectivity, independently of habitat proportion. However, such a comparison would ignore whether the connectivity has regularly or irregularly evolved in time from a high to a low degree.

An ideal test of this hypothesis would be to measure biodiversity and connectivity during a process of habitat destruction (*e.g.* deforestation). Although difficult to undertake, such experiments could be designed in areas where landscape structures change rapidly. This is the case of tropical forested landscapes where the annual rate of deforestation is estimated at 155,000 km^2 (FAO, 1993), and particularly in areas of Amazonian forest in Brazil (as Rondônia and Pará States) where the deforestation rate has been very high during the eighties (INPE, 1992; SKOLE & TUCKER, 1993; FEARNSIDE, 1993; SKOLE *et al.*, 1994). In this case, it would be interesting to model how forest management (defined by the size, shape and spatial arrangement of cutting-units (LI *et al.*, 1993)) and human activities (like cattle ranching, commercial logging or settlements along roads) influence changes in the landscape structure, particularly the forest connectivity. The use of spatial simulation models, like the Dynamic Ecological-Land Tenure Analysis model (DALE *et al.*, 1993*a*, 1993*b*, 1994), would be particularly fruitful.

CONCLUSION

The effect of structural connectivity on biodiversity and extinction processes is a crucial issue. If confirmed, the hypothesis of a structural connectivity threshold

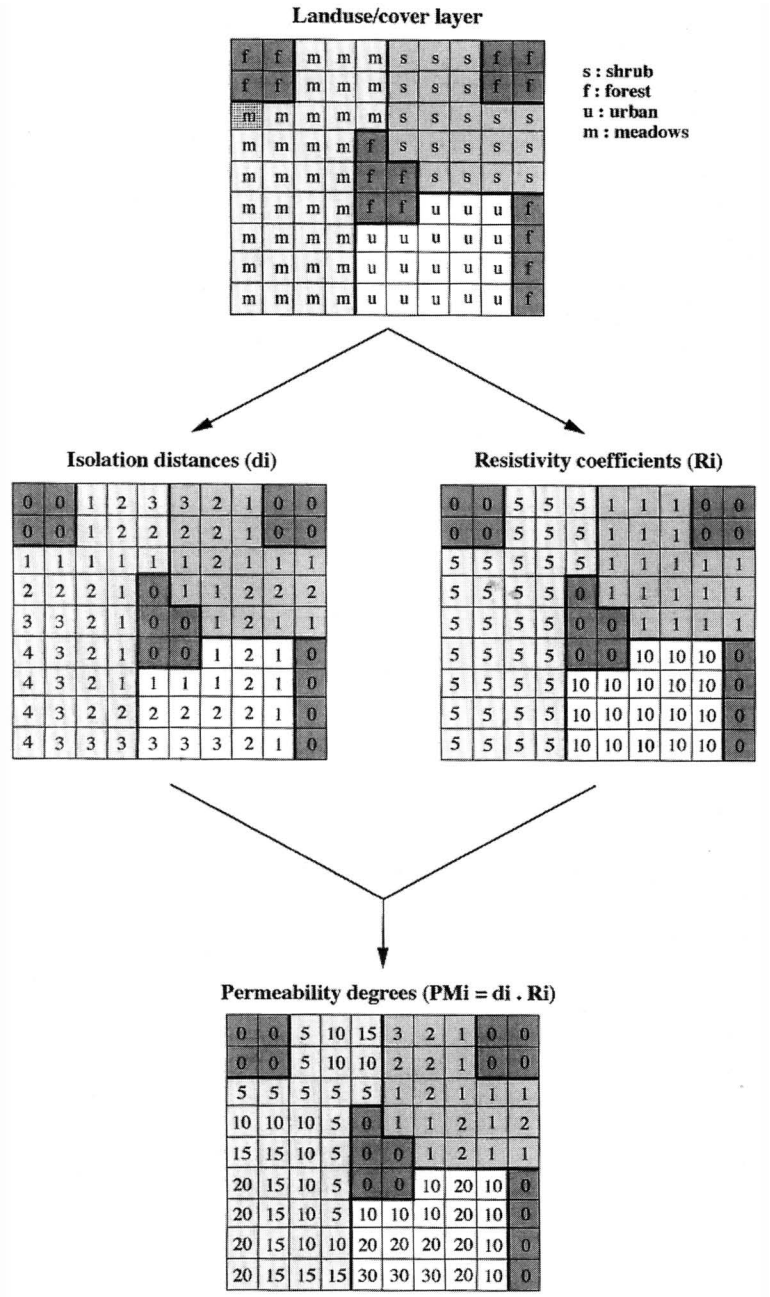

FIG. 5. – Examples of permeability degree (PMi) measurement for forest habitats. Each pixel i is defined by its distance (di) to the nearest forest pixel and by a resistivity coefficient (Ri). The more PMi = di.Ri is, less permeable is the pixel.

may help in setting up a policy of biodiversity conservation. Perspectives of forest management may be considered, particularly in tropical forests. At the present time, the process of deforestation is the most important factor of change in tropical landscapes, and probably the most important issue in conservation biology, given that these forests are supposed to contain more than the half of existing species in the world (WILSON, 1992). We need to understand better the effect of human activity on connectivity as well as the effect of connectivity on the process of species extinction if we are to control the loss of integrity of tropical forested landscapes. Promoting the development of these areas and at the same time maintaining a high degree of connectivity is not unrealistic. It is necessary for management to conserve networks of habitats between natural reserves and to encourage permeable exploitations.

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