Perspective paper

Bridging the gap between ecology and spatial planning in landscape ecology

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Abstract

Landscapes are studied by pattern (the geographical approach) and by process (the ecological approach within landscape ecology). The future of landscape ecology depends on whether the two approaches can be integrated. We present an approach to bridge the gap between the many detailed process studies on species, and applied activities such as landscape evaluation and design, which require integrated knowledge. The approach consists of four components: 1) Empirical case studies of different scales, organisms and processes. 2) Modeling studies to extrapolate empirical studies across space and time. 3) Modeling studies to produce guidelines and standards for landscape conditions. 4) Methods and tools for integration to the landscape level, which can be built into multidisciplinary tools for design and evaluation. We conclude that in the landscape ecological literature, the steps 1 and 2 are well represented, whereas the steps 3 and 4 are mostly neglected. We challenge landscape ecologists to push landscape ecology to a higher level of maturation and to further develop its profile as a problem-oriented science.

Introduction

Landscape ecology is defined as a problem-oriented science (IALE executive committee 1998). It has developed from the growing awareness of environmental problems since the nineteen seventies. Spatial planning and landscape design are disciplines which transfer the knowledge developed in landscape ecology to application. To optimize this process of knowledge transfer, landscape ecology must co-evolve with spatial planning (Ahern 1999). The development of ecologically sustainable landscapes requires that patterns of future landscapes sustain the necessary ecological processes in the landscape. Therefore, we must know how landscape patterns relate to these processes. In this paper we point out that most empirical process studies are of no use to landscape management as long as we fail to transfer the information to the level of problem solving. We concur with Moss (2000), that the justification of landscape ecology as a science requires that this gap between process studies and spatial planning is bridged. Therefore, we think it is necessary to develop an approach for generalizing and aggregating ecological knowledge for application in spatial planning. In this paper, we elaborate such an approach for spatial processes in populations. We focus on biotic processes as we consider that the gap to application in landscape planning for biotic processes is especially wide compared to abiotic processes such as water and nutrient flows.

Why is so much knowledge on ecological processes not applied in spatial planning? We interpret

this in the context of the maturation process of landscape ecology: apparently the merging of geographical and ecological disciplines is not yet complete. To clarify our viewpoint we summarize a bit of history. The first landscape ecologists were geographers (Neef 1982). Zonneveld (1982) regarded the vegetation and soil surveyors as well as geographers as the typical landscape ecologists ('close to the practical holistic landscape scientists'). Early landscape ecology was dominated by pattern analysis and pattern interpretation, for instance in terms of the suitability of the landscape to land use functions (Ružička and Miklos 1982; Haase 1989; Miklos 1989). The holistic entity of the science was stressed, and the notions of landscape homeostasis and biocybernetic regulation were key issues (Zonneveld 1982; Naveh 1987). The Veldhoven proceedings (Tjallingii and De Veer 1982) contained various attempts to apply information theory and thermodynamics as a means of landscape analysis (e.g., Phipps 1982; Veen 1982), but this line of research was never developed to an operational level (but see Li 2000). In a recent special issue of Landscape and Urban Planning devoted to holistic landscape ecology (Naveh 2000) we could not find much progress in the development of a mechanistic basis for a holistic landscape ecology.

On the other hand, landscape ecologists who had their roots in ecology (e.g., Forman 1982) were much more interested in spatial processes linking the landscape pieces together. However, because in the early days ecologists were not yet interested in the role of spatial heterogeneity, there was not much ecological basis for landscape ecologists to build on. In the index of Odum's (1971) handbook the word landscape does not occur and landscape maps only appear, with reference to land use, in the chapter on resources. Similarly, Krebs' (1985) handbook on ecology does not refer to 'landscape', and only three times to spatial heterogeneity. The metapopulation theory (launched by Levins as far back as 1970) was elaborated at the landscape scale by landscape ecologists (e.g., Henderson and Merriam 1985; Fahrig and Merriam 1985; Opdam et al. 1985; Van Dorp and Opdam 1987; Baudry and Merriam 1988; Opdam 1988, 1991), years before this theory became the focus of spatial ecology (Hanski and Simberloff 1997).

