Quartär 67 (2020): 85-103

Geomorphological Diversity and Habitat Variability. A Model of Late Palaeolithic Catchment Composition in Northern Bavaria

Geomorphologische Diversität und Habitatvariabilität. Ein Modell der spätpaläolithischen Catchment in Nordbayern

Florian Sauer[1]* & Thorsten Uthmeier[2]

[1] Collaborative Research Centre 806 "Our Way to Europe", Universität zu Köln, Bernhard-Feilchenfeld-Str. 11, 50969 Köln, Germany; ORCID: 0000-0001-9687-4762; email: florian.sauer@uni-koeln.de
[2] Institut für Ur- und Frühgeschichte, Friedrich-Alexander-Universität Erlangen-Nürnberg, Kochstraße 4, 91054 Erlangen, Germany; ORCID: 0000-0003-1265-061X; email: thorsten.uthmeier@fau.de

Abstract - Due to the lack of adequate data, the environmental and bioeconomic framework of archaeological sites often cannot be investigated. This situation is visible with the Late Palaeolithic in Southern Germany, which is typically represented by surface collections that do not provide ecological information. In this paper, we analyse the topographic composition of site-catchments of Late Palaeolithic sites in Northern Bavaria (Germany). We use a geomorphology-driven approach, which employs the close relationship between local topography and abiotic conditions relevant to plant growth. This way it is possible to model potential regional physiotope diversity and habitat patterning. This methodology allows the analysis of site-environment relationships in cases, when traditional proxies, like palynological or faunal data are lacking or do not provide an adequate spatial extent and resolution. In this paper, site catchment analysis and physiotope diversity estimation for Late Palaeolithic sites in the study area highlight the relevance of relatively specialized landscapes, which provide comparably wet conditions. This indicates the focus of Late Glacial foragers on the exploitation on bioresources associated with wetland and floodplain environments in the study area.

***Zusammenfassung -** Aufgrund der schlechten Verfügbarkeit von Informationsträgern zur prähistorischen Umwelt ist es oftmals schwierig, den ökologischen Kontext und die bioökonomischen Rahmenbedingungen archäologischer Fundstellen zu untersuchen. Besonders deutlich wird diese Situation beispielsweise im Spätpaläolithikum des süddeutschen Raumes. Hier existieren zwar zahlreiche spätpaläolithische Oberflächenaufsammlungen mit zum Teil äußersten hohem Fundaufkommen, diese sind jedoch kaum mit paläoökologischen Informationsträgern assoziiert. In diesem Artikel präsentieren wir die Analyse der spätpaläolithischen Fundstellen im nordbayerischen Raum mittels eines Models, das die topographische Zusammensetzung der Fundstellenumgebung als Indikator für biologische Diversität nutzt. Hierbei wird der enge Zusammenhang zwischen der Geomorphologie und den für das Pflanzenwachstum relevanten abiotischen Umweltbedingungen quantifiziert, um damit die potentielle Nischenvariabilität für Tiere und Pflanzen zu modellieren. Das Modell bietet die Möglichkeit ein Flächenmodell der Rahmenbedingungen zu erstellen und auf diese Weise auch die Veränderung der Bedingungen im Raum zu analysieren. Das Modell wurde mittels geostatistischer Methoden, basierend auf einem Landschaftsmodell des Arbeitsgebietes erstellt. Durch die Berechnung des Topographischen Positionsindex' können morphologisch diskrete Landschaftselemente – Landformen – eingegrenzt werden. Als Resultat kann für die spätpaläolithischen Fundstellen im Arbeitsgebiet zusammengefasst werden, dass eine Bevorzugung von topographisch relativ geringdiversitären Landschaften mit einem Fokus auf feuchtigkeitsaffine Landformen zu erkennen ist.*

Keywords - Late Palaeolithic, geomorphology, environmental modelling, biodiversity, catchment analysis, land use pattern
Spätpaläolithikum, Geomorphologie, Umweltmodellierung, Biodiversität, Catchment Analyse, Landnutzungsmuster

Introduction

The interaction between groups of mobile foragers and the resource-opportunities in the landscape surrounding their sites is central to understanding Palaeolithic hunter-gatherers. On the one hand, this issue has been investigated intensively concerning lithic raw materials (Weißmüller 1995; Floss 1994; Burkert & Floss 2006; Sauer 2016). On the other hand, the research into the exploitation of organic resources by hunter-gatherers is often hampered by insufficient preservation of data carriers. In particular, this holds

---

*corresponding author

This article contains supporting information online at: https://quartaer.obermaier-gesellschaft.de/downloads

true for proxies of local environmental patterning and variability. Furthermore, they typically reflect local conditions and do not provide a comprehensive idea of the regional environmental structuring.

In the project "GIS-based Reconstructions of Late Palaeolithic Land Use Patterns in the North-eastern Bavarian Low Mountain Range", funded by the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG), the focus lay on sites of the arch-backed point technocomplex (ABP; Valde-Nowak et al. 2012) covering the Allerød-Interstadial and the Younger Dryas stadial. The term "Arch-backed point" technocomplex is here preferred over the often-used *Federmessergruppen*. As demonstrated by Sauer and Riede (2019), the taxonomic ambiguity of the *Federmessergruppen* promotes a notion of regionalisation which is not supported by the archaeological record.

