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Predicting plant species richness and vegetation patterns in cultural landscapes using disturbance parameters

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Abstract

A new methodological framework for plant diversity assessment at the landscape scale is presented that exhibits the following strengths: (1) potential for easily standardizable sampling procedure; (2) characterization of disturbance regime; (3) use of selected disturbance descriptors as explanatory variables which probably allow for better transferability than site specific land use types—for example, to evaluate the emerging use of energy plants that pose novel management challenges without historic precedence to many landscapes; (4) analysis of quantitative and qualitative aspects of plant species diversity (alpha and beta diversity). For data analysis, a powerful regression method (PLS-R) was applied. On this basis, after further validation and transferability tests, a practical tool for the development and validation of effective agri-environmental programmes may be developed.

Keywords: Agri-environmental programmes; Alpha diversity; Beta diversity; Fichtelgebirge; Land use; Disturbance; Pattern analysis

1. Introduction

The EU Sustainable Development Strategy, launched by EU leaders in Gothenburg in 2001, assigns priority to halting the loss of biodiversity in the EU by 2010. Accordingly, a variety of agri-environmental programmes was set up to reach this goal. Via these programmes, which support specifically designed farming practices going beyond the baseline level of ‘‘good farming practices’’ (GFP), farmers shall be remunerated for specific efforts made for sustaining ecosystem services, e.g. for management methods supporting species diversity and ecosystem sustainability. Since a new EU law was introduced in 2005 (CAP Reform 2003), which decouples agricultural payments from production or mode of land use, the financial attractiveness of agri-environmental programmes might rise. Now, farmers are paid per ha of arable land or grassland managed, and are no longer subsidized according to the quantity of certain goods produced or land use activity maintained.

However, those programmes are often assumed to have positive influence on biodiversity but this has rarely been proven (Kleijn and Sutherland, 2003). In some cases, programmes even turn out to be ineffective and miss the target (Kleijn et al., 2001). Single programmes in limited areas were successfully set up and evaluated (e.g. Knop et al., 2006) but, especially over large areas, neither the effect of the programmes can be assessed nor does their validation seem feasible (Moser et al., 2002). Most statistical models for predicting species diversity at the landscape level are not transferable to other large areas, as they incorporate extremely detailed information on either abiotic conditions or land use practices. In addition, data collection is often too time-consuming and cost intensive to be used as a standardized tool. Accordingly, an applicable, transferable and standardized method for quantifying biodiversity at the landscape scale is needed to serve three purposes: first, to

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develop guidelines for the design of effective agri-environmental programmes; second, to evaluate their effectiveness for the maintenance of biodiversity; and third, to predict the development of plant species diversity under various land use scenarios.

Thus, the first challenge consists of developing a standardized method for quantifying and indicating biodiversity at these two different levels of observation: within and between plots or patches. The sampling design is based on a systematic grid approach developed for biodiversity assessment in cultural landscapes (Retzer, 1999; Simmering et al., 2006). The second challenge consists of developing a method for assessing the underlying factors that determine plant diversity at these two levels (alpha and beta diversity). For predictions of biodiversity, the variability and heterogeneity of various factors has been tested (e.g. geomorphologic forms by Muller et al. (2004) or land use types combined with soil data by Haberl et al. (2004) or Wamelink et al. (2003)). At the landscape scale, Duelli (1997) points towards variability and heterogeneity of a landscape for explaining species richness, where ‘‘habitat variability’’ describes the difference between land use types or distinct land use patches, and ‘‘habitat heterogeneity’’ indicates the number of such different patches within a given area. Those models that employ land use as a predictor are very precise in their forecasting ability (Waldhardt and Otte, 2003; Waldhardt et al., 2003). However, the number of variables needed is usually too large and sampling often too time consuming to develop an applicable, standardized method from the existing models (Moser et al., 2002). Variables on land use type are easy to collect; however, they are very explicit, may be unique to a certain agricultural region and do not account for novel uses, so that transferability is limited. Thus, the introduction of new crops or altered management practices, as may occur in future or in other regions, cannot be included in the models without additional training data.

