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Relationships between substrate, surface characteristics, and vegetation in an initial ecosystem

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Abstract

Based on a wide range of empirical data we investigated surface and vegetation dynamics in the artificial initial ecosystem “Chicken Creek” (Lusatia, Germany) in the years 2008–2011. We scrutinized three different hypotheses concerning (1) the relations between initial geomorphological and substrate characteristics with surface structure and terrain properties, (2) the effects of the latter on the occurrence of grouped plant species, and (3) vegetation density effects on terrain surface change.

Our data comprise annual vegetation monitoring results, terrestrial laser scans twice a year, annual groundwater levels, and initially measured soil characteristics. Using Generalized Linear Models (GLMM) and Generalized Additive Mixed Models (GAMM) we can mostly confirm our hypotheses, revealing statistically significant relations that partly reflect object or period specific effects but also more general processes which mark the transition from a geo-hydro towards a bio-geo-hydro system, where pure geomorphology or substrate feedbacks are changing into vegetation-substrate feedback processes.

1 Introduction

While a lot of studies on ecosystem development have been conducted in mature ecosystems (e.g. Campbell et al., 2007; Ellenberg et al., 1986; Fränzle et al., 2008; Pennisi, 2010) our information about initial systems is comparably weak. This is remarkable, because initial ecosystems are usually less complex compared to mature systems. Therefore, the study of the development of initial ecosystems could be highly helpful to achieve a better understanding of the complex relationships and feedback mechanisms that are typically found in mature ecosystems (Jørgensen et al., 2000). Tracing the development of such young ecosystems and observing how new relationships and feedbacks emerge with increasing complexity would help to get a better insight on key processes and a basic understanding of their interactions.

Initial ecosystems are also important from a very practical point of view. Worldwide, human activities regularly leave behind huge bare areas (Walker and Willig, 1999; Bradshaw, 1983; Hüttl and Weber, 2001; Schaaf, 2001; Zikeli et al., 2002), which create serious environmental challenges due to their ecological instability and unproductivity. Here, enhanced knowledge is urgently needed for finding optimal ways to transform such landscapes into landscapes, which can be used in a sustainable way by the society.

The land surface is an interface for interlinking a lot of geomorphological as well as biological processes. It can also be seen as an interface where pedosphere, biosphere, hydrosphere and atmosphere are strongly interlinked (Brantley et al., 2007). Subsurface processes like weathering and ground water flow interact here with atmospheric impacts like rainfall, radiation, and wind, and where the biological succession of a bare area starts, it influences back the soil-climate-hydrology system. At the very beginning of ecosystem development, starting with bare ground, these interactions are expected to be especially important (Schaaf et al., 2012).

Scientifically investigated areas, where the first interactions between atmosphere, pedosphere and biosphere are just starting to develop are rare. Among them are areas created by volcanic activity (Bishop, 2002; Dahlgren et al., 1999; del Moral and Wood, 1993; Müller-Dombois and Fosberg, 1998; Friðriksson, 2005) or areas that become exposed after glacier retreat (Cooper, 1923; Matthews, 1992). Rarely, however, the starting conditions at “point zero” are known exactly.

The creation and examination of artificial areas is one approach to close this knowledge gap on processes determining early ecosystem development. Such areas are ideally complete water catchments with a homogeneous substrate, but without any traces of life and therefore without any successional history. Their value for understanding the emerging interactions between atmosphere, pedosphere, hydrosphere and biosphere cannot be overestimated (Schaaf et al., 2011). The 6 ha artificial catchment “Chicken Creek”, established in 2004/05 in the open-cast mining area “Welzow-Süd” near Cottbus, Eastern Germany, was designed to represent the theoretical ideal conditions as close as possible. Here, since nearly seven years, a broad range of key parameters of pedogenesis, geomorphology, vegetation succession and ecosystem development have been studied in high spatio-temporal resolution.

The goal of this study is to scrutinize the following hypotheses by pooling data from different sources, which try to capture the developing complexity in an initial ecosystem:

- Initial geomorphological and substrate characteristics determine the surface's structure and properties of the terrain. The degree of determination of these processes weakens with the ecosystem's development (H1).
- Surface and substrate characteristics determine the plant species groups to be found initially (H2).
- Increasing density of vegetation reduces the erosion and therefore the degree of change of terrain surface structure (H3).

2 Material and methods

2.1 The artificial catchment Chicken Creek

The artificial catchment Chicken Creek with an area of 6 ha was constructed in the open-cast mining area of Lusatia, Germany (51.6049° N, 14.2667° E) in 2004–2005. It is a 2–4 m layer of post-glacial sandy to loamy sediments overlying a 1–2 m layer of Tertiary clay which forms a shallow pan and seals the whole catchment at the base. No further measures of restoration like planting, amelioration or fertilization were carried out; natural succession and undisturbed development is allowed. Due to the artificial construction, subsoil boundary conditions of this site are clearly defined including well documented inner structures as compared to natural catchments. For more details on the constructions process, initial site conditions as well as the monitoring program carried out since 2005 see Gerwin et al. (2009, 2010, 2011) and Schaaf et al. (2011, 2012).

2.2 Data used in this study

A 20 m × 20 m grid for sampling and orientation purposes was established on the catchment area (Fig. 1). The data used in this study cover the sub-area between the gridpoint-lines “A” and “Q” as shown in Fig. 1 which amounts to approximately 5 ha. The other part (the area around the pond in the lower part of the catchment) was excluded from our study, since it is influenced by a high constant water table and evolved into a semi-aquatic ecosystem with very different site conditions.

For the statistical scrutiny of our hypotheses a combined dataset comprising terrain surface information from terrestrial laser scanning (TLS), vegetation information from field records, soil and groundwater information was used. The data sources have different spatial and temporal resolutions. Soil samples were taken only once at the beginning of the study, vegetation records were made once every year in summer time and TLS was done at seven different times between 2008 and 2011.

The spatial data fusion was done on the vegetation monitoring plot scale, assigning the different data sources to the 20 m × 20 m grid points. Temporally, vegetation record data were assigned to the same year’s laser scan data. Thus, dependent on the analysis of interest, the same vegetation record data were assigned to both laser scan measurements of a year. Ground water measurements were assigned as annual means to each vegetation sample plot. For the soil data there was only one measurement, a specific temporal assignment was not possible. Thus, for result interpretation we had in mind that they represent initial conditions and not a temporal development.

As the catchment is sloped downwards from row A to row Q, the distance of any grid point to row A is indicated as DISTA. The time since January 2005 is encoded in the variable TIME with month as yearly fractions (e.g. 6.42 for May 2011) and CALYEAR as the calendar year. The resulting time component of the statistical explanatory variables is identified by the index j and the spatial location by the index i. In Table 1 all variables and indexes used in this study are listed together with their definitions.

2.2.1 Vegetation

Altogether 119 permanent plots for long term vegetation monitoring were established (Zaplata et al., 2010; Fig. 1). Each plot had a square shape of 5 m × 5 m with the above-mentioned grid points in their centers. At each plot all vascular plant species were recorded including cover estimates for each species in 30 distinct percentage classes (Zaplata et al., 2013). Bryophyte covers were estimated in the same way, distinguishing mosses and liverworts. So far, a time series with 7 yr of continuous annual monitoring is available. The plant species occurring in the study period (2008 to 2011) were grouped by (i) lifespan according to Rothmaler (2000), but with only the two categories "annual" and "perennial", (ii) life forms "grasslike", "herb" or "wood" according to Rothmaler (2000); species of the genus *Rubus* were labeled as "wood", and (iii) affiliation to the *Fabaceae* family ("Fabaceae" versus "no Fabaceae"). From this grouping, we calculated for each vegetation plot and measurement the proportions of cover for annual plants (PROPANN), grasslike plants (PROPGRASS), woody plants (PROPWOOD) and *Fabaceae* family (PROPFAB) related to the total plant cover COVTOT (see Table 1).

2.2.2 Soil and groundwater

After completion of the catchment construction, soil samples were taken at each grid-point in a depth of 0–30 cm between October 2005 and April 2006 (see Fig. 1). The samples were air-dried, passed through a 2 mm mesh and analyzed for pH (water extract, Beckmann pH34 glass electrode and WTW pH537), electrical conductivity (EC, Hanna HI 8733 and WTW LF537), texture (sieving and sedimentation procedure with Köhn pipette method), total content of carbon (C_T), nitrogen (N_T) and sulphur (S_T, elementar analyzer Vario EL III), inorganic (carbonate, Scheibler calcimeter) and organic carbon ($C_{org.}$, calculated as difference $C_T - CaCO_3$-C) content.

We assumed the soil data from a grid point being valid for the whole vegetation square. Variables that turned out to be promising for this study in preliminary exploratory data analyses were the percentage of $C_{org.}$ (CORGP), the percentage of skeletal content (SKELCONT), and MSAND, the percentage of medium sand (see Table 1).

