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Research article

Analysis of land-use change in a sector of Upper Franconia (Bavaria, Germany) since 1850 using land register records

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Abstract

This study analyses changes in the landscape of a sector of Upper Franconia (Bavaria, Germany) by comparing land use changes over four time periods (1850, 1900, 1960, 2000). Geodetic and other data derived from the Bavarian real estate tax and land register were entered into various temporal layers of a land register-based vector GIS. This multitemporal GIS permits a precise analysis of the historical structure and development of landscapes on the basis of land plots.

In 1850, the study area was almost exclusively agricultural in structure. Woodlands made up only 18% of the total surface. Rough pastures and wastelands, which covered about 9% of the total surface, were used for grazing. During the first half of the 20th century, the proportion of wooded areas increased considerably. The rough pastures that had formerly been a typical feature of the region nearly disappeared during this period. Agricultural use declined to less than 50% of the total area. In the course of the period between 1960 and 2000, the livestock industry has become an almost exclusively indoor activity. Village development has started spilling over into the adjacent fields. The causes and background of these changes are discussed in detail.

From an ecological standpoint, the land use categories surveyed in this analysis of landscape change can be regarded as vegetation types, thereby constituting habitats for specialized biota. The intensity and frequency of any type of land use creates a certain disturbance regime, which disrupts and controls the succession in a certain way. The concept of categories of change incorporated into the GIS helps to evaluate these habitat types and the rate of change more accurately, e.g. for nature conservation purposes.

Introduction

Landscape ecology emphasizes the spatial characteristics and dynamic relationships of patches (Forman and Godron 1986). By identifying the particular spatial configuration of a landscape, the underlying processes that contribute to the pattern formation can be inferred based on the characteristic composition of the patches in space and time (Urban et al. 1987). In cultural landscapes, anthropogenic processes are of central importance in analyses of structure, dynamics and functions of patches (e.g., Lamarche and Romane 1982; Houghton 1994; Oldfield et al. 2000; Reid et al. 2000). Therefore, ecological studies of cultural landscapes have to be linked closely to the levels of human activities and the hierarchical structure of administrative bodies. In recent years, numerous case studies have focused on both ecological and socio-economic aspects of the transformation of natural landscapes and respective land use changes in Europe (e.g., Sporrong 1998; Pärtel et al. 1999; Verheyen et al. 1999; Cousins et al. 2002; McLure and Griffiths 2002; Petit and Lambin 2002).

These studies have employed a variety of methods to assess and describe landscape change (cf. Riebsame et al. 1994; Olsson et al. 2000; Cousins 2001). We believe that a land plot-level approach provides an accurate way to derive insights about land-use change over the long term as well as how the spatial texture and configuration of a cultural landscape influences anthropogenic ecosystems and their dynamics (cf. Wiens 2002). With the assistance of an attribute database, a model of the past landscape development patterns can support decision-making in landscape planning and biological conservation management (Christensen 1997; Gordon et al. 1995; Gutzwiller 2002; Lambeck and Hobbs 2002).

We use a new standardized method with a high resolution for the precise analysis and evaluation of changes in land use since the mid-19th century in a cultural landscape of Central Europe. This multitemporal cultural landscape information system is based on large scale maps (1:5000). It utilizes more detailed information than traditional approaches with topographical maps and, among other things, integrates land plot-based data such as subsidies, land owner profiles, and soil quality information (Bender et al. in press). The general objectives of this study are to understand the course of cultural landscape change since 1850 at the land-plot level, and to determine its causes.

From an ecological standpoint, this study involves a simultaneous analysis of changes in anthropogenic ecosystems, human disturbance regimes (Pickett and White 1985; Boehmer 1997), patterns of habitat types and distributions of specialized species. Changes in land use patterns have provoked far-reaching ecological effects, the consequences of which now often initiate nature conservation actions (e.g., Jedicke 1998). Over the course of the 20th century, many traditional forms of use (or human disturbance) have been abandoned, and this has resulted in the fragmentation and isolation of anthropogenic ecosystems. For this reason, the goal of our study is also to provide an accurate basis for explaining patterns in species abundance caused by a complex cultural landscape and patterns driven by complex anthropogenic dynamics (cf. Hanski 1999).

With the aid of the multitemporal GIS, we attempted to address the following questions: What was the structure of the landscape around 1850? How were the patches (land plots) used? Which patches changed within which time period? How did they change? And finally: Why did they change?

Methods

Methodology of landscape change analysis

The analysis of landscape change in Central Europe is generally based on topographic and historical maps, air and satellite photographs, land registers which include geodetic survey maps (Figure 1) and land plot records, original surveys of species (where available), as well as various statistical and archival data. Land registers and topographical maps are the principal sources of serial data (Bender et al. in press).

In any assessment of the landscape potential in Central Europe, the period analysed must reach back to the mid-19th century, because the cultural landscapes of this region attained their highest level of ecological and land use diversity during the pre-industrial period (Roweck 1995). The required land register data have been collected comprehensively in large parts of Central Europe since the 19th century (cf. Wagner 1950; Heider 1954; Messner 1967).

The types of land use, ownership status and other attributes are listed (mostly for tax purposes) in the land register's land plot records. The geodetic survey maps document the boundaries of the land plots and also divide each plot of real estate (Eigentumsparzellen) into different sub-plots by type of use (Nutzungsparzellen). Therefore, a database of land plot attributes was compiled from the older land plot records in the archives of the land register for the earlier periods and by entering current data from the automated land tax register (Automatisiertes Liegenschaftsbuch, ALB). This can be complemented by data provided by the agricultural administrations. Nevertheless, in order to make a multitemporal comparison, the terminology for the basic category 'type of use' needs to be adapted, because it may change over time.

A geographical database for a sector of Upper Franconia was created on the basis of current and

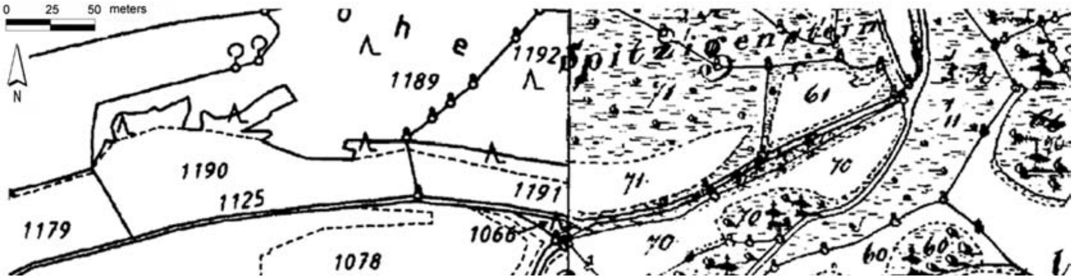

Figure 1. Sections of the current geodetic survey map sheet no. NW 82-11 (left) and the original sheet no. NW 82-10 of 1843 (right), original scale 1:5000. Reproduced by permission of the Bavarian Geodetic Survey, no. 1463/01.