We assume that our approach has the power to overcome this problem of transferability by using disturbance parameters, such as disturbance frequency, size and selectivity, in order to characterize the anthropogenic disturbance regime. These parameters allow a more precise and abstract description of dynamic factors in a landscape than the commonly used surrogate variables of land use type. A surrogate variable provides an indirect measurement effect in situations where direct measurement of effects is not feasible or practical. Disturbance is defined as any relatively discrete event in time, which disrupts community structure, changes resources or the physical environment (Pickett and White, 1985; White and Jentsch, 2001). A disturbance regime is the sum of all disturbances in a given landscape, including interacting disturbances. In order to find suitable factors for the prediction of plant diversity in cultural landscapes, plant species alpha and beta diversity values are correlated with both the land use type and the underlying descriptors of disturbance regime. During the optimization process of the regression models the use of the surrogate variable land-use and the very case specific variable of disturbance type were avoided to demonstrate the predictive potential of disturbance data. The focus is on vascular plants as they are easily monitored and their richness is a good indicator for the richness of many other taxa (Duelli and Obrist, 1998).

Biodiversity implies much more than counting species. It is the sum total of genes, species and ecosystems in a region or the world (quantitative biodiversity), their heterogeneity, turnover or contrast (qualitative biodiversity) and functional biodiversity, including variability of function or ecosystem complexity (CBD, 2001–2005; Beierkuhnlein and Jentsch, 2005). This study incorporates alpha and beta diversity of higher plants as quantitative and qualitative measures of vegetation diversity.

Our central hypothesis was that the variability of disturbance explains plant species richness. Instead of using the common land use types as predictors, it was proposed that the heterogeneity of the disturbance regime is a powerful explanation for plant species richness in cultural landscapes in Central Europe. In order to provide a first test for this hypothesis, an easily standardizable sampling procedure and a mathematical method of data analysis was executed exemplarily in a mid-elevation, rural area in north-eastern Bavaria, Germany.

2. Materials and methods

The study area was located at about 600 m a.s.l. within the Fichtelgebirge in north-eastern Bavaria, Germany. The highest elevation in the Fichtelgebirge is 1053 m a.s.l., geology consists of granite bedrock, precipitation ranges from 600 to 1200 mm/a. Mean annual temperature at the highest elevation is 6 °C, the growing season comprises 4 months. Agriculture, hay and silage production, and forestry are the main forms of land use.

A regular grid of 100 plots was established in a mixed cultural landscape. It spread over an area of 1600 ha (4 km × 4 km). The plots were quadratic and covered 1 ha (100 m × 100 m) each. The grid was positioned randomly inside a part of the investigated region, which was found characteristic for the mountain range of the Fichtelgebirge. The grid was oriented towards North to facilitate plot identification in the field. In each of the plots, areas of different land use/disturbance regime were differentiated and specified as separate patches if their size exceeded 10 m^2 (including footpaths and transition patches of >1 m in width). For each patch, plant species composition, land use and disturbance descriptors were recorded. A classification scheme to characterize the land use and disturbance regime is given in Tables 1 and 2. Important structures, such as riparian zones, paths, hedgerows and transition zones were characterized in the same way as, for example, agricultural areas, forests, meadows or wetlands.

Table 1
Classification scheme of land use

Classes	Sub-classes
Field	Cereal stand
	Maize stand
	Root crop
	Green fodder
	Rape
	Intermediate crop
Path	Footpath
	Field/forest track
	Asphalt road
	Gravel road
	Cobble road
Trees	Single tree
	Grove
	Shrubbery
Fallow land/succession	Young (1–2 years)
	Intermediate
	Older stage (shrubs)
	Old (pre-forest stage)
	Complex
Rock	Single freestanding
	Quarry
	Stonewall/heap
Water body	Running—regulated
	Running—natural
	Standing—artificial
	Spring
	Trench
Boundary	Forest margin
	Field margin
	Meadow margin
	Road margin
	Hedge
	Hedge with trees
	Gallery forest
Grassland	Dry meadow
	Fertile meadow
	Wet meadow
Forest (>100 qm)	Mature spruce stand
	Young spruce stand + mature trees
	Compound spruce forest
	Felling area
	Decidous forest
Settlement	Farm yard
	Single house

2.1. Statistical analyses

Partial least squares regression (PLS-R) was used to describe and analyse the relation between plant species richness within each plot (alpha diversity) and the land-use or disturbance descriptors. Secondly, similarity indices were calculated between plots for species similarity (beta diversity) and similarity of land use or disturbance parameters. These indices were then correlated with each other using Mantel tests.