A total of 26 groundwater gauges were installed in the catchment (Fig. 1). Nine of them were equipped with pressure transducers to register groundwater levels automatically. The levels at the other gauges were measured manually every two weeks. More details are described by Biemelt et al. (2010). We simply attributed the mean annual ground water level in m from the nearest measurement shaft to each grid point, having to tolerate an average distance of 19 m and maximum distance of 53 m from a square midpoint (see Table 1). We used that simple method because no complex assumptions are required as is the case for any interpolation.

2.2.3 Terrestrial laser scans

We used a terrestrial laser scanner (mod. Riegl LMS Z420i) in last target mode to measure 3-D ground surface and vegetation height and density simultaneously. In order to keep the impact on the catchment at a minimum, we only measured from 13 permanently fixed scan positions (Fig. 1), each geo-referenced with 30 DGPS-fixed points (DGPS = Differential Global Positioning System), which allowed us to keep the standard deviation of the georeferencing error below 2.5 cm.

The scan positions were spatially arranged in a way that allowed us to maintain a horizontal measurement resolution of at least 10 cm × 10 cm at a hypothetical horizontal ground surface. Given the limited number of scan positions, this was only possible by mounting the laser scanner on a portable 6 m tower. This height is sufficient for achieving the desired minimum resolution but not too high in order to hit existing vegetation mainly from more lateral, not so much from vertical directions. This is important, because vertically oriented vegetation like grasses is more likely detected from the side, than from above and the side view is better suited to detect vegetation layers under emerging woody plants. See the method comparison by Schneider et al. (2012) for more technical details.

We conducted seven area-wide laser scan campaigns between 2008 and 2011 (September 2008, May 2009, August 2009, April 2010, October 2010, February 2011, and May 2011). Despite it was not easy to find appropriate time windows (for such a campaign several days with clear weather and low wind are required) the measurements were timed so that at least in the years 2009 and 2010 roughly the catchment's state at the beginning and the end of the vegetation period could be covered. With our scans we covered the whole catchment amounting to 6 ha altogether.

The raw laser scan data are three-dimensional point clouds, each point indicating the position where the leaser beam hit an object. In order to separate vegetation from ground surface we divided the covered area into about 200 000 0.5 m × 0.5 m grid cells. On each cell we extracted the minimum vertical coordinate from the point cloud and assumed it to best represent the ground surface level. Our estimate for vegetation height (VEGHEIGHT, see Table 1) on such a cell is the vertical range of point coordinates, i.e. maximum minus minimum vertical coordinate. As a proxy for vegetation density (VEGDENS) on each cell, we took the median vertical coordinate (with the estimated ground level being zero) divided by the estimated vegetation height. This results in a number between 0 and 1. Values near 1 would indicate a high density, because the laser signal will be more often reflected in higher regions if vegetation is dense, resulting in a median nearer the maximum height and for less dense vegetation more reflections are measured at the ground, shifting the median lower. Values near zero result from a small median compared to vegetation height, thus indicating the obvious high penetrability when density is low. The product of vegetation height and vegetation density, which could serve as a rough proxy for biomass, was named VEGDH.

In order to detect rills we used a regression-based approach. For each 0.5 m × 0.5 m laser scan grid cell we took all neighbour cells whose midpoints were inside a radius of 6 m around the midpoint of the central cell. With the horizontal coordinates (x, y) of the cell midpoints as the independent variables and the vertical coordinate (z) of the neighbouring cells' ground level as the dependent variable we fitted a simple ordinary least squares (OLS) regression model of the following form

$$z = a \cdot x + b \cdot y + c + \varepsilon \quad (1)$$

with a, b, c being parameters to be estimated and ε representing the error term. Equation (1) thus represents a plane that after fitting can be interpreted as a smoothened description of the terrain surface in the cell of interest's proximity. If the actual ground level z of the central cell is more than 5 cm lower than the one estimated from Eq. (1), then this cell is assumed to belong to a rill. Visual comparisons with aerial photographs from the catchment show a good concordance with this rill detection method.

In addition to this 6 m neighbour analysis, we used the same method with a 0.8 m radius and calculated the difference between the greatest and the smallest vertical deviation from the regression plane. This can be interpreted as a description of relief energy in the nearest neighbourhood. This potential energy is used as an indicator if the cell is located on a very steep or flat region and thus how large the influence of surface runoff events or seed might be or how likely a successful seed deposition may happen.

To each grid point we attributed every laser scan grid cell with its midpoint inside the corresponding 5 m × 5 m vegetation square and used only those cells further on. This implied two options for data evaluation. First is the extraction and evaluation of sum and mean values from the laser scan data, one number per vegetation square, such as surface roughness or percentage of rill cells. Second is an analysis on the level of single laser scan grid cells. However, preliminary analyses showed that the latter tended to be less revealing than the former while consuming disproportional computing time. Thus, we focussed on the former, more aggregated option. See Table 1 for an overview of the laser scan derived variables.

2.3 Statistical evaluation

As the basic method for our statistical evaluations we chose Generalized Linear Models (GLM's) and Generalized Additive Models (GAM's) because they allow us to deal with different distribution families for the response variable. In addition, GAM's offer a convenient way to incorporate nonlinear effects into the analyses. However, as we take a vegetation square as our basic observation unit, several subsequent observations are available per vegetation square. We covered the resulting autocorrelation by introducing a random effect on vegetation square level. This enlarges GLM's to Generalized Linear Mixed Models (GLMM's) and GAM's to Generalized Additive Mixed Models (GAMM's). See Zuur et al. (2009) for a detailed description of these model types and Pinheiro and Bates (2000) for further information about Mixed Models. Preliminary tests did not indicate any spatial correlation between vegetation squares in the context of this study.

The core of a GLMM in the context of this study is a linear predictor function η of the following form:

$$\eta(X_{1ij},\ldots,X_{qij}) = \alpha + \beta_1 \cdot X_{1ij} + \ldots + \beta_q \cdot X_{qij} + a_i \quad (2)$$

$$a_i \sim \mathrm{N}(0,\sigma_a^2)$$

where $X_1 \ldots X_q$, is a set of q explanatory variables. The indices i and j denote the jth observation on the ith vegetation square. α and β are regression parameters and a_i is a vegetation-square specific random effect. In case of a GAMM, the predictor function enlarges to

$$\eta(X_{1ij},\ldots,X_{qij},K_{1ij},\ldots,K_{nij}) = \alpha + \beta_1 \cdot X_{1ij} + \ldots + \beta_q \cdot X_{qij} + f_1(K_{1ij}) + \ldots + f_n(K_{nij}) + a_i \quad (3)$$

where, in addition, $K_1 \ldots K_n$ is a set of n explanatory variables, and $f_1 \ldots f_n$ is a set of nonparametric smoother functions (cf. Zuur et al., 2009).

The way, how η is transformed into an expected value μ_{ij} for the actual response variable Y_{ij} is defined by the link function g.

$$g(\mu_{ij}) = \eta(X_{1ij},\ldots,X_{qij},K_{1ij},\ldots,K_{nij}) \quad (4)$$

If Y_{ij} is assumed to be normally distributed ($Y_{ij} \sim \mathrm{N}(\mu_{ij}, \sigma^2)$) then the usual link function is identity:

$$\mu_{ij} = \eta(X_{1ij}, \ldots, X_{qij}, K_{1ij}, \ldots, K_{nij}) \tag{5}$$

This is the first of three options we used in this study.

In cases where Y_{ij} was proportional data with a tendency towards overdispersion a quasi-binomial distribution for Y_{ij} with $\mathrm{var}(Y_{ij}) = \tau \cdot \mu_{ij} \cdot (1 - \mu_{ij})$ and the dispersion parameter τ not being fixed to 1 and a logit link

$$\ln\left(\frac{\mu_{ij}}{1 - \mu_{ij}}\right) = \eta(X_{1ij}, \ldots, X_{qij}, K_{1ij}, \ldots, K_{nij}) \tag{6}$$

was used. When $Y > 0$, the assumption of a gamma-distribution for Y_{ij} with $\mathrm{var}(Y_{ij}) = \frac{\mu_{ij}^2}{\nu}$ and ν being the dispersion parameter turned out to be useful in combination with a logarithmic link:

$$\ln(\mu_{ij}) = \eta(X_{1ij}, \ldots, X_{qij}, K_{1ij}, \ldots, K_{nij}) \tag{7}$$

Promising explanatory variables were pre-selected as proposed by Zuur et al. (2009) based on exploratory data analyses such as pairplots and variance-inflation factors. If plausibility considerations, visual data inspections or residual plots suggested (partly) non-linear relationships, a GAMM was chosen instead of a GLMM. In each analysis, we started with the full set of pre-selected explanatory variables, leaving them out stepwise, by AIC comparison and re-fitting each time (Zuur et al., 2009). Model assumptions were confirmed by graphical displays.

For scrutinizing H1, the question if the initial geomorphological and substrate characteristics determine the surface's structure and properties of the terrain, we investigated several response variables (see Table 1):

- RILLR: the proportion of rill cells per vegetation square and measurement. As RILLR represents proportional data, the quasibinomial distribution with logit link was used.
- RELEN: the mean value of the local relief energy of all laser scan cells belonging to one vegetation square. Assuming a gamma distribution combined with the logarithmic link turned out to be most useful for this response variable.
- DHEIGHT, the ground height change (see Table 1 for details) was investigated with a regression model that assumes normal distribution of the response variable and uses the identity link.

