Landscape planning
Nitrogen budget
Riparian buffer zones
Spatial scale
Territorial ecological networks

Scaling in territorial ecological networks

Territorial ecological networks are coherent assemblages of areas representing natural and semi-natural landscape elements that need to be conserved, managed or, where appropriate, enriched or restored in order to ensure the favourable conservation status of ecosystems, habitats, species and landscapes of regional importance across their traditional range (Bennett, 1998). In this study we demonstrate the hierarchical character of territorial ecological networks, recognize common elements and functional differences between hierarchical levels, and analyze the downscaling and upscaling of the functions of ecological networks. Emerging from the examples of ecological networks at different hierarchical levels, we highlighted following common principles: connectivity, multifunctionality, continuity, and plenipotentiality.

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Landscape ecology provides the insight that nature at a landscape level is a relatively dynamic system reacting to a complex of environmental and land use conditions. It has been declared that landscape represents a crucial organizational level and special scale, at which both the effects of global change, as well as site-based biodiversity trends, are apparent, hence, at which appropriate responses will need to be implemented (Hobbs, 1997). The meaningful way in which humans interpret this nature at a landscape scale, and as a modelling instrument in spatial or physical planning, can be called an ecological network (Cook & van Lier, 1994). Most specific initiatives to develop ecological networks meet and suit the specific circumstances evident in the particular geographic and, even more importantly, hierarchical context.

The widely used European-level approach considers territorial ecological networks as coherent assemblages of areas representing natural and semi-natural landscape elements that need to be conserved, managed or, where appropriate, enriched or restored in order to ensure the favourable conservation status of ecosystems, habitats, species and landscapes of regional importance across their traditional range (Bennett, 1998).

In addition to this approach, there are a wide range of names worldwide given to such 'patch and corridor' spatial concepts: greenways in the USA, Australia and New Zealand (Ahern, 1995; Hobbs, 1997; Viles and Rosier, 2001), ecological infrastructure, ecological framework (van Buuren and Kerkstra, 1993), extensive open space systems, multiple use nodules, wildlife corridors, landscape restoration network (Ahern, 1995), habitat networks, territorial systems of ecological stability, framework of landscape stability (Jongman, 1995). In Estonia, a concept of 'the network of ecologically compensating areas' (Mander *et al.*, 1988) has been developed since the early 1980s. This network can be observed as a landscape´s subsystem – an ecological infrastructure – that counterbalances the impact of the anthropogenic infrastructure in the landscape. In comparison with the traditional biodiversity-targeted approach, this concept also considers the material and energy cycling, socio-economic and socio-cultural aspects.

The network of ecologically compensating areas is, like all territorial ecological networks, a multilevel hierarchical system. Their hierarchy emerges from both the spatial range and functions. Although ecological networks are already widely used practice in landscape/territorial planning and nature conservation (Cook and Van Lier, 1994; Ahern, 1995; Jongman, 1995; Bouwma *et al.*, 2002), there are few works available on the hierarchical analysis of territorial ecological networks (Cook, 2002; Villeumier & Prelaz-Droux, 2002).

The main objectives of this study are: (1) to demonstrate the hierarchical character of territorial ecological networks, (2) to recognize common elements and function-

al differences between hierarchical levels of territorial ecological networks; (3) to analyze the downscaling and upscaling of the functions of ecological networks and their spatial distribution.

Considering hierarchy in the application of the ecological network model in practice helps to reflect the complexity of pattern and processes at the landscape level. One of the ways to downscale the functions of an ecological network is to use a strategy based on suitability criteria. This approach helps to reveal, evaluate and exploit the impact of protected and sparsely populated areas on the environment in the broader sense. Likewise, it has been used to identify and measure the suitability of potential sites for ecological network development in residential areas (Miller *et al.*, 1998). As an example, a GIS-based habitat suitability analysis for the designing of national-level ecological networks in Estonia is presented in this paper. For the upscaling approach from the micro-scale ecological network to the meso- and macro-scale level, a nutrient fluxes modeling attempt in riparian buffer zones will be presented. The use of point models step-by-step within elementary watersheds helps to describe the changing gradient of nutrient fluxes along the water filtration path and allows the creation of bridges between the different hierarchical levels of ecological networks.

Roots of the concept

Development of the idea of territorial ecological networks may be largely based on the central place theory elaborated by J.H. von Thünen (1826, 1990), W. Christaller (1933, 1966) and A. Lösch (1954). Enhanced by the Von-Thünen-Christaller-Lösch theory of central places and their hierarchy, Rodoman (1974) used the idea of influence pattern and spatial hierarchy to advance the concept of polarized landscapes. According to this approach, two main poles – centres of human activities (e.g., cities) on the one hand, and centres of pristine (undisturbed) nature (e.g., large forest and swamp areas) on the other hand – create the hierarchical gradient fields of interactions. Thus, it allows the use of the Von Thünen-Christaller-Lösch model for reverse situations, not proceeding from the development of economic but ecological benefit. In this case ecological benefit means first of all less disturbance by human activities (Külvik *et al.*, 2003).