In the study area between the rivers of Danube and Main, ABP sites are usually surface find scatters, collected by avocational archaeologists since the 1960s (Schönweiß & Sticht 1968; Schönweiß 1974; Werner & Schönweiß 1974; Schönweiß 1982, 1989, 1992, 1993, 1997a, 1997b; Süß & Thomann 2009). The small number of excavated sites were primarily investigated in the early 20th century and did not produce sufficient environmental data to adequately describe the surrounding ecological conditions (Hörmann 1913; Gumpert 1933; Tourneau 1933). Since then, only limited research has been conducted in the area (Kaulich 2003, 2004, 2005; an overview can be found with Beck et al. 2009). The research history in the study area led to a plethora of sites lacking associated palaeoenvironmental proxies. Furthermore, the study area yields relatively few palynological samples dating to the Late Glacial Interstadial Complex. This is contrasted by neighbouring core regions, where intensive research on the Late Palaeolithic has been conducted in the last decades. Among others, these are the Neuwied Basin in the Middle Rhine area (Bolus 1992; Baales et al. 1996; Baales 1999, 2001, 2002; Kegler 2002; Bosinski 2007, 2008; Heinen 2008; Gelhausen 2011) the Federsee in Baden-Württemberg (Eberhardt et al. 1987; Jochim 1998; Jochim et al. 1999) and different regions in Bohemia and Moravia (Moník & Pankowská 2020).

In this paper, we employ a modelling-approach that uses physiographic plant geography (PPG) as an indicator of local habitat variability. PPG addresses the close relationship between geomorphology and abiotic environmental factors paramount to biocoenosis (Möbius 1877: 76 - biocoenosis: organisms living and interacting in a habitat and are mutually dependent (e.g. physiotope); phytocoenosis: Plant society inhabiting a specific habitational unit and determined by the prevailing abiotic conditions (e.g. physiotope); zoocoenosis: Faunal society inhabiting a specific habitational unit and determined by the prevailing biotic and abiotic conditions (e.g. physiotope)) distribution (Swanson et al. 1988; Burnett et al. 1998; Zimmermann & Thom 1982). Local biodiversity and environmental patterning are factors, which rarely are subject to investigation in the context of hunter-gatherers (e.g. Parkington et al. 1980; Tallavaara et al. 2018). This can be traced back to the often-problematic preservation of palaeoenvironmental proxies capable of describing local patterns and variability. Their importance to general food procurement and risk management by foragers in different environments is a fundamental element of "optimal foraging theory" (Pyke 1984; Zipf 2012). The significance of biodiversity, particularly in mid- and high latitude environments, has also been stressed quite recently by Tallavaara et al. (2018).

The goal of the overarching DFG-project mentioned above was the analysis of the land-use patterns during the Late Palaeolithic in the Bavarian Central Uplands in Germany. On the regional scale, the numerous sites in this region have never been subject to archaeological investigation. By analysing the Late Palaeolithic site distribution on different levels, it was possible to bring this region to the archaeological discussion (Sauer 2018).

During most of the Upper Palaeolithic, the area under investigation (Fig. 1: a) is – to the current state of archaeological knowledge – uninhabited. Regionally, the Magdalenian site distribution is tethered to the southern escarpments of the Central Uplands (Maier 2015). Only with the beginning of the Late Glacial expansion of the ABP-technocomplex into the Central Uplands can we see an Upper Palaeolithic use of this region and – simultaneously – the access of a different environment, both ecologically and geomorphologically.

In a comprehensive analysis of land-use and settlement patterns (Sauer 2018) the sites were analysed with regards to:

1. Settlement pattern (general spatial characteristics of site-location)
2. Land-use pattern (spatial characteristics of the accessible catchments of the individual sites)
3. Raw material use (analysis of raw material variability and transportation)
4. Techno-typological attribute analysis (assemblage attribute analysis).

While the analysis of the raw material use in the study area was previously discussed in this journal (Sauer 2016), in this paper we aim to elaborate on our investigations regarding the geomorphological conditions within the accessible areas of the individual sites and present the results.