Due to the definition of H1 we did not include any vegetation properties as explanatory variables in these analyses.

In the context of H2, asking if surface and substrate characteristics determine the plant species groups to be found initially, the following set of vegetation properties was chosen as response variables (see Table 1):

- PROPANN: the portion of annual plants related to the total coverage per vegetation square and survey.
- PROPHERB: same for the portion of herbaceous plants,
- PROPGRASS: same for grass including sedge species,
- PROPFAB: same for plants belonging to the nitrogen-collecting *Fabaceae* family
- PROPWOOD: same for woody plant species.

For all these proportions, assuming quasi-binomial distribution and using a logit-link turned out to be the best option. In addition, we also used two laser-scanned vegetation properties as response variables:

- VEGHEIGHT and VEGDENS: the mean vegetation height and vegetation density per vegetation square and survey.

The former was investigated assuming normal distribution and using the identity link while for the latter quasi-binomial distribution with logit-link was applied.

For testing H3, if increasing density of vegetation reduces the erosion, we used DHEIGHT, the laser-scanned surface height changes as a response variable.

We did so in the same way as for H1, but tested several ways of including the laser-scanned vegetation properties VEGHEIGHT and VEGDENS as additional explanatory variables. The other explanatory variables were those that showed significance in the context of H1.

The overarching important components of temporality and spatiality are included in the variables TIME and DISTA.

For all statistical evaluations we used the free software R version 2.15.1 (R Core Team, 2012), namely the package mgcv (Wood, 2006).

3 Results

3.1 Influence of geomorphological and substrate characteristics on surface structure (H1)

The final model for describing the dependency of the portion of rill cells, RILLR, was a GAMM with logit-link (cf. Sect. 2.3, Eqs. 3 and 6):

$$\ln\left(\frac{E(\mathrm{RILLR}_{ij})}{1-E(\mathrm{RILLR}_{ij})}\right) = \alpha + \beta_1 \cdot \mathrm{CORGP}_i + \beta_2 \cdot \mathrm{GAUGE}_{ij} + \beta_3 \cdot \mathrm{TIME}_j + \beta_4 \cdot \mathrm{CORGP}_i \cdot \mathrm{TIME}_j + f_1(\mathrm{DISTA}_i) + a_i \tag{8}$$

The indices i and j, and the random effect a have the same meaning as in Eq. (2), and $E(\mathrm{RILLR})$ represents the expected value of RILLR. CORGP is the percentage of organic carbon in the soil, GAUGE is the mean annual ground water level in m below surface, $f_1(\mathrm{DISTA})$ is a smoother function that represents the effect of DISTA (see Table 1). All explanatory variables show highly significant ($p < 0.001$) effects.

Figure 2 shows the effect of DISTA. Clearly there is a general trend of finding rills more probably the more one moves further downslope, however with a minimum between 50 m and 150 m from row A. Table 2 lists the parameter estimates for α and $\beta_1 \ldots \beta_4$. The parameters for the variables CORGP, GAUGE, and TIME are greater than 0, indicating that the probability to encounter rills increases with the percentage of organic carbon (as measured in 2005), a lower annual ground water level (higher GAUGE) and with time. However, there is also a significant interaction that indicates the influence of CORGP weakens with time.

Testing the local relief energy RELEN the right hand side of the final GAMM model was the same as in Eq. (8), however, due to the logarithmic link function the left hand side is different:

$$\begin{aligned} \ln(E(\mathrm{RELEN}_{ij})) &= \alpha + \beta_1 \cdot \mathrm{CORGP}_i + \beta_2 \cdot \mathrm{GAUGE}_{ij} + \\ &\beta_3 \cdot \mathrm{TIME}_j + \beta_4 \cdot \mathrm{CORGP}_i \cdot \mathrm{TIME}_j + f_1(\mathrm{DISTA}_i) + a_i \end{aligned} \tag{9}$$

The results as presented in Table 3 and Fig. 3 show a strong affinity between the rill probability and the local relief energy. Again, relief energy generally increases with increasing DISTA, however with a minimum at about 100 m from row A (Fig. 3). Relief energy also increases with CORGP (Table 3), lower ground water levels (higher GAUGE) and, expectedly, increases with TIME (parameters $\beta_1 \ldots \beta_3 > 0$), however the negative value obtained for β_4 shows a weakening influence of CORGP with time.

The change of the surface height DHEIGHT, in relation to non-vegetation variables only, yielded a final model of the following GLMM structure:

$$\begin{aligned} E(\mathrm{DHEIGHT}_{ij}) &= \alpha + \beta_1 \cdot \mathrm{MSAND}_i + \beta_2 \cdot \mathrm{GAUGE}_{ij} + \beta_3 \cdot \mathrm{RILLR}_{ij} + \beta_4 \cdot \mathrm{DISTA}_i + \\ &\beta_5 \cdot \mathrm{TIME}_j + \beta_6 \cdot \mathrm{MSAND}_i \cdot \mathrm{TIME}_j + \beta_7 \cdot \mathrm{RILLR}_{ij} \cdot \mathrm{TIME}_j + \beta_8 \cdot \mathrm{DISTA}_i \cdot \mathrm{TIME}_j + a_i \end{aligned} \tag{10}$$

In addition to the afore-mentioned symbols MSAND means the percentage of medium sand (grain size 0.2–0.63 mm) in the soil (as measured in 2005). The parameter estimates and significances are listed in Table 4. Significances are partly weaker than in the models shown above. The effect of MSAND ($\beta_1 < 0$) means that more material (volume) erodes at places where 2005 more medium sand has been found. Lower groundwater levels are connected with greater material export ($\beta_2 < 0$), the more rills we find, the more material is exported ($\beta_3 < 0$). There is a weak, but highly significant tendency towards a surface height increase with increasing DISTA ($\beta_4 > 0$) while time has no significant isolated effect, however the analysis reveals significant time effects in interaction with other variables. Parameter β_6, being significantly greater than 0 indicates that the above-mentioned effect of MSAND weakens with time, and the same is true for the effect of RILLR ($\beta_7 > 0$). A reverse effect is observed for DISTA in interaction with time ($\beta_8 < 0$).

3.2 Influence of surface and substrate characteristics on vegetation structure (H2)

With the proportion of annual plants PROPANN as the response variable the following final model resulted (GAMM with logit-link):

$$\ln\left(\frac{E(\mathrm{PROPANN}_{ij})}{1 - E(\mathrm{PROPANN}_{ij})}\right) = \alpha + \beta_1 \cdot \mathrm{CORGP}_i + f_1(\mathrm{COVTOT}_{ij}) + f_2(\mathrm{CALYEAR}_j) + f_3(\mathrm{GAUGE}_{ij}) + a_i \quad (11)$$

with $\beta_1 < 0$ Table 5 shows a negative correlation between CORGP and the proportion of annual plants. The nonlinear effect of COVTOT, the respective vegetation plot's total degree of coverage in percent (Fig. 4) reveals an optimum at roughly 50 % while the increase at very high degrees of coverage is not significant (broad confidence interval). The proportion of annual plants decreases with the calendar year (Fig. 4), while the probability to find annual plants on a vegetation plot increases with lower groundwater levels (higher GAUGE) roughly in the shape of a saturation curve (Fig. 4).

A very similar final model resulted for PROPHERB, the proportion of herbaceaous plants (GAMM with logit-link).

$$\ln\left(\frac{E(\mathrm{PROPHERB}_{ij})}{1-E(\mathrm{PROPHERB}_{ij})}\right) = \alpha + \beta_1 \cdot \mathrm{CORGP}_i + f_1(\mathrm{COVTOT}_{ij}) + f_2(\mathrm{CALYEAR}_j) + f_3(\mathrm{GAUGE}_{ij}) + a_i \qquad (12)$$

The effects observed for PROPHERB are virtually the same as obtained for annual plants (Fig. 5, Table 6), an optimum pattern for COVTOT, a decreasing curve for the calendar year and a saturation curve for the ground water level, and a negative correlation with CORGP.

The scrutiny of the proportion of grasses (PROGRASS) yielded an even simpler model:

$$\ln\left(\frac{E(\mathrm{PROPGRASS}_{ij})}{1-E(\mathrm{PROPGRASS}_{ij})}\right) = \alpha + \beta_1 \cdot \mathrm{CORGP}_i + f_1(\mathrm{COVTOT}_{ij}) + f_2(\mathrm{CALYEAR}_j) + a_i \qquad (13)$$

Compared to the herbaceous plants, the grasses show an opposing trend. Even though the effect of CORG is just not significant ($p = 0.0633$, Table 7), the grasses seem to be connected to places with higher organic carbon content in the soil. As Fig. 6 shows, the coverage of grasses decreases strongly with the total degree of coverage (COVTOT), while it increases with the calendar year.