Structural components as indicators of functional hierarchy

A network of ecologically compensating areas is a functionally hierarchical system with the following components: (A) core areas, (B) corridors; functional linkages between the ecosystems or resource habitat of a species enabling the dispersal and migration of species and resulting in a favourable effect on genetic exchange (individuals, seeds, genes) as well as on other interactions between ecosystems; corridors may be continuous (linear;

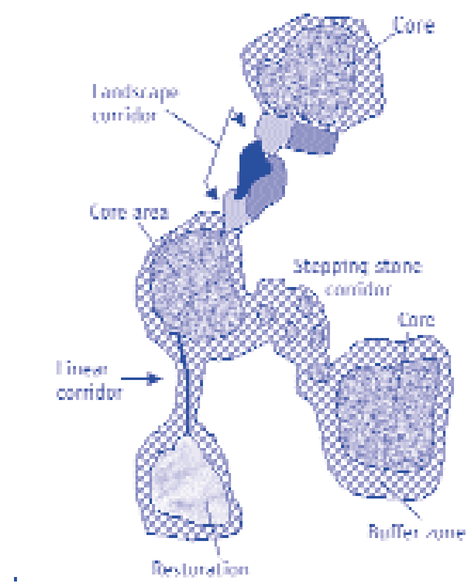

Figure 1. Schematic example of an ecological network (from Bouwma *et al.*, 2002; with permission of ECNC and I. Bouwma).

Saunders *et al.*, 1991), interrupted (stepping-stones; Brooker *et al.*, 1999) and/or landscape corridors (scenic and valuable cultural landscapes between core areas), (C) buffer zones of core areas and corridors, which support and protect the network from adverse external influences, and (D) nature development and/or restoration areas that support resources, habitats and species (Bennett, 1998; Bouwma *et al.*, 2002; Figure 1).

Corridors which provide connectivity between the core areas can be considered as key elements of ecological networks. According to Ahern (1995), ecological corridors and greenways are a linked or spatially-integrated network of lands that are owned or managed for public uses including biodiversity, scenic quality, recreation and traditional agriculture. The viability of certain processes in landscapes is dependent on connectivity (the movement of wildlife species and populations, the flow of water, the flux of nutrients, and human movement). Without connectivity, these processes and functions may not otherwise occur. However, connectivity must be understood in terms of the process or function that it is intended to support.

Movement, which assumes connectivity, is itself the product of evolutionary pressures contributing in many ways to the survival and the reproduction of the animal. Animals move through their home range, but may also move long distances from where they were born and their kin remain. Three kinds of movements can be distinguished (Caughley & Sinclair, 1994):

Local movements- these are movements within a home range and are on smaller scales;

- Dispersal- movement from the place of birth to the site of reproduction, often away from its family group and usually without return to place of birth;
- Migration- movement back and forth on a regular basis, usually seasonally, e.g. from summer range to winter range to summer range.

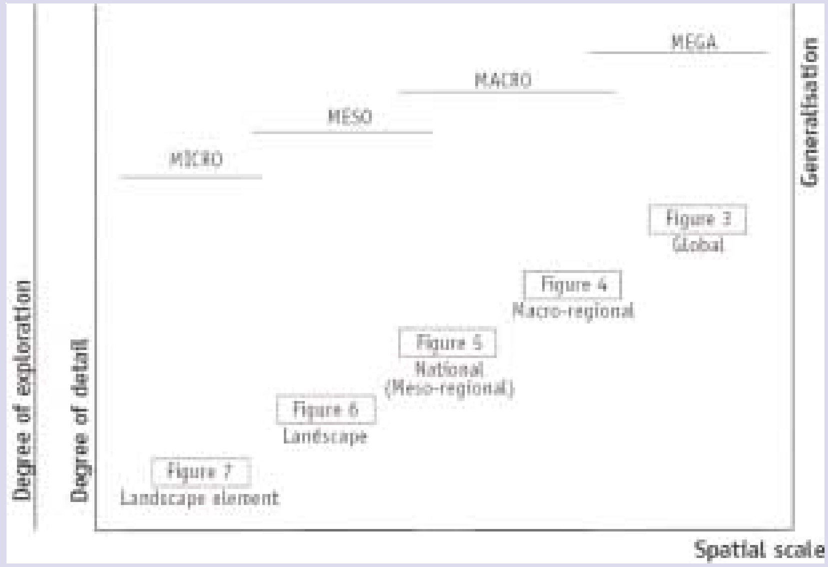

Figure 2. Hierarchy levels of ecological networks and according representative figures of this paper. The degree of detail and the exploredness are increasing and generalization is decreasing towards lower (detail) levels.

Local movements, within the home range of a species for foraging, hiding from enemies and optimizing living conditions, are normally not included in the analyses and implementation of ecological network. However, this kind of movement is most important at lower spatial scales of ecological networks.