The different roots of landscape ecology contributed their own knowledge and methods. Geography contributed the spatial approach and the development of maps as spatially explicit representations of the landscape. Maps are simplified reflections of land-scape functioning, but often this is assumed rather than tested, as is illustrated by the many indices for describing landscape pattern that bear no apparent relation to ecological processes (Schumaker 1996; Vos et al. 2001 a). The geographer Haines-Young (1999) stated it this way: 'Much contemporary work on pattern has focussed on the analysis or description of spatial geometry and has failed to provide any understanding of the significance or meaning of these patterns'. This understanding must be developed within the ecological domains of research.

We argue that the lack of a mechanistic basis for a holistic landscape ecology and, consequently, for spatial planning, is because many empirical and theoretical ecological studies fail to transfer their results in the context of landscape pattern. Most authors of detailed studies do not attempt to bridge the gap to generalization and application (Figure 1). For example, looking through the papers on habitat fragmentation in 'Landscape Ecology', of the 33 papers we classified as such only 11 attempted to make the obtained knowledge about species pattern relationships explicit by a (multiple) regression model, which would allow spatially explicit predictions of species occurrence in landscape patches. Only 2 studies apply a spatially explicit metapopulation model to be able to make predictions on persistence of the species in the landscape (Figure 1, arrow 1). A major gap in this field of landscape ecology is the lack of methods to transfer studies on single species to generalized knowledge on the relation between landscape pattern and biodiversity. While understanding of processes requires a focus on single species distributions and individual behavior, the application of this knowledge in spatial planning requires several steps that are not well developed in landscape ecological methods. In these steps the variety of species' responses to the landscape and the variety of landscape patterns are reduced and generalized, and subsequently made available to users in a form that does not require detailed understanding of ecological processes. In our view, this is why recent landscape planning papers do not use the current body of knowledge on species and landscapes (e.g., Takeuchi and Lee 1989; Bastian and Roder 1998; Duhme and Pauleit 1998; Van Lier 1998). Therefore, future landscape plans are not tested against criteria based on ecological processes (Figure 1, arrow 2).

Moss (1999) considered the geographic and the ecological branches as the 'solitudes' of landscape ecology, referring to the difficult interaction between the two, and postulates that landscape ecology can
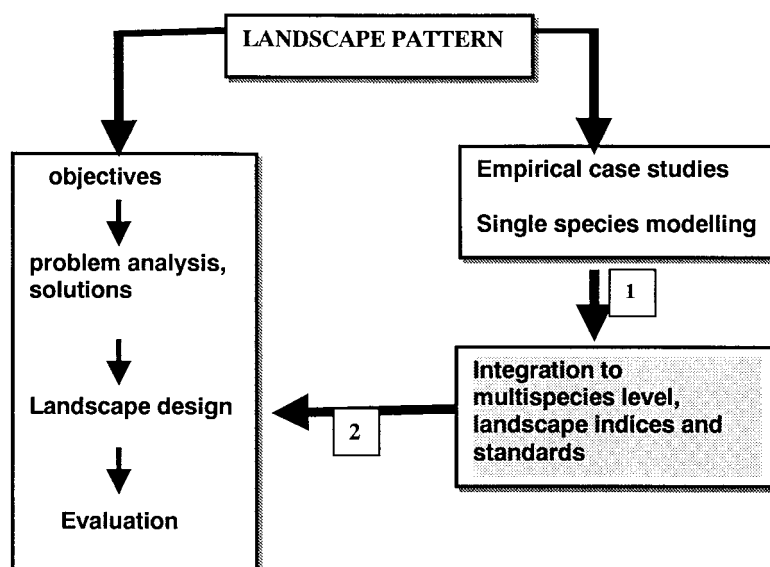
Figure 1. Two distinct approaches within landscape ecology. At the left, the geo-ecological (pattern based) approach, ending up in spatial planning. At the right the bio-ecological (process oriented) approach. The numbered arrows and the gray-shaded bloc indicate where in our view research is underrepresented and the transfer of information is not operating well.

only maturate if the two are merged. Fahrig (1999) illustrated Moss's view by defining landscape ecology as a subdiscipline of ecology: 'Landscape ecology is the study of how landscape structure affects the abundance and distribution of organisms'. We postulate, like Moss (2000), that the future of landscape ecology lies in the understanding of how landscape pattern is related to the functioning of the landscape system, placed in the context of (changing) social values and land use. A necessary step to that goal is the integration of process knowledge from different disciplines. We feel that the knowledge and methods to achieve this integration and apply its results in landscape planning and management are what make landscape ecology unique as compared to other disciplines.