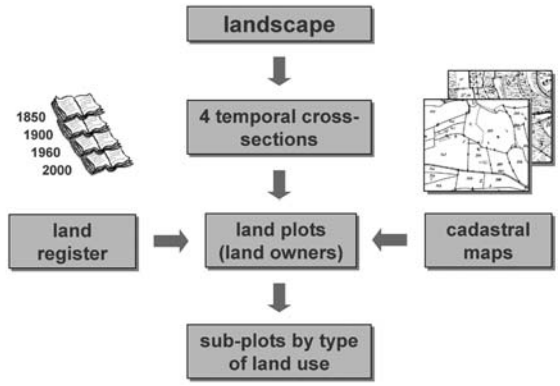

Figure 2. Conceptual model in land resgister-based GIS.

historical cadastral maps at a scale of 1:5000 (Figure 2). The original maps were transferred into raster data, and the spatial features of the ground vegetation were digitized, except where a digital geodetic survey map (Digitale Flurkarte, DFK) already existed. A layer was created for each time period that we investigated (1850, 1900, 1960, 2000), beginning with the most recent and presumably most accurate map, and working backwards in time to the earlier temporal layers. The historical maps only served to identify the changes. Their distortions and projection errors needed to be corrected visually.

The change of the landscape over time was described by means of four temporal layer maps (Figure 3). Maps of landscape change were constructed by successively intersecting the various temporal layers according to categories of change, e.g., from pasture to woodland, beginning with the oldest layer. It then became possible to visualize the changes between any two temporal layers. Compared to a purely statistical evaluation (plot use balance), a geo-relational approach has the advantage of permitting an assessment of development trends. It thus became possible to determine the various changes in cultivation according to the plots' categories of change, i.e., former use vs. subsequent use.

To help explain the causes of landscape change, information from digital terrain models were incorporated into the land register-based GIS and merged with the land plot data. This information equally applies to socio-economic data obtained from geodetic surveys and agricultural administrations (eg. property, farm types), and it provides a means to correlate categories of change with explanatory variables such as soil quality, relief etc. (Bender et al. in press). Vegetation surveys were carried out using the Braun-Blanquet method to analyze vegetation types and plant communities (cf. Mueller-Dombois and Ellenberg 2002).

Study area

The study area is a segment of the Franconian Alb mountain range in Upper Franconia (Bavaria, Germany; Figure 4), which was settled during the early Middle Ages. Dramatic landscape change has occurred in this region in recent decades (Figure 5). Our detailed plot-by-plot approach made it necessary to limit the study area to the district and local levels forming the basic economic units in the history of the cultural landscape. The districts Siegritz, Wuestenstein and Zochenreuth (about 2000 hectares in total; Figure 6) were selected as they encompass the natural and cultural landscape elements typical of the Franconian Alb.

These districts are at different stages of land reallocation: In Siegritz, the process was accomplished in the 1960s, in Wuestenstein the exchange of land plots is currently being initiated, and in Zochenreuth consolidation of the holdings is at the planning stage. Furthermore, the districts vary with regard to their

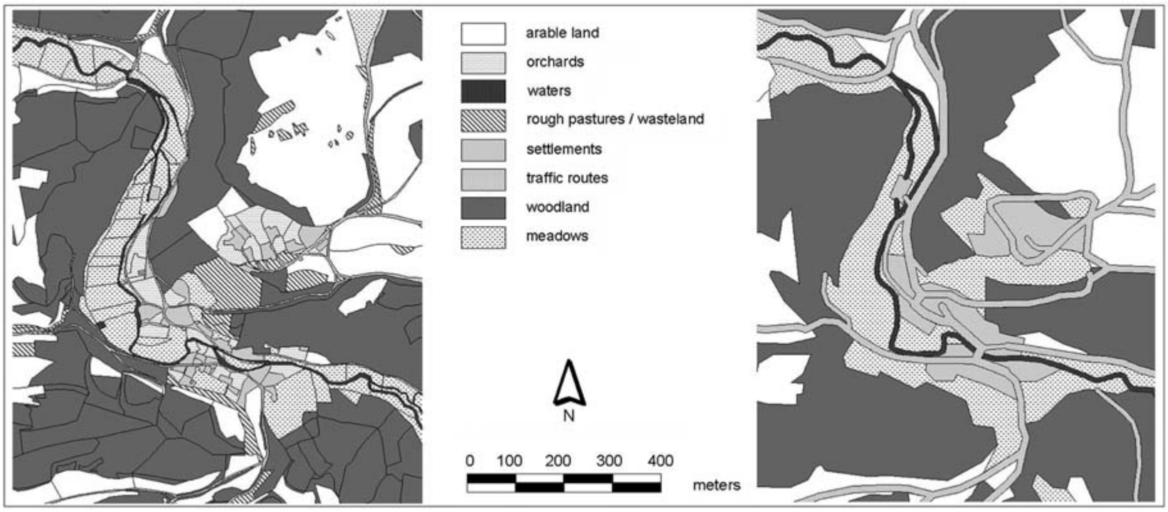

Figure 3. Comparison of two temporal layer maps after evaluation of cadastral maps and topographical maps (section of Wuestenstein district, Franconain Alb).

Figure 4. Location of the study area.

Figure 5. Pottenstein, Franconian Alb (Upper Franconia/Bavaria/ Germany), ca. 1930 (photgraphy by H. Scherzer).

Figure 6. Pottenstein, Franconian Alb at present (photograph by H. J. Boehmer).

settlement history (including both manor villages and peasant villages), the socio-economical categories of villages and farms, and land-use types (full-time and part-time farming, with and without livestock, etc.).

The study area, located at an elevation of 360 to 490 m above sea level, belongs to the Northern

Table 1. Categories of change in the balance of plot use for the districts of Siegritz, Wuestenstein, and Zochenreuth (1850–2000).

area 1850		change 1850–2000								
		arable land	orchards	waters	rough pastures	wasteland	settlements	traffic routes	woodland	meadows
arable land	ha	982.79	0.78	0.19	2.40	2.33	17.69	26.92	331.62	14.70
	%	47.23	0.04	0.00	0.12	0.11	0.85	1.29	15.94	0.71
orchards	ha	2.03	2.04	0.03	0.02	0.3	14.54	0.60	0.10	6.03
	%	0.10	0.10	0.00*	0.00*	0.01	0.70	0.03	0.01	0.29
waters	ha	0.02	0	6.14	0	0	0.01	0.18	0	0.11
	%	*0.00	0.00	0.30	0.00	0.00	0.00*	0.01	0.00	0.01
rough pastures	ha	9.38	0.01	0.03	7.30	0.71	0.61	0.95	48.78	0.22
	%	0.45	0.00*	0.00*	0.35	0.03	0.03	0.05	2.34	0.01
wasteland	ha	9.79	0	0	3.44	2.47	0.85	1.53	93.03	1.35
	%	0.47	0.00	0.00	0.17	0.12	0.04	0.07	4.47	0.06
settlements	ha	0.02	0.11	0.00	0	0.03	6.40	0.14	0.01	0.39
	%	0.00*	0.01	0.00*	0.00	0.00*	0.31	0.01	0.00*	0.02
traffic routes	ha	3.96	0.01	0.01	0.07	0.11	0.33	36.28	0.26	0.14
	%	0.19	0.00*	0.00*	0.00*	0.01	0.02	1.74	0.01	0.01
woodland	ha	20.20	0	0.02	0.47	0.05	1.33	1.71	354.51	1.83
	%	0.97	0.00	0.00*	0.02	0.00*	0.06	0.08	17.04	0.09
meadows	ha	2.07	0.01	0.28	0.25	0.13	2.64	1.86	4.52	48.70
	%	0.10	0.00*	0.01	0.01	0.01	0.13	0.09	0.22	2.34

* between 0.00 and 0.005
% = percentage of total surface area.

