



## Landscape cohesion: an index for the conservation potential of landscapes for biodiversity

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### Abstract

In urbanising landscapes, planning for sustainable biodiversity occurs in a context of multifunctional land use. Important conditions for species persistence are habitat quality, the amount and configuration of habitat and the permeability of the landscape matrix. For planning purposes, these determinants should be integrated into simple indicators for spatial conditions of persistence probability. We propose a framework of three related indices. The cohesion index is based on the ecology of metapopulations in a habitat network. We discuss how an indicator for species persistence in such a network could be developed. To translate this network index into an area index, we propose the concept of spatial cohesion. Habitat cohesion and spatial cohesion are defined and measured for single species or, at best, for species profiles. Since species differ in their perception of the same landscape, different species will rate different values of these indices for the same landscape. Because landscapes are rarely planned for single species, we further propose the index of landscape cohesion, which integrates the spatial cohesion indices of different species. Indices based on these concepts can be built into GIS tools for landscape assessment. We illustrate different applications of these indices, and emphasise the distinction between ecological and political decisions in developing and applying such tools.

### Introduction

The importance to biodiversity of the habitat network spatial pattern and of the landscape matrix was raised in landscape ecology in the late 1980s and widely accepted among population ecologists in the last decade (Henderson and Merriam 1985; Van Dorp and Opdam 1987; Merriam 1988; Opdam 1988, 1991; Fahrig and Merriam 1994; Opdam et al. 1995; Tilman and Kareiva 1997; Wiens 1997; Fahrig 1999; Opdam 2002). Empirical and modeling studies of spatially structured populations at the landscape level showed that the spatial pattern of habitat determines the persistence of natural populations (e.g., Harrison et al. (1988) and Verboom et al. (1991), Sjögren (1991), Dunning et al. (1995), Villard et al. (1995), Thomas and Hanski

(1997), Hanski (1999), Thomas and Kunin (1999), Foppen et al. (2000), Vos et al. (2000)). The spatial structure of the landscape matrix, in which the habitat network is embedded, affects the allocation of dispersing individuals to patches of the network (Dunning et al. 1995; Schumaker 1996; Matthysen and Currie 1996; Sutcliffe and Thomas 1996; Vos et al. 2002). Therefore, we consider the landscape (rather than the ecosystem area) as the functional template for biodiversity.

The landscape is also the spatial unit for many human activities. Land use is a dominant factor in determining landscape pattern, which is also the basis for human perception. Therefore, the landscape is also the functional unit for spatial planning (Ahern 1999; Nassauer 1999). Where nature conservation is

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one of the functions competing for space, quantitative tools that relate the spatial conditions in the landscape to conservation goals are needed (Opdam et al. 1995; Opdam and Wiens 2002). Because planning implies decisions about the future, such tools must have predictive power. Because landscapes are planned for biodiversity rather than for single species, the tools must integrate conditions for a variety of species.

The phases of the planning process require different input from ecologists (Opdam et al. 1995; Harms et al. 1993; Opdam 2002); for example: indicators for problem detection in the diagnosis phase, design rules for sustainable habitat networks in the design phase, and tools for assessing the landscape plan. Since landscape planning is an interactive, transdisciplinary activity, simple images and indicators that can be understood by politicians and stakeholders are indispensable. Maps are useful in communication and should be generated quickly. Also, because often appropriate data are not available, the planning practice demands tools that are independent of actual species distribution data. So we must be able to assess a specific landscape pattern for the *potential* to conserve a specific combination of targeted species. Because conservation is about persistence, this assessment of landscape potential should be functionally linked to population persistence (Opdam et al. 2002).

So our dilemma is that we must be able to 'read' the landscape pattern for its potential to conserve biodiversity, whereas species differ greatly in the spatial scale at which they respond to landscape features, as well as in the features they are responsive to (Andr n 1996; Vos et al. 2001; Fahrig 2001). This implies that there is no simple and direct way to transform landscape features into an index for conservation potential. Existing tools with predictive power either are at the species level and too complex to apply in multi-species planning (metapopulation models), or difficult to generalize and depend on distribution data (empirical regression models). Many landscape indices that were published lack an explicit relationship to population processes and neglect the variation of ecological scales (Verboom et al. 1993; Gustafson 1998; Vos et al. 2001; Opdam and Wiens 2002). We propose that the only way to get there is by (1) analysing the landscape pattern separately for various species and (2) integrating the results into some multi-species index. This leaves us with the task of finding a unifying landscape quality measure that allows an ecological interpretation in terms of persistence or viability. We also need a framework to integrate such measures of

individual species requirements to multi-species indicators at the landscape level (Opdam et al. 2002).

We propose a framework encompassing four components:

1. A system of *ecological profiles*, in which species are classified according to essential characteristics of metapopulation dynamics. A system of ecological profiles minimises the number of spatial analyses one has to do, and makes integration from species to multi-species index easier.
2. An index for *habitat network cohesion* (NC), describing the relationship between the essential characteristics of a habitat network (Opdam 2002) and the persistence probability of a species. NC is an index for a single network. Since we often wish to determine whether the landscape allows sustainability, we also need to find a threshold value related to persistence on the index scale.
3. For a particular species, a planning area may encompass more than one habitat network. *Spatial cohesion* (SC) integrates the values of NC of the networks. Whereas NC is a measure of a habitat network, SC is a characteristic of a region.
4. While NC and SC apply for a specific species or ecological profile, we also need an index at a multi-species level. This index, called *landscape cohesion* (LC), is an overall indicator of the ecological quality of a *landscape region* for biodiversity. It is based on an integration of spatial cohesion indices for a set of ecological profiles. Such an index includes notions of what a society feels as values to be conserved, like choice of species, or acceptable risks of extinction.

