

Integrated Grid Based Ecological and Economic (INGRID) landscape model – A tool to support landscape management decisions

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Abstract

The aim of the INGRID landscape model is to simulate the ecological effects of management schemes for dry grasslands and to calculate costs in order to serve as decision tool for nature conservation agencies. To predict the local and regional risk of extinction of plants and animals with respect to different management scenarios/disturbance regimes, we apply modelling approaches on different scales and levels of hierarchy. We integrate abiotic and biotic state variables, processes and complex interactions in a spatially explicit way into the INGRID modelling shell. Data and parameters necessary for reliable modelling were determined empirically in a study site in southern Germany. Subsystems of the overall model are empirically parameterised and validated by means of extensive field surveys. The INGRID landscape model is still in development to be customised to administrative application. In this paper we give an overview on the landscape modelling shell and demonstrate the general structure of the INGRID landscape model. Preliminary results are exemplified with respect to habitat modelling, nature conservation evaluation, and economic modelling of two management scenarios.

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Software availability

Name of the software: INGRID

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Hardware required: MS Windows™ 32-bit applications

Software required: None

Program language: Borland Delphi

Program size: 2 MB

Availability and cost: at request

1. Introduction

Economic pressure on Central European agricultural systems causes a loss of species-rich ecosystems (Poschlod and Schumacher, 1998; Waldhardt et al., 2003). Instead of traditional and extensive practice to preserve open landscapes, expensive management measures like annual mowing are currently applied. Many abandoned grassland sites became nature reserves with the need to remove standing biomass and to extract nutrients. Consequently, it would be generally desirable to shift from these static, costly conservation measures to dynamic, more cost-effective management regimes.

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This considerable increase in area that needs to be managed by nature conservation authorities on the one hand and a lack of expert knowledge concerning succession under different – especially dynamic – management regimes on the other hand, calls for a predictive tool that integrates nature conservation as well as economic aspects. The Integrated Grid Based Ecological and Economic (INGRID) landscape model offers the possibility to predict ecological benefits as well as economic costs depending on a selected management scenario in a spatially explicit way. Comparison of different scenarios leads to management regimes that combine low management costs with acceptable environmental consequences. We included five different conservation measures in the model: free grazing by goat, sheep, and cattle, as well as infrequent rototilling, and mowing.

With exception of annual mowing, the management systems are characterised by secondary succession which is periodically reset by small scale disturbance events. Therefore, the alternative regimes result in a mosaic of habitat qualities for plant and animal species shifting in space and time. The species' habitats in these shifting mosaics become dynamic with respect to location and time frame affecting colonisation rates and persistence probabilities. In contrast, the classical conservation by mowing conserves low and closed vegetation cover and aims at preventing succession.

Before recommending the proposed cyclic disturbance regimes as an alternative to traditional conservation measures, a number of questions concerning regional species persistence and (inter-)relationships between management, abiotic conditions and biotic response have to be answered. Only if the species' requirements and attributes are met by the long-term spatio-temporal pattern of habitat quality in this mosaic cycle, the proposed dynamic management regime may serve as a cost-efficient alternative.

We empirically studied rototilled and traditionally managed plots on the landscape scale to analyse these management regimes regarding their conservational and economical efficiency in preserving the species richness of dry grasslands (Kleyer et al., 2002). We apply modelling approaches on different scales and levels of hierarchy to assess the risk of extinction of plant and animal species. This requires to integrate static and dynamic modules regarding abiotic and biotic state variables, processes and interactions into a spatially explicit landscape model. There are several examples of successful applications of landscape models for equivalent tasks, especially in forest ecology and management (e.g. Kurz et al., 2000; Li et al., 2000; Liu and Ashton, 1998). Other landscape models explicitly evaluate the effect of management scenarios on habitat quality (Gaff et al., 2000; Li et al., 2000), population persistence of species (Cousins et al., 2003), or carbon stocks (Hill et al., 2003).

To support management decisions, it is essential to integrate abiotic models, ecological models and economic cost assessment (Turner et al., 2000; Jakeman and Letcher, 2003). At best, the management efficiency can be conceptualised as the ratio of ecological gain and economic costs (Pieterse et al., 2002). In any case the information gained by prediction based

on models should be aggregated by a form of multi-criteria analysis (Drechsler, 2000, 2004).

Conservation agencies face an increase of areas that are subject to conservation measures. Often, the funds are not sufficient to use established conservation measures, i.e. mowing, on all areas. New cost-effective methods need to be tested. In order to achieve an optimal allocation of financial resources that leads to conservational success, the comparison of costs and ecological consequences of different management scenarios is essential.

The aim of the INGRID landscape model is to yield ecological as well as economic predictions that are calculated on the basis of spatially explicit management decisions. The management scenarios for each area are interactively assembled by selecting time schedule and type of management. Based on these scenarios, a time series of several years may be simulated yielding three types of result:

- species frequencies and distributions,
- these transferred to conservation values,
- absolute and relative costs of each conservation measure.

Modification of scenarios, e.g. by changing proportion or spatial location of conservation measures, will lead to different simulation results. By comparing several simulation results, the user is able to quantify the trade-off between ecological and economic aspects and may so optimise the management scenario (cf. similar approaches in Rao et al., 2000 or Oglethorpe et al., 2000). In general, the funds are limited and the decision maker tries to achieve the best conservation value possible. In a first step, an established method will be assigned to the most valuable areas. For the other areas, conservation measures will be chosen either by habitat type or by spatial proportions of different measures. Additionally, the proportions of the conservation measures can be modified step by step.

2. INGRID landscape model

2.1. Introduction

The INGRID landscape model was implemented in Borland Delphi™ and integrates several abiotic and biotic modules (see below and Fig. 1), coupled on the basis of a simple grid based Geographic Information System (GIS). An interface to ESRI ArcView® enables the import and export of digital maps. Each module was empirically parameterised and validated by means of extensive field surveys. Combining the modules the landscape model allows:

- (i) scaling and regionalisation, i.e. extrapolating surveys and predicted probabilities of occurrence from plot scale to landscape scale,
- (ii) spatially explicit modelling of processes and interactions between different abiotic and biotic features, and