Franconian Alb. It consists of an Upper Jurassic limestone plateau with calcareous strata and massive dolomitic reefs. The plateau is cleaved by a number of steep valleys that are 70 to 80 m deep. The rivers Aufsess and Leinleiter and their tributaries have gradually excavated their path into the aquifers beneath the Late Jurassic limestone surface.

Within the study area, the plateau of the Franconian Alb has an undulating relief with characteristically wooded hilltops (termed 'Knöcke') and small dry valleys (Figure 6). The plateau sector overlying the permeable calcareous strata is karstified with an arid surface. Soils include rendzic leptosols and cambisols. The mean annual precipitation is about 800 mm, and the average temperature is 7 °C. The natural vegetation consisted of various types of beech forest, depending on local conditions (Hohenester 1989). The mixed and conifer forests that now exist are the result of afforestation and secondary succession (Weisel 1971; Boehmer 1994).

Results

The cultural landscape around 1850

In the mid-19th century, the study area was almost exclusively agricultural in structure. The villages were separated from the surrounding fields by a belt of meadows and sparse orchards. Most of the plateau was subject to agricultural use. Even today, remnants of field terraces provide evidence of the former tillage-pasture rotation typical of the region, the so-called 'Egertenwirtschaft' (Weisel 1971), which is not specifically mentioned in the land register. In some sectors, the cadastral map shows a rotation between tillage and pasture on a much smaller scale than recorded in the land register.

The taxation status of rough pastures was distinct from that of wastelands, but there was hardly any difference in their use or appearance. Both area types (about 10 % of the total surface in 1850) were used for grazing. They were generally located on the slopes of dry valleys and on the eastern hillsides of the Aufsess valley. Patches of wasteland were also a typical feature in the tilled areas of the karstified hills, which were interspersed with dolomite outcrops that could not be removed with the technology available at the time. Rough pastures and wastelands often formed a linear pattern between the fields. So, the livestock could be easily driven from one grazing plot to the next. Extended pasture areas existed in some districts as the result of grazing rights held by non-locals and landlords. Meadows, mostly located in the valleys, were the most intensively used areas of the entire landscape. Irrigation facilitated several hay cuts per

Table 2. Average soil qualities (first Bavarian land taxation, ~1850) and slope gradients in land plots of the districts of Siegritz, Wuestenstein und Zochenreuth by categories of change (1850–2000). The 'soil qualities' do not have units of measure; the background of this concept is the calculation of taxes for the first Bavarian land taxation. In order to evaluate the value ('soil quality') of a certain land plot, the mean annual agricultural yield of sample plots located all over Bavaria was calculated and classified (value classes for arable fields: 1-27; meadows: 1-40; woodlands 0.5−11.5; Heider 1954).

Cat. of change 1850–2000	Plots	Plots (%)	Area (ha)	Area (%)	Av_SQ	Av_SL	Av_ASP	Av_SQ_W	Av_SL_W	Av_ASP_W
arable land – arable land	3207	28.59	982.79	47.23	5.71	3.87	78.98	5.89	3.75	80.35
arable land – meadows	113	1.01	14.70	0.71	6.98	7.03	75.95	8.20	6.17	87.14
arable land – pastures	45	0.40	2.40	0.12	5.13	6.40	77.20	4.45	7.89	68.38
arable land – wasteland	68	0.61	2.34	0.11	4.87	5.96	91.60	4.74	6.12	90.11
arable land – woodland	1482	13.21	331.63	15.94	3.93	7.58	88.05	3.65	7.42	84.58
meadows – arable land	24	0.21	2.07	0.10	13.58	7.10	77.12	17.65	6.11	63.37
meadows – meadows	330	2.94	48.70	2.34	17.45	5.98	84.02	17.67	5.83	82.14
meadows – pastures	6	0.05	0.25	0.01	4.67	3.81	108.42	6.94	9.75	97.52
meadows – wasteland	2	0.02	0.13	0.01	10.50	6.68	66.18	11.66	7.48	72.57
meadows – woodland	17	0.15	4.52	0.22	5.97	8.38	78.55	4.39	10.65	75.76
pastures – arable land	53	0.47	9.38	0.45	2.72	5.52	63.50	2.54	5.81	38.86
pastures – meadows	7	0.06	0.22	0.01	1.43	7.41	73.38	1.27	4.34	71.72
pastures – pastures	37	0.33	7.31	0.35	3.46	7.32	64.94	2.21	8.93	75.84
pastures – wasteland	12	0.11	0.71	0.03	4.00	5.24	33.97	2.73	6.63	33.48
pastures – woodland	143	1.27	48.78	2.34	2.30	8.03	79.29	1.81	9.36	74.21
wasteland – arable land	231	2.06	9.79	0.47	2.88	4.75	80.81	2.71	4.43	87.93
wasteland – meadows	13	0.12	1.35	0.06	0.92	10.49	59.41	1.38	10.39	77.46
wasteland – pastures	19	0.17	3.44	0.17	0.75	8.68	81.24	0.76	11.13	67.84
wasteland – wasteland	65	0.58	2.47	0.12	3.55	5.67	83.39	3.17	5.68	79.27
wasteland – woodland	431	3.84	93.03	4.47	1.69	7.54	86.57	1.20	9.94	85.62
woodland – arable land	100	0.89	20.20	0.97	3.74	5.70	89.21	4.13	3.72	87.03
woodland – meadows	20	0.18	1.83	0.09	4.08	11.15	117.88	3.48	9.65	102.98
woodland – pastures	2	0.02	0.47	0.02	2.50	4.53	98.08	2.97	5.05	54.65
woodland – wasteland	1	0.01	0.05	0.00	3.50	10.39	125.28	3.50	10.39	125.28
woodland – woodland	603	5.38	354.51	17.04	3.45	10.87	97.06	3.58	11.74	91.08
Sum	7031	62.69	1943.04	93.38	5.20	5.93	83.29	5.00	6.43	83.06
Study Area	11216	100.00	2080.86	100.00	6.13	5.79	80.80	5.08	6.41	82.81

Abbreviations: Cat. of change 1850–2000 – categories of change 1850–2000; Plots = number of plots; Plots (%) – % of total plots; Area (ha) – surface area (ha); Area (%) – % of total surface area; Av_SQ – soil qualities, average; Av_SL – slope gradient (in , from DTM 25 by the Bavarian Geodetic Survey), average; Av_ASP = aspect class (south = 180, east/west = 90, north = 0; from DTM 25 by the Bavarian Geodetic Survey), average – ; Av_SQ_W – soil qualities, average (area weighted); Av_SL_W = slope gradient (in °), average, area weighted; 'Av_ASP_W' – aspect class, average (area weighted)

Table 3. Habitat types and plant communities in the districts of Siegritz, Wuestenstein, and Zochenreuth (nomenclature according to CEC 1991; BfN 2000).

Land use categories	Habitat types	Predominant plant communities
settlements	ruderal vegetation	Sisymbrietea, Polygono-Poetea Artemisietea vulgaris,
orchards	fruit orchards, root crops, ruderal vegetation	Glechometalia hederaceae, Convolvuletalia sepium
arable land	cereal crops, root crops	Veronico-Euphorbion, Caucalidion platycarpi
meadows	fertilized meadows, transitional tall herb humid meadows	Arrhenatherion elatioris, Calthion
rough pastures & wasteland	semi-dry calcareous grasslands rock debris swards, thickets	Bromion erecti, Trifolion medii Alysso-Sedion, Berbe ridion vulgaris
woodland	decidous mixed forests coniferous forests	Fagion sylvaticae, Carpinion betuli Pinetum sylvestris

year, in order to produce winter fodder for the livestock.