For the approach of ecological profiles based on ecologically scaled landscape indices, we refer to Vos et al. (2001) and Verboom et al. (2001), Geertsema et al. (2002). The purpose of this paper is to define the three indices as a generic framework (Figure 1) and discuss routes toward application for landscape diagnosis and plan evaluation. However, we do not intend to develop operational methods here. We intend to contribute to building the bridge between process-oriented population knowledge and landscape planning, since we believe that for improving the quality of landscape plans planning concepts should be based on the spatial processes in the landscape (Moss 1999; Opdam et al. 2002). To us, this is the only way toward ecologically sustainable landscapes.

### A theoretical basis for landscape cohesion

A unifying landscape measure requires a unifying theoretical basis. Below, we will explain why we use the metapopulation concept (*sensu* Opdam et al. (1993) and Hanski (1997), Thomas and Kunin (1999)) as a central paradigm. A metapopulation is defined broadly, encompassing mainland-island (one patch in the network is much bigger than the others, Hanski and Simberloff (1997)) and source-sink (some patches are better in quality than others) relationships.

Why do we base our approach on the metapopulation paradigm? In predominantly man-made landscapes, many functions combat for space and sometimes are difficult to combine. Such landscapes appear as checkerboards of ecotopes with different appearances and functions, which are changed due to human land use. If we conceive these ecotopes as a potential habitat network, then the metapopulation is the basis to predict the persistence of species in the network.

An important assumption we make is that spatial configuration of habitat matters in many landscapes under human pressure. With ongoing economic productivity and urban expansion, the spatial density of ecotopes with a conservation focus decreases, while they become smaller and more widely scattered (Figure 1). At the same time the landscape matrix gets increasingly impermeable for organisms that are restricted to these ecotopes. This process is referred to as habitat fragmentation (Opdam and Wiens 2002). Model simulations (Andr n 1994, 1996; With et al. 1996; With and King 1999) indicate a critical threshold in the response of species to ongoing habitat loss. At this *fragmentation threshold* the network population turns into a metapopulation, characterized by temporary absences in suitable habitat patches due to local extinction and delayed reoccupation. With further loss of habitat, the metapopulation passes an *extinction threshold* (Lande 1987; Verboom et al. 1993; Hanski 1997; With and King 1999) and enters a domain of deterministic regional extinction. Below the fragmentation threshold, the configuration of habitat constrains the distribution and persistence of a species. In trying to express this threshold in terms of % habitat in the landscape, (Andr n (1994, 1996); Villard et al. (1999), Vos et al. (2001) and Foppen (2001) showed that this threshold varies greatly between species, but might be expected somewhere below 40% habitat coverage. In many landscapes with a dominant human land use, to many species the

amount of habitat is well below this level. Therefore, landscape planning for nature conservation should focus on the configuration of habitat and relevant elements of the matrix (Opdam 2002).

### Defining network cohesion

For a species to survive in a habitat network, two conditions have to be fulfilled: the dispersal stream across the landscape balances local extinction and recolonization rates, and the total network is large enough to minimise the chance that all local populations go extinct.

The cohesion in the habitat network is the result of the dispersal stream across the landscape and the size of the local populations it links together. All local populations contribute to the dispersal stream, the larger ones more than the smaller ones. The dispersal stream augments with the density of (occupied) habitat in the landscape and the conductivity by landscape elements with relatively high survival chance in the matrix. The stronger the dispersal stream, the higher the proportion of occupied patches. Immigrants may prevent local populations to go extinct and larger and better habitat patches allow bigger and more persistent populations, causing a stronger and more continuous dispersal stream. We propose that network cohesion encompasses the following four landscape components (Figure 2).

- *Habitat quality* is directly related, through population density, to carrying capacity of the patches, to the growth rate of the local populations and consequently, to extinction rate and the intensity of the dispersal stream across the landscape. Below a certain quality level, the population in a patch will go through a process of deterministic extinction (mortality exceeds birth rate), unless it receives enough immigrants from other patches in the landscape.
- *Amount of habitat in the network*. The amount of habitat area has two components: density of the network (amount of habitat per km<sup>2</sup>) and the size of the network (km<sup>2</sup> landscape area over which the network extends). Habitat density is directly related to the size and density of local populations, and consequently to the local extinction rate and the dispersal stream across the landscape. Also, a higher patch density implies shorter average distances between patches, and generates a higher dispersal success.

