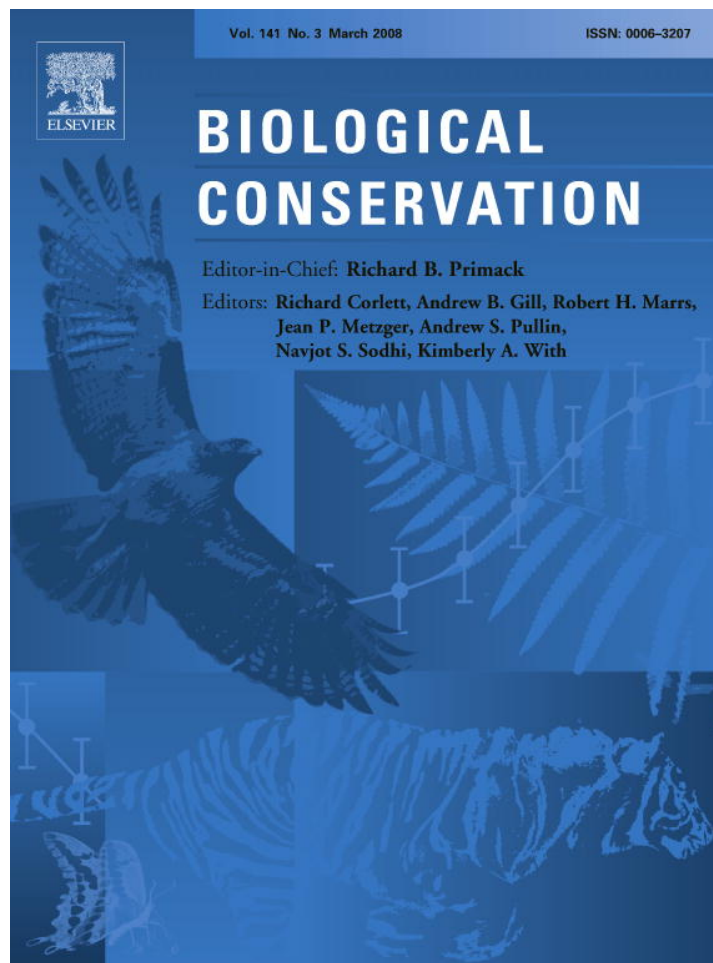


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A landscape model for quantifying the trade-off between conservation needs and economic constraints in the management of a semi-natural grassland community

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ABSTRACT

We present a landscape model to investigate the ecological consequences and costs of different management regimes in semi-natural grasslands. The model integrates dynamic abiotic conditions, management (i.e. disturbance) regime and response of more than 50 characteristic plant and insect species by modelling the dynamics of relevant niche parameters as predictors for species distribution models. We compare our results for exemplary scenarios differing in spatial and temporal scales and exemplary species belonging to different functional groups through several steps of aggregation.

Our analysis aims at the question whether an infrequent massive disturbance by rototilling can serve as a less expensive alternative to annual mowing for preserving the characteristic species composition of open dry grasslands in Southern Germany. Rototilling results in a shifting mosaic determining the habitat quality for plant and animal species that may reduce the survival of local or regional populations.

For some meadow species as well as the encroaching shrub species, rototilling has a detrimental effect on regional habitat quality. Other species, e.g. weeds and annual pioneers, strongly benefit or show only negligible reaction. Since this is a multi-objective problem, there is a no magic bullet in selecting an optimum scenario of measures. But by visualising the trade-off between ecological consequences and costs, our model is a valuable tool for conservation managers providing a sound scientific basis for management decisions relying on available ecological knowledge. It is also an interesting example for a model describing complex communities in a relatively simple way, simultaneously considering the main driving factors.

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1. Introduction

In Europe, many species depend on semi-natural landscapes, which have been created and maintained by long-term low-

intensity land use (Ellenberg, 1986). Today, changes in Central European agriculture cause a loss of species-rich ecosystems that depend on traditional land use (Hodgson et al., 2005; Poschlod et al., 2005). In marginal landscapes, abandonment

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leads to a loss of diverse open landscapes due to secondary succession following the absence of anthropogenic disturbances (e.g. Fischer and Wipf, 2002). Different management regimes are applied to prevent secondary succession and thus minimise habitat and biodiversity loss (e.g. García, 1992; Müller, 2002). In practice, managers have to compromise between ecological benefits and financial costs of management schemes. Reduction of costs can be achieved by reducing disturbance intensity in time or space.

Here, we assess infrequent rototilling as a management regime alternative to annual mowing (Poschlod and Wallis-DeVries, 2002). Rototilling, which is similar to ploughing at depth up to 20 cm, has a massive impact on the vegetation (Fritzsch, 2004). The management schedule allows secondary succession which is periodically reset by rototilling. Compared to annual mowing, disturbance magnitude is increased while disturbance frequency is reduced. Infrequent rototilling establishes a mosaic of habitat qualities for plant and animal species shifting in space and time. Only if species' requirements match the long-term spatiotemporal pattern of habitat quality in this mosaic cycle (Kleyer et al., 2007), rototilling may serve as an alternative to mowing. Therefore, species' sensitivities to both management regimes as well as costs of both procedures need to be integrated into a single model framework to facilitate decision making for managers engaged in nature conservation (Wätzold et al., 2006).

Some recent integrated landscape models explicitly evaluate the effect of management scenarios on habitat quality (Li et al., 2000; Holzkämper and Seppelt, 2007) and population persistence (Cousins et al., 2003; Wintle et al., 2005). But none of these approaches combines the effects of management on multiple species and costs of management.

Our landscape model relates static and dynamic environmental properties to species composition data using species distribution models for a set of 52 plant and five insect species (SDMs, Guisan and Thuiller, 2005). In addition to static predictors, we model the dynamics of abiotic site conditions and disturbances as driving factors for habitat suitability in a spatially explicit way. Thus, the SDMs quantify the shifting mosaic of habitat qualities and predict the effect of management on the spatiotemporal distribution of all 57 species. This allows capturing optimal disturbance intervals to prevent shrub encroachment and to promote annual species of dry grasslands. We quantify the effects of different spatiotemporal scales of disturbance on species' distribution and characterise costs and benefits of different management scenarios. Each module is empirically parameterised and validated by means of extensive field surveys (Fritzsch, 2004; Kühner, 2004; Binzenhöfer et al., 2005; Hein et al., 2007a). Detailed results are shown for eight species belonging to different functional groups (according to Kühner, 2004).