In this paper, we contribute to strategies and methods of data integration by, firstly, identifying what sort of information is required in the various stages of problem solving. This provides us with the landmarks for data integration. Secondly, we present a way from detailed, species-oriented and local, empirical studies to a body of knowledge about the landscape-biodiversity relationship that provides the information required in the consecutive phases of the planning process. We illustrate our approach with examples from our own practice. We focus on habitat networks (Opdam 2001), because we have developed our expertise in that subject. We do not claim to cover the whole scope of landscape ecology, but offer our approach to

our colleagues to test its usefulness in other fields of landscape ecology.

Data required in spatial planning

In decision-making on future landscapes, landscape planners, landscape managers and politicians are involved in a cyclic process (Figure 2). At different points in the cycle different sorts of knowledge are required. The basic condition for a successful use of ecological process knowledge in landscape planning is that this knowledge is tailored for the different steps of this planning cycle.

The cycle starts with a problem definition phase, which is basically a comparison between the future ambitions or goals for the functions of the planning area and the actual situation, in our case maintaining habitat conservation networks in a human dominated landscape. This phase requires clearly defined goals and quantitative measures of success. For example, the planning goal may be to maintain a certain number of identified species with persistent populations, while the measure of success is the number of those species that actually do maintain persistent populations.

In this definition phase we need an *assessment* tool (Figure 2) which may encompass:
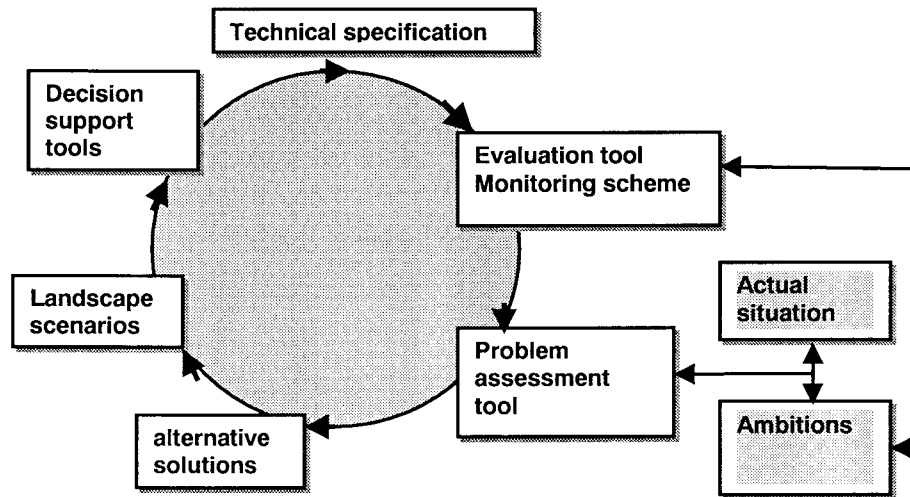- measures for the ecological functioning of the landscape that reflect the policy aims for nature

Figure 2. Information needed in different phases of the planning cycle. It starts with a comparison of the actual suitability of the landscape for selected landscape functions (in our case: biodiversity conservation) with the policy ambitions or goals. This step requires a problem analysis tool. Usually problems can be solved in different ways, which may lead to alternative future landscape options. Then, after choosing the most profitable option, the plan is developed and subsequently evaluated and monitored to see whether the newly developed landscape really does what it is expected to do (planning cycle adapted from Harms et al. 1993).

conservation; for example the number of species in sustainable habitat networks, the percentage of actual or potential species present;

– landscape standards required for persistent (meta) populations of target species, for example minimum amount of habitat or minimum landscape cohesion (Opdam et al. submitted);

– a spatially explicit tool to assess whether and where these conditions are actually realized in the planning area.

This assessment tool may take various forms. For example, one may use empirical data to determine the network of suitable habitat for the species and define the occupied patches, and use an incidence-based model (Hanski 1994; Ter Break et al. 1998; Vos et al. 2000) to transfer the distribution pattern to a measure related to persistence. Alternatively, one may use ecologically-scaled landscape indices to determine for which species profile the landscape provides conditions for persistence (Vos et al. 2001a), or use a GIS (geographic information system) model based on landscape cohesion assessment to determine the potential of the landscape for a set of target species (Opdam et al. submitted). In many cases, time will not allow extensive field sampling and subsequent analyses. Therefore, quickly applicable tools, which are able to assess the conditions of the landscape independent of species distribution data, are preferable (Opdam 2001).