Spatial hierarchy

Most specific initiatives to develop ecological networks – either theoretically or in practice – consider the specific circumstances evident in the particular hierarchical context. The most practicable is the approach that proceeds from the traditional scaling of maps in cartography: 1:500; 1:1000; 1:5000; 1:10,000; 1:50,000; 1:100,000, 1:500,000 etc. Mander *et al.* (1995) intuitively defines the network components at four levels: (a) mega-scale: large natural core areas (>10,000 km²) and their buffer zones, sometimes connected with corridors; (b) macro-scale: large natural core areas (>1000 km²) surrounded by buffer

zones and connected with wide corridors or stepping-stone elements (width >10 km); (c) meso-scale: small core areas (10-1000 km^2) and connecting corridors between these areas (e.g., natural river valleys, semi-natural recreation areas for local settlements; width 0.1-10 km); (d) micro-scale: small protected habitats, woodlots, wetlands, grassland patches, ponds (<10 km^2) and connecting corridors (stream banks, road verges, hedgerows, field verges, ditches; width <0.1 km; Figure 2).

The hierarchical scaling is similar to the classification of core areas based upon insights regarding the minimum required area to sustain viable populations of species (e.g., of European importance). According to this system, very large areas (critical size: >5 km^2; guarantees the long-term survival of all populations), large areas (critical size: 1-5 km^2; when isolated this area may suffer some loss of species; connection or area enlargement is required), and areas with a sub-optimal size (70-100% of species can maintain viable populations, the most demanding species can only be maintained or restored by enlargement and/or connections with comparable habitats by corridors); Bouwma *et al.*, 2002).

Mega-scale ecological networks can be considered at the global level. The Human Footprint Map can serve as a basis for determining global ecological networks (Figure 3; Sanderson *et al.*, 2002). The macro-scale of ecological networks is represented by regional-level activities like the Pan-European Ecological Network (PEEN) or national-level projects. In the Czech Republic, Slovak Republic and the Netherlands, territorial ecological networks are implemented and legislatively supported. In Estonia, Lithuania and Poland, networks are designed and some aspects accepted by law. In Hungary, Latvia, Switzerland and Ireland, network design is under development, and local or landscape-level ecological networks have been established in some parts of the territory of several European

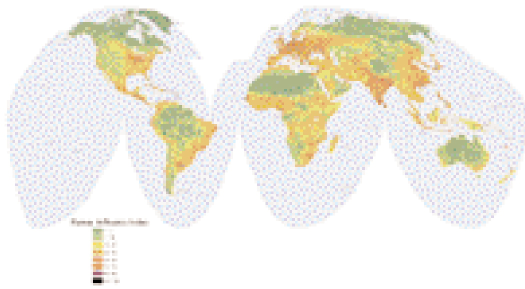

Figure 3. The map of the Human Footprint as a basis for the ecological network system at the global scale (Sanderson *et al.*, 2002). Summarized factors of anthropogenic pressure have been used, such as the Human Influence Index, which is the quantitative basis for the map. Adopted from www.ciesin.columbia.edu/wild_areas/. The full list of biomes is available at *www.wcs.org/humanfootprint*.

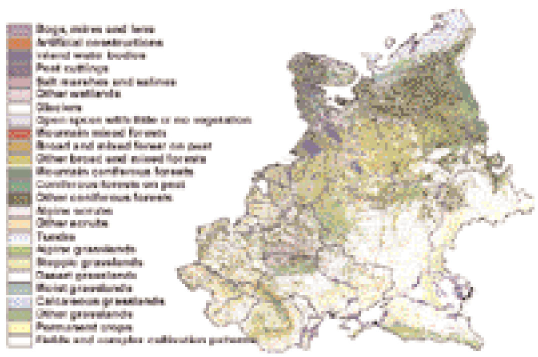

Figure 4. Habitat map of the Pan-European Ecological Network (PEEN) for Central and Eastern Europe as a basis for the PEEN indicative map. Adopted from Bouwma *et al.* 2002.

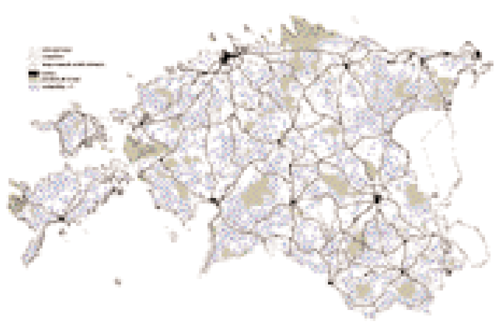

Figure 5. Suitability for the ecological network in Estonia (adopted from Remm *et al.*, 2003) as an example of an ecological network at the meso-regional (national) level. Dark grey patches indicate protected areas (relative suitability value >1.0), whereas grey areas have a suitability value of 0.5-1.0, and are mostly local core areas, various buffer zones and corridors; towns are shown in black.