Material and Methods

The area under investigation is composed by five third-order environmental landscape units: the Keuper-Lias-Land, the Franconian Alb, the Upper Palatinate Valley, the Franconian Thuringian Uplands and the Upper

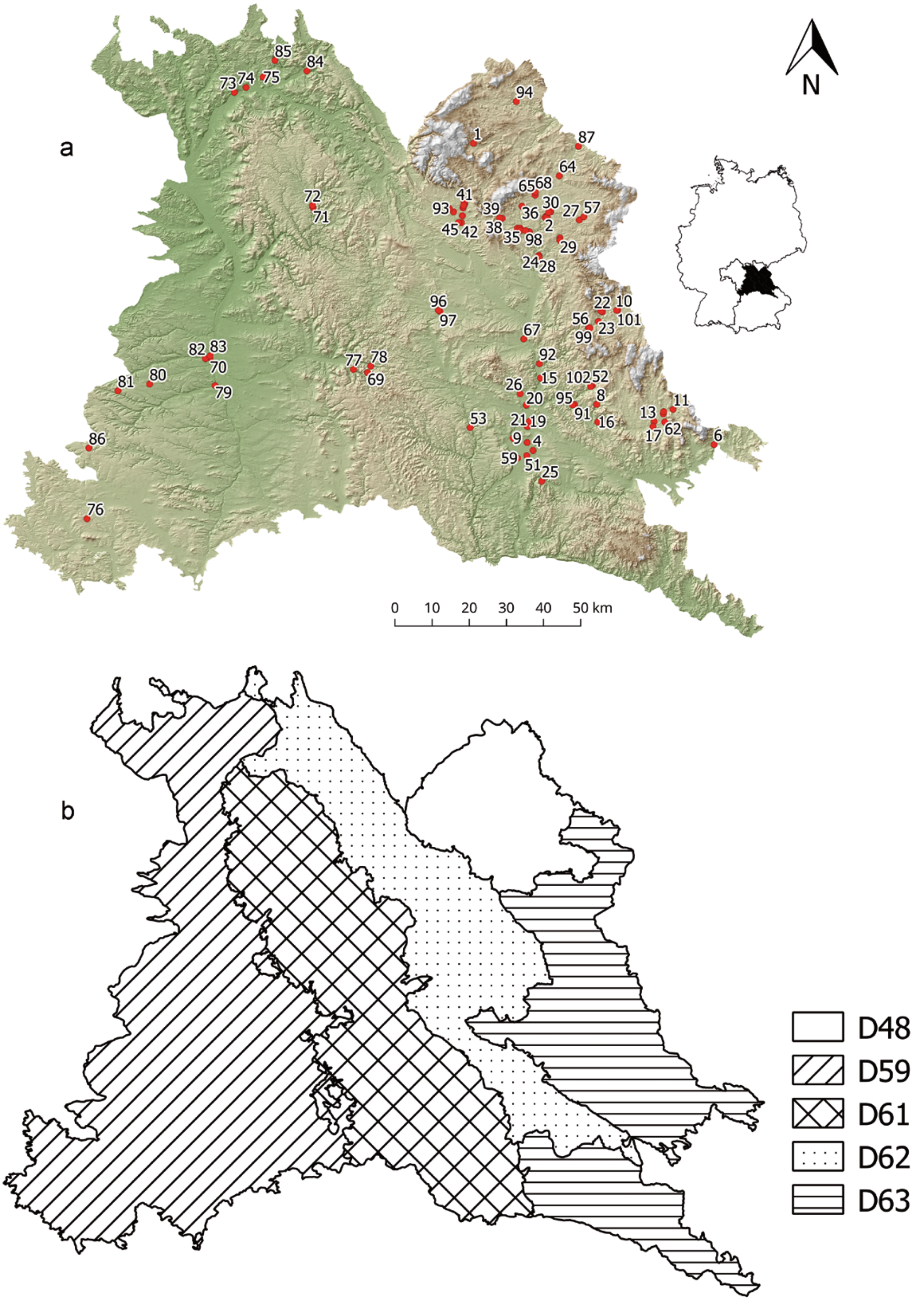

Fig. 1. Study area in Northern Bavaria and environmental subdivision: (a) Distribution of sites used in this case study. A comprehensive list of sites with WGS84 coordinates is enclosed in the supplementary data table (SI14). The insert shows the location of the study area in Germany; (b) D48: Franconian Thuringian Range, D59: Keuper Lias Land, D61: Franconian Alb, D62: Upper Palatinate Valley D63: Upper Palatinate Forest (Geodata: GADM – Global Administrative Areas, Naturräumliche Gliederung Bayerns – Bayerisches Landesamt für Umwelt).

Abb. 1. *Arbeitsgebiet in Nordbayern und die Naturräumliche Gliederung: (a) Verteilung der in dieser Fallstudie genutzten Fundstellen. Eine vollständige Liste der Fundplätze mit WGS 84 Koordinaten befindet sich in der Zusatzdatentabelle (SI 14). Die kleine Zusatzkarte zeigt die Lage des Arbeitsgebietes in Deutschland; (b) D48: Fränkisch-Thüringisches Mittelgebirge, D59: Keuper Lias Land, D61: Fränkische Alb, D62: Oberpfälzer Hügelland D63: Oberpfälzer Wald (Geodaten: GADM – Global Administrative Areas, Naturräumliche Gliederung Bayerns – Bayerisches Landesamt für Umwelt).*

Palatinate Forest (Meynen et al. 1962a; Meynen et al. 1962b). These units provide an analytical subdivision of the study area, which will be maintained in the geostatistical analysis of the topographical makeup (see also Mischka 2007).