Once the problem is defined, the next step requires a set of *possible solutions* (Figure 2). These may take the form of simple and qualitative indications, for example minimum area rules for ecosystems based on the key patch approach (Verboom et al. 2001; Opdam and Wiens 2001). In many cases, one solution will promote only some of the target species, whereas other species are neutral or even negatively affected. Also, different solutions may have different chances of being implemented, given social and economic restrictions. For instance, a mosaic of small elements may be easier to mix with agricultural claims than developing a large key patch.

Finding the optimal combination of options in a multifunctional context is a complex process, which can be guided by supplying *landscape scenarios* and *decision support tools* (e.g., Harms et al. 1993). In this step, alternative options for the landscape are assessed and compared. It requires the same type of information as discussed under problem definition, but the tools must have predictive power. An analysis of the present situation is of no use here.

After choosing for the most cost-effective option, the new landscape plan is designed and constructed. This phase asks for *technical specifications*, such as templates for corridor types for particular species profiles, or required dimensions of fauna underpasses.

The final stage is an assessment of the success of the plan after implementation. *Monitoring* the effects

of the landscape change is important to validate the model's predictions, to improve the quality of the predictive toolbox and, most importantly to allow for a further planning round or implementation phase if the goals are not met. We suggest that the method used earlier for comparing alternative scenarios could be used. In this case, the conditions for biodiversity in the restored landscape are compared to the conditions required for attaining the targets. We consider that landscape ecologists should provide such monitoring schemes.

So, depending on the stage in the planning process, we may need either simple rules and concepts or rigorous quantitative tools. In all cases, except when the planning is aimed at a single species, rules, concepts and tools must apply for a combination of species. In the next section we present the strategy that we developed to obtain this information.

Strategy of data integration

The steps we distinguish in the research strategy are depicted in Figure 3. Empirical knowledge should be the basis of any scientific rule. Field studies may focus on pattern analysis at the population level or measure spatial processes on individuals in connection with the landscape structure.

Studies of distribution patterns in a landscape network

Characteristically, populations in landscapes are spatially structured and their performance may be affected by the spatial characteristics of the habitat network in the landscape and the structure of the matrix in between. The observed distribution patterns represent snapshots in the dynamic interaction between distribution patterns of species and spatial processes, governed by the landscape pattern and landscape change. Differences in habitat patch occupancy over a landscape region are interpreted as the effect of landscape pattern on population processes. For instance, information about the significance of corridor elements in the matrix for birds can be obtained by correlating presence/absence patterns with characteristics of the patch network and the density of hedgerows in the landscape matrix (e.g., Van Dorp and Opdam 1987). Also, we obtain indications of the degree of fragmentation at which species are affected by habitat configuration and matrix characteristics. If different species are compared in the same landscape, we obtain information about the between-species variation in response to landscape variation. Usually, such studies produce notions about concepts and solutions, rather than reliable tools for evaluation and prediction. Spatially explicit regression models can be applied to define whether and where there is a problem for the species (e.g., Vos and Chardon 1998), but because they are based on correlations the uncertainty of such results is considerable.

Process studies at the level of populations and individual movements

A next step in empirical studies is measuring processes at the level of local populations. The dynamics of network populations can be understood by the extinction and recolonization rates of local populations. Most importantly, for understanding the relation between these processes and the landscape pattern, such measures should be related to patch and matrix characteristics (Vos et al. 2001a). Dispersal is one of the key processes for population persistence in a landscape network (Opdam 1988; Wiens 1997). The dispersal stream across a landscape is the result of decisions of individuals in response to landscape pattern, concerning velocity, choice of directions, probability of crossing borders, etc. Dispersal studies should include the role of landscape structure on distance and direction of dispersal movements, particularly the influence of corridor and barrier structures in the matrix (Vos et al. 2001b).