Table 2
Classification scheme of disturbance regime

Disturbance type	Felling (undefined)
	Clear felling
	Femel felling
	Felling due to beetle damage
	Felling for density control
	Removal of dead wood
	Wood storage and movement
	Skidding track
	Collapsed tree
	Biomass input
	Wild boar disturbance
	Compactation by trampling
	Compactation by vehicles
	Pond drainage
	Agricultural use
	Mowing
	Flooding
	Pesticides
	Building works, soil/rock movements
Dimension space	
Disturbance size	Punctiform/linear
	1/4 of areal
	1/2 of areal
	3/4 of areal
	Complete areal
Disturbance form	Linear
	Laminar
	Punctiform
Disturbance distribution	Homogen
	Heterogen
Dimension time	
Disturbance frequency	Every 100 years
	Every 10 years
	Annual
	Twice a year
	Three times a year
	Greater than three times a year
	Steady in time
	Steady intense in time
Disturbance seasonality	1. Quarter of the year
	1. +4. Quarter
	1. −3. Quarter
	1. −4. Quarter
	2. Quarter
	2. −3. Quarter
	2. −4. Quarter
	3. Quarter
	3. −4. Quarter
	4. Quarter
Disturbance duration	<1 day
	<1 week
	<1 month
	<1 year
	>1 year
Selectivity of disturbance	None
	Age
	Species
	Location
	Land parcel boundary

Several regression analyses (PLS-R) were carried out, including different sub-sets of the data as explanatory variables, to predict species richness within plots. Four different sub-sets of data were used: (a) the quantitative and qualitative land-use data (Table 1; results in the text) to be used as a reference value of desirable predictive power, (b) the number of patches differentiated within each plot and all disturbance descriptors (Table 2; results in Table 3 model I), (c) the disturbance descriptors only (Table 2; results in Table 3, model IV) and (d) parameters of disturbance frequency and seasonality only (Table 2; results in Table 3, model VI). Each of the three disturbance models (Table 3, models I, IV, VI) were then optimized by selecting only significant parameters and by reducing the number of variables to a few easily collected parameters. The significance of the variables for the model was determined by uncertainty tests carried out within a full cross validation (jack-knifing procedure). The further selection process was achieved by excluding variables that explain redundant variance. This was easily accomplished by the comparison of the principal component specific loading weights and visual selection from the ordination plot.

In addition to the qualitative variables, such as ‘‘disturbance event restricted to the third quarter of the year’’ in the form of presence/absence data (Tables 1 and 2), quantitative fuzzy variables were used: ‘‘number of different land-use classes‘‘, ‘‘number of different land-use sub-classes’’, ‘‘number of different patches’’, ‘‘number of different disturbance frequencies’’ and ‘‘number of different disturbance seasonalities’’ that occur within each plot.

Partial least squares regression (PLS-R) is a further development of principal component regression (PCR), where the explanatory variables are bundled with the help of a principal component analysis (PCA) and the derived components replace the independent variables during the regression (Bastien et al., 2005). PLS-R was used, as it allows the mix of quantitative and qualitative explanatory variables within the same analysis. With PLS-R, over-fitting by strongly correlated variables, as often found in multiple regression analyses, is avoided as the number of factors is reduced to only a few principal components. Using PLS-R, the complete set of factors can be included in the analysis—in contrast to step-wise procedures of multiple regressions, the reduction or grading of variables is not necessary (ter Braak and de Jong, 1998; Abdi, 2003, for applications see, e.g. Dangles et al., 2004).