2. Materials and methods

2.1. Study area and data sources

The generic landscape model is applied to the nature reserve "Hohe Wann" located in the Hassberge area in Lower Franconia, Germany (50°03'N, 10°35'E, extent: 7 × 3 km²). The study area is characterised by heterogeneous geological substrates

(Triassic Sand and Gypsum Keuper). It is characterised by a mosaic of dry grasslands and shrubs within a matrix of arable land and forestry (Rudner et al., 2007).

Habitat types, land use, and soil properties were mapped between 2000 and 2002 (Eibich, unpubl. data). Data sets regarding the incidence of plant and animal species as well as habitat features covering the full gradient of succession in the landscape were surveyed on 91 plots following a stratified random design (plant species: see Kühner, 2004; butterfly, moth, grasshopper, and bush cricket species: see Hein et al., 2007a). A digital elevation model was constructed from aerial photographs by photogrammetry. Daily meteorological data were provided by the Bavarian agro-meteorological network for the period from 1991 to 2005.

2.2. Model structure and elements

The INtegrated GRID-based landscape model INGRID bases on a simple grid-based geographic information system with a spatial resolution of 10 × 10 m². It relates disturbance caused by management, topographic and edaphic conditions as well as dynamics of soil water to species composition as conceptually depicted in Fig. 1. Species composition is modelled by SDMs as the sum of occupancies of individual species (cf. Peppler-Lisbach and Schröder, 2004; Ferrier and Guisan, 2006). The different types of predictor variables used in the SDMs – topography, disturbance regime, static and dynamic soil conditions – are provided by several modules (see below).

Each simulation starts with the definition of management scenarios. The scheduled regime is translated into disturbance-related parameters (scenario generator, cf. Table 1). A simple, process-based simulation is used to calculate local soil water dynamics depending on site conditions and disturbance regime (abiotic module). We end up with sets of static and dynamic predictors for each patch under management. SDMs are then applied annually to depict the shifting mosaic of habitat suitability for all species (biotic module). Simultaneously, the economic module calculates annual management costs. Table 1 illustrates the underlying sequence of modules that are processed during a simulation (top to bottom).

2.2.1. Management scenario generator

Management scenarios are characterised by the spatiotemporal pattern of disturbance (either rototilling or mowing)

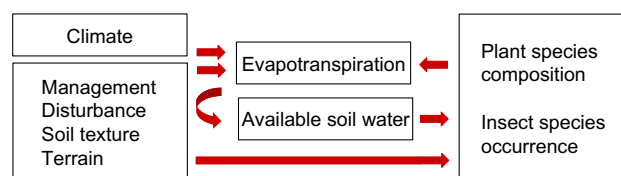


Fig. 1 – Processes and relationships considered in the integrated landscape model INGRID: species composition is affected by (i) management and related disturbance, (ii) static soil and terrain parameters as well as (iii) available soil moisture. The latter is driven by climate and evapotranspiration which itself depends on plant cover (after Schröder, 2006a).

depending on (i) frequency (in terms of return intervals: e.g. 1, 2, 3, or 5 years), (ii) spatial extent (between 0% and 100%), and configuration (automatically, i.e. either randomly or economically, or individually allocated for a set of appropriate habitat types). The resulting parameters (cf. Table 1) are updated with an annual time step to serve as predictors in the biotic module.

2.2.2. Abiotic module

The abiotic module simulates abiotic site conditions depending on climate and management regime. It consists of three sub-modules (A to C) that provide input data for the simulations.

A – Digital terrain model and static soil conditions By digital terrain analysis we quantified site characteristics like elevation, slope, and aspect as well as more complex topographic parameters such as potential solar radiation (Wilson and Gallant, 2000). During a detailed soil survey, soil texture and pH were mapped among other parameters (Eibich, unpubl. data). Available water capacity was calculated from soil texture according to AG Boden (1994).

B – Regionalisation of climate conditions Data from a reference climate station (Köslau: 50°03'52"N, 10°40'17"E, 400 m a.s.l.) located in the direct vicinity of the study area were regionalised by a multiple regression model to cover the entire study area (cf. Daly et al., 1994). This model was derived from data considering 11 climate stations within a 50 km radius. It describes yearly mean temperature and precipitation as a function of elevation and luv/lee situation.

C – Climate time series, time series of soil and plant parameters To calculate the dynamics of water supply for plants (see below) the following parameters are provided: (i) meteorological time series with a daily time step from 1991 to 2005 (air temperature, sum of precipitation, mean relative humidity, wind speed, and global radiation), (ii) topographic parameters, since they alter the above variables, (iii) soil properties that are relevant for soil water dynamics, and (iv) plant cover parameters for calculating evapotranspiration.

2.2.3. Modelling the dynamics of abiotic site conditions

The calculation of potential and actual evapotranspiration as well as soil water content (Rudner et al., 2007) follows Wendling et al. (1984) as described in DVWK (1996). Potential evaporation after Penman (1956) is corrected with respect to vegetation effects following the (dual) crop coefficient approach (Allen et al., 1998). Via these coefficients, evapotranspiration and plant available soil water depend on the interplay of management and local soil properties. For each simulation year, the amount of plant available soil water during April and June is aggregated to monthly sums which are used as explanatory variables for SDMs in the biotic module (cf. Table 1).

2.2.4. Biotic module: species distribution models (SDMs) regarding plant and insect species – shifting mosaic of habitat qualities

To assess management effects on regional diversity, we estimated and applied predictive SDMs. We used SDMs to predict the spatial distribution of 52 plant and five insect species in response to the following predictor variables (cf. Table 1, examples given below):

- (i) Dynamic disturbance variables depending on the management schedule, e.g. disturbance depth or week of first disturbance.
- (ii) Dynamic soil variables depending on climate and disturbance, e.g. amount of plant available water in April.
- (iii) Dynamic variables that depend on the succession taking place after disturbance, e.g. habitat type (only for insect models, derived from expert knowledge, Rudner pers. comm.).
- (iv) Static predictors depicting soil and terrain conditions, e.g. slope.