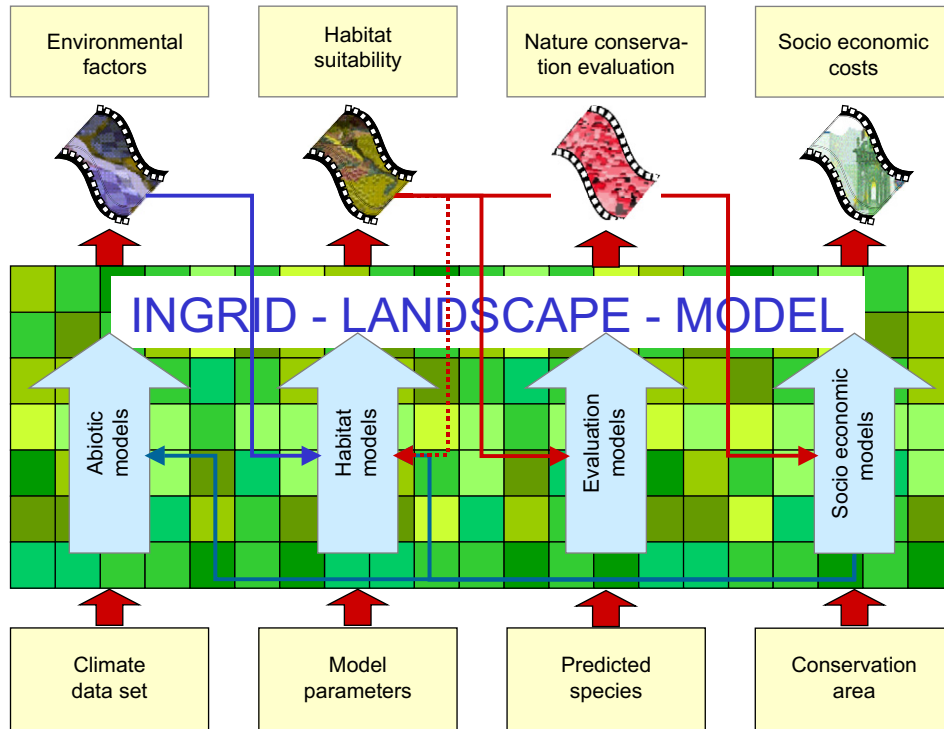


Fig. 1. Internal structure of the INGRID landscape model. The four modules are inter-related by data exchange as depicted by arrows.

(iii) assessing ecological values (nature conservation evaluation) as well as economic costs (costs of conservation measures) of any of the management scenarios.

The management regimes comprise frequency, spatial extent and temporal sequence of conservation measures. It depends on these parameters if rototilling can be considered a cost-effective alternative for the conservation of open dry grasslands that helps to preserve biodiversity.

2.2. Model structure

The INGRID landscape model comprises of the following modules (see also Fig. 1).

2.2.1. Maps

We used static input maps of e.g. elevation, slope, and aspect as well as more complex topographic parameters, like plan and profile curvature, potential insolation and topographic wetness index. These parameters were derived by means of digital terrain analysis on the basis of a digital elevation model with 5 m resolution using GIS (cf. Moore et al., 1991; Wilson and Gallant, 2000; Florinsky et al., 2002). Additionally, we derived some static soil parameters from the soil map according to AG Boden (1994). These parameters are necessary for calculating soil water conditions: sand, silt, and clay content, pore volume, field capacity, available water capacity, and hydraulic conductivity. Others serve as predictor variables in plant habitat models, e.g. field capacity and pH value.

2.2.2. Abiotic model

The calculation of potential and actual evapotranspiration (after Penman, cf. Fisher et al., 2005) as well as soil water content follows the simple approach of Wendling et al. (1984). It does not take lateral flow paths into account. Potential evaporation is corrected with respect to vegetation effects following the (dual) crop coefficient approach after Allen et al. (1998). The abiotic model calculates the dynamics of potential and actual evaporation as well as plant available water (Rudner et al., 2004; Schröder et al., 2004). Via the crop coefficients these values depend on the management regime chosen. The simulation yields chronosequences.

2.2.3. Habitat models

Statistical habitat models predict the shifting mosaic of habitat qualities for plant and animal species as well as the spatial distribution of the species (cf. Guisan and Zimmermann, 2000; Reich et al., 2000). We used logistic regression to estimate habitat models for 52 plant species and 5 insect species. The analyses were carried out using S-Plus 6.1 applying the HMISC and DESIGN libraries provided by Harrell (2001). We used a backward stepwise procedure for model selection, allowing linear and quadratic responses. Habitat model performance was evaluated by $R^2_{\text{Nagelkerke}}$ regarding model calibration and AUC regarding model discrimination (see Hosmer and Lemeshow, 2000; Manel et al., 2001) after internal validation with bootstrapping (Verbyla and Litvaitis, 1989; Steyerberg et al., 2001; Opperl et al., 2004). We checked for strong correlation between environmental variables (according to Fielding and Haworth, 1995).

2.2.4. Nature conservation evaluation models

Based on the species predictions, each grid cell is rated with respect to three different criteria (rarity, cultural landscape, wilderness) as well as biodiversity. Evaluation factors ranging from 1 to 5 were predefined for each species. The rarity value was assigned in dependence on regional abundance consulting a distribution atlas (Schönfelder and Bresinsky, 1990). The values for the criteria “cultural landscape” and “wilderness” were assigned according to the importance of the species for the vegetation in the historic cultural landscape, dominated by viticulture and semi-natural dry grassland, or in the potential natural vegetation, respectively. Concerning rarity the maximum factor of all predicted species in a cell is retained. For the other two criteria the mean value of the predicted species is employed (Fig. 2). The biodiversity value represents the share of predicted species with respect to the potential species pool. The result is transformed to the range from 1 to 5. During a simulation run the frequency distribution of the evaluation levels is shown, resulting from an aggregation over the whole study area. On the information level, the predicted frequency of the modelled species is stored.

2.2.5. Economic models

Financial models calculate the costs of the management scenarios regarding the time schedule and spatial management regime. The calculation of the costs is based on parameters like frequency (e.g. each year or every third year), effective

working time, time for preparation of machines, labour costs, capital costs, and costs for farm machines (after Kuratorium für Technik und Bauwesen in der Landwirtschaft, 1998). The effective working time depends on site parameters like area, slope, soil type, accessibility and distance to the next site or farm. As at steep slopes rototilling has to process upwards, additionally the orientation of the sites with respect to slope and thus the length of the possible rototilling tracks is relevant. Short tracks require frequent turning of the machines.

2.2.6. Scenario wizard

The scenario wizard allows a guided interactive definition of management scenarios following different paths. For areas with fixed conservation measures those may be predefined and fixed for the scenarios. The management type may be assigned to single areas by habitat type or by setting up proportions of different types. In the next step, the time schedule is fixed for each area. Furthermore, a set of options concerning the simulation has to be specified. In the last step, the habitat models have to be specified and assigned to the selected simulation run. The scenario wizard serves also to modify scenarios.