Range of planning area	Administrative levels	Hierarchical level of core area	Diameter of core areas	Width of corridors	Planning levels in Estonia	Spatial scale (Fig. 32; Mander et al., 1995)
1–1.5*10^5 km	Earth's geographical space					
1 – 1.5*10^4 km	Geopolitical areas					
1 – 1.5*10^4 km	Group of large countries, cultural , ldistricts,large groups of countries	Global I	>1000 km	>300 km		MEGA
3 – 5*10^3 km	Large country	Global II	500 – 1000 km	200 – 300 km		MEGA
1 – 1.5*10^3 km	Group of small countries, large group of states or provinces	Regional-large	300 – 500 km	100 – 200 km		MACRO
300 – 500 km	Small country, small group of provinces or states	Regional-small	100 – 200 km	30 – 50 km	National	MACRO
100 – 150 km	Districts, small group of counties, group system of settlement groups	National-large	30 – 50 km	10 – 20 km	National District	MESO
30 – 50 km	County, large group of parishes	National-small	10 – 20 km	3 – 5 km	District	MESO
10 – 15 km	Small group of parishes, large town	District (county)-largebig	3 – 5 km	1 – 2 km	District Comprehensive	MESO
3 – 5 km	Parish, town, a part of large town, large group of villages	District (county)-small	1 – 2 km	300 – 500 m	Comprehensive	MESO
1 – 2 km	Part of town, settlement, countryside of protected area, group of villages	Local I	300 – 500 m	100 – 200 m	Detailed	MICRO
300 – 500 m	Larger group of buildings, quarter, village, field complexmassive	Local II	100 – 200 m	30 – 60 m	Detailed	MICRO
100 – 200 m	Countryside, the group of buildings with it's surrounding land, field, sectionpartition of forest	Detailed I	30 – 50 m	10 – 20 m	Detailed	MICRO
30 – 50 m	Homes and house with it's closer surroundings	Detailed II	10 – 20 m	3 – 6 m		MICRO
10 – 20 m	Apartment, a part of a house					MICRO
3 – 5 m	Space occupied by moving person, room					
1 – 2 m	Personal space of one person					

Table 1. Hierarchical levels of planning the ecological network.

countries such as Germany, Belgium, UK, Italy, Spain, Portugal, Russia, and the Ukraine (Bouwma *et al.*, 2002). Landscape-level ecological networks are designed or implemented on a wide range of spatial scales, from macro- and meso- to micro-scale projects. The most significant research on both species migration and dispersal, as well as on energy and material fluxes has been carried out at this level (see Forman, 1995; Farina, 2000). Likewise, the most detailed analysis and implementation schemes have been established at micro-scale (Figure 2).

Spatial hierarchy is closely associated with the planning levels of ecological networks. Table 1 presents a possible system of administrative levels, the range of planning areas, as well as the levels and size of core areas and connecting corridors. Experiences gained from the development of the concept of the ecological network in Estonia are presented as an example for the national-level approach. The challenge of the ecological-network approach is to integrate ecological principles, biodiversity, and landscape conservation requirements into spatial planning procedures and other land use practices.

Functions of territorial ecological networks

Ecological networks are viable because they provide mul-

tiple functions within a specific and often limited spatial area, and these functions can be planned, designed and managed to exist compatibly or synergistically (Jongman, 1995).

According to a broader concept, ecological networks (networks of ecologically compensating areas) preserve the following main ecological and socio-economical functions in landscapes (Mander *et al.*, 1988):

I. Biodiversity.
- Refuges for species (incl. genetic variability).
- Migration and dispersal tracts for biota.

II. Material and energy flows.
- Material accumulation, recycling and regeneration of resources.
- Barrier, filter and buffer for nutrient fluxes.
- Dispersal of human-induced energy.

III. Socio-economic development and cultural heritage.
- Supporting framework (e.g., recreation area) for settlements.
- Compensation and balancing of inevitable outputs of human society (e.g., supporting traditional rural development).

The relative importance of the ecological functions of the system of ecologically compensating areas depends on the spatial scale (Table 2). This varies, however, across both space and time. Based on the experience of landscape evaluation for regional and landscape planning in the countries of Central and Eastern Europe (Bastian & Schreiber, 1999), one can assume that the biodiversity support (refuge function) is more important at the macro-scale level than at the medium or micro-level. Larger natural areas with heterogeneous structure can support more species than medium- or small-size core areas (Caughley & Sinclair, 1994). On the other hand, as migration corridors and dispersal tracts, the medium-level corridors play a key role in connecting core areas of different scales. Accordingly, in the Human Footprint Map (Figure 3), for instance, areas of high value on the Human Influence Index (e.g., large areas in North America and densely populated Europe) still have remarkable high biodiversity with a list of species comparable to the period before significant anthropogenic pressure began. This is largely supported by the connectedness of natural core areas of different size. Material accumulation, the regeneration of resources, the filtering and buffering effects of material and energy fluxes need more space, and therefore their importance is greater on higher hierarchical levels (Table 2). On the other hand, the highest relative importance of all functions can be found at the meso-scale level, which integrates the national, landscape and some detail scale approaches (Table 2, Figure 2). This is one of the explanations – next to cost and complexity – of the relatively high number of studies and implementation experiences of ecological networks at the landscape level.