94 sites (Fig. 1: a) assigned to the ABP technocomplex are known in this area, but only three of these are excavated locations, which were investigated in the early 20th century (Steinbergwand b. Ensdorf: Hörmann 1913; Gumpert 1933; Pottenstein: Tourneau 1933; Hohler Fels b. Happurg: Kaulich 1996). Traditionally, these sites were assigned to the "Atzenhof group", however, this subcultural classification is only of research-historical interest today (Schönweiß 1974, 1992; Ikinger 1998; Beck et al. 2009; Sauer & Riede 2019). Sufficient stratigraphic information is not available for any of the excavated locations. Therefore, the excavated sites do not provide more detailed information than the surface collections, which probably represent multiple occupations. This is also indicated by the raw material use (Sauer 2016, 2018). Several sites contain raw materials from opposite directions (e.g. Danube-area and North-German Lowlands). Among the available archaeological assemblages mostly relatively large lithic scatters (>200 pieces) were included in the dataset. Single finds and very small find scatters were not included, since their attribution to the Late Palaeolithic is not robust. Including the potential functional variability of assemblages in this study would be pertinent for understanding the interaction of foragers with the landscape surrounding their sites. However, the shortcomings of surface collections have led us to exclude the analysis of assemblage-composition in this study and solely investigate the location in relation to the surrounding topographic conditions.

In the context of settlement pattern analysis (see introduction), the general locational characteristics of the sites were examined. It showed that most of the Late Palaeolithic sites were placed relatively close to the major river courses with a southern and south-western orientation and a preferential settlement of moderate slopes (for a comprehensive analysis of the locational characteristics see Sauer 2018). This also indicates that deposition of Holocene sediments has not influenced site visibility on a large scale, which is also demonstrated by the location of sites like the Late Palaeolithic open-air sites of Sarching (Heinen 2005) or Oberweiherhaus (Sauer 2018), the Magdalenian site of Barbing (Geyer 2013) or the Gravettian site of Salching (Weißmüller 1987) near to the recent floodplain.

Prior to modelling, all sites were evaluated regarding their typological assignment to the ABP complex (based on the information provided by the Bavarian heritage administration) and the admixture of diagnostic tools of other time phases, particularly from the Mesolithic (Sauer 2018). Arch-backed points were seen as an unequivocal proxy of a Late Palaeolithic occupation. Furthermore, backed bladelets, burins on end-retouch and end-scrapers made on medium-sized flakes (length ~25 mm) are valid indicators as they typically accompany ABP assemblages (e.g. Bolus 1992; Baales 2002; Kegler 2002). The raw material composition shows long distance movements between the Danube Basin, Bohemia and the Flint Line (The southernmost transportation of glacially moved Baltic flints) in the North German Plain (Sauer 2016).

The range of the Franconian Alb represents the centre of the study area (Fig. 1: b. D61). It is a Jurassic ridge characterized by expressed geomorphological heterogeneity with extended high plains interrupted by steep canyons. Adjacent to the west lie the lowlands of the Upper Triassic Keuper-Lias Land (Fig. 1: b. D59), which is an area of low morphological variance. It is primarily composed of reworked alluvial terraces. A comparable situation becomes apparent to the East of the Franconian Alb. Here, the Upper Palatinate Valley (Fig. 1: b. D62; Middle and Upper Triassic) receives the runoff water provided by the Alb, the highlands of the Franconian Thuringian Range (Fig. 1: b. D48; Silur) and the Upper Palatinate Forest (Fig. 1: b. D63). The Upper Palatinate Forest's geology is composed of the crystalline basement, where limited erosivity of the metamorphic bedrock (mostly gneiss and granite) leads to a smaller amplitude in morphology as opposed to the Jurassic limestone of the Alb. One result is a great number of small river-valleys in the Upper Palatinate Forest, while a small number of comparably large channels drains the Franconian Alb.

As it is often the case in landscape archaeological investigations, the distribution of Late Palaeolithic locations in the study area is biased by different factors. Among these, surveyor activity and modern land use can be considered the most influential to the modern distribution pattern. Research traditions led to a greater number of known surface collections in the east of the study area (Upper Palatinate Forest). We respond to this skewed distribution pattern by a two-tracked data analysis: The results will be evaluated with regard to (1) the entire study area as well as (2) the five individual environmental landscape units.

Palaeoenvironmental Data

The available palynological dataset is not directly related to archaeology and mostly tied to the highland areas of the Upper Palatinate Forest and the Danube Basin (Stalling 1987; Knipping 1989; Hahne 1991; Hahne 1992; Kortfunke 1992; Küster 1992). During the Allerød-Interstadial (Fig. 2), the area of interest was covered by a dense pine-birch forest dominated by *Betula*. With the advent of the Younger Dryas (Fig. 2), the frequencies of *Pinus* increase slightly, but no major change in vegetation is indicated (Frenzel 1983). Only in the subalpine and alpine regions in Southern Bavaria, more expressed vegetational changes have been observed (Lang 1962; Schmeidl