Predictions of persistence

The approaches mentioned thus far concern distribution of species in a habitat network. However, conservation is primarily focussed on persistence. Therefore, an important step in building up our knowledge basis for landscape planning is that we determine under which conditions landscape networks allow persistence. Hence, we must be able to translate distribution patterns into persistence estimates. This requires either individual-based mechanistic metapopulation models (Lindenmayer and Lacy 1995; Lindenmayer and Possingham 1995; Smith and Gilpin 1997; Foppen et al. 2000a) or incidence function metapopulation models (e.g., Verboom et al. 1991; Thomas and Hanski 1997; Vos et al. 2000). Verboom et al. 2001 combine the two models for one purpose.
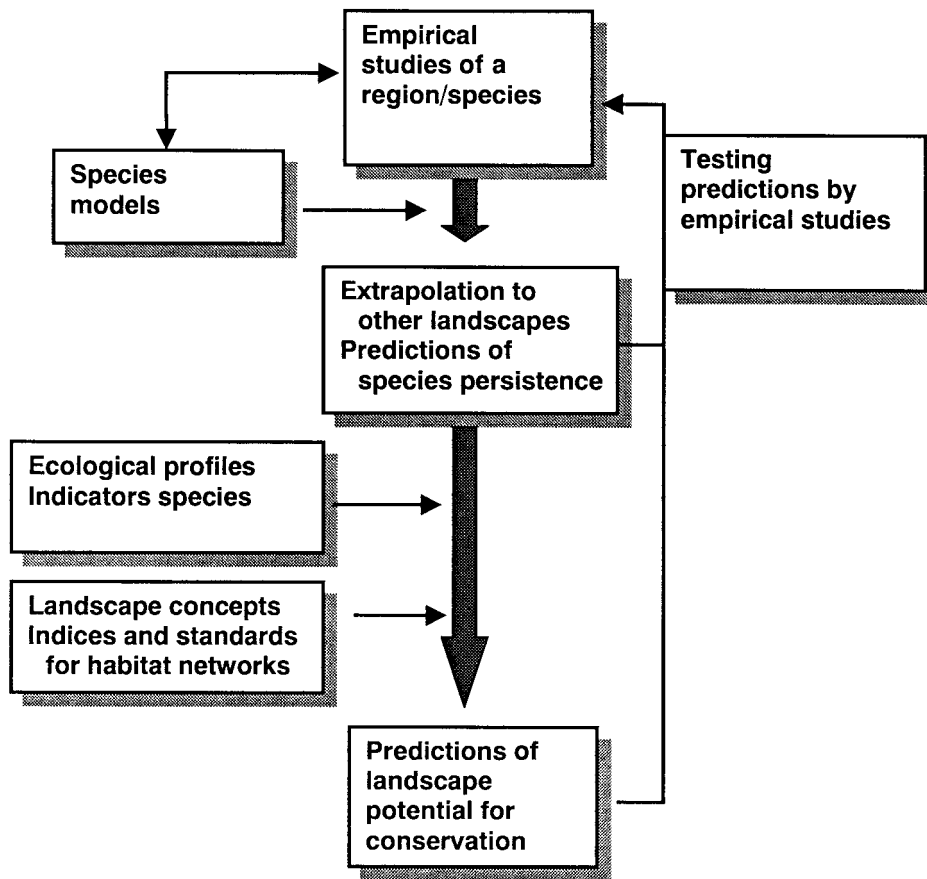
Figure 3. Steps in the research strategy. From top to bottom, the results of empirical studies are transferred to other landscapes and to predictions of persistence, whereas in the subsequent steps the single species level is left for a multi-species level that allows predictions on the potential of the landscape. These predictions can be validated by empirical data.

Generalization to other landscapes

Most empirical studies encompass only a minor part of all variation in landscape configuration that is encountered in landscape planning. Therefore, application in landscapes outside the range of variation is problematic. Also, similar problems arise if species have different responses to landscape configuration in different parts of their geographical range (Mönkkönen and Reunanen 1999) .

There are various approaches to overcome this problem. Case studies might be repeated in areas with different configurations of the habitat network to test the validity of empirically obtained regression models (Taylor 1991). Alternatively, metapopulation models can be used as a tool for extrapolation across a landscape gradient. For instance, such models can detect critical thresholds for landscape cohesion (Andrén 1996, Vos et al. 2001a).

Aggregation to multi species level, generating simple landscape indicators and design rules

Strictly speaking, no two species are alike regarding the landscapes they need for survival. But as landscapes are not planned for single species, the challenge is to find similarities between species. These similarities form the basis to classify species into ecological profiles, and generate rules for sustainable landscapes for these profiles (Vos et al. 2001a; Opdam et al. 2002; Verboom et al. 2001).