Beta diversity – the turnover in species composition along a gradient (according to Whittaker, 1972) – can be calculated with so-called proximity measures. For the analysis on hand, the Sørensen Similarity Index was used. Similarity between neighbouring plots concerning their land use and disturbance characteristics for presence/absence data was calculated with the Sørensen Index as well, while the Bray-Curtis Index was used for quantitative variables. Beta diversity of plant species and the corresponding similarity of land use or disturbance regime between neighbouring plots were then correlated using Spearman ρ correlation. Significance was determined using Mantel tests (1000 iterations). The following Software was used: SIGMAPLOT 9.0 (Systat, 2004), The Unscrambler v8.0 (CAMO, 2003), R 2.1.1. (R Developing Core Team, 2005), VEGAN 1.6-10 (Oksanen et al., 2005) and ARCGIS 9.1 (ESRI, 2005).

3. Results

Predictive power of the qualitative and quantitative land-use data for alpha diversity was high ($R^2 = 0.75$, root mean square error: 15.9 (11%), number of variables: 54 and

Table 3
PLS-R models predicting plant species richness (alpha diversity) using disturbance data

Selection of explanatory variables	Number of PLS axes	R^2	RMSE	Prediction error in %	Number of variables
I. Number of zones within each plot + all disturbance parameters (quantitative and qualitative)	3	0.76	15.3	10	43
II. Reduction to significant variables (after jack-knifing)	2	0.77	15.0	10	17
III. Reduction by eliminating redundant information	2	0.73	16.4	11	4[a]
IV. All disturbance parameters (quantitative and qualitative)	3	0.73	16.52	11	42
V. Reduction to significant variables (after jack-knifing)	2	0.74	15.9	11	17
VI. Parameters of disturbance frequency and seasonality (quantitative and qualitative)	2	0.72	16.8	12	12
VII. Reduction to significant variables (after jack-knifing) and by eliminating redundant information	2	0.72	17.0	12	4[b]

Three different subsets of the data were selected as starting point for the modelling process (see models I, IV and VI). Maintaining high model quality, the explanatory variables are then reduced step by step leading to models III, V and VII. RMSE: root-mean-square-error of prediction (typical error) from full cross-validation.

[a] Model variables: number of zones within each plot, number of different disturbance seasonalities, disturbance during the first quarter of the year, disturbance during the second quarter of the year.

[b] Model variables: number of different disturbance seasonalities, number of different disturbance frequencies, disturbance during the forth quarter of the year, disturbance during the second quarter of the year.

number of PLS axes: 3). As it was attempted to reach good predictions without including explicit land use data this information was not used for further models. Table 3 presents the results of different PLS-R Models which reached equally high predictive force including disturbance data, only. The initial set of variables consisted of the complete set of disturbance parameters and the absolute number of recorded patches within each plot (Table 3, model I-III). The model quality (model I) was high ($R^2 = 0.76$). The process of variable reduction lead to a final number of four model parameters (via models II to III). The model quality remained high ($R^2 = 0.73$). The number of differentiated patches within each plot was excluded within models IV–VII. In model IV–V, the parameters included were limited to the disturbance regime. The predictive power remained high ($R^2 = 0.74$). The dynamic components of the disturbance regime (disturbance frequency and seasonality) showed major predictive forces within model V (not shown). Therefore further models were calculated selecting the parameters of disturbance frequency and seasonality as initial variables (models VI and VII). The parameters of disturbance frequency and seasonality predicted 72% of the variability of species richness (model VI). Again, the reduction of variables brought forward a model including only four variables (model VII) with high model quality and high predictive power ($R^2 = 0.72$). The results showed good fit concerning the predicted species richness versus observed species richness (Fig. 1). The remaining significant variables for this prediction are: (1) number of disturbance frequency types, (2) number of disturbance seasonality types, (3) the presence or absence of disturbance events restricted to the second quarter of the year and (4) the presence or absence of disturbance events restricted to the forth quarter of the year (Table 3, model VII).