Global Human Footprint and Last of the Wild: ecological networks at a global level

The map of the Human Footprint, worked out by Columbia University, USA, is a global driver of conservation crises on the planet and may be considered as a base for ecological networks at the global level (Figure 3). Analysis of the Human Footprint Map indicates that 83% of the land's surface is influenced by one or more of the following factors: human population density greater than one person per square kilometer, location within 15 km of a road or major river, occupied by urban or agricultural land uses, within 2 km of a settlement or railway, and/or producing enough light to be regularly visible to a satellite at night. About 98% of the areas where it is possible to grow rice, wheat or maize (according to FAO estimates) are similarly influenced. Summarized factors have been used as

Functions	Macro-scale	Meso-scale	Micro-scale
Biodiversity			
Refuges for species (incl. genetic variability)	high	medium	low
Migration and dispersal tracts for biota	low	high	medium
Material and energy flows			
Material accumulation, recycling and regeneration of resources	high	medium	low
Barrier, filter and buffer of nutrient fluxes	low	medium	high
Dispersal of human-induced energy	high	medium	low
Socio-economical development and cultural heritage			
Supporting framework (e.g., recreation area) for settlements	low	high	medium
Compensation and balancing of inevitable outputs of human medium society (e.g., supporting traditional rural development)	high	low	

Table 2. Relative importance of the effects of ecological and socio-economic function classes of system of ecologically compensating areas at different scales.

Human Influence Index that is the quantitative base of the Human Footprint Map (Sanderson *et al.*, 2002). However, human influence is not an inevitably negative impact – for instance, the hierarchical concept of ecological networks (ecological infrastructure) shows remarkable solutions that allow people and wildlife to co-exist. Nature is often resilient if given half a chance. Hopefully, human beings will be in the position to offer or withhold that chance.

The map of the Last of the Wild, which represents the largest least influenced areas in all of the biomes of the world and in all of the world's regions (Sanderson *et al.*, 2002) is a kind of inversion of the Human Footprint map. They represent a practical starting point for long-term conservation: places where the full range of nature may still exist with a minimum of conflict with existing human structures. If we wish to conserve wildlife and wild places and have a rich and beautiful environment for ourselves, we need to find ways to diminish the negative impacts of human influence, while enhancing the positive impacts.

PEEN as an example of ecological networks at the regional level

One of the most important channels for the implementation of the Pan-European Biological and Landscapes Diversity Strategy (PEBLDS), approved by the 3rd Conference of Ministers of the Environment of 55 European countries entitled 'An Environment for Europe', held in Sofia on 25 October 1995, is the establishment of the PEEN. The participating states have agreed that the network should be established by 2005. The PEEN will contribute to achieving the main goals of the PEBLDS by ensuring that a full range of ecosystems, habitats, species and their genetic diversity, and landscapes of European importance are conserved; habitats are large enough to place species in a favourable conservation status; there are sufficient opportunities for dispersal and migration. The development programme for the PEEN will design the physical network of core areas, corridors, restoration areas and buffer zones. The programme includes the following actions: a) the elaboration of the criteria on the basis of which the network of core areas, corridors, restoration areas and buffer zones will be identified, taking the biogeographical zones of Europe into account; b) the selection of the ecosystems, habitat types, species and landscapes of European importance; c) the identification of the specific sites and corridors by way of which the respective ecosystems, habitats, species and their genetic diversity, and landscapes of European importance will be conserved and, where appropriate, enhanced or restored; d) the preparation of guidelines that will ensure that actions taken to create the network are as consistent and effective as possible. A coherent European Ecological Network of Special Areas of Conservation (SAC) is being set up under the title Natura 2000 by each of the EU Member States (as defined in the Habitats Directive (92/43/EEC Article 3). This network, composed of sites hosting the natural habitat types and species listed in Annexes I and II of the Habitats Directive, will enable the natural habitat types and the species' habitats concerned, to be maintained or, where appropriate, restored at a favourable conservation status in their natural range. However, the SAC concept considers only protected or designated areas, while the

PEEN concept also covers large undisturbed areas and their connecting corridors outside protected or designated areas. In addition, many other functions of ecological networks, such as control of energy and material fluxes, are considered by the PEEN concept.

One of the first activities of the PEEN development programme is the Indicative Map of the PEEN for Central and Eastern Europe, which is mainly based on the habitat classification and suitability analysis (Figure 4; Bouwma *et al.*, 2002).

Suitability of habitats for ecological network at national level

We consider an ecological network design to consist of three principal layers: (1) general topographical features like coastlines, the water network, major roads, and place names for locating the network portrayed, (2) habitat-based field of suitability for the ecological network, calculated from network values of landscape features using a predefined algorithm, (3) the ecological network as an administrative decision. The second layer serves as a tool supporting decision-making, while the third layer consists of the traditional components of an ecological network, such as core areas, corridors, buffer zones, and nature development/restoration areas (Remm *et al.*, 2003).