Examples

Developing guidelines and assessment tools for corridors

The resistance of the landscape for dispersing individuals is an important component of connectivity in

human-dominated landscapes, where boundaries between habitat patches are sharp and the permeability of boundaries and the matrix will vary greatly (Wiens 1997; Bennett 1999). In nature conservation practice, the protection of zones with high permeability, so-called corridors or linkages, are being implemented to enhance successful dispersal of organisms (e.g., NPP 1990; Bonner 1994; IUCN 1995; Jongman and Troumbis 1996; Bennett 1999; Vas et al. 2001b). There is a need for general rules for effective corridor design.

Empirical case study on individual movements in a landscape

Vos et al. (submitted) started at the level of the individual moving through the landscape. Tree frogs (*Hyla arborea*) were taken as organisms suitable for field studies and representative of small-sized ground moving organism. In field experiments, the behavior of radio-tagged tree frogs in an agricultural landscape, which resembles the matrix between suitable habitat patches for this species, was registered. These experiments provided data on movement speed and turning angle, as well as the probability of crossing boundaries (Figure 4). Such data identify that landscape elements have different effects on frog movement, and thus influence the direction and speed of movement. For quantitative application in landscape planning, such data have to be generalized to other landscape patterns and aggregated to the landscape level.

Generalization to other landscapes

To extrapolate these individual and local scale observations to differences in connectivity between landscapes, the simulation model SMALLSTEPS was calibrated on the observed movement paths (Vos et al. 2002). To test the reliability of the model predictions, the model was tested in a different study area, comparing the predicted transition of individuals between populations with actually observed dispersal events (Vos, unpublished data). Vermeulen (1995), Tischendorf and Wissel (1997) and Haddad (1999) also followed this approach with spatially explicit movement models based on individual-level studies of movement on a micro scale. These models can be used to generate simple connectivity values of different types of landscapes for the particular species under study. Such values can be put into a GIS model to assess or predict connectivity of a planning landscape. Another application is to determine the effectiveness

of alternative corridor designs (Figure 5). However, the applicability in spatial planning is limited since the connectivity values are species specific, and will at best hold for species with comparable reactions to landscape heterogeneity.

Aggregation to multi species level

In the next step (Figure 3), in which more general corridor requirements for species complexes are developed, the connectivity estimates obtained for different species will be aggregated. This step is still in progress. The basic goal is to establish, for a range of species, the key characteristics that determine corridor effectiveness in landscapes with different degrees of habitat fragmentation. Species with comparable corridor requirements are then grouped into similar corridor profiles. To develop such a framework, simulation studies with model species in computer-generated landscapes help to generate ecological profiles (Vos et al. 2001a). A profile represents a range of species with similar sensitivity to landscape resistance. Each profile is connected to a basic corridor type. In constructing profiles, we need to consider variation in habitat-specific movement velocity, dispersal mortality, habitat preferences, and boundary behavior in different landscape configurations. The modeling of the impact of corridor width and movement attributes by Tischendorf and Wissel (1997) is a good example of this approach.

Developing guidelines and assessment tools for effective habitat networks

In the Netherlands marshlands are important to nature conservation. To safeguard marshland biodiversity, marshland areas are planned to function as a habitat network, including marshland restoration and new corridor zones. For the Dutch government it is important to know whether the plans are adequate to reach the goal, and where enlargement of existing areas, development of stepping stones and corridor zones will be most effective.

Empirical case studies: inferring significance of network configuration from distribution pattern