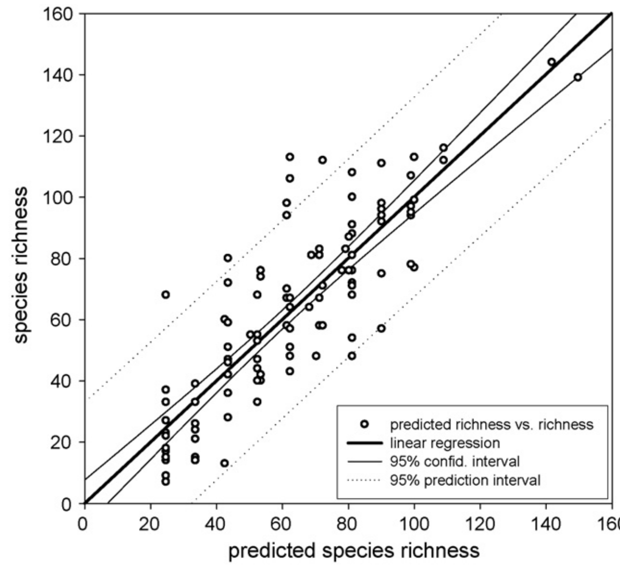

Fig. 1. Predicted plant species richness per plot vs. observed richness. The parameters of the underlying model are documented in Table 3, model VII.

The patterns of alpha diversity (Fig. 2a) were found very dissimilar to the pattern of beta diversity (Fig. 2b). To analyse underlying factors correlated with beta diversity pattern, species similarity of neighbouring plots was correlated with the corresponding similarity of the land use and disturbance parameters (Table 4). The highest Spearman ρ coefficient was found when correlating species similarity values with the data sub-set including all variables used to characterize disturbance (see Table 2). If similarity of disturbance regime was calculated including only the subset with different frequencies of disturbance, correlation changed by only a little and remained high (Table 4). In summary, the variability of disturbance rhythm was a powerful predictor for beta diversity patterns of vegetation.

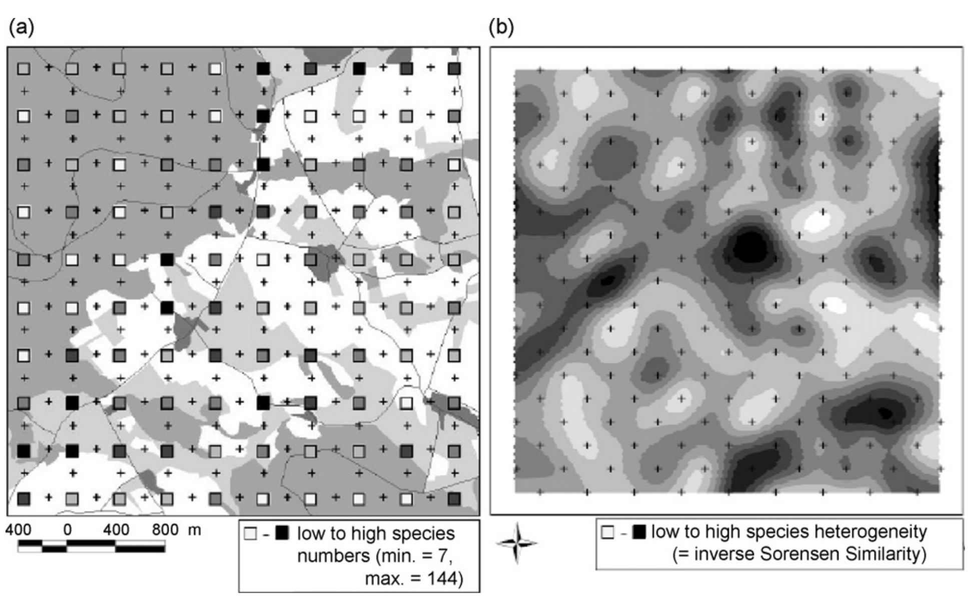

Fig. 2. Patterns of (a) alpha and (b) beta diversity (here expressed as negative Sørensen similarity). The squares mark the sample plots, + marks the points half way between the plots, where beta diversity values were calculated. Beta-diversity was interpolated over the area via kriging.

Table 4
Correlation of plant species beta diversity (species similarity) with the similarity patterns of land use and disturbance regime

Data sub-set used for correlation with beta diversity	Spearman ρ
Similarities of the complete disturbance regime data incl. land use classes and sub-classes	0.75
Similarities of land-use classes and sub-classes	0.69
Similarities of disturbance regime	0.76
Disturbance regime: dimension time only (Table 1b)	0.68
Disturbance regime: frequency only (Table 1b)	0.59

The Spearman ρ coefficients are significant according to Mantel tests ($p < 0.001$).