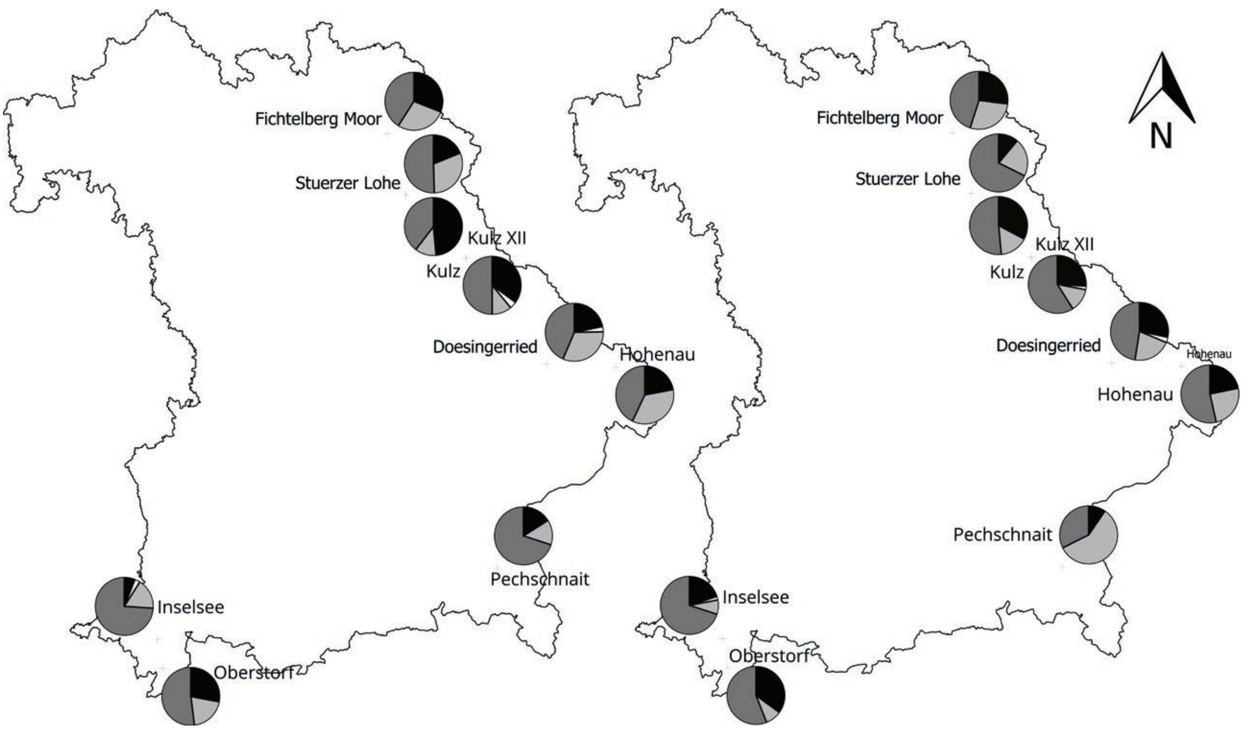

Fig. 2. Palaeovegetational setup of Bavaria in the Allerød-Interstadial, left; Palaeovegetational setup of Bavaria on the Younger Dryas stadial, right (image from: Sauer 2018); black: weeds, dark grey: pine (*Pinus*), light grey: birch (*Betula*), white: willow (*Salix*).

Abb. 2. *Paläovegetation in Bayern während des Allerød-Interstadials, links; Paläovegetation in Bayern während der Jüngeren Dryas, rechts (Bildquelle: Sauer 2018); schwarz: Gräser, dunkelgrau: Kiefer (Pinus), hellgrau: Birke (Betula), weiß: Weide (Salix).*

1971; Küster 1992; Stojakowits et al. 2014). Archaeological sites providing palynological or archaeozoological information directly related to Late Palaeolithic layers are not present in the study area. The ABP layer D of the site of Zigeunerfels (Sigmaringen) in Baden-Württemberg west of the study area reflects a more continental climate with a mean annual temperature of only 3.7-4.0 °C and an annual precipitation of 542 to 619 mm. Both values are considerably lower than today (Fahlke 2009: 92f).

Theoretical Framework

Given the absence of palaeoenvironmental data for the numerous ABP sites in the study area, a different approach was explored to provide information on the potential bioresources in the catchments of the various sites. The methodology is based on the close relationship between landscape morphology and the abiotic factors that are paramount for the presence and growth of different plant communities (plant community: phytocoenosis; Neef 1968; Zimmermann & Thom 1982; Swanson et al. 1988; Parker & Bendix 1996; Burnett et al. 1998; Kratochwil 1999; Schwabe 1999; MacMillan & Shary 2009; Barka et al. 2011; Hobohm 2011; Sauer 2018, 2020). It is best circumscribed by 'Thienemann's first basic principle on biocoenoses', which states: "*The more variable the environmental conditions of a habitat complex, the larger the number of its coenoses/synusia*" (Hiltermann 1982; Kratochwil 1999: 20; Smith & Smith 2009: 445).