Marshland birds are often absent in suitable habitat and their presence is related to the amount and spatial configuration of habitat. Studies on the distribution of bird species in the Dutch marshland network found that small and abundant species, like the
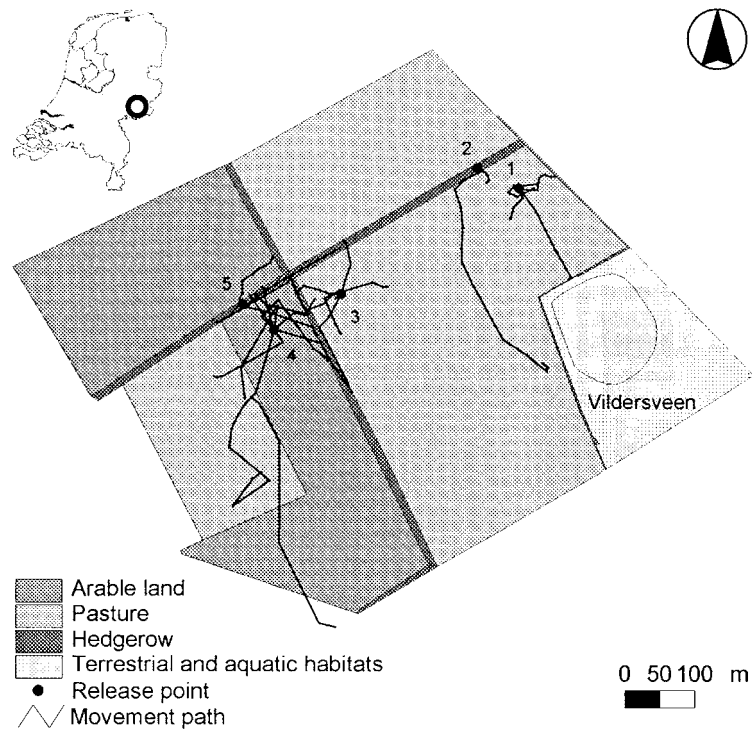
Figure 4. Observed movement patterns of displaced tree frogs in an agricultural landscape (from Vos et al. submitted). Inset map shows study landscape location in The Netherlands.

Reed Warbler (*Acrocephalus scirpaceus*), as well as large mobile species, like the Bittern (*Botaurus stellaris*) are affected by habitat configuration (Foppen et al. 2000b; Foppen & Chardon 2002). Empirical regression models were constructed which explained presence/absence as a function of size of marshland patches and their relative position within the network (Foppen et al. 2000a; Verboom et al. 2001; Foppen & Chardon 2002). These models have been used to predict the effect of planned marshland in the research area in comparison to the original situation (e.g., Opdam et al. 1995).

Transferring distribution data to persistence

We developed species specific modules of a spatially explicit individual-based model called METAPHOR (Foppen et al. 1999, 2000a,b; Vos et al. 2001a). With this model we simulated the dynamics of a metapopulation of several marshland birds like Reed and Sedge Warbler (*A. schoenobaenus*), Great Reed Warbler (*A. arundinaceus*) and Bittern.

Parameterization of the species-specific parameters was based on literature data, empirical studies (Foppen et al. 2000a,b) and calibrated on distrib-

ution patterns of the species (SOVON 1987). The predictions of this model can be used to determine whether the observed habitat network permits a long-term persistence of the network population of a certain species.

Generalization to other landscapes

The METAPHOR marshland bird model can also be used to make predictions of persistence for landscapes other than the study area. For that we have to assume that the observed relations between dispersal and metapopulation processes also hold for other landscapes. Validating the model on distribution data should test this assumption.

We used the species-specific modules of the METAPHOR model to evaluate and compare several marshland management scenarios (Foppen et al. 2000b). The scenarios tested the possible implications of stopping the reed-cutting regime, or restoring 1500 ha of marshland, or both. These combinations resulted in very different amounts of suitable breeding area (mainly reed vegetation) per marshland and for the whole country. Running a 'marsh warbler' and 'bittern' module of METAPHOR for these scenarios

——— **1cm = 250m**

Figure 5. Application of the movement model SMALLSTEPS, based on parameters estimated from the observation of field patterns (Figure 4). The model is used to measure connectivity of a landscape for the tree frog in various landscape scenarios.

indicated the impacts on persistence and occupation pattern for these species in the Netherlands (Figure 6).

Aggregating to multispecies level; rules for application

For a further aggregation to the multi-species level we distinguished two ecological profiles, respectively representing small marshland songbirds and marshland herons (Foppen et al. 2000b). General rules for minimal key patch size were developed for each of these

Table 1. Population sizes (in pairs at carrying capacity) in two landscape configurations as a result of METAPHOR simulations for a 'marsh heron' and a 'marsh warbler'. Indicated are the average size and the range for a network with and without a key population (KP). Based on Verboom et al. (2001).