For the proportion of woody plants (PROPWOOD) a simple GLMM resulted:

$$\ln\left(\frac{E(\mathrm{PROPWOOD}_{ij})}{1-E(\mathrm{PROPWOOD}_{ij})}\right) = \alpha + \beta_1 \cdot \mathrm{COVTOT}_{ij} + \beta_2 \cdot \mathrm{CALYEAR}_j + a_i \qquad (14)$$

Only two explanatory variables show a significant relationship in this context. Trivially, the proportion of woody plants increases with time (CALYEAR). Less expectedly, the probability of finding woody plants decreases as the total coverage on a vegetation square increases (Table 8).

The final model for the proportion of Fabaceae (PROPFAB) resulted in the following structure:

$$\ln\left(\frac{E(\mathrm{PROPFAB}_{ij})}{1-E(\mathrm{PROPFAB}_{ij})}\right) = \alpha + \beta_1\cdot\mathrm{GAUGE}_{ij} + f_1(\mathrm{COVTOT}_{ij}) + f_2(\mathrm{CALYEAR}_j) + f_3(\mathrm{SKELCONT}_i) + a_i \tag{15}$$

with SKELCONT representing the soil's skeletal content in percent as measured 2005.

As Table 9 shows, there is a positive correlation between lower ground water levels and the occurrence of *Fabaceae* ($\beta_1 > 0$). Up to skeletal contents of 10 % and up to total degrees of coverage of about 20 %, their proportion is positively correlated with both variables (Fig. 7). Remarkably, the occurrence of *Fabaceae* over time showed a maximum in the years 2008 and 2009 (Fig. 7).

VEGHEIGHT, the mean vegetation height as obtained from laser scans was described with the following model:

$$E(\mathrm{VEGHEIGHT}_{ij}) = \alpha + \beta_1\cdot\mathrm{COVTOT}_{ij} + \beta_2\cdot\mathrm{GAUGE}_{ij} + f_1(\mathrm{CALYEAR}_j) + f_2(\mathrm{DISTA}_i) + a_i \tag{16}$$

Figure 8 (left) shows that vegetation height increases with time, expectedly in an exponential pattern as it is typical for initial growth processes. The same figure (Fig. 8, right) reveals a clear trend of increasing vegetation height with the distance from gridrow A. Groundwater levels (dryer conditions) and coverage degrees are positively correlated with vegetation height ($\beta_1 > 0$, $\beta_2 > 0$, Table 10).

No significant relations of other variables with the laser-scanned vegetation density VEGDENS could be identified.

3.3 Influence of vegetation structure on surface structure (H3)

In order to scrutinize H3 we took the model formulation from Eq. (8) which relates the change of the laser-scanned surface height DHEIGHT with soil and surface variables, but added different combinations of the laser-scanned vegetation height VEGHEIGHT, vegetation density VEGDENS, and TIME, all referring to the beginning of the period during which DHEIGHT occurred. We found that including the product of VEGHEIGHT · VEGDENS = VEGDH in interaction with time yielded the best model:

$$\begin{aligned} E(\mathrm{DHEIGHT}_{ij}) = \alpha + \beta_1 \cdot \mathrm{MSAND}_i + \beta_2 \cdot \mathrm{GAUGE}_{ij} + \beta_3 \cdot \mathrm{RILLR}_{ij} + \beta_4 \cdot \mathrm{DISTA}_i + \\ \beta_5 \cdot \mathrm{TIME}_j + \beta_6 \cdot \mathrm{MSAND}_i \cdot \mathrm{TIME}_j + \beta_7 \cdot \mathrm{RILLR}_{ij} \cdot \mathrm{TIME}_j + \beta_8 \cdot \mathrm{DISTA}_i \cdot \mathrm{TIME}_j + \\ f_1(\mathrm{VEGDH}_{ij}, \mathrm{TIME}_j) + a_i \end{aligned} \tag{17}$$

Compared to the model without vegetation data as explanatory variables (Eq. 10, Table 4), the parameter estimates for $\beta_1 \ldots \beta_8$ are very similar (Table 11), thus, there is no contradiction between this and the other model. However, the nonlinear vegetation effect pronouncedly shows a vegetation effect that counteracts erosion. The higher and denser the vegetation (i.e. the greater VEGDH), the stronger this effect, which also changes with time (Fig. 9). In the first observation period (start September 2008) the correlation is somewhat weak and almost linear but in the following two periods, the curve becomes more and more bent upwards, the VEGDH-value where the bend starts moving down to smaller VEGDH-values from the second to the third observation period. This indicates that even with the same VEGDH-values the stabilizing effect of vegetation increases with time.

4 Discussion

Surface structure in the study area is mainly influenced by geomorphological characteristics. The slope degree of the area is not the same throughout the area, but shows a maximum in the lower part (rows L to P in Fig. 1). This is reflected (or at least indicated) by the pronounced and partly nonlinear effects of the downhill distance from grid row A (DISTA) on the frequency of rills (RILLR), the local relief energy (RELEN), and the ground surface height change (DHEIGHT). The pronounced minima for the downhill distance effect (DISTA) for the rill frequency and the local relief energy (Figs. 2, 3) seem to indicate a special local situation: they are located just downhill an area where, due to the construction works of the catchment, many rills take an perpendicular course to the main slope direction.

Gullies are channeling surface runoff. This results in a further incision both in depth and uphill – a kind of a positive feedback, which is strongly supported by our model for the ground surface height change (DHEIGHT, Table 4), especially by the significant effects of the rill frequency (RILLR) and the interaction effect of the downhill position (DISTA) with time.

Although the portion of organic carbon (CORGP) is strongly correlated with rill intensity, it seems most likely that this parameter is a proxy for the general substrate properties. The same could be true for parameter MSAND. According to Gerwin et al. (2010), CORGP strongly correlates with clay content. In general, soil texture in the western part of the catchment is dominated by loamy sands, whereas in the eastern part pure sands dominate. These differences are reflected in the spatial extent and form of the erosion gullies being narrower and deeper in the western part, but shallower and wider in the eastern part (Schaaf et al., 2012). Surface runoff dominated catchment hydrology at least in the early years resulting in gully formation and transport of large sediment amounts that were deposited in the lower part of the hill slope and in the pond (Schaaf et al., 2012). While doing so surface runoff and erosion transported mainly finer textured material, resulting in even coarser texture at the uphill surface substrates. This could explain the decreasing influence of the substrate proxy variables CORGP and MSAND with time.

Besides such transport effects, the weakening effects of initial surface and soil properties with time reflect the increasing influence of vegetation coverage (see H3).

In summary, our results strongly support H1. Geomorphology (slope degree) and substrate properties like grain size distribution and resulting differences in groundwater levels affect the system strongly and result in fundamental changes in geomorphology all over the area, but with main effects where the slope degree is highest. The developing vegetation cover, however, reduces the influence of these factors in the course of time, leading to an increasing conservation of the structures that developed earlier.

Some of our results concerning the influence of surface and substrate characteristics on vegetation structure (H2), to which belongs the decrease of annuals as well as the increase of grasses and especially woody species in the course of time, and the general increase of vegetation height over time prove some basic assumptions of "succession science" (e.g. initial pioneers are followed by perennial grasses). Despite a scientific history of well over a century (Cutler, 2010) even this is noteworthy. For a long time in Central Europe "succession science" was regarded with suspicion, until its methodological approaches became more precise (Frey and Lösch, 2004). Projects exclusively using chronosequences (probably the most) lack the spatial coverage for a quantitative analysis on vegetation change, both, in the sense of spatial patterns over time and in the sense of temporal pattern in space (Baasch, 2010). Still vast uncertainty exists about the ratio of exogenous processes (e.g. soil properties) to endogenous processes (e.g. dispersal, biotic community processes) during succession. In view of the above and considering also previous publications (Zaplata et al., 2011a, 2013) which give hints that dominant species' dispersal over the area might be regarded as nonvarying in space, a particular contribution of H2 and our study system takes shape.

Annual species – most of them being pioneers – were preferentially and expectedly found at places with less organic carbon that means with low water and nutrient storage capacities (as mentioned before organic carbon might act as a proxy for general substrate properties), and lower groundwater levels. It was found also in a low-pH system that particularly stressful places were almost exclusively colonized by pioneers (Baasch, 2010).

In line with basic assumptions, the annual species' portion decreases with time (Fig. 4). However, the foregoing notwithstanding, during the first years of the succession two annual species (*Conyza canadensis*, *Trifolium arvense*) were successively dominating (Zaplata et al., 2011b) and hence their portion increases with increasing vegetation cover (COVTOT) but does not change with COVTOT values beyond 50 % (Fig. 4). The existence of a succession phase governed by *Trifolium arvense* (*Fabaceae*) in 2008–2009 means, that many (adjacent) vegetation plots had similar covers of this plant species (Zaplata et al., 2013). The "optimum" shortly before COVTOT = 50 % (Fig. 4) might reflect the "preferential cover range" of *T. arvense*. Apparently this phase is recapitulated in an optimum calendar year effect for the occurrence of *Fabaceae* (Fig. 7). In previous studies we show a temporal trend in the manner of optimum curves for both cover (Schaaf et al., 2012) and regularity of the cover (Zaplata et al., 2013) for the two dominant species in a very detailed way.