The variability of environmental conditions relates to the variability of topography. Landscape morphology is a major driver of abiotic gradients, like the distribution of surface water, solar radiation and disturbance factors (wind, fire etc.). Also, lithological and pedological properties are profoundly influenced by the local topography (Guisan & Zimmermann 2000: Fig. 3). Since plants and plant-societies are not distributed randomly, but rather associated with the specific needs of the respective phytocoenosis (Schwabe 1999: 101), the heterogeneity of vegetation is determined by, among other factors, the region's variation in topography, given equal large scale climatic conditions (Zimmermann & Thom 1982: 47; Hunter et al. 1988: 376ff ; Schwabe 1999: 79). Highly variable topography provides a multitude of different physiotopes (Physiotope: Spatial unnit of relatively homogenousgeomorphic properties which determine interactions between abiotic (e.g. wetness) and biotic (e.g. plant cover) components; Schwabe 1999: 101), which in turn can generate a great variety of phyto- and zoocoenoses. Conversely, morphologically uniform landscapes will result in relatively low levels of geomorphologically controlled biodiversity, since growth conditions are similar throughout the entire region (Schaefer 1999: 52-54). Consequently, in this article physiotopes are understood as "*topographical unit[s] in which […] certain definable and often homogeneous stable conditions […] prevail*" (Schwabe 1999: 79; also: Neef 1981) and therefore are considered to be "*plot*

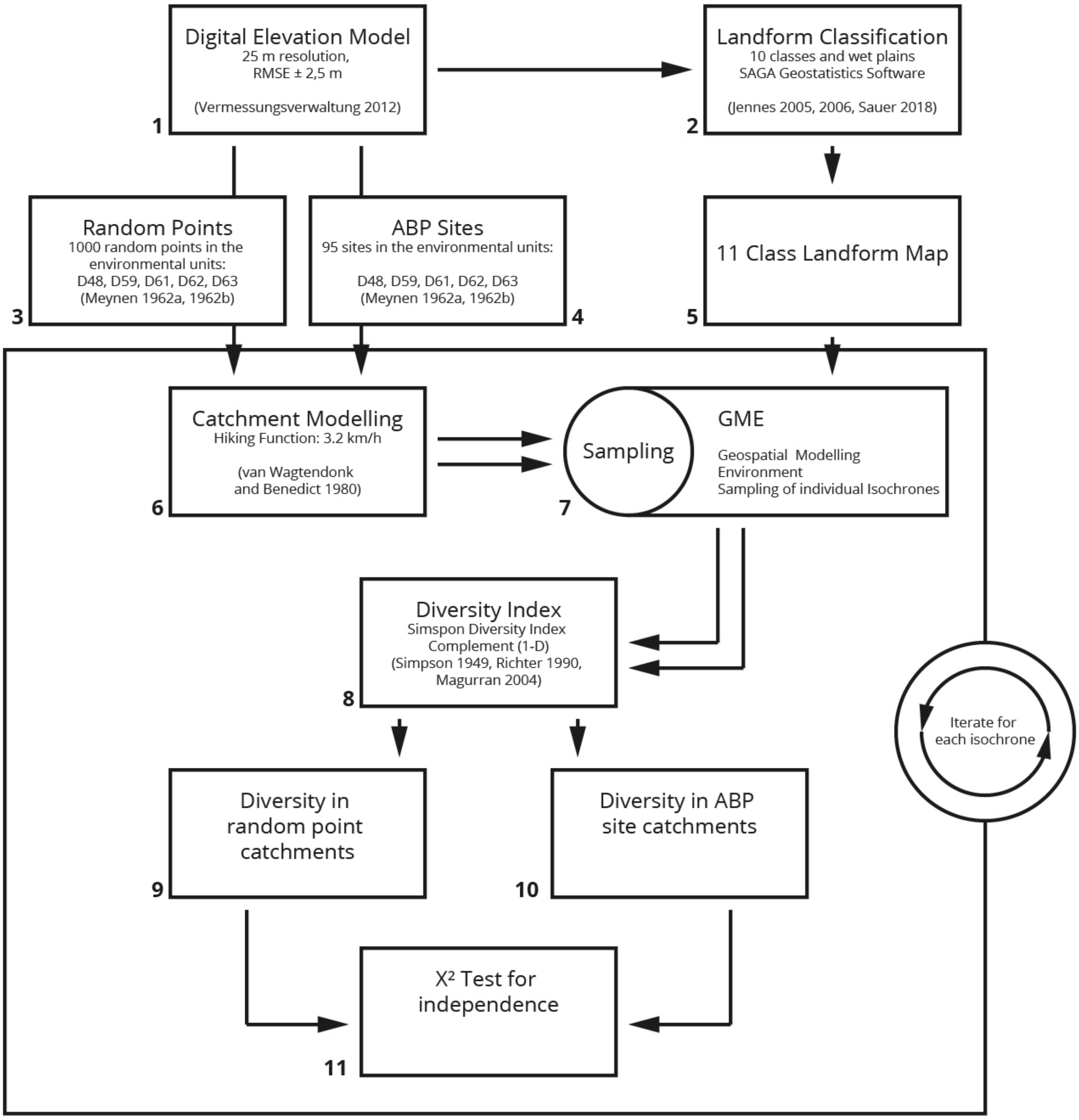

Fig. 3. Flowchart of the modelling approach; the individual steps are numbered and reflected in the text.