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|--|--|---|
|  | <b>Habitat Network</b><br>• single network   | <b>Landscape</b><br>• multiple networks   |
| <b>Ecological profile</b><br>• single species / ecological profile<br>• single ecosystem | <b>Network cohesion</b><br><i>Sustainability of habitat network</i><br>(yes or no) | <b>Spatial cohesion</b><br><i>e.g. number of sustainable networks, % patches belonging to sustainable network</i> |
| <b>Biodiversity</b><br>• multiple species / ecological profiles<br>• multiple ecosystems |  | <b>Landscape cohesion</b><br><i>e.g. % of ecoprofiles with conditions for persistence</i>                         |

| Definitions  |   |
|--|---|
| <p><b>Network cohesion (NC).</b> An index for the sustainability of a habitat network for a particular species or ecological profile, based upon the size, quality and configuration of habitat elements of the network as well as on the permeability of the matrix. The minimum required network cohesion is the point above which the conditions allow persistence of the metapopulation.</p> <p><b>Spatial cohesion (SC).</b> An index for the sustainability of a landscape area for a particular species or ecological profile. SC is composed of the NC values for a region.</p> <p><b>Landscape cohesion (LC).</b> An index for the ecological quality of a landscape, based on the integrated potential for sustainability of a series of ecological profiles. These profiles differ in habitat and spatial scale.</p> <p><b>Habitat network.</b> The association of habitat patches in a landscape that potentially can be connected by a fair amount of dispersal, so that dispersal between patches in the network allows for recolonization and diminishes local extinction.</p> <p><b>Patch.</b> A spatially continuous piece of habitat of a species, limited by non-habitat.</p> | <p><b>Network population.</b> The spatially structured population in a habitat network, consisting of local populations connected by dispersal. A metapopulation is a particular type of a network population.</p> <p><b>Matrix.</b> The landscape between the habitat patches. The matrix of species A can be the habitat of species B and vice versa.</p> <p><b>Ecological profile.</b> A set of characteristics based on three components: ecosystem type, extinction related characteristics (e.g., area requirements), and recolonization related characteristics (dispersal distance, etc).</p> <p><b>Connectivity.</b> <math>CO_{ij}</math> is a measure for the number of potential connections between patch <math>i</math> and patch <math>j</math>, <math>CO_i</math> = patch connectivity (<i>sensu</i> Hanski (1994)).</p> <p><b>Sustainable.</b> A habitat network or landscape is sustainable for a species (true species or ecological profile) if the metapopulation of the species that inhabits it (or could inhabit it) is viable, i.e., has a high probability to survive for a long time (e.g., over 95% in a period of 100 years).</p> |

*Box 1.* Schematic representation of the relationship between network cohesion, spatial cohesion and landscape cohesion. Landscape cohesion is the ultimate goal as a tool for landscape planning. However, only network cohesion for species can be determined using ecological process knowledge. Therefore we propose a hierarchical approach in which first network cohesion is assessed (per species per network). Second, on the basis of network cohesion, spatial cohesion is assessed (per species for a planning region). Third, spatial cohesion assessments are combined into landscape cohesion (for multiple species, for a planning region). Note that no biodiversity assessment of habitat networks is possible, because species usually differ in how they perceive and function in habitat networks.

- *Spatial distribution of habitat* (combining patch size, shape and configuration). Patch perimeter/area ratio (and patch shape in general) may affect the extinction rate and the proportion of individuals leaving the habitat, whereas

configuration affects dispersal success. Since larger patches have smaller extinction rates and a smaller proportion of edge area where habitat quality may be lower, their contribution to the dispersal stream is relatively great.

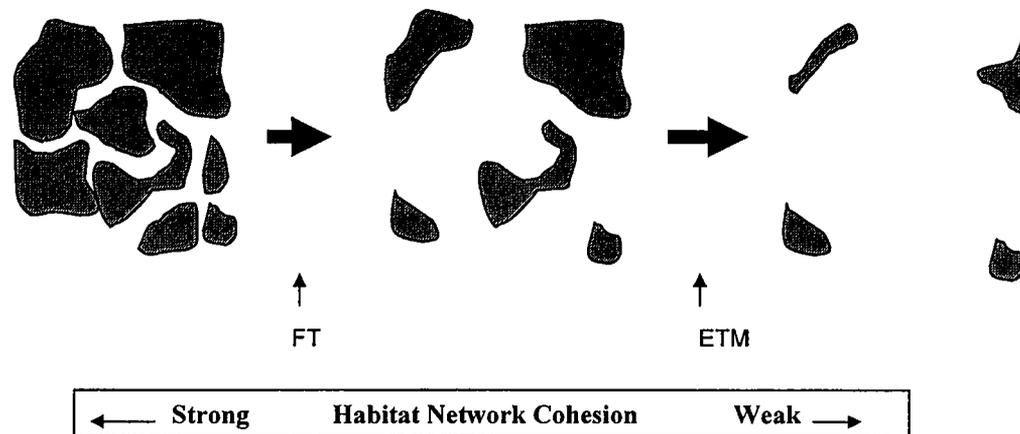


Figure 1. Along a gradient of increasingly intensive land use and decreasing habitat coverage, a species living in remnant habitat is confronted with a decreasing cohesion of the spatial pattern of its habitat. The two thresholds are the fragmentation threshold (FT) and the extinction threshold of the metapopulation (ETM).