Woodlands only made up 18.2% of the total surface in 1850. Most of the wooded areas were located on the shaded western slope of the Aufsess valley and on hillsides too steep for sheep grazing. The less intensive use of these plots may also have been due to their distance from the farmsteads.

Changes from 1850 to 1900

There was little change in land use between 1850 and 1900. The wooded area increased by 1%, marking the beginning of a process that was to assume enormous importance in the following period. The increase mostly took place on former wasteland areas, which were either planted with pine or underwent gradual succession processes.

Changes from 1900 to 1960

There was considerable building activity in the towns during the first half of the 20th century. Settlements increased by several hectares, mostly due to sealing (i.e., paving or extensive construction) on many farmyards and the reclassification of orchards adjacent to homesteads as part of the settled area in the land register. This led to a corresponding decrease in garden plots and adjacent arable land.

Agricultural use declined to less than 50% of the total area with one contributing factor being the cessation of the tillage of marginal soils (Table 1, Table 2). The upper plateau, which had been largely devoid of woods before 1900, acquired a pattern of tilled fields and wooded stands with dolomite outcrops at the center.

We investigated the effect of including the soil quality classes and slope gradients designated in the two oldest 19th century land registers and correlating them to subsequent changes in use (Table 2). The expected general trend towards the less intense use of plots with low fertility was only partly confirmed, particularly in the case of cultivated (tilled) plots. The average fertility of the fields converted to woodlands was somewhat lower than that of the fields remaining under cultivation. The same applies to the rough pastures. One interesting result, however, was that the rare clearing of wooded areas was not strongly related to their fertility, but rather depended on reasons that remain to be identified. An analysis of the slope gradients of plots showed the expected correlation with changes in use, with changes being minor in cultivated plots having little inclination, whereas plots with steep slopes were frequently converted to woodland (Table 1).

The proportion of wooded surface in the districts doubled to about 40% during this time period. In the case of Wuestenstein, for instance, wooded areas increased by 212 hectares in 60 years. In particular, former rough pastures and wastelands were either planted or abandoned, so that this category virtually disappeared except for a small remnant of 2% of the surface area of the landscape. On the plateau, the pattern of the woodlands at this time often followed the linear arrangement of the former wastelands. Woodland areas inside the agricultural sector were rarely planted. Rather, woodland expansion occurred in these locations as a result of natural regeneration along the edges of the ancient wooded plots.

Analysis of the landscape maps and comparisons of the proportions of land use areas does not indicate any changes in the valley meadows. Nevertheless, labor shortages have clearly resulted in less intense use, as evidenced by the decay of the irrigation ditches (Hoffmeister 1966).

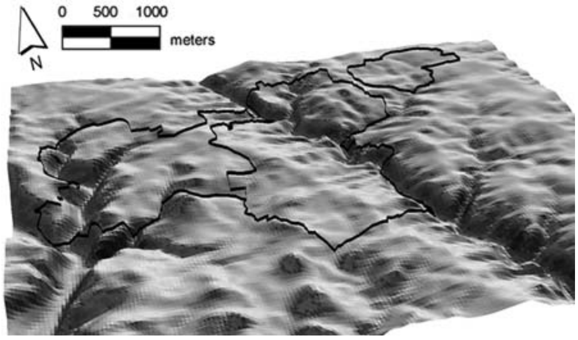

Figure 7. Digital terrain model of topographical map TK 25, sheet 6133 (Muggendrof) showing the district boundaries of the study area. Database: DTM 50 by the Bavarian Geodetic Survey.

Changes from 1960 to 2000

Fewer changes in the landscape were identified for the period of 1960 to 2000 when compared to the preceding period, even though structural transformation continued (Figure 7). Statistically, the principal modifications included an increase in the road network due to extensive construction in the 1960's and a decrease in garden areas (by 11.5 hectares in the Wuestenstein district, 17.7 hectares in the total study area). Town development continued to spill over into the adjacent fields. In some townships, farmyards were even relocated outside of the villages. The manorial villages formerly characterized by part-time farming expanded into the adjacent landscape because of the construction of new houses at the edges of towns during the 1980s and 1990s. A clear delimitation between the village and the fields no longer existed. The settlements and the road network now comprised over 5% of the total area.

In traditional peasant villages, the comparatively large farms now use the adjacent meadows for permanent pasture, providing an outdoor run for cattle otherwise kept in sheds. The livestock industry has become an almost exclusively indoor activity in the course of the period of 1960 to 2000. Its importance can only be assessed by evaluating the agricultural statistics and by analyzing the crops. About 65% of the farms still raise livestock (1999 Agricultural Census). Fodder crops were grown on 25% of the tilled fields in the study area in 1999.

A comparison of the temporal layers for the years 1960 and 2000 shows that the tilled surface has increased somewhat, even at the expense of wooded areas. Apparently, it is more profitable to clear unproductive pine and spruce woods and use them for farming, rather than to replant them with trees. According to a survey, this development is reinforced by a great demand for arable land that cannot be satisfied by additional leases. This trend is likely due to the fact that crop farmers must increase in size in order to remain economically viable until the increment of productivity is used up and farm hands must be hired, although the farmers actually can't afford paying for outside help.

Discussion

Socio-economic changes

Farm size and agricultural production

In 1850, the average size of an agricultural property (a spectrum including small land plots owned by craftsmen and other workers up to small and medium sized farms) was approximately 10 hectares with the largest property having an area of 40 hectares. These plots were primarily used for subsistence farming. As a result, a mixture of agricultural activities was most suitable, including cultivated land, grazing pastures, livestock farming (also for fertilizer production) and specialized crops (e.g., fruits). Private forests of various sizes were often integrated into the agricultural endeavors as well, these making up 70% of the entire forested areas (Weisel 1971).

Since 1850, the landscape has undergone continuous structural changes. Until the end of World War II, the main goal was to increase agricultural production in order to safeguard the availability of food for the growing population. Since the end of the 1960s, the overriding concern has been securing farmer incomes (Henkel 1995). At the same time, the conversion of mixed agricultural ventures to specialized livestock operations (dairy production, beef or pork breeding and production) was implemented. Following the trend toward general motorization and the possibility to commute, a tendency developed toward part-time farming. Over time, these farms gave up livestock farming as a result of the high labor costs. Nevertheless, the high labor burden of whole families secured a continued intensive usage of the pastures, whereby a strong appreciation of agriculture and a strong bond to land ownership is expressed. As a result of a lack of heirs willing to continue farming, it has been a concern that previously cultivated plots will be left fallow (Hümmer 1976). However, farmers willing to increase their holdings have purchased almost all of the fields that have come up for sale as they themselves must expand in order to remain profitable. The purchase of additional lands is limited, however, by increments of productivity because the average farmer cannot afford to hire farmhands.