***Abb. 3.** Flussdiagramm des Modellierungsvorgangs; die Einzelschritte sind nummeriert und im Text wiedergegeben.*

areas for vegetation relevés" (Schwabe 1999: 79) which "*can be defined geomorphologically and topographically*" (Schwabe 1999: 79; also: Thannheiser 1992; Leser 1996). Hence, a greater variability of physiotopes translates to a greater variability of biocoenoses (biocoenosis: phyto- and zoocoenoses populatinng a given habitat; Kratochwil 1999: 26).

Within a climatic period (e.g. the Allerød-Interstadial as a phase of a relatively continuous climatic regime within the Late Glacial Interstadial Complex), these interrelationships between vegetation and physiotopes can be observed on multiple scales. Microforms, like small pits, may accumulate water after rainfall in summer providing a microhabitat for a comparatively short time. At the same time, in a regional context rainfall will result in heightened flow velocities in the river systems, promoting release and redistribution of nutrients. While these general principles can be deduced from uniformitarian studies, the assumption that the recent relief is an adequate approximation of ancient morphology is another matter. Landscape morphology is not stable and more likely to differ from its current state with greater temporal distance (Summerfield 1991: Tab. 1.2). Since this approach employs modern geomorphology as a proxy to estimate levels of relative potential biodiversity, the analytical scale must be set in relation to the geomorphological change since the time-period in question. This issue is addressed by primarily using the geomorphic properties of macroscale topographic units (Summerfield 1991: 12) as representatives of physiotopes. These macroscale units range on a temporal scale of about 10^7 years proving them comparably unchanged at least on the temporal scale addressed in the context of the Upper Palaeolithic (Summerfield 1991: Tab. 1.2). By using these large-scale entities, comparably large areas throughout Europe (e.g. the Central Upland Belt composed of the Massif Central, French and Swiss Jura, German Central Uplands, Carpathians etc.) can be investigated. Only areas, which experienced strong Late Glacial and Holocene transformation should be treated with caution, even though macroscale geomorphological change likely plays only a minor role.

Landforms (discrete expressions of topographic composition like hills, mountains, canyons etc.; component of the *landscape* as the entirety of *landforms*) are representations of physiotopes that are relatively stable on the temporal scale in question (Summerfield 1991). However, this stability cannot necessarily be assumed for all settings. Volcanic or coastal environments may be subject to drastic changes in the shape of the landscape within relatively short periods of time. In these cases, a special assessment of the situation and the modeling of palaeotopography is necessary. Estimating potential or relative biodiversity by landform diversity as a representative of physiotope diversity is, to a certain degree, independent of prevailing climatic conditions. Landform variability generally influences growth conditions (extreme habitats were basic growth conditions like sufficient humidity or temperatures do not prevail are an exception to the rule: e.g. deserts, ice deserts). In the approach presented here, we do not employ specific biocoenoses to model ecological variability. We understand physiotope diversity as a strictly relative representative of potential interbiocoenotic diversity determined by topographically controlled abiotic gradients (the diversity of different ecological communities as opposed to the intrabiocoenotic diversity as a value of species diversity within a physiotope or habitat: Kratochwil 1999: 5).

Methodology

To use landforms as representatives of physiotopes on the macroscale, they have to be derived from a digital elevation model (Fig. 3: 1; DEM; 25 m resolution, RMSE ± 2.5 m) of the study area (Vermessungsverwaltung 2012). In this article, landforms are classified by employing the Topographic Position Index (TPI; Fig. 3: 2 & Tab. 1) based landform classification algorithm (Guisan et al. 1999; Weiss 2001; Jennes 2005; Jennes 2006), which is part of the SAGA geostatistics software (Conrad et al. 2015). The TPI is used to assess the relative position of raster cells in a DEM by evaluating a raster-cell's position relative to the mean elevation within a given radius. Positive TPI-values reflect higher relative altitude, negative ones reflect lower relative position than the surrounding landscape. The selected radius for calculating the TPI influences the resulting values. For the study area, the classification was conducted using 25 m DEM for Bavaria (Vermessungsverwaltung 2012).

When the TPI-values are compared on two different scales, e.g. a small neighborhood (SN) and a large neighborhood (LN), the results are classified according to threshold values. As a result, the DEM is classified into 10 different landforms, which are set by the algorithm (the 10 classes are set by the SAGA "TPI-based landform classification" algorithm, which classifies the SN and the LN axis using the standard deviation; Jennes 2006; Tagil & Jenness 2008: Fig. 4). In this article, analytical landform-classes are italicized. Since SN and LN are of central importance to the modelling results, their scales must be selected in accordance to the question at hand. Low scale-values will result in the pronunciation of small morphological units of short temporal stability. Higher scale-values reflect larger morphological units, which are less susceptible to morphological change over time.