The SDMs track the spatiotemporal dynamics of predictors and calculate the annual occurrence probabilities of

Table 1 – Concept of information flow: INGRID integrates several modules that are processed from top to bottom

Module	Input	Result	Format	Predictors for SDMs	Unit
Scenario generator	Management scenario	Management and related disturbance regime	Dynamic	Disturbance frequency Disturbance depth First week of disturbance	[yr ⁻¹] [cm] [calendar week]
Abiotic module	Terrain & disturbance parameters	Terrain parameters	Static	Slope sin (Aspect), cos (Aspect) Potential solar radiation	[°] [1] [kWh/m ²]
	Soil & plant cover conditions	Static soil parameters	Static	pH Available water capacity	[1] [mm]
	Climate data	Evapotranspiration and soil water dynamics	Dynamic	Plant available soil moisture in April Plant available soil moisture in June	[mm/month] [mm/month]
Biotic module	All predictors	Predicted species occurrences	Dynamic	–	[P] or [0 1]
Economic module	Management regime	Management costs	Dynamic	–	[k€/yr]

The modules are linked by interacting processes and exchange of information since each module yields relevant inputs for others. For instance, the scenario generator module helps to generate management scenarios which are represented as maps of disturbance-related parameters such as frequency and depth for each year of a simulation. These disturbance parameters serve – among others – as input variables for (a) the abiotic module calculating a chronosequence of maps of plant available water, (b) the biotic module calculating the spatiotemporal pattern of habitat quality and predicting species composition, and (c) the economic module calculating management costs. All predictor variables considered in the biotic module are given with their units.

the species. Dynamic predictors are applied annually. If, for a patch, the scenario schedules rototilling in every third year and no management in the remaining years and rototilling starts in the first year, the predictor *disturbance depth* is set to -5 cm in that specific year, but to 200 cm (i.e. no disturbance) in the second and third year. Due to the change in plant cover and evapotranspiration, management also affects soil water dynamics yielding dynamic amounts of plant available water. The year-to-year dynamics of habitat suitability are driven by all types of dynamic predictors.

As SDMs, we used logistic regression models estimated on observed training data using R 2.2.0 (R Development Core Team, 2005). After checking for multicollinearity between predictors (Fielding and Haworth, 1995), we applied backward stepwise model selection considering linear and quadratic terms (R packages Hmisc and Design, Harrell, 2001). We assessed SDM performances with respect to calibration (R_N^2 after Nagelkerke, 1991) and discrimination (area under the receiver-operating-characteristic curve, AUC, Fielding and Bell, 1997) after internal validation via bootstrapping (Verbyla and Litvaitis, 1989). Model residuals were checked for spatial autocorrelation by calculating Moran's I (R package spdep, Bivand, 2002).

All species presence–absence data were sampled according to the principle of space-for-time substitution (Pickett, 1989). Consequently, we use these models to extrapolate and predict the species' distribution for the entire study area. Regression models assume equilibrium conditions in the response of species to habitat factors. Since this assumption is often violated after strong disturbances such as rototilling, we considered results of yearly frequency analyses conducted on experimental plots after rototilling (Fritzsche, 2004) by introducing a correction term for species that showed significant changes in frequency in the first years after management. Biotic interactions are not explicitly considered in this approach since the dynamics are mainly driven by disturbance.

Each SDM yields (i) a habitat suitability map with predicted occurrence probabilities, and (ii) resulting response surfaces to facilitate model evaluation. In order to derive species distribution maps, we applied P_{fair} as species-specific classification threshold according to Bonn and Schröder (2001), (i.e. sensitivity equals specificity) by applying AUC_ROC (Schröder, 2006b).

To derive aggregated measures of species performance, we calculated the number of habitat units for each species. Habitat units sum the predicted occurrence probabilities in the study area (cf. U.S. Fish & Wildlife Service, 1980). For further temporal aggregation, we use either minimum or mean occurrence probabilities during a simulation period (HU_{min} vs. HU_{mean}). HU_{mean} corresponds to the 'optimistic' assumption that a species is able to recover after a period of low habitat quality or local extinction as soon as habitat quality thresholds are reached again. HU_{min} , however, corresponds to the 'pessimistic' assumption that the minimum occurrence probability during a simulation governs the species performance. This may even result in permanent local extinction if habitat quality is below the threshold (e.g. P_{fair}).

2.2.5. Economic module: management costs

The costs of each management scenario depend on management frequency and inputs of labour and of capital invested (calculated according to KTBL, 1998). Labour costs depend on patch area, slope and orientation, soil properties, mean patch distance, and accessibility. The landscape model calculates management costs for each patch considering all these factors. Mowing and rototilling differ in demand for labour and capital per unit of area as well as in the relative proportions of both factors. Rototilling has higher labour productivity and benefits more from economies of scale than mowing – even though rototilling was carried out only in upslope-direction due to local conditions.

3. Results

3.1. Validation of the abiotic module

The abiotic module is successfully validated with independent data provided by the Department of Agriculture of the City of Würzburg. Fig. 2 shows simulated and observed dynamics of the plant available water content for two sites with different soil types between September 2001 and March 2005. Nash and Sutcliffe (1970) model efficiencies were 0.81 (loess soil) and 0.58 (clayey soil). This criterion ranges from minus infinity to 1, with higher values indicating better agreement. A value of 0 indicates that the observed mean is as good a predictor as the model.

3.2. Species distribution models (SDMs)

Table A1 in Appendix 1 provides an overview of model estimates and performance criteria. Altogether, there are only four plant species (*Bromus hordeaceus*, *Inula conyzae*, *Lolium perenne*, and *Rosa canina*) that do not respond to any dynamic predictor variable; they show constant predicted probabilities for both management systems. All other species do respond

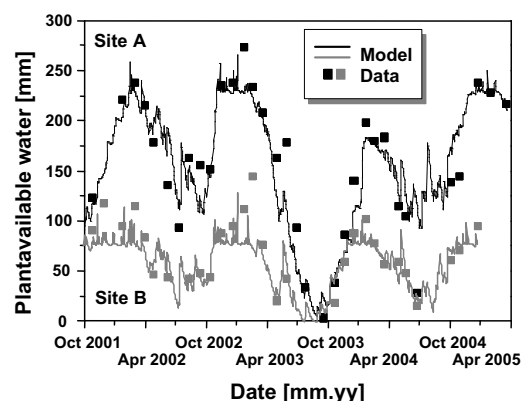


Fig. 2 – Validation of the abiotic module: plant available water dynamics for two independent sites located outside the study area in Lower Franconia; site A: eroded orthic luvisol on loess (Seligenstadt, 49°50'39"N, 10°06'11"E, 281 m a.s.l.) and site B: vertic cambisol on clay stone (Hohenroth, 50°18'56"N, 10°10'00"E, 300 m a.s.l.). Nash-Sutcliffe model efficiencies were 0.81 (site A, black) and 0.58 (site B, grey).