However, the proportion of annual plants' (to which *T. arvense* belongs) steady decrease means that the perennials on the whole had disproportionate growth rates, even during the dominance phases of the two annual species.

What has been found for annuals is in many respect also true for herbaceous plants and for *Fabaceae* (Fig. 7), simply because most of the herbaceous plants at the beginning of the succession are annuals, and a dominating species of this group (*Trifolium arvense*) belongs to the Fabaceae family.

For the grasses, however, we found just the opposite temporal trend than for the herbs. Each year their share on the total community (Fig. 6) increased. Grass species like *Agrostis capillaris* and *Calamagrostis epigejos* increased strongly (Zaplata et al., 2011b), and we expect a continued rise in the importance of the grasses. Again in contrast to the herbaceous plants, the grasses dominate plots with low total coverage (Fig. 6). Hence, grasses are important contributors on more sparsely covered plots. In such a way they may rule severely habitable subareas, but not the study system as a whole. This fact supports the assignment of the studied time span to the (first) successional stage of herbaceous vegetation (Zaplata et al., 2013). Only two explanatory variables, total degree of coverage and calendar year, showed a significant relationship in this context (Fig. 6, Table 7).

The same applies for the woody plants, with an increasing share on the total community and – unexpectedly – a decreasing probability of finding them on vegetation squares with higher total cover (Table 8). We suggest a reverse situation in future. Latest, when there are several crown layers formed by differently sized trees, their joint covers will prevail about the total covers of pure herb and grass plots. We also suggest that detailed analyses, possibly in combination with experiments, could reveal what possibly suppresses the successful establishment of woody species at subareas of the study site. Based on considerations about resource limitation-driven competition modes by Hara (1993) and Weiner (1990), we hypothesize that our finding indicates that during the observed time span plant growth in the catchment was mostly limited by the soil bound resources water and nutrients. Under such conditions the tree competition strategy to invest in vertical size does not pay off so much as it does when the vectorially distributed resource light is limiting. As long as this is not the case, trees may often face disadvantages in competition with non-woody plants.

We also found that overall vegetation height is by trend greater on more densely vegetated plots (Table 10). We may interpret that (i) simply as consequence of particularly stressful growth places, (ii) the high proportion of per se low-growing annuals there, or (iii) as an effect of beginning light competition which comes, however, hardly from trees yet. At this point we would like to emphasize the contribution from this extensive study here "just" is the evidence that there is a positive relationship between taller and denser vegetation. Even for the clarity of this very "basic" seeming result, prerequisites such as the spatial explicitness (the tracking of the individual fate of the vegetation squares) had to be fulfilled.

Our finding that vegetation height tends to be greater when the distance to the groundwater table is higher probably reflects a spurious correlation resulting from the coincidental temporal distribution of dry years co-occurring with ongoing succession. On the other hand there are, however, indications that at least some of this effect might be attributable to the intrinsic characteristics of the system. For example, the first dominant plant species, the aforementioned *Conyza canadensis*, reached the greatest growth heights in 2006, which was the driest year so far in the time series. In the course of time a decrease in size was registered even for some perennial species like *Artemisia vulgaris*, *Hypericum perforatum* and *Hieracium umbellatum*, whose sometimes still existing prior-year shoots were taller evidenced by comparison during the vegetation square survey.

In conclusion, the results of the separate analyses of plant functional groups (annuals, herbs, *Fabaceae*, grasses, woody plants) are in line with "succession theory", e.g. the decreasing proportions of annuals and herbs and the increasing proportions of grasses and woody species. The latter two were underrepresented on denser vegetated plots. It might seem paradoxical at first sight, considering them as the superior competitors. However this underlines the exceptional nature of early succession. With such results, this study supports a non-neutral view of ecosystem assembly during succession (cf. Nee and Stone, 2003). From our second hypothesis' point of view (surface and substrate characteristics determine the plant species groups to be found initially) we can summarize that it is partly true. Some few substrate characteristics already correlate in different ways with the occurrence of certain plant groups (cf. Baasch, 2010). Expectedly, woody plants show the weakest connection to substrate properties, the weak but significant connection we found between the occurrence of the N-collecting *Fabaceae* and the soil skeletal content (Fig. 7) is plausible as well.

Introducing vegetation properties into the model for the surface height change (DHEIGHT) clearly confirmed our third hypothesis – the increasing density of vegetation reduces the erosion and therefore the degree of change of terrain surface structure. Remarkably VEGHD, the product of the laser-scanned vegetation height with the laser-scanned vegetation density VEGDENS – a proxy for biomass – performed best as the vegetation-related explanatory variable. The effects of all other substrate and geomorphology variables stayed virtually the same as in the DHEIGHT model without any vegetation variables used in the context of our first hypothesis. Thus, there apparently are no inconsistencies which would hamper the interpretation. As Fig. 9 shows, the terrain-stabilizing effect of vegetation increases in the course of time, even for the same values of VEGHD. This may be interpreted as the result of positive (reinforcing) feedbacks between vegetation and substrate (vegetation establishment stabilizes the surface which supports further vegetation establishment) while vegetation growth itself appears to be also driven by positive feedback as can be seen from the exponentially shaped calendar year effect on vegetation height in Fig. 8. As typical in many kinds of initial systems, not only in ecosystems (Sterman, 2002), positive feedbacks seem to dominate the surface and vegetation dynamics of the investigated artificial catchment Chicken Creek.

5 Conclusions

Although some of our findings must be considered to reflect incidental relationships, they mostly confirm all three hypotheses. The initial geomorphology and substrate properties have indeed an effect on the surface formation processes. We find positive (reinforcing) feedback mechanisms like the tendency of rills to deepen. However such pure substrate or geomorphology induced effects weaken with time, while vegetation establishes increasingly and differentiatedly introducing new, (currently positive) feedbacks. These consist in mutually reinforcing stabilisation of surface and vegetation, but also in vegetation growth processes. In general our analyses show a transition from a geo-hydro towards bio-geo-hydro-system as defined in Elmer et al. (2013).

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Table 1. Names, data source and description of the variables used in this study.

Source	Variable	Description	Unit
TLS	RILLR$_{ij}$	Proportion of laser scan cells classified as belonging to a rill related to the total amount of laser scan cells per vegetation plot	
TLS	RELEN$_{ij}$	Mean value of local relief energy (0.8 m radius neighbourship)	m
TLS	DHEIGHT$_{ij}$	Mean ground surface elevation changes between September 2008–May 2009, May 2009–April 2010, and April 2010–February 2011. Positive values of DHEIGHT indicate an increase of the surface height indicating a net gain of substrate material in the vegetation square, while negative values indicate a net substrate material export (erosion) from the respective square.	m
TLS	VEGHEIGHT$_{ij}$	Mean vegetation height	m
TLS	VEGDENS$_{ij}$	Mean vegetation density surrogate	
TLS	VEGDH$_{ij}$	Product of VEGHEIGHT$_{ij}$ and VEGDENS$_{ij}$	
VEG	PROPANN$_{ij}$	Proportion of annual plant cover related to total plant cover	
VEG	PROPHERB$_{ij}$	Proportion of herbaceous plant cover related to total plant cover	
VEG	PROPGRASS$_{ij}$	Proportion of grass like plants cover related to total plant cover	
VEG	PROPWOOD$_{ij}$	Proportion of woody plants cover related to total plant cover	
VEG	PROPFAB$_{ij}$	Proportion of cover of plants belonging to the *Fabaceae* family related to total plant cover	
VEG	COVTOT$_{ij}$	Total degree of plant coverage	
SOIL	CORGP$_{i}$	Percentage of organic carbon in the soil	
SOIL	SKELCONT$_{i}$	Perentage of skeletal content in the soil	
SOIL	MSAND$_{i}$	Percentage of medium sand (0.2–0.63 mm) in the soil	
AQ	GAUGE$_{ij}$	Mean annual ground water level below surface	m
	DISTA$_{i}$	Distance from the row of the grid point to the row A on the catchment (see Fig. 1)	m
	TIME$_{j}$	Time in years since January 2005, months included as fractions of years	a
	CALYEAR$_{j}$	Calendarial year	a

TLS: derived from laser scans, available for each laser scan grid cell, aggregated for each vegetation plot.
VEG: derived from the vegetation monitoring, summer of each year.
SOIL: values from soil samples in 2005 at the center of each vegetation plot.
AQ: values assigned from the nearest of the ground water gauges, yearly averages.
Indices:
i values for a specific location (gridpoint), constant over time.
j values for points in time, spatially independent.
ij values for a specific point in time, at a specific location.