Cultivation and land conditions

Lands on the upper plateau within the study area are comprised predominantly of cultivated land. Meadows were always scarce in these areas. Around 1850, the arable land that was farmed by using a three-field crop rotation system ('gebundene Dreifelderwirtschaft') was splintered into numerous tiny plots (divided by stone ridges) as a result of the traditional division of family estates among heirs. Crop beds 60–75 cm wide and 25–30 cm high, so-called 'Bifänge', were created from the relatively shallow soil of stony fields. These crop beds were used for growing grains such as rye, barley, and oats with crops yields only exceeding sowings by a factor of two or three (Weisel 1971). Tuber crops and modest feed crops were grown in the proximity to the villages on relatively fertile garden plots, which were not integrated into three-field crop rotation.

Since approximately 1900, efforts were being made to intensify production on the more favorable lands. This resulted in an increase in the production of feed crops. Since the adoption of grass-clover plantings in the beginning of the 1920s, solid feed crop production occurred in this region. This gradually laid the foundation for specialized livestock farming. The current cultivation spectrum encompasses, with the application of fertilizers and pesticides, approximately 50% grains, 25% feed crops, besides predominantly oil crops and corn. In the Agricultural Land Use Management Plan (BayLBA 1986), the cultivated land plots of the upper plateau are classified as 'cultivated locations with favorable production conditions' with subsidized fallow land playing as of yet a minor role (5%) in the region's management.

Land re-allocation and rural development

Due to the irregular block and short strip plots, the district of Siegritz was characterized by different property configurations. The results of the land re-allocation proceedings carried out between 1962 and 1975 were dominated by the agricultural political objective of the largest possible augmentation of production. Requirements for nature and landscape protection were not yet anchored in the general awareness of planners and farmers. Stemming from this situation, it is understandable that small structures such as hedgerows, groves and rocky knolls were destroyed and leveled in order to create field areas with large plots and straight field rows (Hümmer 1986).

In noticeable contradiction to the Siegritz district, the Wuestenstein district still consists of multi-structured forest-field transitions, abundant hedgerows and relatively small land plots. The land re-allocation within the district of Wuestenstein was first arranged in 1988 and will be implemented in the near future. It is bound by very different visions than those common to Siegritz. Nature protection interests were strongly considered; landscape planning is a central component of the procedures. In general, the landscape scenery should be preserved and the biotope composition enhanced. Construction of field rows began in 1998 with the topographical and historical conditions acting as the basic model.

Sheep farming in the Franconian Alb

Slopes of valleys and knolls were best utilized for sheep grazing. As a result of the increasing demand for wool since the Middle Ages, a feudal sheep raising system was established with grazing rights existing on a multitude of local districts. Around 1800, 15 of these manorial sheep farms in the Franconian Alb had arisen each owning on average of 1000 sheep (Weisel 1971). With the dissolving of the feudal grazing rights in the 1900s, the community owned sheep farms previously suppressed by grazing right limitations temporarily flourished (Jacobeit 1961), so that the number of sheep reached its peak around 1850. Afterwards, competition from overseas and the emergence of import tariffs for wool and market sheep at the Paris market all resulted in rapid decline in herd sizes (in Upper Franconia: from 177,000 sheep in 1863 to 78,500 in 1883). Pastures abandoned by community owned sheep farms were taken by wandering shepherds (transhumance) temporarily coming up at the end of the 19th century (Hornberger 1959).

Indeed, the intensification of the agricultural production detracted available land from the already declining sheep farms. The continual decline in the amount of arable farmland since 1850 took place primarily through the abandonment of so-called 'Egerten', plots formerly used in tillage-pasture rotation. Sheep farming was also hindered as a result of the abandonment of fallow (Brachzelgen) in favor of feed crops. Opportunities for grazing on harvested fields were lost because of their rapid mechanical plowing, and the further interference of sheep migration between grazing areas due to increasing traffic and settlement densities. Abandoned pastures and Egerten, which were initially designated as wastelands in the land plot records, became noticeably shrubby.

While the traditional rough pasture grassland has dwindled away from about 15% of the total area of the Franconian Alb to about 1% today (9% to 1% in our study area), sheep farming arrived at its lowest point in the 1960s as many of the herds of the municipality (and other shepherds) were abandoned. In 1967, there were only 8170 sheep left in the northern Franconian Alb. As a result of additional paddock farming, the inventory has since then increased so that in 1994 there were still seven sheep farmers with herds including as many as 500 ewes (1994 Agricultural Census).

Meadow cultivation in the valleys of the Franconian Alb

The history of meadow irrigation in the study area reaches back to the Middle Ages. In the time between 1850 and World War I, the Bavarian law of irrigation enabled an enormous cultural and technical revival, above all through new irrigation co-ops and ever more elaborate irrigation constructions. Reports from the early 20th century show that the irrigation constructions were not in good condition (Hoffmeister 1966). The insufficient work force resulted in the neglect of irrigation systems. Despite this, the majority of farms were still reliant on these irrigation systems in the 1960s. Many small hobby farms required cheap feed for their few livestock. The valley pastures have been farmed almost entirely without irrigation since around 1970. The fields have become generally drier, except in areas with springs where it becomes wet due to the decaying irrigation ditches. Today, the meadows in valleys are classified as land with unfavorable production conditions. Full-time farmers prefer to farm large meadow areas without extensive upkeep costs. The modern part-time farmers often switch from livestock or mixed farming to solely crop production because it is less labor intensive. Nevertheless the use of hay cuts from valley meadows has not ceased. As a result, suitable fields are farmed with intensive application of fertilizers, pesticides and modern machines, while the rest of the land lies fallow and is threatened by afforestation.

Ecological and Conservation Aspects

Agricultural intensification has led to a widespread decline in farmland biodiversity as measured across many different taxa (cf. Benton et al. 2003). The cessation of pasture grazing and the subsequent reforestation have continuously reduced the availability and accessibility of habitats to many species. Today, many of these species have significance for nature conservation in Germany (e.g., Bundesamt für Naturschutz 1998, 2000). Habitat fragmentation entails numerous ecological consequences, such as changes in food availability, obstruction of dispersal pathways, isolation of habitat sectors, segregation of populations, and may reduce areas or population sizes to levels below maintenance thresholds. Finally, it may lead to the extinction of specialized species (cf. Fahrig and Merriam 1994; With and Christ 1995; Kleyer et al. 1996; Jaeger 2002).

We regarded the classes of land cover surveyed in our analysis of landscape change as types of vegetation cover, that constitute habitats for specialized plant species, insects, birds etc. The classifications of settlement, orchard, arable land, meadow, rough pasture, wasteland and woodland in the cadastral register have been assigned to plant communities determined in field surveys (Table 3; cf. Gauckler 1938; Ellenberg 1996). The multitemporal GIS was employed to compare proportions of those habitat types and to assess how, when and why the sizes of the different types have changed.

Rough pastures and wasteland, for instance, have been defined as potential sites of the limestone grassland *Gentiano-Koelerietum pyramidatae* (gentian-hairgrass turf; *Bromion erecti*), which is listed in Bavaria as an endangered plant community (Walentowski et al. 1991). The reduction of rough pastures and wastelands equally represents a loss in potential habitats for vascular plants characteristic of the region's limestone grasslands, e.g., *Koeleria pyramidata, Cirsium acaule, Bromus erectus*, *Phleum phleoides*, *Carex caryophyllea*, *Pimpinella saxifraga*, *Medicago lupulina*, and *Pulsatilla vulgaris*.