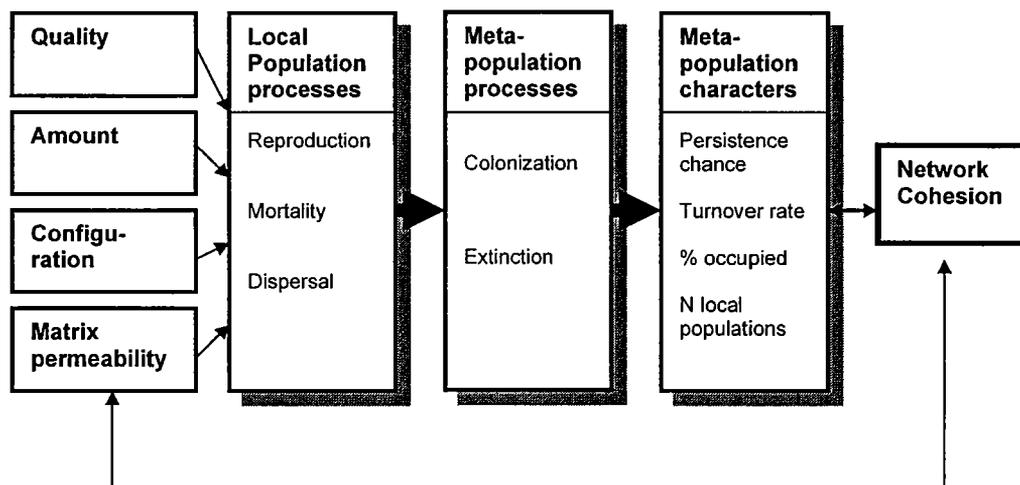


Figure 2. The functional relationship between the four components of habitat networks (four blocks left) and the concept of network cohesion proceeds; via local population processes (left column), metapopulation processes (middle column) and metapopulation characteristics (right column). The aim of network cohesion assessment is to infer habitat network cohesion directly from the four network components.

- *Matrix permeability* affects the costs of dispersal, and hence dispersal success. Barriers and corridors, types of boundaries and their arrangement in space all influence dispersal success, and consequently the colonization rate of patches and the support of small local populations.

These features all affect local population processes and dispersal, and thereby local extinction and recolonization (Figure 2).

Clearly, the components of habitat network cohesion are species specific. Species perceive landscapes at different scales, live in different ecosystem types and, while dispersing, have different preferences for or are differently affected by elements of the landscape matrix. So, a particular ecosystem network may be functionally totally different to species with diverging perceptions of scale, distance or barriers.

### Defining habitat networks

The basic map of the planning area shows patches of several ecosystem types. We describe a procedure allowing the delimitation of the habitat network for a single species. First, generate a map of habitat patches. Basically, this is a habitat suitability modeling step. Any ecosystem patch is assessed for its size and quality whether it is good and large enough to contain at least one reproductive unit of a species. Patches so close that they fit the scale of individual home ranges are fused to a single habitat patch. Patches suitable as habitat but too small to contain a reproductive unit are not rated as habitat patches, but count as elements in the matrix. Second, determine habitat networks. Two habitat patches belong to the same network as long as the distance is less than most dispersal distances. The euclidean distance between the patches is ecologically scaled with the permeability of the landscape matrix. To determine the maximum patch distance, we suggest to neglect rare long distance events, which will contribute little to the equilibrium dynamics of a metapopulation. For instance, we use a maximum distance which includes 90% of all dispersal events.

The result of the delimitation procedure is a map per species of the planning area with one or several habitat networks. Note that if a network extends beyond the borders of the planning area, the external part should be included in the delimitation procedure, because the sustainability assessment should of course be based on the whole network. The next challenge is to determine for any network whether it is sustainable.

### Calculating network cohesion

In this section, we discuss available methods to compute network cohesion. This discussion will put us strongly in the dilemma between theoretically preferred and practically useful. First, we give the basic demands of a calculation method, and subsequently we discuss which of the available methods meets this standard.

Because we need a landscape index that is functionally linked to population persistence, any habitat cohesion index should be ecologically-scaled. Rather than area and distance, we measure carrying capacity and distance scaled to the specific dispersal distance (true or ecological distance). Vos et al. (2001) showed

that ecologically-scaled landscape indices have a much higher predictive power than non-scaled landscape indices. Most existing network algorithms in metapopulation literature are not suitable for this purpose, because these must be calculated from species distribution data for any particular area. Some algorithms need estimates of the extinction rates  $e_i$  and colonization rates  $c_{ij}$  of a metapopulation in the habitat network of the species (e.g., Hanski (1994)). Recent theoretical attempts by Frank and Wissel (1998, 2002) and by Ettienne and Heesterbeek (2001) produced transition matrices for habitat networks with unequal patches and asymmetrical configurations, and calculated the sustainability of a network from the eigenvalues of the transition matrix generated by the metapopulation model. The transition matrix contains the transition probabilities between the different states of the metapopulation, e.g., (0,0,0,0) is a state with four patches, all extinct, and (1,1,1,1) is a state with all four occupied. However the transition matrix has the size of  $2^n \times 2^n$ , and therefore calculations with more than  $\sim 10$  patches are impossible with most current computers (Ettienne and Heesterbeek 2001). Likewise, Frank and Wissel (1998, 2002) derived an approximation formula for the sustainability of larger asymmetrical metapopulations. All these approaches could generate minimal values for habitat cohesion of sustainable networks, but they need lots of empirical data for parameterization and are therefore not generally applicable.