Table 2. Parameter estimates and significances for the model estimating the portion of rill cells (RILLR) as shown in Eq. (8). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect *a* in Eq. (8) is 0.5456. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: RILLR increases (decreases) with increasing values of the respective predictor variable.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	−8.1121	0.5397	***
CORGP	↑	β_1	10.4752	2.0661	***
GAUGE	↑	β_2	1.0374	0.1753	***
TIME	↑	β_3	0.8624	0.0820	***
CORGP · TIME	↓	β_4	−1.7634	0.3555	***
f_1(DISTA)		Nonparametric smoother	See Fig. 2		***

Table 3. Parameter estimates and significances for the model estimating the local relief energy (RELEN) as shown in Eq. (9). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (9) is 0.1119. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: RELEN increases (decreases) with increasing values of the respective predictor variable.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	−5.5417	0.2758	***
CORGP	↑	β_1	5.7311	1.1252	***
GAUGE	↑	β_2	0.5085	0.0894	***
TIME	↑	β_3	0.5726	0.0434	***
CORGP · TIME	↓	β_4	−1.0869	0.2031	***
f_1(DISTA)		Nonparametric smoother	See Fig. 3		***

Table 4. Parameter estimates and significances for the model estimating surface height change (DHEIGHT) as shown in Eq. (10). Significance levels: ***: $p<0.001$, **: $p<0.01$, *: $p<0.05$. The variance of the random effect a in Eq. (10) is 0.0002. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: DHEIGHT increases (decreases) with increasing values of the respective predictor variable. Thus, ↓ indicates a tendency towards erosion while ↑ indicates trends that counteract erosion.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	−0.0414	0.0825	
MSAND	↓	β_1	−0.0031	0.0015	*
GAUGE	↓	β_2	−0.0286	0.0058	***
RILLR	↓	β_3	−0.2559	0.0970	**
DISTA	↑	β_4	0.0006	0.0001	***
TIME		β_5	0.0226	0.0169	
MSAND · TIME	↑	β_6	0.0007	0.0003	*
RILLR · TIME	↑	β_7	0.0429	0.0217	*
DISTA · TIME	↓	β_8	−0.0002	0.0000	***

Table 5. Parameter estimates and significances for the model estimating the proportion of annual plants (PROPANN) as shown in Eq. (11). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (11) is 0.1594. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: PROPANN increases (decreases) with increasing values of the respective predictor variable.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	0.2551	0.0868	**
CORGP	↓	β_1	−1.7067	0.4431	***
f_1(COVTOT)		Nonparametric smoother	See Fig. 4		***
f_2(CALYEAR)		Nonparametric smoother	See Fig. 4		***
f_3(GAUGE)		Nonparametric smoother	See Fig. 4		***

Table 6. Parameter estimates and significances for the model estimating the proportion of herbaceous plants (PROPHERB) as shown in Eq. (12). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (12) is 0.0855. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: PROPHERB increases (decreases) with increasing values of the respective predictor variable.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	0.6254	0.0685	***
CORGP	↓	β_1	−0.9162	0.3481	**
f_1(COVTOT)		Nonparametric smoother	See Fig. 5		***
f_2(CALYEAR)		Nonparametric smoother	See Fig. 5		***
f_3(GAUGE)		Nonparametric smoother	See Fig. 5		***

Table 7. Parameter estimates and significances for the model estimating the proportion of grasses (PROPGRASS) as shown in Eq. (13). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (13) is 0.1489.

Variable	Parameter	Estimate	Std. Error	Significance
	α	−1.9460	0.0783	***
CORGP	β_1	0.7366	0.3960	$p = 0.0633$
f_1(COVTOT)	Nonparametric smoother	See Fig. 6		***
f_2(CALYEAR)	Nonparametric smoother	See Fig. 6		***

Table 8. Parameter estimates and significances for the model estimating the proportion of woody plants (PROPWOOD) as shown in Eq. (14). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (14) is 3.1987. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: PROPWOOD increases (decreases) with increasing values of the respective predictor variable.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	−1118.7522	98.9546	***
COVTOT	↓	β_1	−0.0119	0.0018	***
CALYEAR	↑	β_2	0.5542	0.0493	***

Table 9. Parameter estimates and significances for the model estimating the proportion of Fabaceae (PROPFAB) as shown in Eq. (15). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (15) is 0.2288. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: PROPFAB increases (decreases) with increasing values of the respective predictor variable.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	−2.6636	0.1723	***
GAUGE	↑	β_1	0.8693	0.1301	$p = 0.0633$
f_1(COVTOT)		Nonparametric smoother	See Fig. 7		***
f_2(CALYEAR)		Nonparametric smoother	See Fig. 7		***
f_3(SKELCONT)		Nonparametric smoother	See Fig. 7		***

Table 10. Parameter estimates and significances for the model estimating the laser-scanned vegetation height (VEGHEIGHT) as shown in Eq. (16). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (16) is 0.0074. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: VEGHEIGHT increases (decreases) with increasing values of the respective predictor variable.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	0.3851	0.0367	***
COVTOT	↑	β_1	0.0007	0.0003	*
GAUGE	↑	β_2	0.0879	0.0301	**
f_1(CALYEAR)		Nonparametric smoother	See Fig. 8		***
f_2(DISTA)		Nonparametric smoother	See Fig. 8		***

Table 11. Parameter estimates and significances for the model estimating surface height change (DHEIGHT) as shown in Eq. (17). Significance levels: ***: $p < 0.001$, **: $p < 0.01$, *: $p < 0.05$. The variance of the random effect a in Eq. (17) is 0.0006. Trend: qualitative illustration of linear predictor variables' significant influences. ↑, ↓: DHEIGHT increases (decreases) with increasing values of the respective predictor variable. Thus, ↓ indicates a tendency towards erosion while ↑ indicates trends that counteract erosion.

Variable	Trend	Parameter	Estimate	Std. Error	Significance
		α	−0.0427	0.0253	
MSAND	↓	β_1	−0.0024	0.0004	***
GAUGE	↓	β_2	−0.0392	0.0032	***
RILLR	↓	β_3	−0.0215	0.0072	**
DISTA	↑	β_4	0.0004	0.0000	***
TIME	↑	β_5	0.0189	0.0038	***
MSAND · TIME	↑	β_6	0.0007	0.0000	***
RILLR · TIME	↑	β_7	0.1075	0.0016	***
DISTA · TIME	↓	β_8	−0.0002	0.0000	***
f_1(VEGHD, TIME)		Nonparametric smoother	See Fig. 9		***

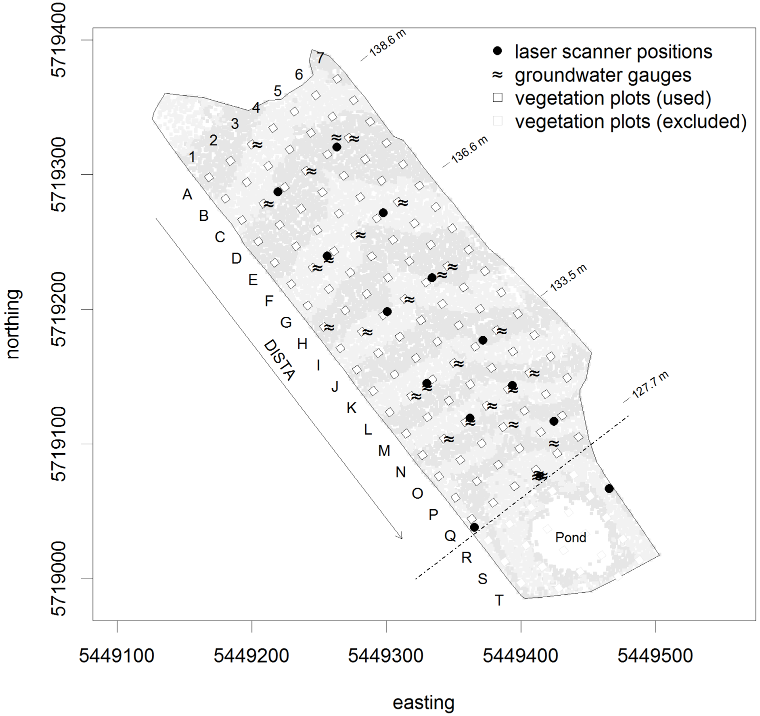

Fig. 1. Map of the Chicken Creek area (with Gauss-Krüger Zone 5 coordinates) showing locations of the data sources (vegetation plots, laser scanner positions, groundwater gauge positions) relevant for this study. Vegetation plots are identified by row (A–T) and column (1–7). In this work only rows A-Q were used. The variable DISTA as shown in the figure indicates the distance of a point from row A. Ground heights a.s.l. are given as mean values from the laser scan September 2008 around the centerpoints of vegetation plots A6, F6, L6 and Q6.