4. Discussion

The analyses confirm the high predictive power of land use data for diversity of plant species (alpha and beta diversity), but they also bring forward the possibility to substitute information on land use with selected parameters of the disturbance regime for prediction. Even the quantitative variable ‘‘number of patches differentiated within each plot’’ needed not be added to the model to derive a good predictive force. This demonstrated the high forecasting ability of disturbance descriptors. The diversity of disturbance rhythm characterized by disturbance ‘‘frequency’’ and ‘‘seasonality’’ most accurately described alpha diversity of plant species at the plot scale. Diversity of disturbance rhythm was also highly correlated with beta diversity of vegetation at the landscape scale. Accordingly, the use of disturbance frequency and seasonality as a mechanistic expression of the diversity of rhythm in land use provides enough information for characterizing the main variability of plant diversity in the study area. The application of a prediction scheme based on disturbance frequency and seasonality could therefore be of relevance for the creation and evaluation of agri-environmental programmes.

Prediction models for the pattern of beta diversity have not yet been included in our analyses. However, the good fit in Spearman correlation comparing the similarity of species and disturbance parameters between plots indicated the potential of disturbance parameters to describe plant species similarity patterns. The evaluation of the impact of agri-environmental programmes on beta diversity via disturbance data would be an important development.

The question of transferability and the possible necessity of inclusion of further factors such as soil type will have to be a matter of further investigation. According to Waldhardt et al. (2004), soil type is also a factor of major relevance in predicting plant species richness in agricultural ecosystems. However, because land use is partially determined by soil type, much of the patchiness in soil type is strongly correlated with land use type and consequently with parameters of the anthropogenic disturbance regime. It might therefore not be necessary to include soil characteristics in the models if disturbance data are used. An example of such a correlation is the low frequency of mowing in either nutrient poor meadows or wet meadows. In both cases, local plant species richness is inversely correlated with disturbance frequency. This agrees well with theory from disturbance ecology (Huston, 1994; White and Jentsch, 2001). However, in regions of high geological variation, the soil characteristics might be necessary factors for good predictions. Additionally, there is further potential to ameliorate the models by including interaction terms. Such an optimization process, however, will only be useful on a wider data basis, as otherwise the local specificity of the area will be overrepresented in the model. Applicability of the method for future evaluation and prediction of plant species diversity is very high, because the necessary data acquisition can be reduced to sampling only a small set of disturbance parameters. Furthermore, sampling is very effective due to the use of a systematic grid (Austin, 1981; Beierkuhnlein, 1999) and shortcomings of a preferential sampling design are minimized (Colbach et al., 2000).

A general problem of all agri-environmental programmes is that, though land use may be changed due to funding, regeneration of plant diversity is often limited due to a lack of soil seed banks, seed input and recruitment (Bischoff, 2005). Also, remaining chemical and structural soil properties may hinder the performance of many species (Dupouey et al., 2002). Therefore, the main target of environmental programmes has to be the conservation of existing species richness. In very homogeneous landscapes, where species diversity has already declined, the validation process can only take place after several years of regeneration plus specific restoration plans. Otherwise, validation with the present models would dramatically overestimate actual species richness.

In contrast to other approaches of predicting species richness (e.g. Schwab et al., 2002; Dauber et al., 2003; Ernoult et al., 2003; Wilson et al., 2003; Waldhardt et al., 2004), the use of disturbance data offers the advantage of allowing for easy adaptation to upcoming, novel types of land use, e.g. new crops such as energy plants. This is an additional strength in contrast to the widely used evaluation systems based on indicator species. Plant species richness seems a better indicator for ecosystem functioning and sustainability of a landscape than indicator species (Loreau et al., 2001; Beierkuhnlein and Jentsch, 2005; Hooper et al., 2005). However, the use of rare species to define areas of special protection status, as outlined in the FFH guidelines, is an important supplement to an approach for cultural landscapes as presented here.

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