to dynamic predictors: (i) disturbance alone (38 species), (ii) dynamic soil conditions alone (two species), or both (13 species), and on static predictors (soil conditions: 31 species; topographic variables: 38 species). Table A1 also presents model performances with respect to calibration (R_N^2) and discrimination (AUC) after internal validation via bootstrapping. Fig. 3 depicts AUC-values showing very good model performances for most species – even in case of low prevalences. We detected significant spatial autocorrelation in model residuals for four plant species only: *Avenula pubescens*, *Poa pratensis*, *Petrorhagia prolifera*, and *Prunus spinosa*.

3.3. Local dynamics

The landscape model yields management costs and spatially explicit time series of predicted species occurrences for each scenario. Before stepping through different modes of aggregation, we present species-specific results for a single patch. We compare annual mowing, the reference scenario, with rototilling each third year, taking place in the years three, six, and nine. Local dynamics are exemplified by a set of seven plant species representing different functional types (Kühner, 2004) and one endangered insect species (Binzenhöfer et al., 2005) (Fig. 4).

In case of annual mowing, habitat quality is more or less stable for most species except *Knautia arvensis* and *Centaurea jacea* (Fig. 4A). The variation in habitat quality of the latter two species reflects fluctuating soil conditions. For rototilling, habitat quality exhibits four different response types (Fig. 4B).

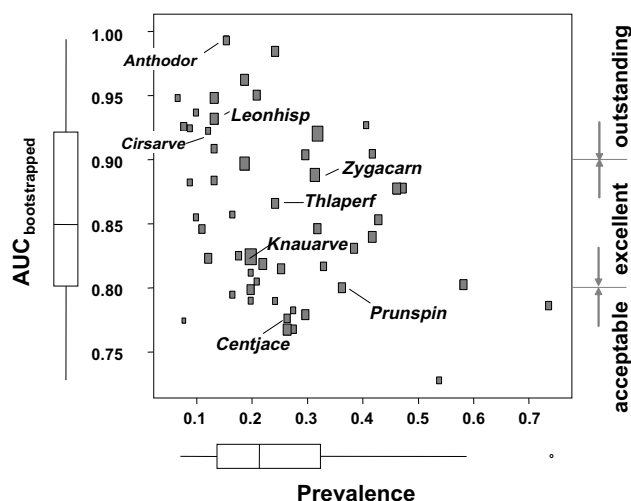


Fig. 3 – Relationship between model performance (in terms of AUC = area under ROC-curve), prevalence, and model complexity for 57 species distribution models after bootstrapping with 300 replicates. AUC-values are classified according to Hosmer and Lemeshow (2000). Symbol sizes are proportional to the number of model parameters ranging from 1 to 10 but show no clear pattern regarding performance. Exemplary species are flagged (species labels: Anthodor, *Anthoxanthum odoratum*; Centjace, *Centaurea jacea*; Cirsarve, *Cirsium arvense*; Knauarve, *Knautia arvensis*; Leonhisp, *Leontodon hispidus*; Prunspin, *Prunus spinosa*; Thlaperf, *Thlaspi perfoliatum*; Zygacarn, *Zygaena carniolica*).

There are species with only marginal reaction, like *Anthoxanthum odoratum*. Other species reveal discrete peaks in the year after management (*C. jacea*, *Leontodon hispidus*, *Thlaspi perfoliatum*) or show some additional tailing (*Cirsium arvense*). In contrast, habitat quality for *K. arvensis* collapses in the years of rototilling (3, 6, 9). Other species like *P. spinosa* exhibit increasing habitat quality during succession while collapsing in the year after rototilling. *Zygaena carniolica* is predicted to completely vanish if a patch is rototilled. *K. arvensis*, *C. arvense*, and *T. perfoliatum* benefit most from rototilling: Their mean occurrence probabilities over a simulation period of 10 yrs relative to annual mowing are 698%, 520%, and 378%. This indicates that the local mean occurrence probability under rototilling of, for instance, *T. perfoliatum* is almost 4 times higher than in the reference scenario (100%). In contrast, *C. jacea*, *L. hispidus*, *P. spinosa*, and *A. odoratum* perform worse with mean occurrence probabilities relative to annual mowing of 73%, 47%, 47%, and 40%, respectively.

3.4. Regional dynamics

When local dynamics are aggregated over the total study area by calculating habitat units, the overall pattern of species benefiting (>100%, i.e. *C. arvense*, *K. arvensis* and *T. perfoliatum*) or suffering from rototilling (<100%, i.e. all other species in Figs. 4 and 5) is preserved. Fig. 5 considers a scenario with rototilling every third year on one half of the area and annual mowing on the other. The figure presents habitat units aggregated over a ten year simulation in terms of absolute values (HU.min vs. HU.mean in Fig. 5A) and relative to the reference scenario (Fig. 5B). As Fig. 5A reveals, the species differ extremely with respect to regional habitat quality. A combined view on regional habitat qualities for both scenarios and all 57 species is given in Appendix 2 (Fig. A1).

3.5. Comparison of all scenarios

Habitat area for *C. arvense* and *K. arvensis* increases with the spatial proportion of rototilling (left axes in Fig. 6) and exceeds the scores yielded by the reference scenario. In contrast, we observe a generally negative effect for *P. spinosa*, *Z. carniolica*, and *L. hispidus*. *Leontodon* shows the same performance as in the reference scenario only if both mowing and rototilling are applied annually. These quite unlikely and expensive scenarios are also the only ones with a positive effect of rototilling on *C. jacea*. For *T. perfoliatum*, the effect of the spatial proportion of rototilling depends on the return interval. This species exhibits a strong increase in habitat area if the return interval for rototilling is lower than five years which nicely corresponds to the results of a detailed process-based model (Pagel et al., 2008). In *A. odoratum* the proportion of rototilling reveals only a negligible effect, as holds for the return intervals.