2.2.7. Simulation

Simulations can be run based on a management scenario for periods of one or more years as far as climate data are available. The amount of plant available water is calculated

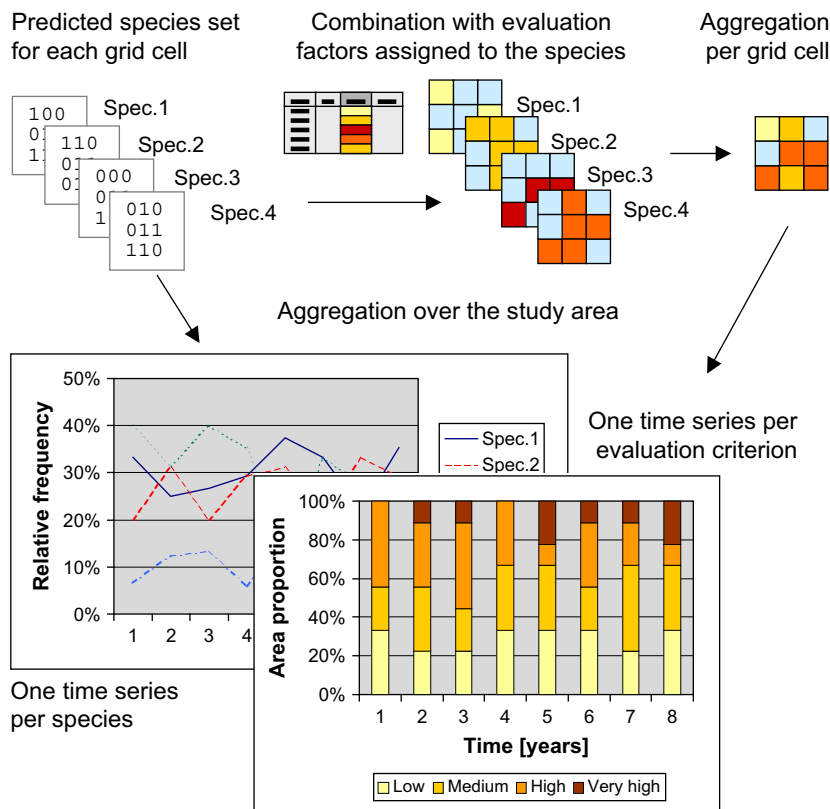


Fig. 2. Information flow during the nature conservation evaluation procedure: based on the species predicted occurrences, the relative frequency of each species is retained as a time series. The predicted species combination per grid cell yields ratings for three different evaluation criteria which are displayed as time series, too.

with a daily time step. Integration regarding selected months yields a dynamic predictor variable for habitat modelling (Fig. 3). Changes in predictor variables caused by the management regime are updated on a yearly time step. Calculation of habitat suitability, and economic costs as well as the evaluation are carried out yearly. Results are displayed in charts as time series.

3. Case study: the nature reserve “Hohe Wann”, Southern Germany

3.1. Study area and data sources

The empirical studies in order to parameterise the INGRID landscape model have been carried out from 2000 to 2003 in the nature reserve “Hohe Wann”. It is located in the Hassberge area in Lower Franconia, Germany (50°03' N, 10°35' E, see Fig. 4) that belongs to the “Franconian escarpment landscape”.

The area of investigation with an extent of about 7 km × 3 km is characterised by heterogeneous geological substrates, i.e. Triassic sand and gypsum Keuper as well as the traditional system of inheritance by equal division resulting in extremely small agricultural areas. South-facing slopes that receive higher-than-average insolation are either used as vineyards, or they are fallow land after abandonment. They can be characterised as a mosaic of dry grasslands and shrubs within a matrix of arable land and forestry (see Fig. 5).

The surveys of habitat types, land use and soil characteristics were carried out between 2000 and 2002. The incidence of plant and animal species as well as habitat features were measured on 91 plots following a stratified random sampling design (Hein, 2004; Binzenhöfer et al., 2005).

3.2. Scenarios

Five management scenarios for the study area Hassberge are shown as exemplary applications of the landscape model. The scenarios were created by using the scenario wizard.

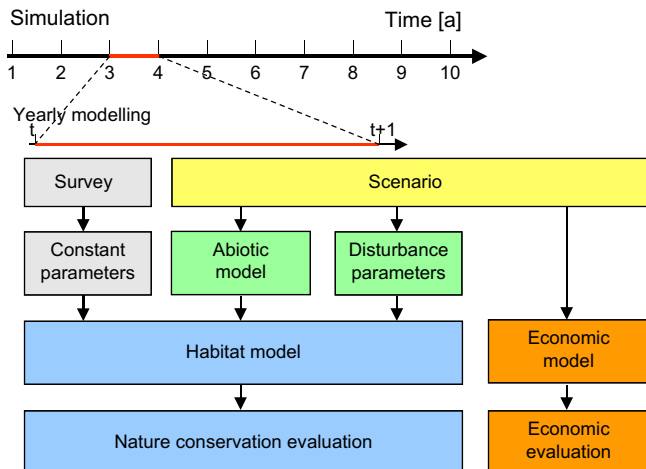


Fig. 3. Flowchart of a simulation run: the graph shows the calculation steps that are applied for each single year of a 10-year simulation run.

They are related to the entirety of the dry grassland, extensively used meadows and fallow land in the referred nature reserve.

In the scenarios the proportions of rototilled and mowed areas were set to 90/10 (scenario I), 70/30 (II), 50/50 (III), 30/70 (IV), and 10/90 (V). An interval of three years was chosen for rototilling. Mowing will take place annually. The scenarios are summarised in Table 1. Fig. 6 shows cut-outs of maps regarding the scenarios I, III, and V.

3.3. Results

3.3.1. Habitat modelling

The landscape model enables the application of habitat models to different disturbance scenarios. Habitat models quantify habitat quality with respect to the environmental conditions (Guisan and Zimmermann, 2000; Ortigosa et al., 2000). Applying these models for spatio-temporally varying environmental conditions – as we do e.g. for available soil water – yields a predicted shifting mosaic of habitat qualities (cf. Chiarello et al., 1998).