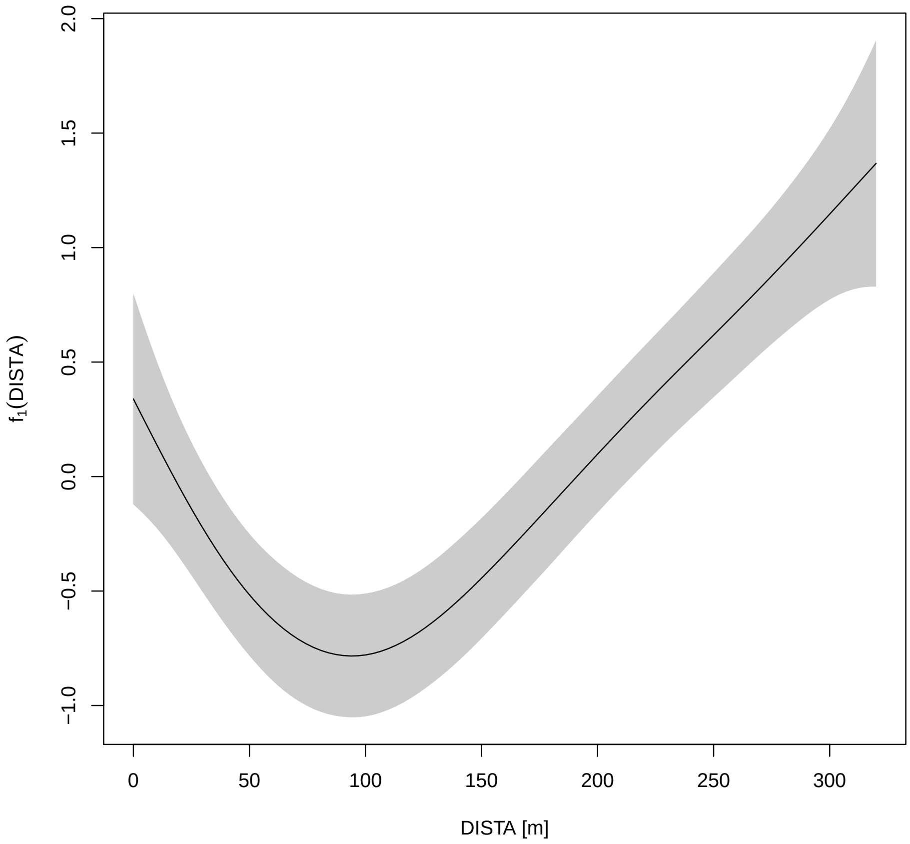

Fig. 2. Nonlinear effect of a vegetation square's distance from gridrow A (DISTA) on the portion of rill cells (RILLR) (see Eq. 8). Shaded: 95 %-confidence area.

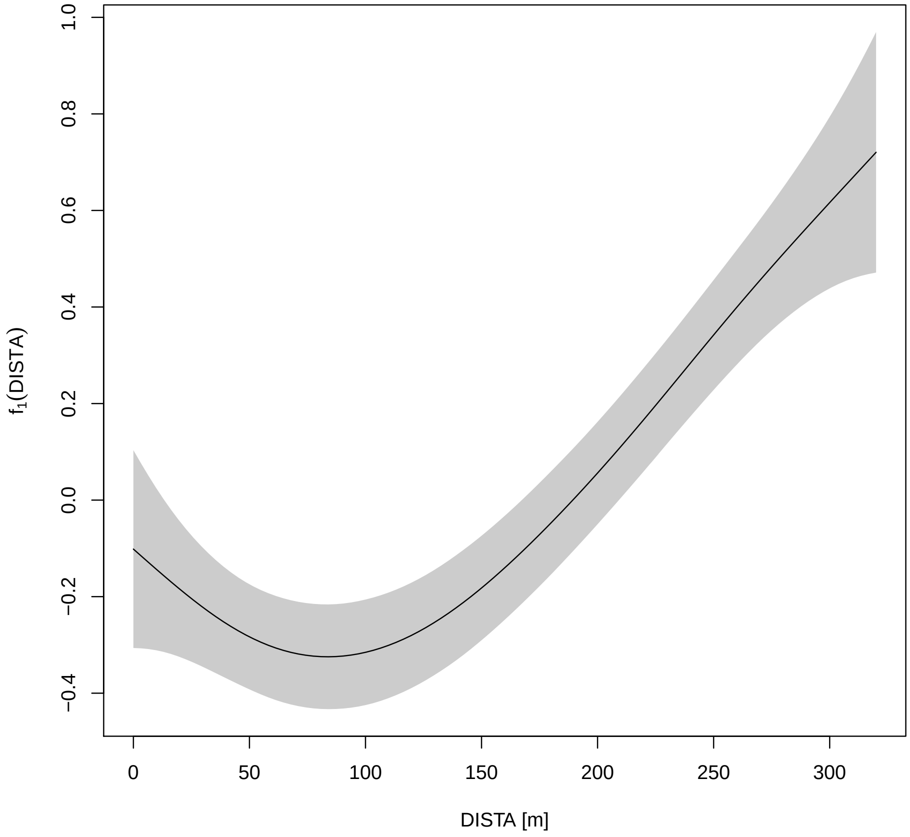

Fig. 3. Nonlinear effect of a vegetation square's distance from gridrow A (DISTA) on the local relief energy (RELEN) (see Eq. 9). Shaded: 95 %-confidence area.

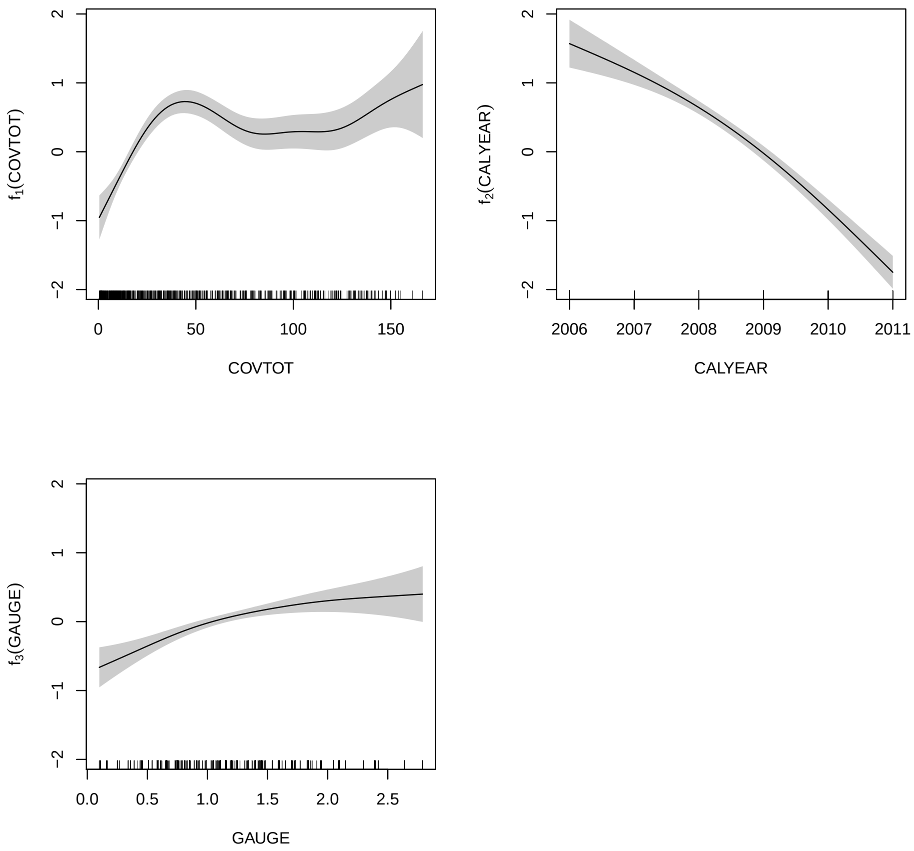

Fig. 4. Nonlinear effects of the total degree of coverage (COVTOT), calendar year (CALYEAR), and ground water level (GAUGE) on the proportion of annual plants (PROPANN) (see Eq. 11). Shaded: 95 %-confidence area.

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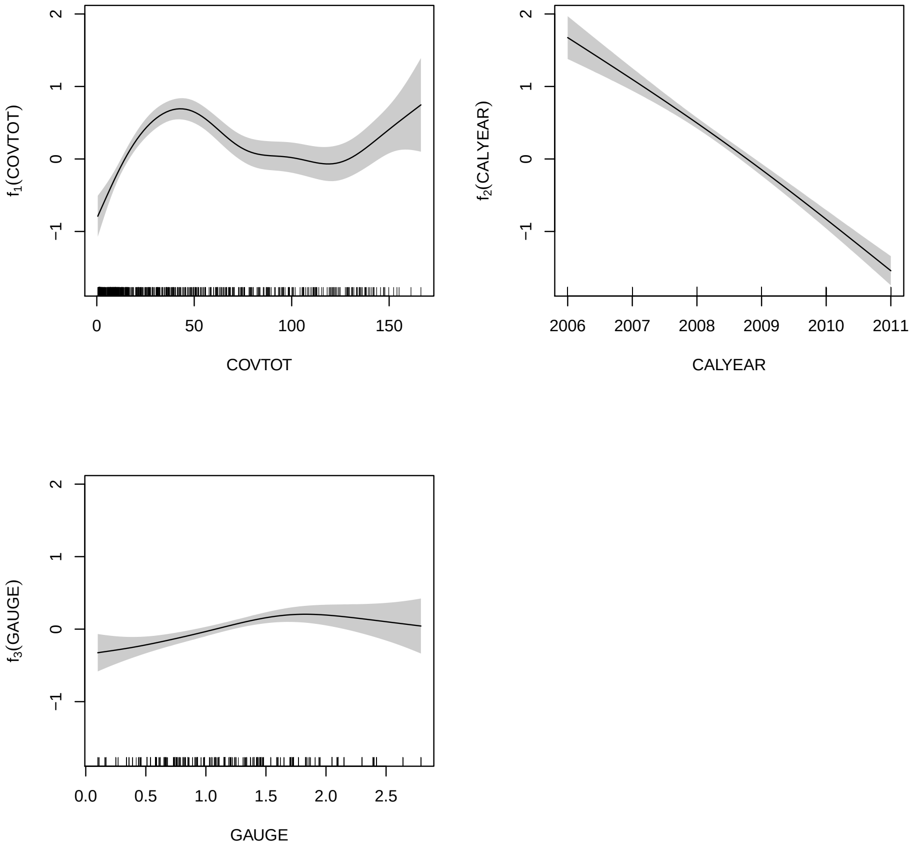

Fig. 5. Nonlinear effects of the total degree of coverage (COVTOT), calendar year (CALYEAR), and ground water level (GAUGE) on the proportion of herbaceous plants (PROPHERB) (see Eq. 12). Shaded: 95 %-confidence area.