In order to create a habitat map, which served as a basis for the ecological networks suitability map, several modifications were made to the Estonian CORINE land cover map (Meiner, 1999; Remm *et al.*, 2003). All habitats, linear structures and designated areas were ranked according to their expert-assessed values (from 0 to 10) based on their naturalness, rarity and potential influence on biodiversity and landscapes. Each square on the grid (1 x 1 km) is supposed to have a certain suitability for the establishment of an ecological network (PS). The suitability of a square kilometre is determined mainly by the square's habitat structure but also by the location of the grid square relative to main migration routes of species and by management and legislation. The direction and magnitude of the influence of these factors on the PS is called the ecological network value (ENV; Remm *et al.*, 2003). We assign ENVs to the habitat classes as non-negative real numbers (e.g., 0 – presence of the factor excludes the square from the ecological network, 1 – neutral influence, 2 – twice as good as the average, the factor doubles the suitability estimation of a square 10 – the factor improves by ten times the suitability of a square). A multiplicative (logarithmic) scale is suggested because it allows the use of zero value to designate absolutely unsuitable conditions. The overall suitability [PS] of a square kilometre unit is calculated as a log product of the suitability values of all categories.

The ENV of a habitat class is given as an expert decision considering the importance of certain habitats for wildlife diversity in Estonia, and the distribution of endangered taxons in habitats according to the Red Data Book of Estonia (Remm *et al.*, 2003): The mean PS-value of a square kilometre is 0.897, and the median 1.006; the minimum value is 3.648 and the maximum 3.75. The most common network suitability is between 1.0 and 1.5. As a rule, the ecological network suitability of protected areas is higher than that of non-protected areas.

The mean natural-PS value of square kilometers that contain more than 80% protected area is 1.34, and the mean natural-PS of those square kilometers that do not include protected area is 0.819. The relative amount of protected area correlates positively with natural suitability for the ecological network. Nearly one half (47.4%) of ecologically highly valuable areas (PS >1.0) are under nature protection in Estonia. On the other hand, this means that more than one half is not protected administratively (Figure 5).

Habitat mosaic of the cultural landscape: Ecological network at landscape level

Landscape level is the most integrative among all the spatial scales of ecological networks. On the one hand, there are a great many definitions and, respectively, concepts of landscape, which makes the planning aspects very comprehensive and multifunctional. In landscape ecology, most commonly a mosaic of habitats is understood as a landscape (Forman, 1995; Farina, 2000). Due to long-term human impact and land use dynamics, European landscapes have been significantly altered. Valuable habitats in coastal and alpine areas, especially various grasslands and forests, but also wetland ecosystems in Europe as a whole have decreased dramatically in area. In large territories of high-level economic development, most natural ecosystems have been destroyed and pushed to the margins by dominant land uses such as agriculture, industrial forestry and urban development. In Europe as a whole, both homogenisation and fragmentation are the main driving factors of landscape change. As a result of fragmentation, mainly relatively small and often isolated natural areas have survived. In this mosaic, and some larger and less disturbed (semi)natural ecosystems (ecologically compensating areas) and hedgerows and riparian zones connecting them create an ecological network (infrastructure) in the cultural landscape (Figure 6), supporting the multifunctional character of the landscape.

Also, marginalisation, now dominating in Eastern, Central and Northern Europe as a main driving force of landscape change, initiates the dramatic loss of valuable seminatural ecosystems (Mander & Jongman, 1998). Some of the main functional aspects of these landscapes are connectivity and connectedness (Baudry & Merriam, 1988). The former measures the species' migration and dispersal processes by which sub-populations of organisms are interconnected into a functional demographic unit: metapopulations on different equilibrium levels (Hanski *et al.*, 1995). Connectedness refers to the structural links between elements of the spatial structure of a landscape and can be described from mappable elements (Bouwma *et al.*, 2002). The importance of metapopulation principles, partly derived from the island biogeography theory (MacArthur & Wilson, 1967; re-published in 2001; Opdam, 1991), is the acknowledgement that the survival of species involves more than solely maintaining nature reserves; ecological linkages are needed and must be included in spatial plans. Likewise, corridors between core areas and buffers around sensitive areas can provide important control of energy/material fluxes.

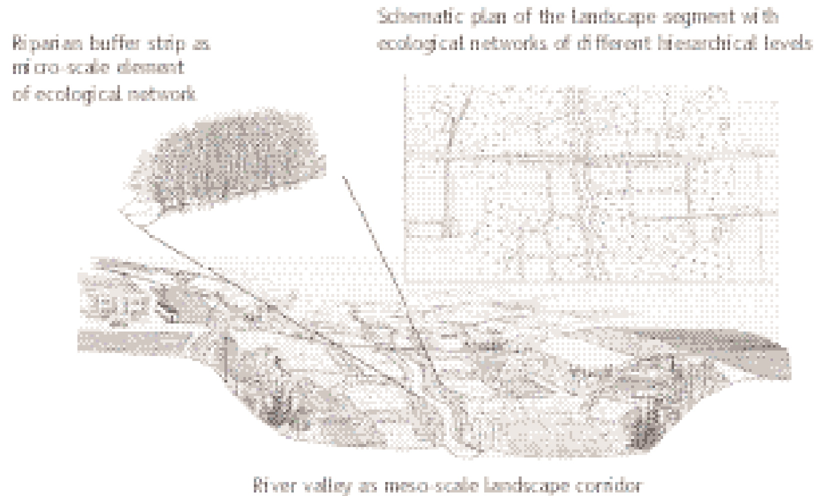

Figure 6. River valley with small-grain landscape pattern within intensively-used large-grain agricultural fields as a multifunctional landscape corridor. Hedgerows and other ecologically compensating areas in the traditional agricultural landscape of the river valley serve as examples of the ecological network at the micro-scale.