For all plant species, except *P. spinosa*, a longer return interval for rototilling decreases the number of habitat units (right axes in Fig. 6). *P. spinosa* as well as *K. arvensis* benefit also from longer return intervals for mowing. The overall pattern of species benefiting (*C. arvense*, *K. arvensis*, and *T. perfoliatum*) or suffering from rototilling (*A. odoratum*, *C. jacea*, *L. hispidus*, *P. spinosa*, and *Z. carniolica*) is preserved if the return interval

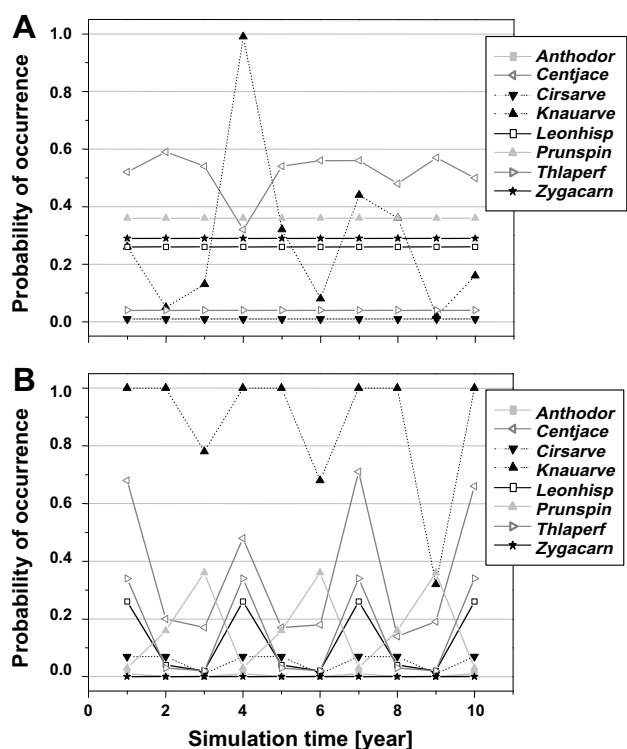


Fig. 4 – Local annual dynamics considering habitat quality for eight species simulated over 10 years for two different scenarios. (A) Annual mowing, (B) rototilling each third year, taking place in year 3, 6, and 9 (species labels: see Fig. 3).

for rototilling does not exceed five years. In *Z. carniolica*, there is only a negligible effect of return interval.

3.6. Scenario effects on costs

Costs differ strongly across scenarios (Fig. 7A and C). The management currently applied in the area – annual mowing – is the most expensive one. Rototilling significantly reduces costs of management (Fig. 7A). This is due to the lower return interval of rototilling (i.e. three years compared to annual mowing in Fig. 7). The area-dependent costs decrease for each type of management if it is applied to larger proportions of the landscape (Fig. 7B). This reduction is more pronounced in case of rototilling since it takes more advantage from economies of scale. Fig. 7C presents the costs relative to annual mowing for all scenarios depicted in Fig. 6.

Generally, the bigger the proportion of rototilled patches and the less frequently the measure is applied, the less expensive is the management.

3.7. ‘Optimum’ scenarios

In order to facilitate selecting ‘optimum’ scenarios, one can plot species performances against total management costs relative to annual mowing (Fig. 8) visualising the trade-off between costs and each ecological criterion.

Shrub encroachment by *P. spinosa* is one of the major threats for the open landscape under study. Fig. 8A shows that there are many possibilities to reduce its occurrence

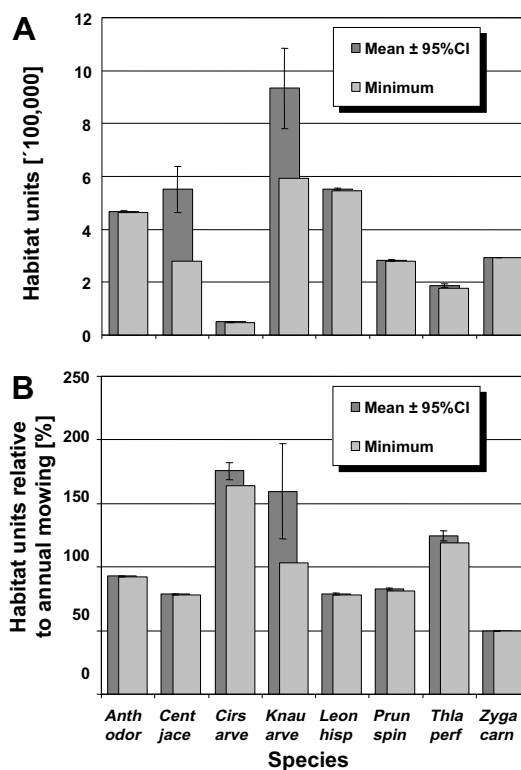


Fig. 5 – Minimum (*HU.min*) and mean habitat units (*HU.mean*) spatiotemporally aggregated over 10 year simulations of the scenario presented in Fig. 4B regarding the eight exemplary species; (A) absolute values, (B) relative to reference scenario, i.e. annual mowing (species labels: see Fig. 3). The presented results refer to all 14 145 cells under management (i.e. 141.45 ha, from an overall of 986.71 ha). For comparison: an occurrence probability of 0.5 for all these cells is equivalent to $HU = 707\ 250$.

more effectively by rototilling. In contrast, dry grassland annuals like *T. perfoliatum* benefit from rototilling. They can be easily promoted applying less expensive scenarios (Fig. 8B). The third species, *Z. carniolica* (Fig. 8C), is an endangered burnet moth (Binzenhöfer et al., 2005) that suffers if rototilling is applied. So, for this species – similar to others (cf. Fig. A1) – saving money reduces regional habitat suitability.

4. Discussion

4.1. Model structure

Our landscape model integrates abiotic models, species distribution models, and economic models to facilitate an integrated assessment of management scenarios regarding ecological and economic criteria. Based on extensive field surveys, the model extrapolates our results from plot scale to landscape scale.