We implemented logistic regression habitat distribution models estimated for 91 randomly stratified plots (e.g. Kühner and Kleyer, 2003; Hein, 2004; Kühner, 2004; Binzenhöfer et al., 2005). We modelled the probability of occurrence for 52 plant and 5 animal species with performances ranging from acceptable to outstanding according to

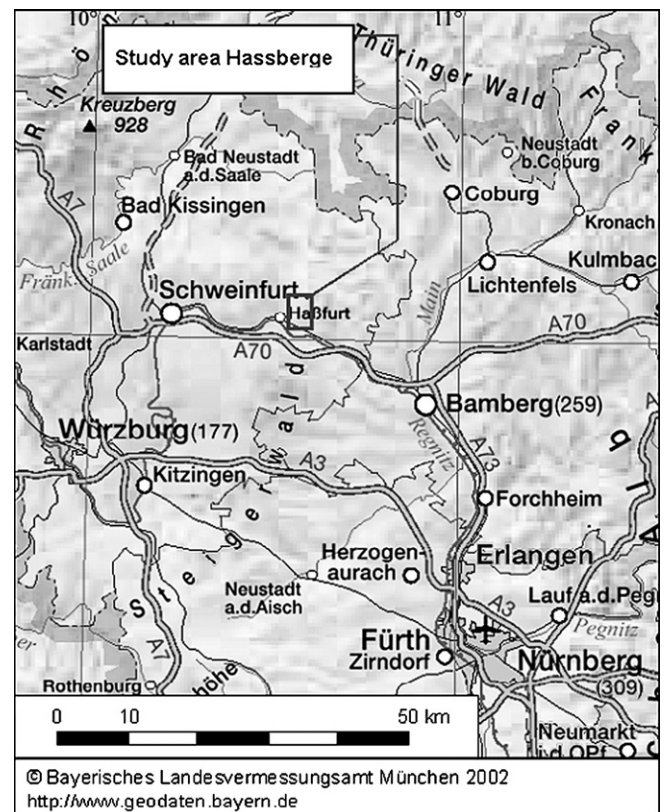


Fig. 4. Map of Franconia (northern Bavaria, Germany) with the Hassberge study area.

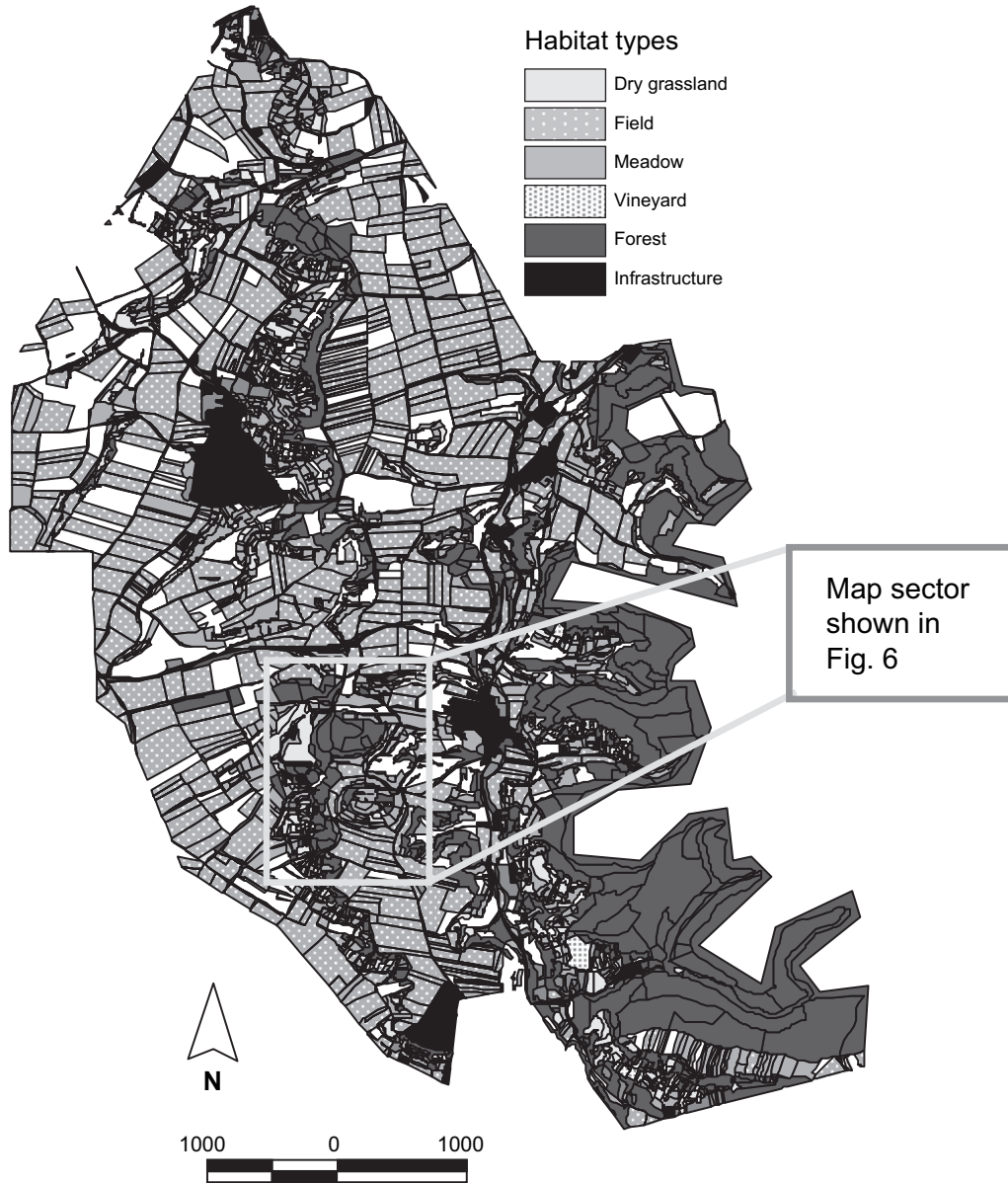


Fig. 5. Map of habitat types within the nature reserve “Hohe Wann” within the Hassberge area.

Hosmer and Lemeshow (2000) (Fig. 7). The models were validated internally with bootstrapping to yield realistic estimates of model performance (cf. Verbyla and Litvaitis, 1989; Pepler-Lisbach and Schröder, 2004). AUC-values significantly decrease with increasing prevalence ($p = 0.011$). This may indicate more specific niches yielding better models for less abundant species. Prevalences for these species ranged from 0.066 (*Bromus sterilis*) to 0.74 (*Poa pratensis*) with a median of 0.20 (Fig. 7). We checked for spatial autocorrelation in the residuals by calculating Moran’s I using Crimestat 2.0, detecting significant spatial autocorrelation in model residuals in case of 5 plant species (*Achillea millefolium*, *Dactylis glomerata*, *Petrorhagia prolifera*, *Prunus spinosa*, *Salvia pratensis*) and one animal species (*Platycleis albopunctata*).

Based on maps of environmental variables (like habitat type, soil properties, land use, slope, aspect, insolation,

wetness index, amount of plant available soil water between April and June, etc.) we use these habitat models to calculate the probability of occurrence for the entire study area, i.e. we perform a spatial extrapolation from our 91 sample plots. Further, these habitat suitability maps may be transformed to maps showing matrix versus suitable habitat using classification

Table 1
Application of two management types according to five management scenarios (area size, ha)

a	Scenario 1		Scenario 2		Scenario 3		Scenario 4		Scenario 5	
	r	m	r	m	r	m	r	m	r	m
	(90%)	(10%)	(70%)	(30%)	(50%)	(50%)	(30%)	(70%)	(10%)	(90%)
1	41.6	13.9	31.8	38.7	23.6	69.5	14.1	97.4	4.6	125
2	41.6	13.9	37.5	38.7	23.2	69.5	14.3	97.4	4.9	125
3	42.4	13.9	31.5	38.7	23.1	69.5	13.7	97.4	4.7	125

a, year; r, rototilling; m, mowing.