Alternatively, we proposed an approach based on the set of carrying capacities  $\{CC_i\}$  and the connectivity structure  $\{CO_{ij}\}$  of the habitat network, following the two Ecologically Scaled Landscape Indices presented by Vos et al. (2001). The first Ecologically Scaled Landscape Index (ESLI), called the *average patch carrying capacity* (ACC), integrates the average patch area and the individual area requirements of a species in a particular patch type. The individual area requirement is based on data about density or home range size in various vegetation types (habitat quality), which is taken from literature. The second ESLI is the *average connectivity of the patches* (ACO) of a habitat network. Connectivity of a single patch is defined as the sum of the contributions of all patches within the dispersal range to the overall dispersal stream, weighted by the area of the patches, and the distance (after Verboom et al. (1991) and Hanski (1994), among others). In this algorithm, distance can easily be replaced by ecological distance by

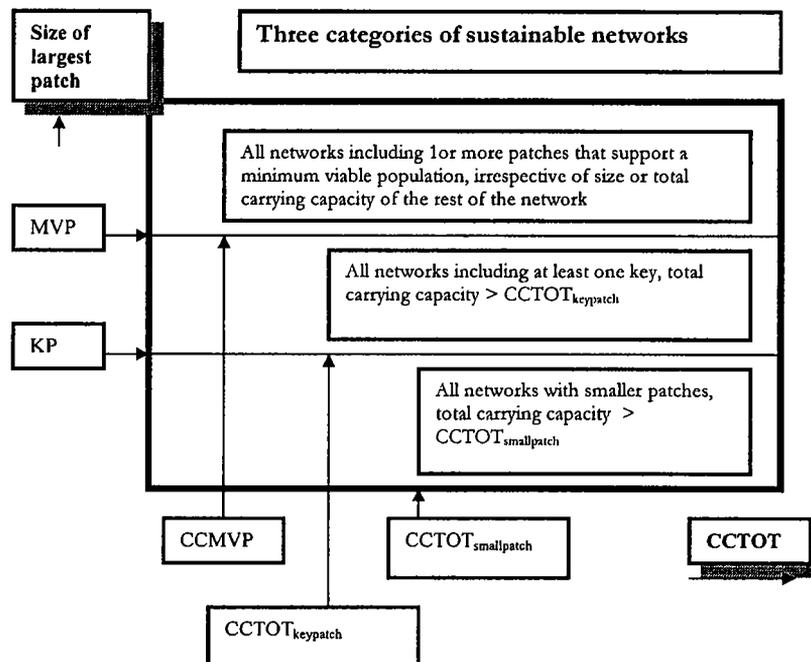


Figure 3. Schematic representation of the definition of three categories of networks. The vertical axis represents the size of the largest patch in three classes (MVP, KP and patches smaller than KP). The horizontal axis represents the total network area needed for sustainability. The scales of x and y-axes differ. See text for further explanation.

weighing it with the relative resistance of the landscape.

*Network cohesion* (NC) then is the combination of the two ESLI's:  $NC = (ACC, ACO)$ , in which ACC is the average carrying capacity and ACO the average connectivity of the patches in a landscape area. The threshold below which the metapopulation goes extinct due to loss of cohesion we call minimum Network Cohesion ( $NC_{min}$ ). The threshold could in theory be depicted by a line in a plot relating the two ESLI's (see Vos et al. (2001)).

ACC and ACO do not account for the probability that metapopulations in small habitat networks go extinct just by chance. A second problem with this approach is that the role of patch size variability in controlling local extinction is not well addressed. There is evidence that the presence of large and/or well-connected patches in the network has a relatively strong contribution to persistence (Frank and Wissel 2002; Verboom et al. 2001; Adler and Nuernberger 1994). Hence, we developed a more practical approach, based on the assumption that the largest patch has the largest contribution to persistence (Verboom

et al. 2001). In stead of ACC and ACO we focus on the patch with the largest carrying capacity of the network (CCMAX) and, subsequently, on the carrying capacity of the total network (CCTOT). The procedure follows three steps (Figure 3):

1. Scanning the network for a patch that exceeds the carrying capacity of a minimum viable population, that is a population that can be persistent without the rest of the network. The theory of minimum viable populations (MVP) predicts that any network with a patch large enough for an MVP should be persistent, regardless the presence of other patches in the network, and therefore independently of the average patch carrying capacity or patch connectivity.
2. Scan the network for a key patch (KP), a patch large enough to contain a local population with an extinction chance of 5% in 100 years, given an immigration rate of 1 individual per generation (Verboom et al. 2001). A network with a key patch is sustainable if the total carrying capacity exceeds the critical bottom level  $CCTOT_{keypatch}$ .

3. Networks without a key patch are assessed on the basis of CCTOT<sub>smallpatch</sub> only. Note that CCTOT<sub>smallpatch</sub> has a different value than CCTOT<sub>keypatch</sub> in case 2, because networks without a key patch need more area to be sustainable (Verboom et al. 2001)

Of these various approaches, the last method is the only one that is practically useful. The price for its practical value is a loss of detail: the dominant aspect of configuration is the presence or absence of a (very) big patch. For the rest of the network-configuration is simplified to the critical (ecologically-scaled) distance from the key patch. This restriction will be a problem in planning networks that lack a key patch. Therefore, we conclude that the theoretically preferable methods should be further developed.

The probabilistic nature of the underlying processes implies that KP and CCTOT are dependent on the extinction chance that is assumed in the model calculations. Essentially, this is a political decision. We propose to define this critical level at 95% in 100 years, accepting that 5% of the habitat networks will lose the species in the next century if the landscape would remain constant. We assume that networks that lose species will be recolonized sooner or later due to rare events of successful long distance dispersal. For very isolated networks, one could consider lower levels of risk.