An important advantage is that we model the response of a large set of species to simultaneously modelled abiotic dynamics as a consequence of various management scenarios. Concurrently, we calculate the respective management

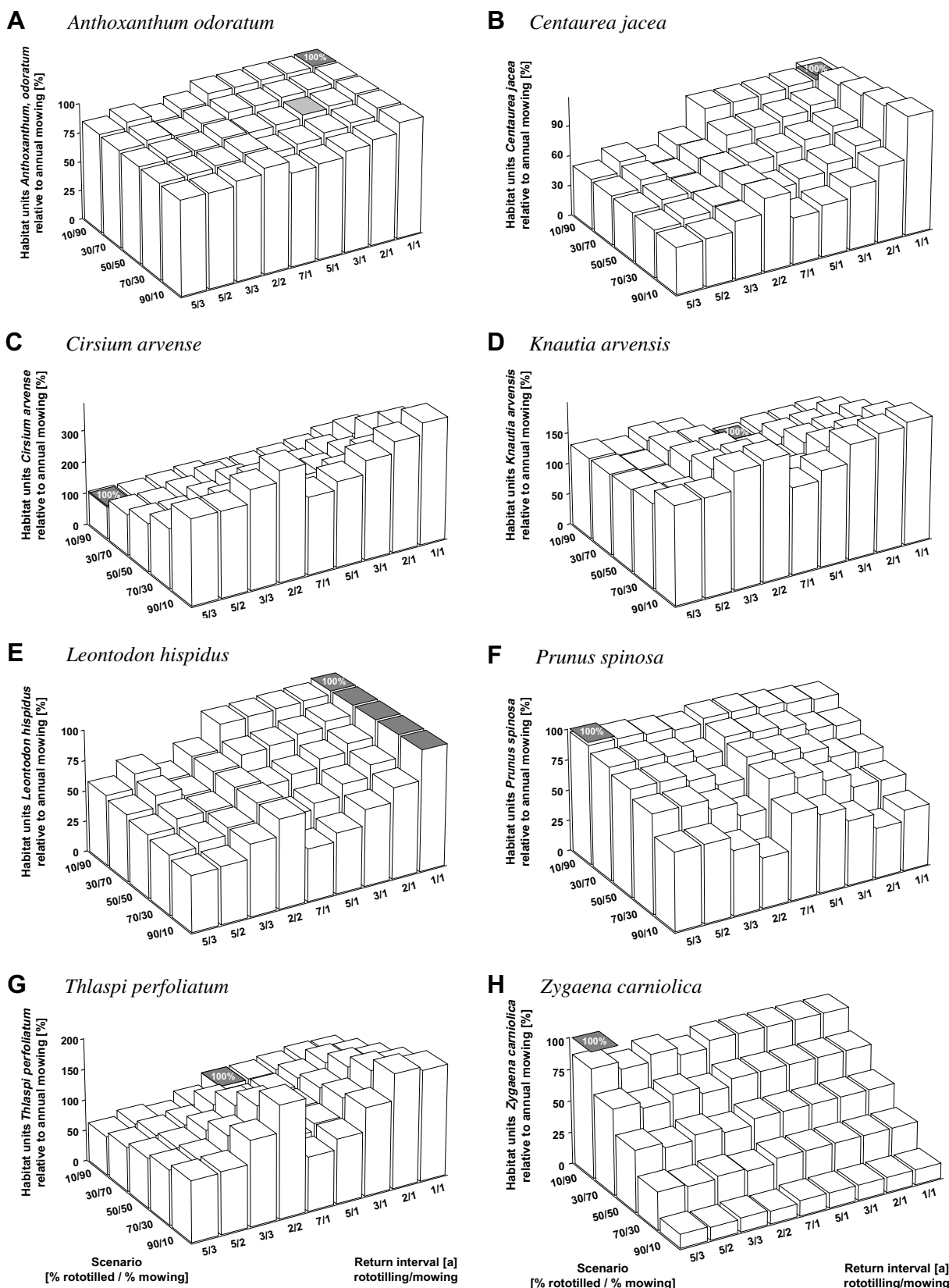


Fig. 6 – Performance of eight species (A–H) for different proportions of rototilling and mowing and different return intervals relative to the reference scenario annual mowing (i.e. 100% as labelled at any suitable position in the plots). The bars show *HU.mean*-values, i.e. mean occurrence probabilities from ten year simulations summed over all cells of the study area. To facilitate comparison with Fig. 5, the scenario with 50% tri-annual rototilling and 50% annual mowing is labelled light grey in (A).

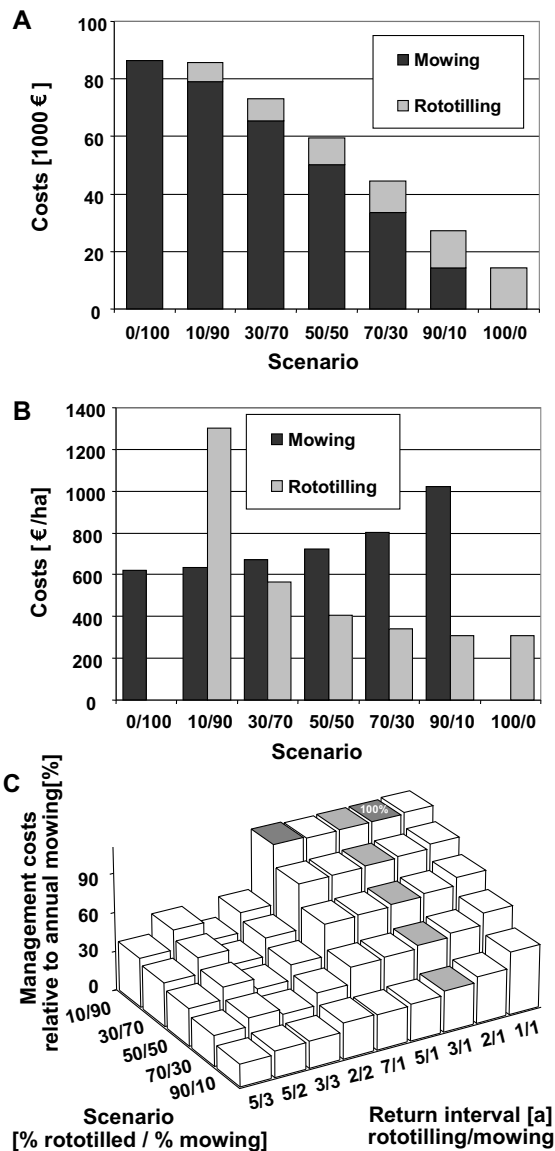


Fig. 7 – (A) Mean annual management costs [1000 €] and **(B)** mean area-dependent costs [€/ha] assigned to both types of management. These data are derived from 10-year simulations with rototilling every third year and annual mowing with different spatial proportions. The respective scenarios are marked light grey in **(C)** which depicts the costs relative to the reference scenario (100% annual mowing) for all scenarios shown in Fig. 6.

costs to enable the selection of appropriate management regimes. Alternatively, a much smaller set of indicator species could have been considered (e.g. Hein et al., 2007a; Holzkämper and Seppelt, 2007), but for that the umbrella effect of selected indicators has to be shown first (e.g. Bonn and Schröder, 2001; Maes and Van Dyck, 2005). Our model is also different from community-level succession models because it tracks the fate of each single species by modelling a species-specific shifting mosaic of habitat qualities.