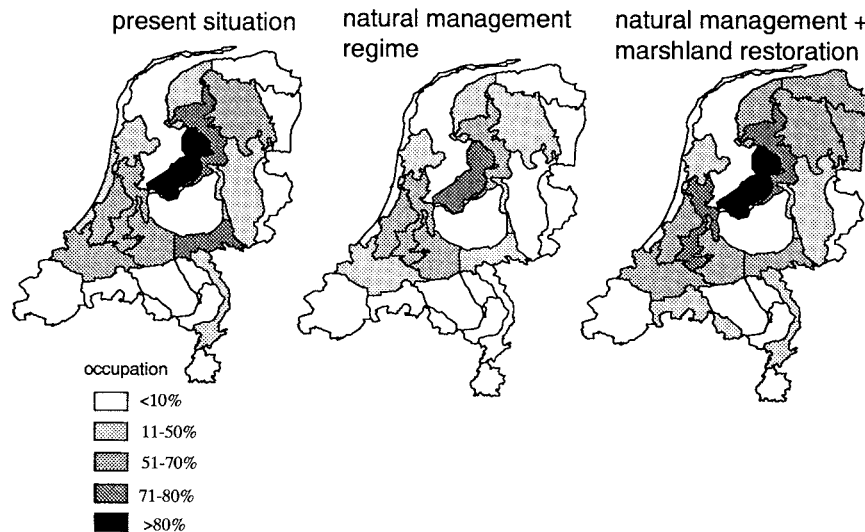| Species	KP	Network with KP	Network without KP
Marshheron	20	83 (62–190)	122 (97–1009)
Marshwarbler	100	130 (120–175)	150 (132–160)

Figure 6. Occupation probability in different landscape regions in the Netherlands, as predicted by a METAPHOR Bittern model. Occupation is presented relative to carrying capacity as an average saturation. Geographical classification based on soil and geomorphologic cues. Presented are three situations. From left to right: present situation, present location of marshlands with a natural management regime (after stopping reed cutting) and the National Ecological Network scenario (with restoration and change to natural management regime). Based on Foppen et al. (2000b).

species profiles (Table 1, Verboom et al. 2000). A key patch is a habitat patch in a network with a very small probability of going extinct (<5% in 100 years), based on an assumption of one immigrant per generation. We used our empirical data on presence/absence of marshland birds and the resulting predictive regression models to estimate the size of key patches for species profiles (Verboom et al. 2001). The METAPHOR model was used to test these estimates in different landscape configurations. Also, by using this model we extrapolated the standards for one patch to standards for a total network of patches (Verboom et al. 2001, Table 1).

These rules were built into the rule based model LARCH (Chardon et al. 2000), which is able to determine quickly the potential for conservation of a habitat network, independently of species distribution data. In the case of the marshland birds it was used to evaluate the proposed national ecological network plan and several alternatives (see Opdam et al. 2002, Groot Bruinderink et al. 2002; Verboom et al. 2001).

Conclusion

In our view, the integration of ecological and geographical research lines (in the context of socio-economic conditions) is the core activity of landscape ecology. It is absolutely necessary to obtain that in-

tegration when we want to design and develop landscapes on a sound ecological basis, rather than just designing a landscape pattern which might seem adequate for some years, but which bears no relationship to the natural processes in the landscape system.

We presented the ecological part of this mechanistic knowledge basis as a knowledge pyramid in four layers:

1. Empirical case studies on many different scales, organisms and processes.
2. Modeling studies to extrapolate empirical studies across space and time
3. Modeling studies to produce guidelines and general rules.
4. Tools for integration to the landscape level, so that application in multidisciplinary landscape studies becomes possible.

We conclude that in the landscape ecological literature, steps 1 and 2 are well represented, whereas steps 3 and 4 are mostly neglected. Steps 1 and 2 are also claimed by spatial ecology (With and King 1999; Fahrig 1999). We challenge landscape ecologists to pay much more attention to steps 3 and 4 to bridge the gap between knowledge development and knowledge application. Accomplishing this will give landscape ecology a much stronger profile, and we will proceed a step towards landscape design based on ecological processes. Our approach was devel-

oped in our own practice, and it remains to be seen to what extent it makes sense in other parts of the world. The Netherlands has a strongly urbanizing landscape, where humans dominate the landscape and land use functions compete strongly for space. Spatial planning is widely accepted. Nature and landscape values are becoming strong components in the competition for space, and politicians and managers ask for quantitative tools to consider the cost-effectiveness of measures in the landscape. In this context there is a great need for quantitative ecological knowledge at the landscape level. We postulate that this is typical for urbanizing areas in the world, where nature is considered an important part of the green environment. We invite landscape researchers to share their experience with us with respect to the sort of information needed in landscape management, and other strategies to build up the mechanistic knowledge base to support that need.

Acknowledgements

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