### Defining spatial cohesion

Network cohesion is an index for one single habitat network, whereas a planning area may contain a number of networks for one species. If so, we need an index telling us how good that area is for some species. The calculation of this index requires aggregation, for which both ecological and political decisions have to be made. It entails decisions whether one sustainable network is enough, whether 50% should be sustainable, or even all networks. Possible aggregated indices are:

1. Percentage of habitat patches which are part of a sustainable network.
2. percentage of habitat area which is part of a sustainable network.
3. the sustainability of the most sustainable network in the landscape area.

In the first and second index, networks are classified as either sustainable or not. Alternatively, one can

rank networks according to degrees of sustainability, e.g., by dividing the index scale in three classes nearly sustainable, sustainable and highly sustainable. Again, when calculating spatial cohesion, one should include parts of any network that extend beyond the border of the planning area.

### Defining landscape cohesion

For a landscape, a landscape cohesion (LC) index could be obtained by aggregating the SC-indices for the species 1-n ( $SC_1, SC_2, \dots, SC_n$ ). Depending on the type of spatial cohesion, one may obtain different sorts of LC-indices, with different applications. We distinguish two basic types:

1. LC-indices for the state of conservation of biodiversity. Examples are:
  - % species in sustainable networks in any part of the region.
  - % of species with at least 50% of habitat patches in a sustainable network. The 50% level is arbitrary.
  - % of area that are part of a network of either one of the following classes: nearly, moderately, highly sustainable network.

This index tells us which part of the biodiversity is protected, with various levels of ambition.

2. LC-indices for the effect of changing the network. An example is: % of area with at least 50% of the species sustainable. Again, the 50% level is arbitrary. This index tells us how much of the nature area in the planning region has a 'good' status, and is helpful to explore the effect of adding extra nature area

Again, these indices involve political decisions about the set of target species involved in the assessment, about the definition of 'good' and about the ambition level of conservation (in the examples, arbitrarily set at 50%). Also, we assume in this index that all species are considered of equal conservation value.

The type of application determines which index is the most useful. Consider, for example, the following applications.

1. *Goal setting.* If Landscape Cohesion is a measure of spatial quality, a point along the measure serves as a goal of conservation policy. The index type 1 is well suited for goal setting.
2. *Monitoring.* Instead of surveying species abun-

dance over the years, the monitoring of the policy success can be surveyed with spatial cohesion from digitised air photos or satellite images and compared to the goal set under 1. Indices of type 1 are probably preferable for this purpose.

3. *Bottleneck detection.* Maps of index type 2 on a patch basis will show landscape regions where few species or ecological profiles find sustainable habitat. Such regions may be regarded as bottlenecks in the landscape cohesion, and in a further step one may search for sites where adding habitat yields a relatively large increase in landscape cohesion.
4. *Supporting decisions between options for landscape development or between alternative solutions.* For example, the index type 2 may compare locations for adding new habitat, expressing the effect in terms of the amount of existing habitat that turns into the 'good' status. An index type 1 would show the option under which most species are best protected.
5. *Integration with other land use functions.* One may explore which solutions make the best chances for integrating biodiversity conservation with other land use functions, for instance indicators for the historic landscape value, or for the quality of the landscape as perceived by humans. This allows optimisation of functions in a planning context. Index 2 is probably most suited for that.

In the Netherlands, spatial cohesion indices are used in conservation policy and landscape planning since 1997. The national report on the state of nature (Anonymus 1997) published an assessment of the increase of nature quality in case the national ecological network would be developed with emphasis on the largest nature areas possible under the restrictions of other land use functions (Figure 4). In this case one has chosen a simplified representation of the LC-map. Alternatively, a map on a grid basis was produced for the recent National Spatial Planning Framework (Figure 5). Landscape cohesion was also the basis for an assessment of the potential barrier effect of highways crossing the national ecological framework (Reijnen et al. 2000). Here, the index compares the network with and without infrastructure, thus showing the potential increase in landscape cohesion if measures to minimise the barrier effect are taken. This assessment is used as a basis for an action programme to solve the effect of the most important barriers. A good example of an application using a type 2 index is not yet available. However, examples of assessments with SC-indices did affect political decisions on where to

develop corridor zones (Reijnen and Koolstra 1998; Foppen 2001).

## Discussion

### *The significance of landscape cohesion*

Almost all attempts to develop a landscape-based predictor of biodiversity need species distribution data. Approaches based on the species-area relationship lack the spatial configuration component (for example Margules et al. (1988) and Pressey and Nicholls (1989), Lomolino (1994)). Multiple regression models of species occurrence in landscapes do include the effect of spatial configuration (e.g., Van Dorp and Opdam (1987), Vos and Chardon (1998) and Villard et al. (1999)), but are of restricted value if applied outside the study region (Verboom et al. (1993) and Opdam and Wiens (2002)). Metapopulation models are superior to these methods in being based on spatial processes and generally applicable. Some are useful in practice because they are spatially explicit, quite realistic and calibrated on distribution data (Lande 1987; Doak 1989; Lindenmayer and Possingham 1995; Lindenmayer and Lacy 1995; Possingham et al. 1994; Smith and Gilpin 1997). However, because these models are species specific and need extensive parameterisation and calibration efforts, we consider them impracticable for landscape planning purposes. Incidence function models for metapopulations (Hanski 1994; Wahlberg et al. 1996; Thomas and Hanski 1997; Ter Braak et al. 1998; Vos et al. 2000) are more practical, but still depend on distribution data of species.

Alternatively, landscape pattern indices are independent of species data and simple enough to be of practical use in planning. There is a near infinite number available, both simple and complex. However, usually these measures are statistical constructs which have not been calibrated on species distribution and persistence data, which implies that their ecological meaning is unknown (Schumaker 1996; Gustafson 1998; Vos et al. 2001).