The concept of categories of landscape change incorporated into the GIS helped to evaluate these habitat types more precisely. For instance, the categories of change rough pasture / wasteland – woodland – woodland – woodland and rough pasture / wasteland – rough pasture / wasteland – woodland – woodland (Figure 8), which correspond to afforestation in the 1850–1900 and 1900–1960 periods, denote the sparse pinewoods (steppe-heath pine forest; after Gauckler 1938) that have become characteristic of the Franconian Alb. In contrast, the ancient woodlands of the category of change woodland – woodland – woodland – woodland represent mixed beech and hornbeam forests (*Fagion sylvaticae*, *Carpinion betuli*), which are – as a consequence of their continual woodland history and decreasing use – already closely related to the potential natural vegetation.

These analyses facilitate the evaluation of the feasibility and utility of studies of landscape change in the planning of ecosystem restoration. One example is the ability to restore a desirable habitat, such as limestone grassland. It can be determined whether the envisioned aggregate (which may now be shrubs, wooded, or tilled) was formerly a rough pasture, and when the change in use occurred. Historical drove tracks can be accurately reconstructed. As a result, the likelihood of successful restoration of limestone grassland at the site in question can be assessed, since the age of a plots seed bank is of crucial importance for the reestablishment of *Bromion erecti* grasslands (Bonn and Poschlod 1998). The categories of change (Figure 8) thus represent a tool for decision-making and help to determine the effort involved in achieving a desired result in a given area.

According to Wiens (2002), the components of a landscape can be partitioned into features of composition, structure, and processes. In our example, the patches making up the landscape are nearly entirely of anthropogenic origin. This means that the flows of organisms are to a large extent determined by anthropogenic processes, which are driven by anthropogenic mechanisms like mowing, grazing, and forestry (Anand 1994; Boehmer 1997). Current recommendations for biodiversity conservation emphasize the need to conserve multi-scale ecological patterns and processes that sustain the full complement of biota and their supporting ecosystems (cf. Poiani et al. 2000; Turner et al. 2001). If spatial and temporal heterogeneity and complexity are critical elements in this function of ecosystems, then it is important to maintain the mechanisms driving these processes (Anand 1994; Christensen 1997).

Who is driving the processes creating the pattern of cultural landscapes? From an ecological point of view, we understand the patterns of a cultural landscape as a mosaic of patches of different human disturbance regimes (or artificial/anthropogenic disturbance regimes; Pickett and White 1985). The intensity and frequency of any type of land use creates a certain disturbance regime, which disrupts and controls the successional trend in a certain way (Boehmer 1997). Limestone grassland species are dependent upon grazing regimes for their continued existence, species from meadows are dependent on mowing regimes and controlled irrigation, and the pine forests' typical species in our study area are dependent on forest litter extraction. Losses and changes of those land use types cause a lack of typical human disturbance regimes, with a consequent loss of typical mechanisms that create ecosystems supporting specialized biota. Therefore, conservation concepts for anthropogenic plant communities have to consider the benefits of traditional land-use systems, e.g., land-use-rotation for the spatial distribution and maintenance of endangered field weeds (Waldhardt 2003).

The types of land use that are listed in the land register's land plot records help dividing the land plots into different patches by type (including frequency and intensity) and history of use precisely. By using those attribute data, the application of the land-plot based multitemporal GIS facilitates determination and quantification of current and historical disturbance regimes. This provides a useful source of information for conservation purposes and further biodiversity research e.g., on plant functional types in relation to disturbance and land use (cf. Poudevigne and Baudry 2003; Rusch et al. 2003).

Conclusions

A land plot-based multitemporal GIS provides an accurate basis for the analysis of long-term cultural landscape change. This approach can be applied to all areas of Central Europe where continual land-register data have been compiled since the early 19th century (e.g., Germany, Austria). It is advantageous particularly for description and quantification of land use change at the local level. Thus, this method can be employed e.g., to a detailed reconstruction of ancient landscapes, the identification and explanation of human induced processes, and to landscape planning purposes as well. Since cultural landscape change entails serious ecological consequences, such as fragmentation and loss of habitats, specific knowledge about the background of disadvantageous processes is fundamental for the success of nature conservation measures. Particularly conservation concepts for endangered species and

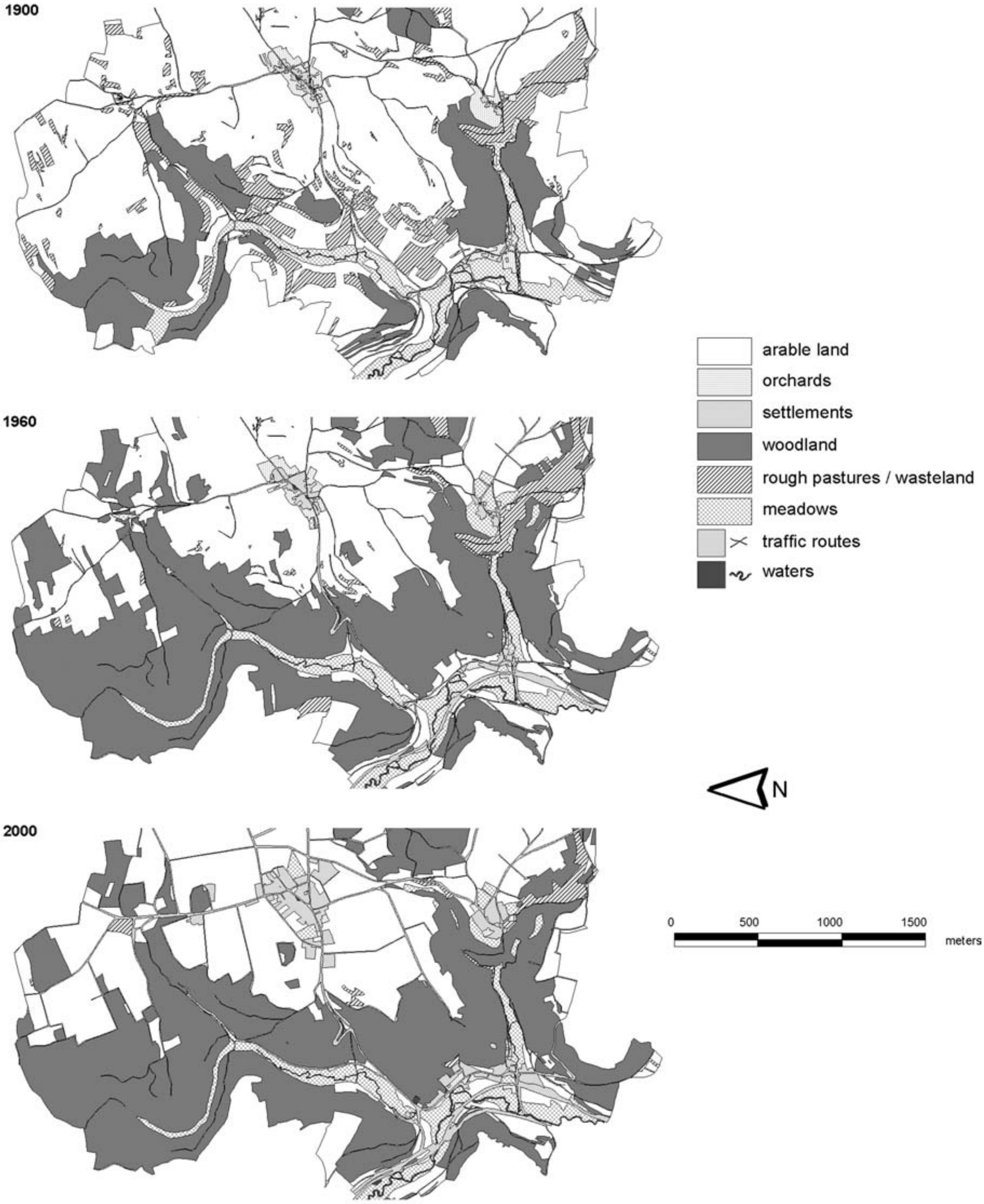

Figure 8. Maps of the distribution of land use categories 1900, 1960, 2000 in the Siegritz district (Franconian Alb).

communities that are supported by traditional land-use systems (e.g., sheep grazing) have to consider the historical distribution of suitable habitats. The land plot-based multitemporal GIS facilitates a precise reconstruction of habitat patterns and human disturbance regimes at any time since 1850.