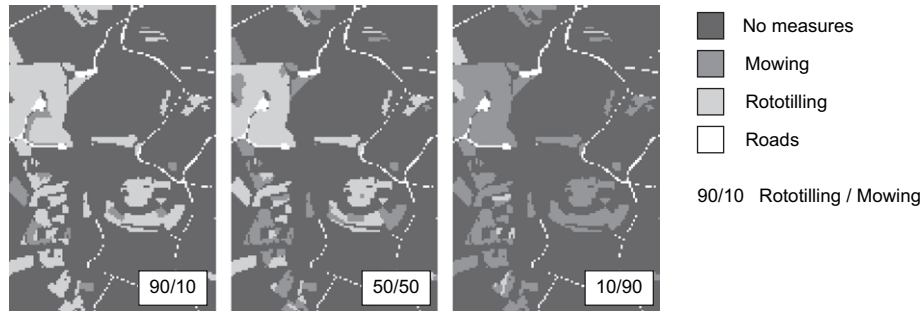


Fig. 6. Cut-outs of the scenario maps I, III, V (cell size 10 m).

thresholds (cf. Schröder and Richter, 1999; Ortigosa et al., 2000; Larson and Sengupta, 2004; Binzenhöfer et al., 2005).

Although, habitat models assume equilibrium conditions, there are some issues that allow their application in a dynamic context. Applying space-for-time substitution (Pickett, 1989), we use time-dependent predictor variables. Predictors directly describing the disturbance regime in terms of frequency as well as depth of disturbance integrate over longer time periods but they directly affect the soil water balance according to their dynamics. Bare soil after rototilling differs in evaporation rate compared to vegetated soil. This aspect is taken into account when calculating time-dependent predictors (e.g. amount of plant available soil water between April and June).

As a case species the annual plant *Thlaspi perfoliatum* was chosen. Fig. 8 depicts the steps in applying the habitat model. The species' spatial distribution was found to depend on the frequency of disturbance and on air capacity of the top soil (cf. maps in Fig. 8). After bootstrapping the model showed an excellent performance (Nagelkerke- $R^2 = 0.439$ and $AUC = 0.866$).

The species showed a unimodal response regarding the disturbance frequency, meaning that the probability of occurrence reaches its maximum for intermediate frequencies (around once per year, what is expected for an annual plant). The response with respect to the second predictor variable air capacity is sigmoidal. Since the regression coefficient is negative, the species was found to avoid soils with high air capacity, i.e. soils that dry fast.

To include the dynamic aspects related to the management applied we used results of frequency analyses conducted on experimental plots (Fritzsich, 2004): if a species revealed significant increase or decrease in the first two years after management, we increased or decreased the probabilities of occurrence estimated by the habitat models.

The application of the habitat model with respect to the five scenarios changes the spatial distribution of habitat quality (three scenarios are shown in Fig. 6). Overall, *T. perfoliatum* would benefit from rototilling. In Fig. 9 the predicted frequencies of six species are compared for all five management scenarios and the reference scenario.

3.3.2. Nature conservation evaluation

The highest rarity values decrease with the increasing share of rototilled areas. This reflects primarily the decrease of

Zygaena carniolica, the species with the highest rarity value. Rototilling has a weak influence on the value of the criterion 'cultural landscape'. The proportion of cells with very high values decreases slowly with an increasing proportion of rototilled areas. The number of cells with low values of the criterion 'wilderness' increases with increasing proportion of rototilling. This was expected as rototilling is an intensive cultivation method (Table 2).

The distribution of biodiversity values for different scenarios shows that the proportion of cells with medium diversity as well as the proportion of cells with very high diversity increase weakly at the expense of cells with high diversity.

3.3.3. Modelling of management costs

For the five described scenarios, the costs of the different management types were modelled in a spatially explicit way. We assumed that half of the area could be mown by a rotary cutter and the other part by clearing saws when calculating the costs of mowing. With an identical management area of 139.5 ha the scenarios imply costs that differ considerably (Figs. 10 and 11). A scenario with a high proportion of rototilled patches and an interval of three years is the most

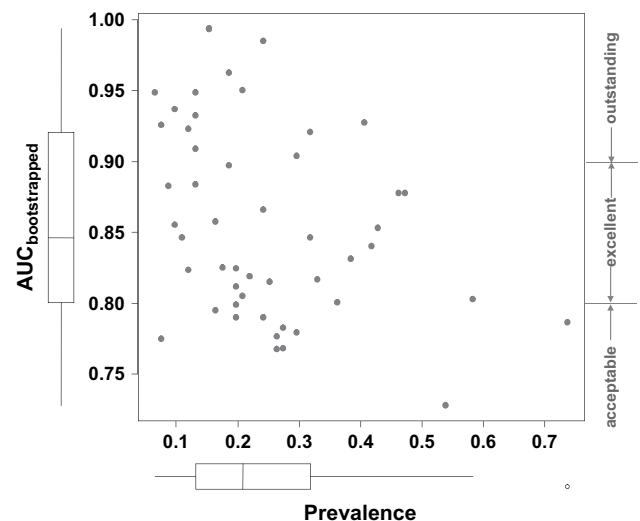


Fig. 7. Performance of the habitat models estimated for 52 plants species: AUC-values after bootstrapping plotted against prevalence. The AUC-values classified according to Hosmer and Lemeshow (2000) depict model discrimination.