With the proposed framework we build a bridge between generic, but ecologically non-significant, landscape indices and the persistence probability of species populations at the landscape level. Applying landscape cohesion does not require species distribution data. The framework we present has a modular structure, and can therefore be easily improved when

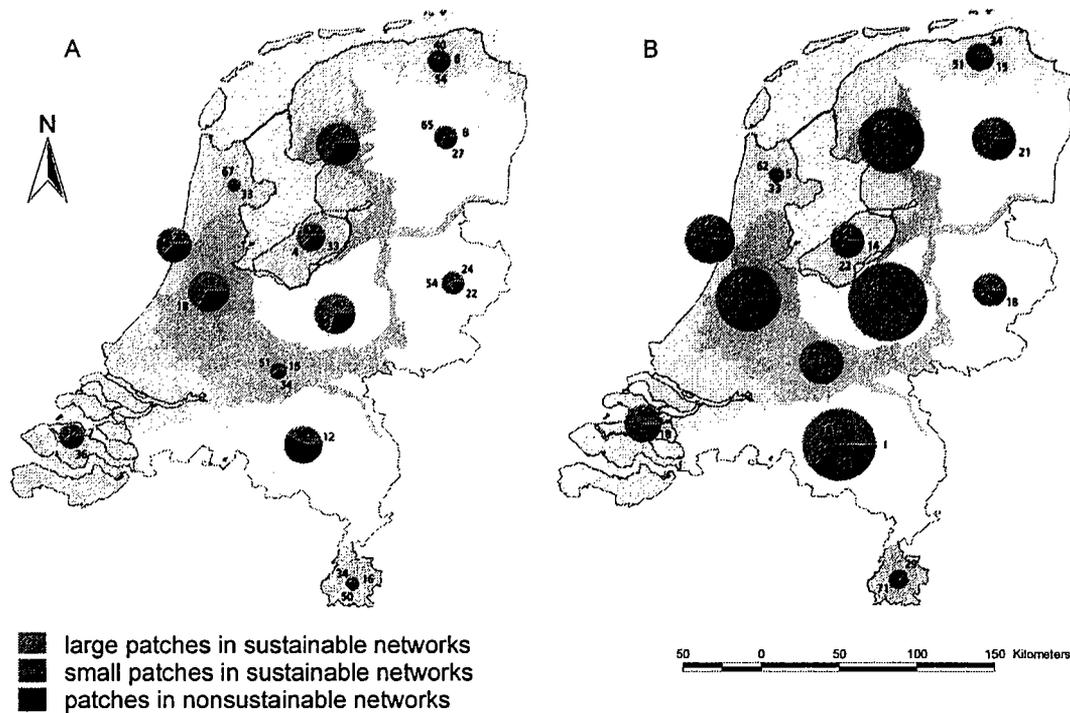
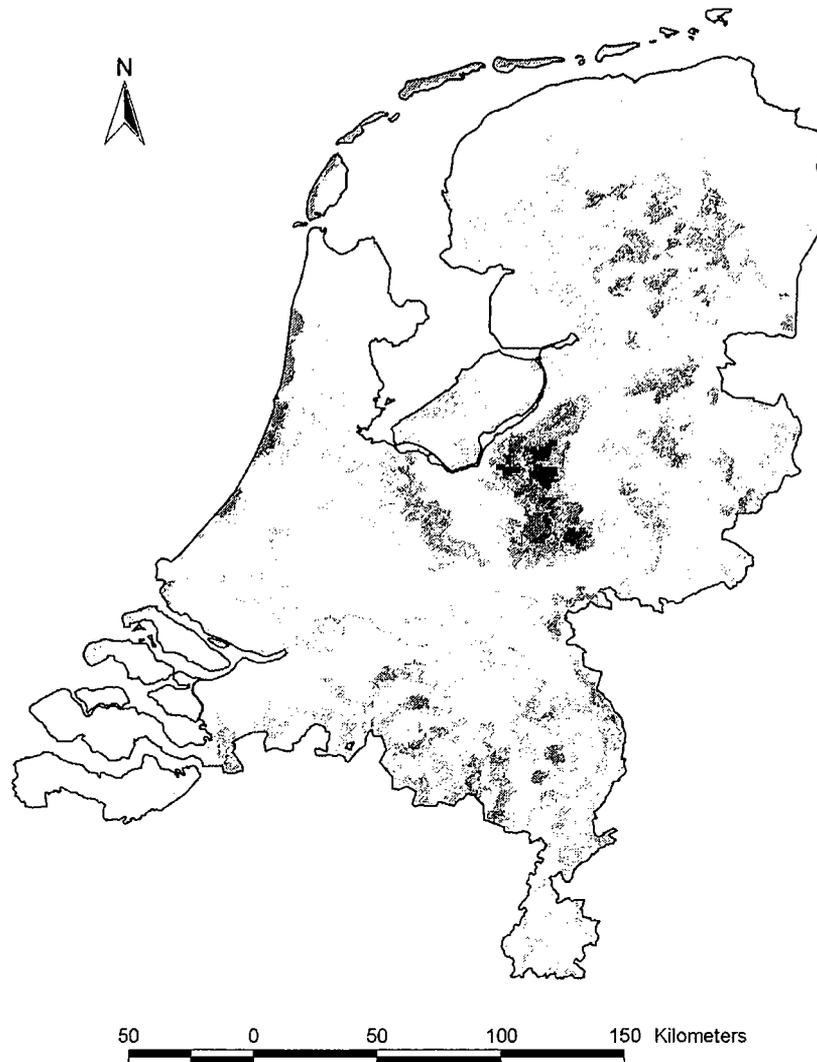