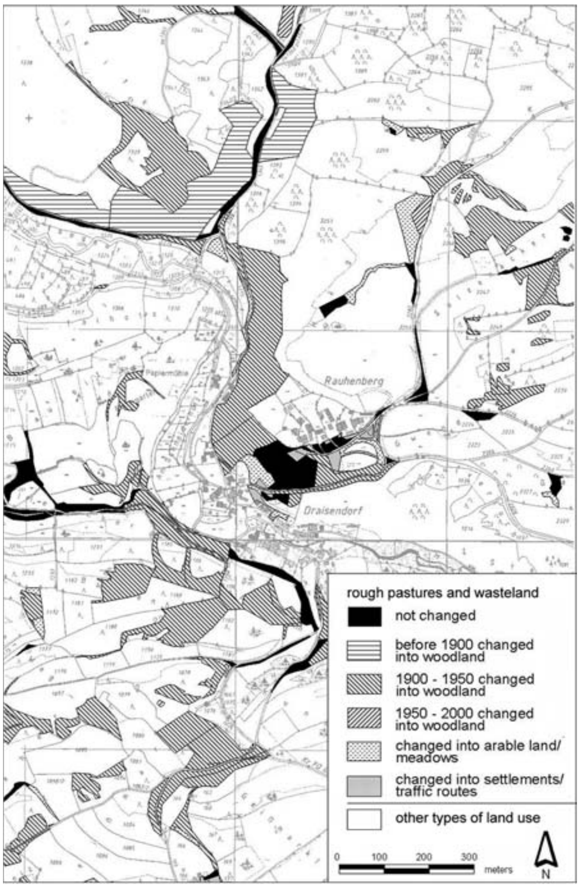

Figure 9. Categories of change in rough pastures and wastelands in the district of Wuestenstein (Franconian Alb).

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References

Anand M. 1994. Pattern, process, and mechanism – The fundamentals of scientific inquiry applied to vegetation science. Coenoses 9: 81–92.

Bayerische Landesanstalt für Betriebswirtschaft und Agrarstruktur (BayLBA; ed.) 1986. Agrarleitplan für den Regierungsbezirk Oberfranken. München, Germany.

Bender O., Boehmer H.J., Jens D. and Schumacher K.P.2005. Using GIS to analyse 200 years of cultural landscape change in Southern Germany. Landscape and Urban Planning.70: 111–125.

Benton T.G., Vickery J.A. and Wilson J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology and Evolution 18: 182–188.

Boehmer H.J. 1994. Die Halbtrockenrasen der Fränkischen Alb – Strukturen, Prozesse, Erhaltung. Mitteilungen der Fränkischen Geographischen Gesellschaft 41: 323–343.

Boehmer H.J. 1997. Zur Problematik des Mosaik-Zyklus-Begriffes. Natur und Landschaft 72: 333–338.

Bonn S. and Poschlod P. 1988. Ausbreitungsbiologie der Pflanzen Mitteleuropas. Quelle and Meyer, Wiesbaden, Germany.

Bundesamt für Naturschutz (ed.) 1988. Rote Liste gefährdeter Tiere Deutschlands. Schriftenreihe für Landschaftspflege und Naturschutz 55. Landwirtschaftsverlag, Münster, Germany.

Bundesamt für Naturschutz (BfN; ed.) 2000. Verzeichnis und Rote Liste der Pflanzengesellschaften Deutschlands. Schriftenreihe für Vegetationskunde 35. Landwirtschaftsverlag, Münster, Germany.

Christensen N.L. 1997. Managing for Heterogeneity and Complexity on Dynamic Landscape. In: Pickett S.T.A., Ostfeld R.S., Shachak M. and Likens G.E. (eds), The Ecological Basis of Conservation. Heterogeneity, Ecosystems, and Biodiversity. Chapman and Hall, New York, New York USA, pp. 167–186.

Commission of the European Communities (CEC; ed.) 1991. CORINE biotopes manual. Habitats of the European Community. Office for Official Publications of the European Communities, Luxembourg.

Cousins S.A.O. 2001. Analysis of land-cover transitions based on 17th and 18th century cadastral maps and aerial photographs. Landscape Ecology 16: 41–54.

Cousins S.A.O., Eriksson A. and Franzén D. 2002. Reconstructing past land use and vegetation patterns using palaeogeographical and archaeological data: A focus on grasslands in Nynäs by the Baltic Sea in south-eastern Sweden. Landscape and Urban Planning 61: 1–18.

Ellenberg H. 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer Sicht. Ulmer, Stuttgart, Germany.

Fahrig L. and Merriam G. 1994. Conservation of fragmented populations. Conservation Biology 8: 50–59.

Forman R.T.T. and Godron M. 1986. Landscape Ecology. Wiley, New York, New York USA.

Gauckler K. 1938. Steppenheide und Steppenheidewald der Fränkischen Alb in pflanzensoziologischer und geographischer Betrachtung. Berichte der Bayerischen Botanischen Gesellschaft 23. Munich, Germany.

Gordon D.R., Provencher L. and Hardesty J.L. 1995. Measurement Scales and Ecosystem Management. In: Pickett S.T.A., Ostfeld R.S., Shachak M. and Likens G.E. (eds), The Ecological Basis of Conservation. Heterogeneity, Ecosystems, and Biodiversity. Chapman and Hall, New York, New York USA, pp. 262–273.

Gutzwiller K.J. 2002. Using Broad-Scale Ecological Information in Conservation Planning. In: Gutzwiller K.J. (ed.), Applying Landscape Ecology in Biological Conservation. Springer, New York, New York USA, pp. 357–359.