SDMs have been widely used in conservation biology to quantify habitat quality, assess the effect of environmental changes, and derive management decisions (e.g. Milsom

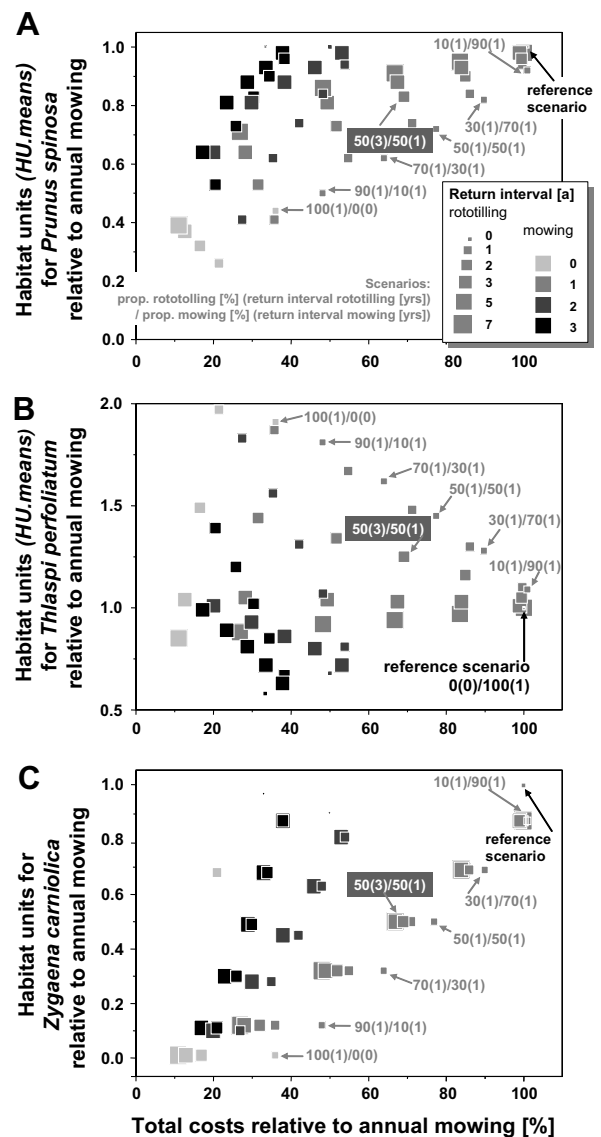


Fig. 8 – Exemplary species performance against total management costs relative to the reference scenario (100% annual mowing) given for all scenarios. (A) Habitat units (HU.mean) for *Prunus spinosa*, (B) for *Thlaspi perfoliatum*, and (C) for *Zygaena carniolica*. Exemplary scenarios are indicated to clarify the different proportions of rototilled and mown areas. These scenarios were chosen for the ease of presentation only. They exemplify the effect of spatial proportion of rototilled area over the entire gradient from the reference scenario 0(0)/100(1) to the extreme opposite annual rototilling of the entire area, i.e. 100(1)/0(0). To facilitate comparison with Figs. 5–7, the scenario with 50% tri-annual rototilling and 50% annual mowing is labelled. Symbol size and grey scale depict the combination of return intervals for rototilling and mowing. These properties together with the spatial proportion of each management type control the costs of each scenario relative to the reference scenario.

et al., 2000; Fischer et al., 2004; Pöyry et al., 2005; Wilson et al., 2005; Buse et al., 2007). Innovatively, we apply SDMs

in a dynamic environment by considering the dynamics of driving factors. By means of SDMs, we calculate time series of occurrence probabilities for time series of predictor variables that are explicitly modelled within the landscape model. Since important predictors are related to soil water dynamics, our approach can be interpreted as an ecohydrological model (Schröder, 2006a).

The use of static SDMs – assuming equilibrium – for predictions in a dynamic context (Guisan and Theurillat, 2000) is justified by applying the space-for-time substitution, i.e. analysing conditions that are similar to future conditions at different locations (e.g. species' occurrence with respect to the habitat's position on a succession gradient). The models describe only the probability of species occurrence, thus neglecting population dynamic processes. This may be a source of error. Comparing the two aggregated measures of occurrence probabilities during a simulation run ($HU.min$ vs. $HU.mean$), however, provides means to assess potential effects of important population dynamic processes. If $HU.min \leq HU.mean$, the species runs frequently through “bottlenecks” of low abundance and may be sensitive to stochastic extinction processes or may not be able to re-colonize all potentially suitable areas. In another study (Pagel et al., 2008), we applied a detailed process-based population dynamic model to assess the effect of rototilling scenarios on only one single species, *T. perfoliatum*. But because this model approach is comparatively data hungry it can not be applied to a large set of species.

Since ecological assessment bases on SDMs in our model, we emphasised the evaluation of SDMs. The majority of the models exhibit excellent model discrimination and good or satisfactory model calibration after internal validation (Fig. 3, Table A1). We detected residual spatial autocorrelation only in case of four plant species. So, neglecting additional spatial predictors seems justified in 93% of all species. Anyhow, introducing neighbourhood interactions by considering spatial predictors, e.g. proportion of suitable habitat within a specific radius, may improve model performance as shown for butterflies by Binzenhöfer et al. (2005). Additionally, spatial attributes like patch size, isolation or connectivity (Binzenhöfer et al., 2008) may serve as proxies for spatial effects on population dynamics. However, this type of predictors could not be obtained for the entire species set in the present study.

The simulated scenarios differ from the landscape sampled. Although available as experimental fields, rototilled plots are underrepresented in the training data and conditions after rototilling are probably not adequately met in the training data. There is a trade-off between obtaining excellent models for real conditions and less adequate models regarding the scenarios. Consequently, gradients of main driving forces should be sampled as long as possible to cover the whole range of possible scenario options.