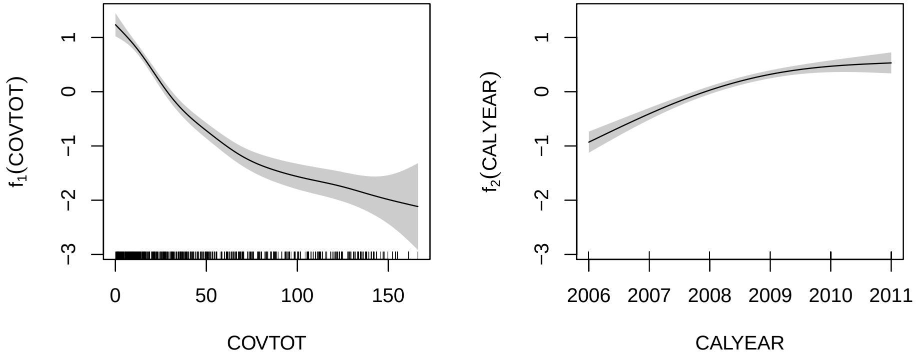

Fig. 6. Nonlinear effects of the total degree of coverage (COVTOT), and calendar year (CALYEAR), on the proportion of grasses (PROPGRASS) (see Eq. 13). Shaded: 95 %-confidence area.

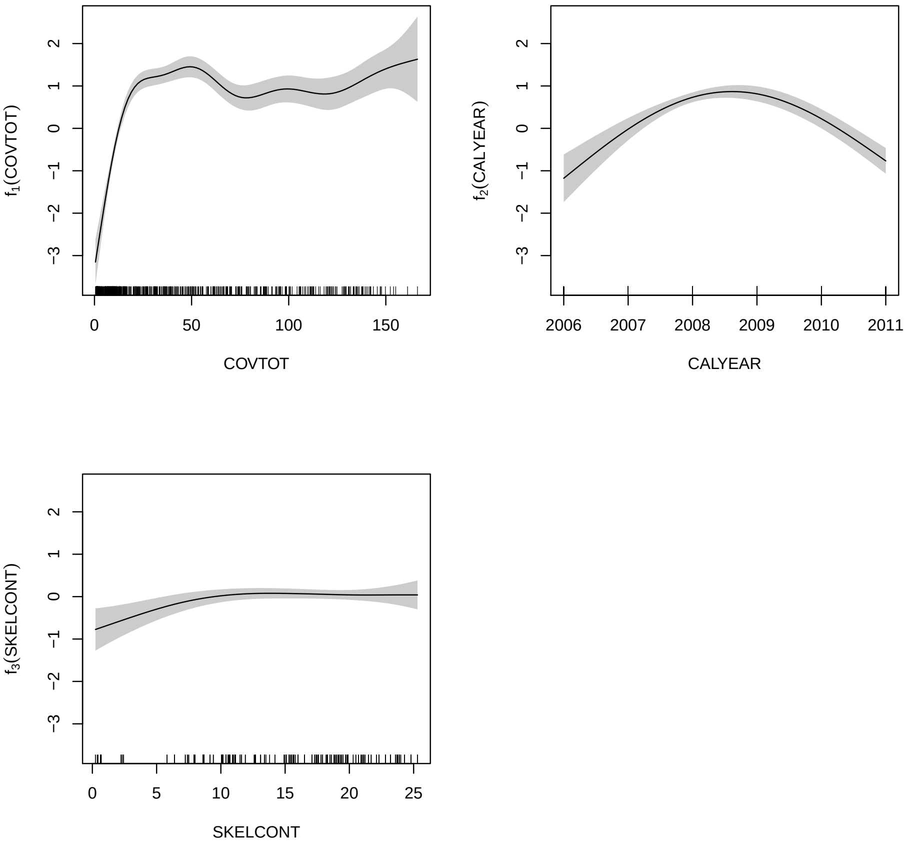

Fig. 7. Nonlinear effects of the total degree of coverage (COVTOT), and calendar year (CALYEAR), and skeletal content (SKELCONT), on the proportion of Fabaceae (PROPFAB) (see Eq. 15). Shaded: 95 %-confidence area.

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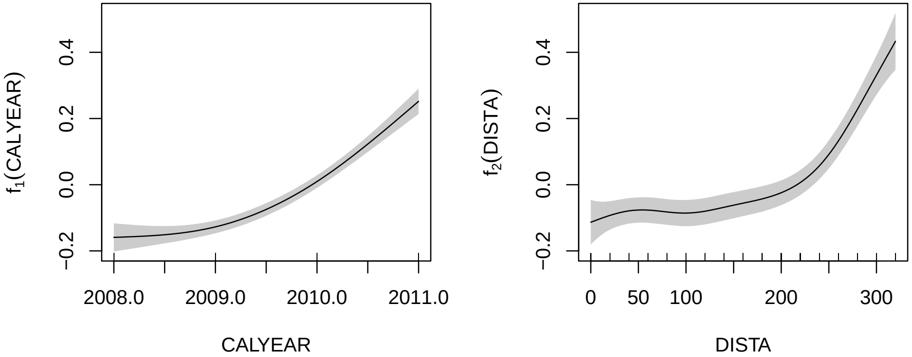

Fig. 8. Nonlinear effects of the calendar year (CALYEAR), and distance from gridrow A (DISTA), on the laser-scanned vegetation height (VEGHEIGHT) (see Eq. 16). Shaded: 95 %-confidence area.

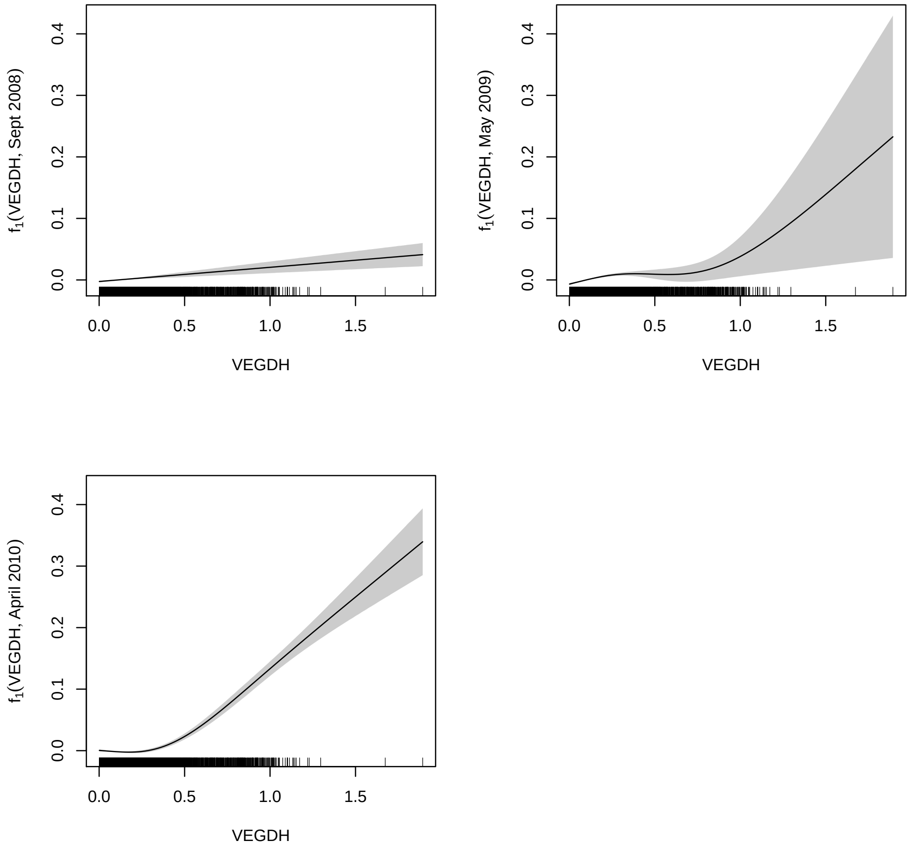

Fig. 9. Nonlinear effect of the product of vegetation density and vegetation height (VEGDH) at different times on the surface height change (DHEIGHT) (see Eq. 17). Shaded: 95 %-confidence area.