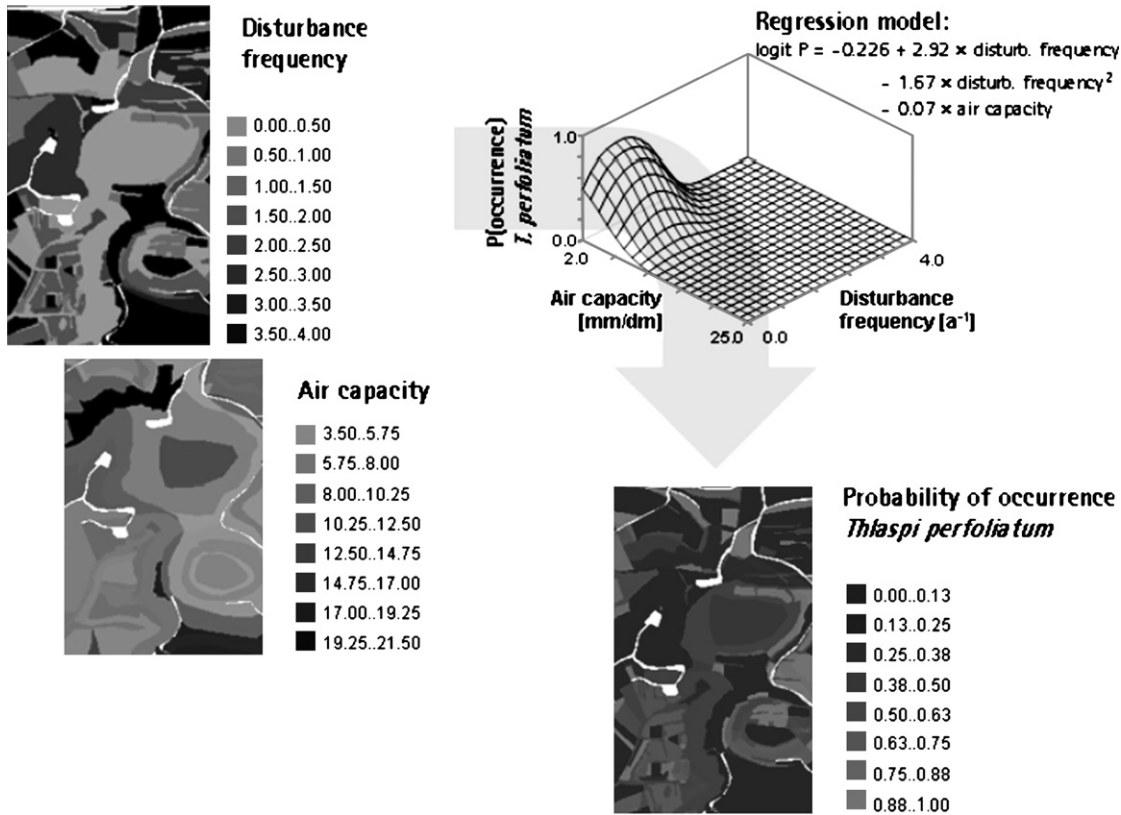


Fig. 8. Application of an exemplary habitat model for *Thlaspi perfoliatum*: maps of predictor variables (left), regression equation (top right), response surface and derived map of predicted occurrence probabilities (bottom right).

economic solution (27,000 €). With decreasing proportion of rototilled areas the rototilling costs decrease slowly and the mowing costs increase considerably. The area-dependent costs for mowing are almost stable (600–670 €/ha). The relative costs of rototilling depend heavily on the patch sizes and the distance between the patches (frequent transposing, higher relative amount of fixed costs). There is an upper threshold above which the relative rototilling costs are more or less stable (scenario 2: 32 ha/a) and a lower threshold below which the costs explode (scenario 4: 14 ha/a).

4. Conclusion

Based on comprehensive field surveys, the INGRID landscape model aims to integrate abiotic models, habitat models and economic models. Using the landscape model, in the study area a number of different management scenarios can be evaluated considering their nature conservation value related to their management costs. The results may build the basis of decisions concerning the management of concrete sites, using alternative management systems like rototilling. The application of the landscape model seems especially relevant in situations where the development of sites should be confronted with the costs of the development. A large number of scenarios can be evaluated in a short time period. The crux is the comparison of nature conservation values and management costs. As the nature conservation values reflect a mean value of the species that are predicted for a cell, the

disappearance of species is only detectable by changes in the biodiversity chart. Therefore, we recommend to study the results on the species development also before making management decisions in order to have sufficient and detailed information on the species level.

To minimise uncertainty of management decisions, we integrated habitat models into the landscape model. The aggregation of ecological information in the nature conservation evaluation module corresponds to the multi-criteria analysis

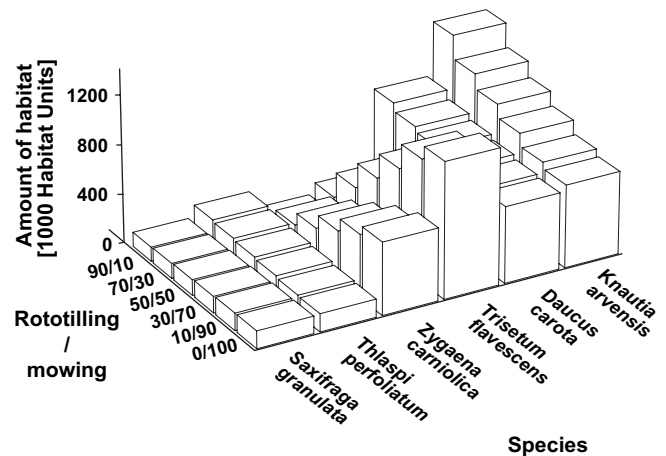


Fig. 9. Predicted habitat units (occurrence probability × area) for selected species regarding the five management scenarios described in comparison to the reference scenario (100% mowing).

Table 2
Nature conservation evaluation for five management scenarios (% grid cells averaged over 10 years)

Scenario	1	2	3	4	5
<i>r/m</i>	90%/10%	70%/30%	50%/50%	30%/70%	10%/90%
Rarity					
v	11	29	47	66	83
h	17	14	10	6	3
l	72	57	43	28	14
Cultural landscape					
v	12	11	10	10	9
h	86	87	88	89	90
m	2	2	1	1	0
Wilderness					
m	88	91	93	95	98
l	12	9	7	5	2
Biodiversity					
m	29	42	54	67	81
l	71	58	46	33	19

Evaluation levels: v, very high; h, high; m, medium; l, low; *r/m*, ratio rototilling/mowing.

‘scoring’ described by Drechsler (2004). The weighting problem is tackled in the evaluation factors that are assigned to each species in the species database. This leads to transparent evaluation results. In the aggregation procedure, the results are not condensed to one single number but to several values with respect to different evaluation criteria as postulated by Pieterse et al. (2002). In addition, objective information is provided with the results concerning the development of single species in order to enable the best decision possible. The target species problem, however, remains unsolved by the landscape model. As hitherto the manager has to set priorities, especially if there are trade-offs between species depending on different management types.

In contrast to Crist et al. (2000), the conclusion on biodiversity in the INGRID landscape model is based on the prediction of single species applying habitat models that integrate the modification of environmental factors. This procedure yields quantitative results concerning the spatial distribution. As

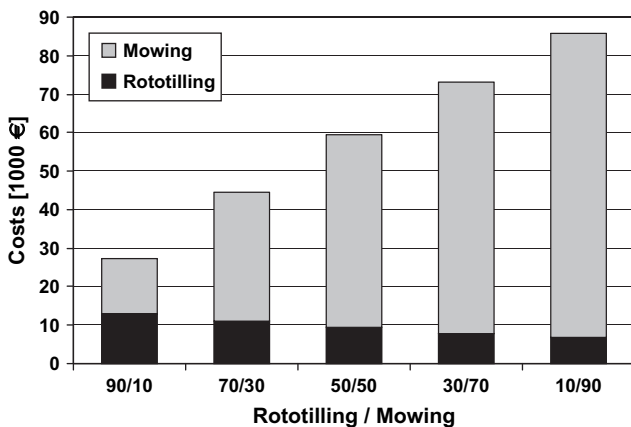


Fig. 10. Absolute annual management costs [1000 €/a] for five different scenarios (90/10 indicates the area ratio rototilling/mowing).