Hanski I. 1999. Metapopulation Ecology. Oxford Univ. Press, Oxford, UK.
Heider J. 1954. Das bayerische Kataster. Geschichte, Inhalt und Auswertung der rentamtlichen Kataster, Lager- und Grundbücher in Bayern sowie der zugehörigen Flurkarten. München-Pasing, Bayerische Heimatforschung 8. Germany.
Henkel G. 1995. Der Ländliche Raum. Teubner, Stuttgart, Germany.
Hoffmeister S. 1966. Über Bewässerungswiesen im Einzugsgebiet der Wiesent von Forchheim bis Streitberg. MA Thesis, Department of Geography, University of Erlangen, Erlangen, Germany.
Hohenester A. 1989. Zur Flora and Vegetation der Fränkischen Alb. In: Tichy F. and Gömmel R. (eds), Die Fränkische Alb. Neustadt a.d. A., Schriften des Zentralinstituts für fränkische Landeskunde und allgemeine Regionalforschung an der Universität Erlangen-Nürnberg. Germany, pp. 77–94.
Hornberger T. 1959. Die kulturgeographische Bedeutung der Wanderschäferei in Süddeutschland. Remagen, Forschungen zur deutschen Landeskunde 109, Germany.
Houghton R.A. 1994. A worldwide extent of land-use change. BioScience 44: 305–313.
Hümmer P. 1976. Soziale Entwicklungen und ihre räumlichen Auswirkungen im Agrarbereich erläutert an einem Beispiel aus der nördlichen Fränkischen Alb. Mitteilungen der Fränkischen Geographischen Gesellschaft 21/22: 527–535.
Hümmer P. 1986. Flurbereinigungsverfahren in Franken. Fallbeispiele im Vergleich. In: Hopfinger H. (ed.), Franken – Planung für eine bessere Zukunft? Ein Führer zu Projekten der Raumplanung. Carl, Nürnberg, Germany, pp. 285–310.
Jacobeit W. 1961. Schafhaltung und Schäfer in Zentraleuropa bis zum Beginn des 20. Jahrhunderts. Berlin, Veröffentlichungen des Instituts für deutsche Volkskunde 25, Germany.
Jaeger J. 2002. Landschaftszerschneidung: eine transdisziplinäre Studie gemaß dem Konzept der Umweltgefährdung. Umweltgefährdung, Ulmer, Stuttgart, Germany.
Jedicke E. 1998. Raum-Zeit-Dynamik in Ökosystemen und Landschaften. Naturschutz und Landschaftsplanung 30: 229–236.
Kleyer M., Kaule G. and Settele J. 1996. Landscape Fragmentation and Landscape Planning, with a Focus on Germany. In: Settele J., Margules C., Poschlod P., Henle K. (eds), Species Survival in Fragmented Landscapes. Kluwer, Dordrecht, The Netherlands, pp. 138–151.
Lamarche H. and Romane F. 1982. Analyse landschaftlicher Veränderungen aufgrund sozioökonomischer und ökologischer Kriterien am Beispel einer südfranzösischen Gemeinde. Natur und Landschaft 57 (12): 458–464.
Lambeck R.J. and Hobbs R.J. 2002. Landscape and Regional Planning for Conservation: Issues and Practicalities. In: Gutzwiller K.J. (ed.), Applying Landscape Ecology in Biological Conservation. Springer, New York, New York USA, pp. 360–380.
McLure J.T. and Griffiths G.H. 2002. Historic Landscape Reconstruction and Visualisation, West Oxfordshire, England. Transactions in GIS 6: 69–78.
Messner R. (ed.) 1967. 150 Jahre österreichischer Grundkataster 1817–1967. Ausstellungskatalog. Bundesamt für Eich- und Vermessungswesen, Wien, Austria.
Mueller-Dombois D. and Ellenberg H. 2002. Aims and Methods of Vegetation Ecology. The Blackburn Press, Caldwell, New Jersey, USA.
Oldfield F., Dearing J.A., Gaillard M.-J. and Bugmann H. 2000. Ecosystem processes and human dimensions – The scope and future of HITE (Human Impacts on Terrestrial Ecosystems). PAGES Newsletter 8: 21–23.
Olsson E.G.A., Austrheim G. and Grenne S.N. 2000. Landscape change patterns in mountains, land use and environmental diversity, Mid-Norway 1960-1993. Landscape Ecology 15: 155–170.
Pärtel M., Mändla R. and Zobel M. 1999. Landscape history of a calcareous (alvar) grassland in Hanila, western Estonia, during the last three hundred years. Landscape Ecology 14: 187–196.
Petit C.C. and Lambin E.F. 2002. Impact of data integration technique on historical landuse/land-cover change: Comparing historical maps with remote sensing data in the Belgian Ardennes. Landscape Ecology 17: 117–132.
Pickett S.T.A. and White P.S. (eds) 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego, California, USA.
Poiani K.A., Richter B.D., Anderson M.G. and Richter H.E. 2000. Biodiversity Conservation at Multiple Scales: Functional Sites, Landscapes, and Networks. Bioscience 50: 133–146.
Poudevigne I. and Baudry J. 2003. The implication of past and present landscape patterns for biodiversity research: introduction and overview. Landscape Ecology 18: 223–225.
Reid R.S., Kruska R.L., Muthui N., Taye A., Wotton S. and Wilson C.J. 2000. Land-use and land-cover dynamics in response to changes in climatic, biological and socio-political forces: the case of southwestern Ethiopia. Landscape Ecology 15: 339–355.
Riebsame W.E., Parton W.J., Galvin K.A., Burke I.C., Bohren L., Young R. and Knop E. 1994. Integrated modelling of land use and cover change. BioScience 44: 350–356.
Roweck H. 1995. Landschaftsentwicklung über Leitbilder? Kritische Gedanken zur Suche nach Leitbildern für die Kulturlandschaft von morgen. LÖBF-Mitteilungen 20: 25–34.
Rusch G.M., Pausas J.G. and Leps J. 2003. Plant Functional Types in relation to disturbance and land use: Introduction. Journal of Vegetation Science 14: 307–310.
Sporrong U. 1998. Dalecarlia in central Sweden before 1800: a society of social stability and ecological resilience. In: Berkes F. and Folke C. (eds), Linking Social and Ecological Systems. Management practices and social mechanisms for building resilience. Cambridge University Press, Cambridge, UK, pp. 67–94.
Turner M.G., Gardner R.H. and O'Neill R.V. 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer, New York, New York, USA.
Urban D.L., O'Neill R.V. and Shugart H.H. 1987. Landscape Ecology. BioScience 37: 119–127.
Verheyen K., Bossuyt B., Hermy M. and Tack G. 1999. The land use history of a mixed hardwood forest in western Belgium and its relationship with chemical soil characteristics. Journal of Biogeography 26: 1115–1128.
von Haaren C. 2002. Landscape planning facing the challenge of the development of cultural landscapes. Landscape and Urban Planning 60: 73–80.
Wagner H. 1950. Die Entwicklung des Katasters in Württemberg. Stuttgart, Innenministerium Württemberg-Baden, Germany.
Waldhardt R. 2003. Die Bedeutung von Landnutzungsdynamik für die Vielfalt der Ackerwildkrautflora in einer peripheren Kulturlandschaft. Nova Acta Leopoldina NF, Nr. 328: 237–247.
Walentowski H., Raab B. and Zahlheimer W.A. 1991. Vorläufige Rote Liste der in Bayern nachgewiesenen oder zu erwartenden Pflanzengesellschaften. Band 2. München, Berichte der Bayerischen Botanischen Gesellschaft 62, Germany.

Weisel H. 1971. Die Bewaldung der nördlichen Frankenalb. Ihre Veränderungen seit der Mitte des 19. Jahrhunderts. Erlangen, Erlanger Geographische Arbeiten 28, Germany.
Wiens J.A. 2002. Central Concepts and Issues of Landscape Ecology. In: Gutzwiller K.J. (ed.), Applying Landscape Ecology in Biological Conservation. Springer, New York, New York, USA, pp. 3–21.
With K.A. and Christ T.O. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446–2459.