Figure 4. Maps of the LC-index based on 10 ecological profiles for 13 Geophysical regions in the Netherlands in three categories. A) situation in 1997, B) expected situation after completing the national ecological network (from Anonymus (1997)). To assess the biodiversity potential of the landscape, we distinguished three main ecosystems in the Netherlands: forest, heathland and marshland. For each ecosystem we chose ecological profiles that covered the range of bird and mammal species in that ecosystem. For each ecological profile, we determined the habitat networks and the network cohesion. We distinguished three categories of sustainability on a patch basis: large patches (key patches) in sustainable networks, small patches in sustainable networks and patches in nonsustainable networks. For each profile the areas in these categories were summed up per region, resulting in a spatial cohesion index. These indices were subsequently summed up and the percentages are shown in the figures. The size of the circles is proportional to the total area of habitat of the ecosystems in the region.

knowledge increases. Other approaches to estimate habitat network cohesion can also be fit into the framework.

Landscape cohesion is developed for landscapes dominated by farming and urban development. In such landscapes, habitat patches in the landscape matrix are distinct, and their coverage is so low that the persistence of many species depends on the cohesion of the habitat network rather than on, simply, habitat coverage. In such landscapes conservation planning is part of a multifunctional landscape planning process with many stakeholders. Such a process requires scientific data, but ultimately depends on the expression of human values (Theobald et al. 2000). Scientists must present their knowledge in a transparent way, and make assumptions and uncertainties explicit. Rule-based assessment models based on LC help to

meet these conditions. Setting goals for biodiversity conservation is a cultural and social activity, guided by science but done by the public (cf. Margules (1999)). Scientists help in decision making by showing the relation between nature quality gain and efforts and investments necessary. As long as the goals are subject to political debate, LC-based tools are useful in showing the conservation potential of various future options, as well as how much space is involved. Once a goal is made explicit, LC based tools can be used to compare alternatives to achieve it. Hence, various types of output based on LC play a role at different moments of the planning cycle.



*Figure 5.* Map of LC-index for 18 ecological profiles (from Hoogeveen (2001)). To assess the biodiversity potential of the landscape, we distinguished three main ecosystems in the Netherlands: forest, heathland and marshland. For each ecosystem we chose ecological profiles that covered the range of the bird, mammal, reptile and butterfly species in that ecosystem. Per ecological profile the habitat networks were defined. The spatial cohesion for each habitat patch was assessed, based on its own size and the habitat patches in the network. Per ecological profile this resulted in a grid-based map where patches had a good cohesion or not. Good is defined here as being part of a sustainable network with at least one key patch (Pouwels et al. 2002; Verboom et al. 2001). All the maps were overlaid and the ecological profiles with a good spatial cohesion were counted for each grid cell, resulting in numbers between 0 and 18. The colours on the map represent species number (0–18). This spatially explicit LC-index is especially useful for bottleneck evaluations (application 3). Light coloured areas that are near to dark coloured areas may be improved by connecting patches. Light coloured areas that are more or less solitary can only be improved by improving the quality or enlarging patches. Large light coloured areas need further investigation. It may be useful to calculate the LC-index per ecosystem, because bottlenecks are usually solved per ecosystem. Aggregation of the map can be used for the other applications. For example the gridcells with more than 9 species (50%) can be counted.

*A note on choosing species for landscape cohesion assessment*

The choice of species for landscape cohesion assessment appears critical. Can the results be manipulated by choosing certain species for conservation while disregarding others? We argue that species or ecological profiles are part of the tool kit and not targets themselves. We propose to use a matrix of ecological profiles (Vos et al. 2001) along a gradient of relevant dispersal distances (e.g., 100 m, 1000 m, 10,000 m) and relevant individual area requirements (e.g., 1 ha, 10 ha, 100 ha). Furthermore we choose species with different movement strategies (e.g., flying and non-flying, the latter perceive major roads and canals as barriers) and different ecosystem preferences that are relevant for the planning region (e.g., forest, marshland, grassland). A broad variety of species (true or profile) is recommended.

*Do we know enough about metapopulation ecology?*

The answer depends on the level of detail that is required for the application. LC is not a proper method when there is a lot of detail required. For example, when the role of habitat quality should be investigated or a management plan for a particular species is prepared, an individual-based mechanistic metapopulation model might be a better tool. Landscape cohesion based methods are pretty rough, much detail is exchanged for simplicity and generality. For most regional planning, however, this is sufficient. The planning context is extremely uncertain, and therefore requires tools with corresponding robustness. That is not to say that we do not need improvements of the knowledge basis. Opdam (2002) listed priorities for development of landscape cohesion assessment.

We do not believe that the variation in space and time across landscapes is simply too high for making any generalisation at all (Mönkkönen and Reunanen 1999). We propose to look for similarities rather than for differences among species and ecosystems. We cannot afford waiting with applying our knowledge until we know enough: that will never be the case. "Land use decision making will not wait for scientists to get it right" (Theobald et al. 2000). We consider the development of practical LC-based methods as a necessary way to go.

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