Riparian buffer zones as ecological network at micro-level

Riparian buffer zones are often considered to be multifunctional elements of rural landscapes that serve as examples of ecological networks at the most detailed level. In agricultural areas of Estonia, the preferable land-use alternative is perennial grassland (buffer zone) in combina-

tion with a forest or bush buffer strip directly on river banks or lake shores (Mander *et al.*, 1997). In some countries the complex structure of buffer zones is officially recommended or legislatively stated. For instance, in the U.S., the recommended complex buffer zone consists of three parts which are perpendicular to the stream bank or lake shore (sequentially from agricultural field to water body): a grass strip, a young (managed) forest strip and an old (unmanaged) forest strip (Lowrance *et al.*, 1984). Riparian buffer zones have the following essential functions: (1) filtering of polluted overland and subsurface flow from intensively managed adjacent agricultural fields; (2) protecting the banks of water bodies against erosion; (3) filtering polluted air, especially from local sources (*e.g.*, large farm complexes, agrochemically treated fields); (4) avoiding intensive growth of aquatic macrophytes by canopy shading; (5) improving the microclimate in adjacent fields; (6) creating new habitats in land/inland water ecotones; and (7) creating greater connectivity in landscapes due to migration corridors and stepping-stones (Mander *et al.*, 1997).

According to the hierarchy level of ecological networks, the relevance of buffer functions differs significantly. For instance, the impact of the shading effect is extremely local. Likewise, water and bank protection functions are very important on the micro-scale (local level of one or a small group of fields) and have no significant relevance on a regional, i.e. macro-scale. On the other hand, biological functions like creation of connectivity in landscapes due to migration corridors and stepping-stones is more relevant on higher hierarchical levels (Mander, 2001).

Filtering of polluted overland and subsurface flow is the key function of buffer zones (Peterjohn & Correll, 1984; Pinay & Décamps, 1988; Jordan *et al.*, 1992; Vought *et al.*, 1994). For instance, three biological processes can remove nitrogen: (1) uptake and storage in vegetation; (2) microbial immobilization and storage in the soil as organic nitrogen; and (3) microbial conversion to gaseous forms of nitrogen (denitrification: see Pinay *et al.*, 1993; Weller *et al.*, 1994; nitrification: see Watts & Seitzinger, 2000; Wolf & Russow, 2001). Various biophysical conditions control the intensity of these processes, and therefore the variability of that intensity is very high. For instance, gaseous emissions and plant uptake can vary from <1 to 1600 and from <10 to 350 kg N ha^{-1} yr^{-1}, respectively (Mander *et al.*, 1997). Thus different processes can play a leading role in nitrogen removal. The efficiency of removal also depends on input fluxes and nitrogen pools in the systems. Therefore a comprehensive budget analysis is needed to model and control the N flows in riparian ecosystems. In Figure 7, the nitrogen budget in a riparian grey alder stand is presented as an example of such modeling (Mander *et al.*, 2003).

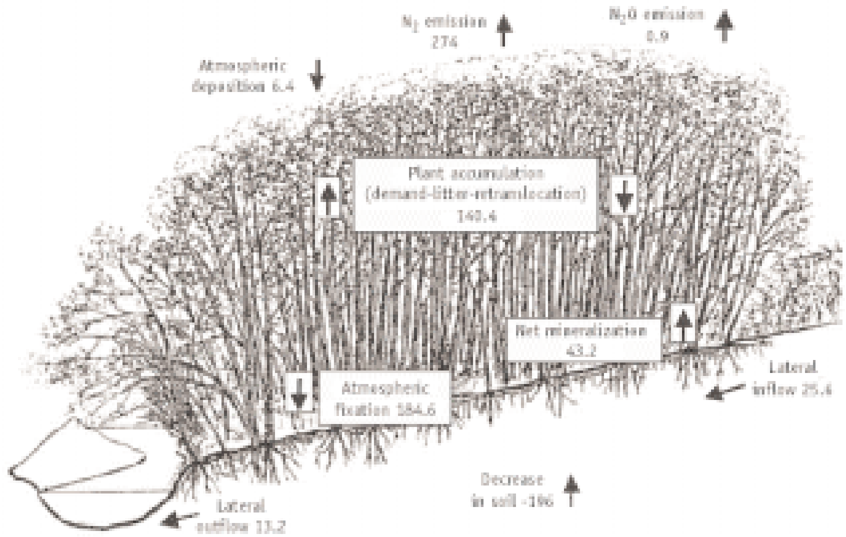

Figure 7. Nitrogen budget of a 15-year riparian grey alder stand (kg ha^{-1} yr^{-1}) as an example of the buffering function of ecological network elements (corridors and buffers) at the micro-scale level. Adopted from Mander *et al.*, 2003.