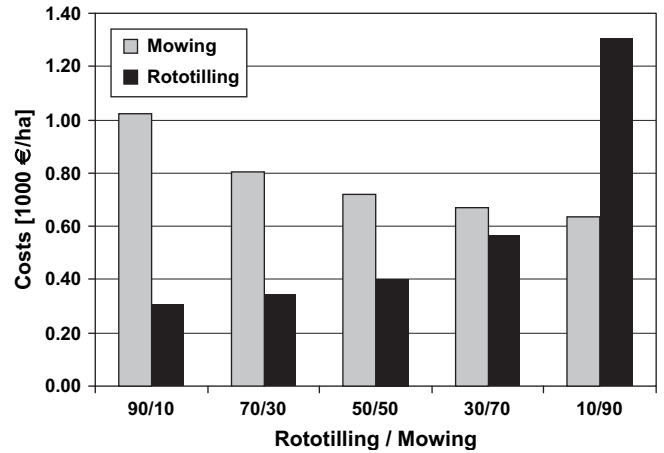


Fig. 11. Relative management costs [1000 €/ha × a] for five different scenarios (90/10 indicates the area ratio rototilling/mowing).

a measure of ‘extinction’, we have chosen the fall of the incidence function (derived from habitat models) below a critical threshold (p_{crit}), although we are aware that dynamic (meta-) population models (e.g. Akçakaya, 2000; Biedermann, 2004) may be more realistic (especially with small populations). On the other hand, it is not a trivial task to obtain sufficient data to parameterise those models for so many species. Thus, habitat models can be used to deal with many species and yield a rough prediction of changes in biodiversity.

Furthermore, the landscape model may be useful for the prediction of future development within environmental planning processes (e.g. impact assessment). However, further developments of the INGRID landscape model, like integration of population dynamic models or economic models for pasture management, are necessary in order to achieve more accurate predictions of the biodiversity of plants and animals as well as management costs. The inclusion of an expert module that will run simulations for a number of modified scenarios and enable sensitivity analyses will be the next step in the development of the landscape model. Sensitivity analyses may also help to study the role of error propagation (Håkanson, 1999) on model results.