The important question of error propagation is often ignored when coupling models. In this respect, the detection of species occurrences as well as the quantification of disturbance and costs may not be problematic. Uncertainty in regression coefficients is reflected by their confidence intervals and related hypothesis tests. Since model performances are good after internal validation, we assume that this part

of the landscape model is sufficiently robust. But we see a higher potential of errors in the regionalisation procedure of climate and soil data. Additionally, the approach to model abiotic conditions is rather simple though sufficient for its purpose. But since the possible sources of errors are identical for different scenarios, and because all results are analysed relative to one reference scenario, this point may not be critical for scenario assessment.

4.2. Model results

Different spatiotemporal scales of rototilling affect the abiotic conditions and thus the potential distribution of plant and animal species. As our results show, infrequent rototilling can serve as a cost-effective alternative to annual mowing preserving biodiversity of open dry grasslands. But there is a trade-off: The larger the proportion of rototilled area, the more money can be saved (Fig. 7), but the more loss of habitat has to be expected for the majority of species (Figs. 6,8, A1). As expected, representatives of plant functional types show different response to the scenarios. The SDMs implemented differ slightly from those plot-based models presented by Kühner (2004) as well as Hein et al. (2007a), because they consider only data available for the entire landscape. Thus, they are not the best models possible, but the best models applicable for predictions on landscape scale (cf. Hein et al., 2007b). Additionally, it was not possible to estimate significant models for plant species with extremely low prevalences. As these rare species are of significant conservation interest, they may be implemented as expert knowledge-driven models (cf. Petit et al., 2003), if accounting for these species is desirable.

The resulting relationship between management regimes and calculated habitat suitabilities corresponds to the known ecological behaviour of the selected species (Bundesamt für Naturschutz, 2005). Meadow species depending on annual mowing such as *C. jacea* and *L. hispidus* suffer from the dominance of tall forbs that gain weight with increasing mowing intervals. The effect of rototilling is mainly explained by the larger disturbance interval. More competitive species like *K. arvensis* benefit from a larger management interval. Weeds like *C. arvensis* obviously benefit from rototilling as do annuals like *T. perfoliatum*. Longer disturbance intervals decrease the habitat suitability as shown by process-based population dynamic models (Pagel et al., 2008). Species that propagate vegetatively, like *P. spinosa*, are more affected by rototilling than by mowing. For these species, short management intervals have a stronger effect. Rototilling turned out to control shrub encroachment better than mowing.

5. Conclusion and implications for conservation

Conservation management is strongly constrained by economic considerations. Our landscape model guides management decisions by visualising the trade-off between management costs and ecological consequences regarding a large set of grassland species. Therefore, it is a valuable

Table A1 – continued

Label	PV5	PV5 ²	PV6	PV6 ²	PV7	PV7 ²	PV8	PV8 ²	PV9	PV9 ²	PV10	PV10 ²	PV11	PV11 ²	PV12	PV12 ²
Trifprat	3.13	-0.67	0.00	0.00	0.00	0.00	0.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trifrepe	1.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.00	0.00
Trisflav	0.00	0.00	-5.60	0.00	0.60	-0.01	0.00	0.00	-1.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Veroarve	0.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.90	2.37	0.00	0.00	0.00	0.00	0.00	0.00
Verocham	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Vicisati	0.00	0.44	0.00	0.00	0.00	0.00	0.00	0.00	-1.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Violhirt	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.35	-0.01	0.00	0.00	0.00	0.00
Insect species	Label	R ² N	AUC	P _{fair}	Intercept	Potential solar radiation	Fallow land	Intensively managed meadows	Hedges	Extensively managed meadows	Fringes	Dry grasslands				
<i>Zygaena carniolica</i>	Zygacarn	0.55	0.88	0.39	-0.86	-0.0071	-0.26	-0.45	0.65	8.93	10.87	11.15				
<i>Coenonympha arcania</i>	Coenarca	0.34	0.75	0.57	-9.20	0	0	8.10	18.41	9.55	18.41	9.40				
<i>Metriopectera bicolor</i>	Metrbico	0.21	0.71	0.47	-12.09	0.0037	0.08	6.52	5.74	7.22	6.86	8.22				
<i>Stenobothrus lineatus</i>	Stenline	0.33	0.77	0.51	-15.25	0.0054	0.11	7.98	-0.53	8.28	8.44	9.87				
<i>Platycleis albopunctata</i>	Platalbo	0.49	0.91	0.14	-22.02	0.0090	0.12	0.16	-0.92	7.41	10.15	9.21				

Predictors for plant models: PV1, pH; PV2, available water capacity; PV3, disturbance depth; PV4, disturbance intensity; PV5, disturbance frequency (aboveground); PV6, disturbance frequency (belowground); PV7, week of first disturbance; PV8, cos(aspect); PV9, sin(aspect); PV10, slope; PV11, available soil moisture (April); PV12, available soil moisture (June). Reference category for insect models considering habitat types: crop land.

Appendix 2

See Fig. A1

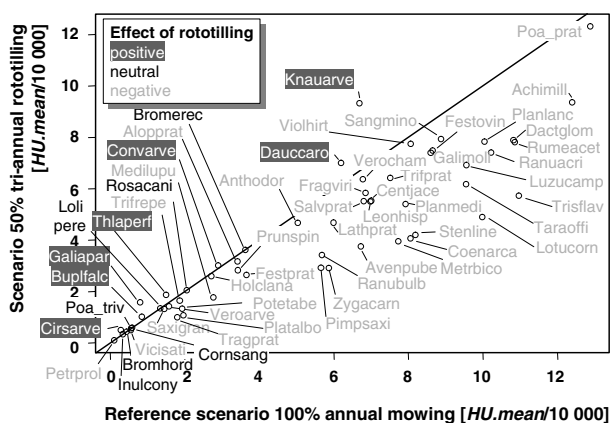


Fig. A1 – Regional habitat qualities aggregated over a simulation period of 10 years in terms of habitat units derived from mean occurrence probabilities (HU.mean) comparing two different scenarios: reference scenario (100% annual mowing) vs. 50% tri-annual rototilling and 50% annual mowing (species labels: cf. Table A1 in Appendix 1).

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