Discussion and conclusions

Emerging from the examples of ecological networks at different hierarchical levels, the following common principles can be highlighted. First, the most important and specific principle of ecological networks is *connectivity*. Together with connectedness, these are the main functional aspects in the landscape that are of importance for the dispersal and persistence of populations, and the supporting/controlling of the flow of water, the flux of nutrients, and human movement. According to Baudry and Merriam (1988) connectivity is a parameter of landscape function, which measures the processes by which sub-populations of organisms are interconnected into a functional demographic unit. Connectedness refers to the structural links between elements of the spatial structure of a landscape, which can be described from mappable elements. Sometimes biological connectivity (e.g. functional patterns) and landscape connectedness (e.g., physical connection of similar landscape elements) match, as in the movements of small forest mammals along wooded fencerows from one woodlot to another (Henein and Merriam 1990). Sometimes they do not match, as in the case of ballooning spiders (Asselin and Baudry 1989).

Structural elements differ from functional parameters. For some species connectivity is measured in the distance between sites, whereas for other species the structure of the landscape and connectedness through hedgerows represents the presence of corridors and barriers. Area reduction will cause a reduction of the populations that can survive, and in this way an increased risk of extinction. It also will increase the need for species to disperse between sites through a more or less hostile landscape.

Second, the principle of *multifunctionality* states that ecological networks always bear several functions, which are coherent to landscape functions at the relevant hierarchical level (see Bastian & Schreiber, 1999). Therefore the planning of networks following only one principle (dispersal and migration of species) may mislead the planning purposes.

Third, the principle of *continuity* means that the functioning of a network at a certain hierarchical level is only guaranteed if the full spectrum of a networks' hierarchy is performed.

In practical terms this means that ecological networks should be maintained or if necessary created at all levels. We assume that the network at lower hierarchical levels supports the biodiversity and material cycle control at the adjacent higher levels. For example, it is very complicated to support endangered species at higher scales of large areas (e.g. large and homogeneous forest plantations) if the ecological infrastructure is absent at the lower levels (e.g. meso- and micro-level habitats). Considering that principle, the hierarchical levels between adjacent levels in the hierarchy may integrate functions and characteristics prevailing at neighbouring levels. Therefore, for instance, ecological and socio-economic functions have the highest relative importance in meso-scale networks (Table 2).

Fourth, according to the principle of *plenipotentiality* (considering causal relationships between levels of hierarchy, such as causal constraints and determinations of lower-level phenomena by high-level phenomena and *vice versa*), there are no specific scale-limited functions of ecological networks. The relative importance of various functions varies depending on the hierarchical level, and planning strategies should therefore follow these variations. For instance, at the global (mega-scale) level, the leading functions of the networks are to control the global balance of CO_2 and other greenhouse gases. At the micro-level, local biodiversity support and the control of nutrient fluxes are dominant.

At the global level one art of the solution of biodiversity lies in conserving the Last of the Wild -- those few places that are relatively less influenced by human beings in all ecosystems around the globe, and give the opportunity for their connectedness (Sanderson *et al.*, 2002). It allows better stewarding of natural processes across the gradient of human influence through conservation science and action. The most important part of the solution for human beings, as individuals and through institutions and governments, however, is to moderate their influence in return for a healthier relationship with the natural world. On the other hand, at the micro-level, small-scale variations of land-use patches and their ecotones may compensate the excess nutrients.

The concept of territorial ecological networks can be considered a new paradigm in nature conservation and ecosystem management. The functions of ecological networks (biodiversity support, energy and the regulation of material fluxes, cultural and socio-economic functions) and their proportions are coherent within the hierarchy of networks. Therefore different management principles and strategy are required on different hierarchical levels. Further activities in the research, design and implementation of territorial ecological networks should concentrate on the development of coherent planning and management schemes at higher hierarchical level up to the global scale. In addition, the upscaling of ecological networks' functions and their spatial distribution is one of the priorities in the further development of this new concept of nature conservation.

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Abstract

This paper draws attention to and discusses the hierarchical nature of territorial ecological networks, and in this context their structural and functional aspects are debated. The focus of the article is on implementation and is illustrated with a number of examples, including the Pan-European Ecological Network as an example of ecological networks at the regional level and the riparian buffer zones as an ecological network at the micro-level. The upscaling and downscaling of ecological networks' functions and spatial distribution are discussed.

The paper suggests that the functions of ecological networks (biodiversity support, energy and material fluxes' regulations, cultural and socio-economic functions) and their shares depend on the level of those networks in the hierarchy. Furthermore, the functions depend on and are complementary to the simultaneous existence of ecological networks at several levels. Therefore, in land-use planning and conservation practice on different hierarchy levels, different and coordinated management principles and strategies are required.

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