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References

- AG Boden, 1994. *Bodenkundliche Kartieranleitung*. E. Schweizerbart'sche Verlagsbuchhandlung, Hannover.
- Akçakaya, H.R., 2000. Conservation and management for multiple species: integrating field research and modeling into management decisions. *Environmental Management* 26 (Suppl. 1), 75–83.
- Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop evapotranspiration – guidelines for computing crop water requirements. FAO Irrigation and Drainage Paper 56. FAO – Food and Agriculture Organization of the United Nations, Rome.
- Biedermann, R., 2004. Modelling the spatial dynamics and persistence of the leaf beetle *Gonioctena olivacea* in dynamic habitats. *Oikos* 107, 645–653.
- Binzenhöfer, B., Schröder, B., Biedermann, R., Strauß, B., Settele, J., 2005. Habitat models and habitat connectivity analysis for butterflies and burnet moths – the example of *Zygaena carniolica* and *Coenonympha arcania*. *Biological Conservation* 126, 247–259.
- Chiarello, E., Amoros, C., Pautou, G., Jolion, J.-M., 1998. Succession modeling of river floodplain landscapes. *Environmental Modelling & Software* 13, 75–85.
- Cousins, S.A.O., Lavorel, S., Davies, I., 2003. Modelling the effects of landscape pattern and grazing regimes on the persistence of plant species with high conservation value in grasslands in south-eastern Sweden. *Landscape Ecology* 18, 315–332.
- Crist, P.J., Kohley, T.W., Oakleaf, J., 2000. Assessing land-use impacts on biodiversity using an expert systems tool. *Landscape Ecology* 15, 47–62.
- Drechsler, M., 2000. A model-based decision aid for species protection under uncertainty. *Biological Conservation* 94, 23–30.
- Drechsler, M., 2004. Model-based conservation decision aiding in the presence of goal conflicts and uncertainty. *Biodiversity and Conservation* 13, 141–164.
- Fielding, A.H., Haworth, P.F., 1995. Testing the generality of bird-habitat models. *Conservation Biology* 9, 1466–1481.
- Fisher, J.B., DeBiase, T.A., Qi, Y., Xu, M., Goldstein, A.H., 2005. Evapotranspiration models compared on a Sierra Nevada forest ecosystem. *Environmental Modelling & Software* 20, 783–796.
- Florinsky, I.V., Eilers, R.G., Manning, G.R., Fuller, L.G., 2002. Prediction of soil properties by digital terrain modelling. *Environmental Modelling & Software* 17, 295–311.
- Fritzsch, K., 2004. Plant response to changes in disturbance magnitude. PhD thesis, University of Oldenburg, Germany. Available from: <<http://docserver.bis.uni-oldenburg.de/publikationen/dissertation/2004/fripla04/pdf/fripla04.pdf>>.
- Gaff, H., DeAngelis, D.L., Gross, L.J., Salinas, R., Shorosh, M., 2000. A dynamic landscape model for fish in the Everglades and its application to restoration. *Ecological Modelling* 127, 33–52.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135, 147–186.
- Håkanson, L., 1999. Error propagations in step-by-step predictions: examples for environmental management using regression models for lake ecosystems. *Environmental Modelling & Software* 14, 49–58.
- Harrell, F.E., 2001. *Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis*. Springer, New York.
- Hein, S., 2004. The survival of grasshoppers and bush crickets in habitats variable in space and time. PhD Thesis, University of Würzburg, Germany. Available from: <<http://opus.bibliothek.uni-wuerzburg.de/opus/volltexte/2004/914/>>.
- Hill, M.J., Braaten, R., McKeon, G.M., 2003. A scenario calculator for effects of grazing land management on carbon stocks in Australian rangelands. *Environmental Modelling & Software* 18, 627–644.
- Hosmer, D.W., Lemeshow, S., 2000. *Applied Logistic Regression*. Wiley, New York.
- Jakeman, A.J., Letcher, R.A., 2003. Integrated assessment and modelling: features, principles and examples for catchment management. *Environmental Modelling & Software* 18, 491–501.
- Kleyer, M., Biedermann, R., Henle, K., Poethke, H.J., Poschlod, P., Settele, J., 2002. MOSAIK: semi-open pasture and ley – a research project on keeping the cultural landscape open. In: Redecker, B., Fink, P., Härdtle, W., Riecken, U., Schröder, E. (Eds.), *Pasture Landscape and Nature Conservation*. Springer, Heidelberg, pp. 399–412.
- Kühner, A., Kleyer, M., 2003. Habitat models for plant functional types in relation to grazing, soil factors and fertility. *Verhandlungen der Gesellschaft für Ökologie* 33, 248.
- Kühner, A., 2004. Habitat models for plant functional types in response to management and disturbance. PhD thesis, University of Oldenburg, Germany. Available from: <<http://docserver.bis.uni-oldenburg.de/publikationen/dissertation/2005/kuehab04/pdf/kuehab04.pdf>>.
- Kuratorium für Technik und Bauwesen in der Landwirtschaft, 1998. *Landchaftspflege: Daten zur Kalkulation von Arbeitszeiten und Maschinenkosten*. KTBL-Schriften-Vertrieb im Landwirtschaftsverlag, Münster.
- Kurz, W.A., Beukema, S.J., Klenner, W., Greenough, J.A., Robinson, D.C.E., Sharpe, A.D., Webb, T.M., 2000. TELSA: the tool for exploratory landscape scenario analyses I. *Computers and Electronics in Agriculture* 27, 227–242.
- Larson, B.D., Sengupta, R.R., 2004. A spatial decision support system to identify species-specific critical habitats based on size and accessibility using US GAP data. *Environmental Modelling & Software* 19, 7–18.
- Li, H., Gartner, D.I., Mou, P., Trettin, C.C., 2000. A landscape model (LEEMATH) to evaluate effects of management impacts on timber and wildlife habitat. *Computers and Electronics in Agriculture* 27, 263–292.
- Liu, J., Ashton, P.S., 1998. Formosaic: an individual-based spatially explicit model for simulating forest dynamics in landscape mosaics. *Ecological Modelling* 106, 177–200.
- Manel, S., Williams, H.C., Ormerod, S.J., 2001. Evaluating presence–absence models in ecology: the need to account for prevalence. *Journal of Applied Ecology* 38, 921–931.
- Moore, I.D., Grayson, R.B., Ladson, A.R., 1991. Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. *Hydrological Processes* 5, 3–30.
- Oglethorpe, D., Hanley, N., Hussain, S., Sanderson, R., 2000. Modelling the transfer of the socio-economic benefits of environmental management. *Environmental Modelling & Software* 15, 343–356.
- Oppel, S., Schaefer, H.M., Schmidt, V., Schröder, B., 2004. Habitat selection by the pale-headed brush-finch, *Atlapetes pallidiceps*, in southern Ecuador: implications for conservation. *Biological Conservation* 118, 33–40.
- Ortigosa, G.R., De Leo, G.A., Gatto, M., 2000. VVF: integrating modelling and GIS in a software tool for habitat suitability assessment. *Environmental Modelling & Software* 15, 1–12.
- Peppler-Lisbach, C., Schröder, B., 2004. Predicting the species composition of mat-grass communities (Nardetalia) by logistic regression modelling. *Journal of Vegetation Science* 15, 623–634.
- Pickett, S.T.A., 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed.), *Long-term Studies in Ecology*. Springer, Heidelberg, pp. 110–135.
- Pieterse, N.M., Verkroost, A.W.M., Wassen, M., Olde Venterik, H., Kwakernaak, C., 2002. A decision support system for restoration planning of stream valley ecosystems. *Landscape Ecology* 17 (Suppl. 1), 69–81.
- Poschlod, P., Schumacher, W., 1998. Rückgang von Pflanzen und Pflanzengesellschaften des Grünlands – Gefährdungsursachen und Handlungsbedarf. *Schriftenreihe für Vegetationskunde* 29, 83–99.
- Rao, M.N., Waits, D.A., Neilsen, M.L., 2000. A GIS-based modeling approach for implementation of sustainable farm management practices. *Environmental Modelling & Software* 15, 745–753.
- Reich, R.M., Lundquist, J., Bravo, V.A., 2000. Spatial relationship of resident and migratory birds and canopy openings in diseased ponderosa pine forests. *Environmental Modelling & Software* 15, 189–197.
- Rudner, M., Biedermann, R., Schröder, B., Kleyer, M., 2004. Assessing management systems for the conservation of open landscapes using an integrated landscape model approach. In: Pahl-Wostl, C., Schmidt, S., Jakeman, T. (Eds.), *iEMSs 2004 International Congress: "Complexity and Integrated Resources Management"*. International Environmental Modelling and Software Society, Osnabrück.
- Schönfelder, P., Bresinsky, A., 1990. *Verbreitungsatlas der Farn- und Blütenpflanzen Bayerns*. Ulmer, Stuttgart.
- Schröder, B., Richter, O., 1999. Are habitat models transferable in space and time? *Zeitschrift für Ökologie und Naturschutz* 8, 195–205.

- Schröder, B., Rudner, M., Biedermann, R., Kleyer, M., 2004. Ökologische & sozio-ökonomische Bewertung von Managementsystemen für die Offenhaltung von Landschaften – ein integriertes Landschaftsmodell. *UFZ-Bericht*, 9/2004, 121–132.
- Steyerberg, E.W., Harrell, F.E., Borsboom, G.J.J.M., Eijkemans, M.J.C., Vergouwe, Y., Habbema, J.D.F., 2001. Internal validation of predictive models – efficiency of some procedures for logistic regression analysis. *Journal of Clinical Epidemiology* 54, 774–781.
- Turner, R.K., van den Bergh, J.C.J.M., Söderqvist, T., Barendregt, A., van der Straaten, J., Maltby, E., van Ierland, E.C., 2000. Ecological-economic analysis of wetlands: scientific integration for management and policy. *Ecological Economics* 35, 7–23.
- Verbyla, D.L., Litvaitis, J.A., 1989. Resampling methods for evaluation of classification accuracy of wildlife habitat models. *Environmental Management* 13, 783–787.
- Waldhardt, R., Simmering, D., Albrecht, H., 2003. Floristic diversity at the habitat scale in agricultural landscapes of Central Europe – summary, conclusions and perspectives. *Agriculture, Ecosystems & Environment* 98, 79–85.
- Wendling, U., Müller, J., Schwede, K., 1984. Ergebnisse von Verdunstungsmessungen über Gras mit einem Off-line Datenerfassungssystem. *Zeitschrift für Meteorologie* 34, 190–202.
- Wilson, J.P., Gallant, J.C., 2000. *Terrain Analysis: Principles and Applications*. Wiley, New York.