In this study, we decided to favour the TPI-based landform classification algorithm as presented by Guisan & Weiss (1991) as well as Guisan & Zimmermann (2001) over its variation (TPI divided by the standard deviation of the elevation) presented by De Reu et al. (2013). The DEV-algorithm pronounces small morphological units stronger than the TPI. This generates more "noise" of small, local units and does not serve the purpose of reflecting general trends in our study area. This decision is justified by the scale of analysis, with a focus on large scale topographic entities. The TPI better reflects the dichotomy between low-lying, topographically moderate landscape elements and the heterogeneous uplands allowing for the analysis of general trends in the study area.

For processing, large TPI ranges were chosen. A small neighbourhood range of 0 m and 800 m (elevation deviation in a 2 km^2 area) and a large neighbourhood range of 0 m and 3,000 m (elevation deviation in a 28 km^2 area) were selected. This value range was employed to gain a representation of macroscale topographic units, which do not react to relatively short-timed micro- and mesoscale events which cannot be reliably determined for the Upper Palaeolithic period. Topographic variability on the scale of river terraces is therefore not represented by the landform modelling approach making the results robust on the long temporal scale and applicable for analysis.

Since large regions in the study area, particularly the lowland-areas (specifically the Keuper-Lias land and the Upper Palatinate Valley), are prone to the accumulation of surface water, the landform category of the *plains* was reclassified into *plains* and *wet plains* to accommodate the wetness in the area. This was achieved by employing a threshold topographic

Landform type	Small neighbourhood TPI (SN)	Large neighbourhood TPI (LN)
Canyon/V-shaped valley	--	--
Valley/U-shaped valley	0/-	--
Midslope drainages	--	++
Upland drainages	-	+
Plains	0 (Slope ≤ 5°)	0 (Slope ≤ 5°)
Wet plains	0 (Slope ≤ 5°, TWI > ø TWI Canyon)	0 (Slope ≤ 5°, TWI > ø TWI Canyon)
Open slopes	-/+ (Slope > 5°)	-/+ (Slope > 5°)
Upper slopes	-/+	++
Local ridges	++	--
Midslope ridges/ small hills in plains	++	-/+
High ridges	++	++

Tab. 1. Landforms as provided by the TPI-based landform classification and their general morphological values (See also: Jennes 2006).

Tab. 1. *Landformen wie sie durch den TPI-basierenden Landform-Klassifikationsalgorithmus wiedergegeben werden und ihre generellen morphologischen Charakteristika (Siehe auch: Jennes 2006).*

wetness index (TWI) for areas of high potential topographic wetness.

To do this, the DEM was smoothed to eliminate small topographic features (SAGA Gauss Filter: Standard deviation: 2; radius: 15 cells; search mode: circle; 2 passes) and the TWI was calculated. The TWI reflects the local tendency for precipitation accumulation by estimating upslope contributing area and slope as determinants for topographically controlled hydrological processes (Beven & Kirkby 1979; Sørensen et al. 2006). The resulting indices for soil moisture are, like other topographically controlled values (Zimmermann & Thom 1982), influencing biocoenosis distribution (Giesler et al. 1998). Within the model, *canyons* were the landforms with the highest TWI-levels (13.41) due to the expressed accumulation of surface water. Therefore, the mean TWI-value of this class was used to reclassify the *plains*. Areas in the *plains* showing a TWI exceeding the mean *canyon*-TWI were reclassified into *wet plains* (resulting in a mean TWI for the *wet plains* of 14.14). In the end, the DEM was classified into 11 landforms ranging from the flat *plains* and *wet plains* to the *high ridges* and *canyons* in morphologically pronounces landscapes (Fig. 3: 5 & Fig. 4). These 11 morphological units are regarded as physiotopes determining biocoenosis presence.

To analyse the relationship between site and surrounding landscape, the landform composition in the respective catchments (Vita-Finzi et al. 1970; Higgs & Vita-Finzi 1972) were sampled. A catchment is regarded to be the area around a site which is subject to exploitation by the prehistoric foragers with a same-day return. The area beyond the limit of a catchment is not subject to exploitation without the setup of a new camp and locations (resdential mobility: Binford 1980; Binford 2001). In any case, the present study is not aiming at identifying a specific subsistence strategy (e.g. collectors or foragers) nor the related settlement pattern and its site types (e.g. base camp, field camp, special task site, location etc.) according to, for example, Binford (1980). Instead, we focus on a comparative analysis of the landform diversity in a defined spatial area to deduce hypothesis about factors that have influenced the ecological aspects of the site catchment. From a methodological point of view, the distinction between different types of site function is in this study less relevant, because the placement of any type of site follows a prior decision and any type of camp and location provides a catchment of potentially exploitable landscape.

Site catchments were modeled using a hiking function, which estimates traveling speed in relation to the local slope based on a walking speed of 3.2 km/h on level ground (van Wagtendonk & Benedict 1980; Uthmeier et al. 2008 ; Sauer 2016). The catchment-isochrones were calculated for every site (Fig. 3: 4) to a maximum time distance of four hours as well as for a set of 1,000 randomly placed points for statistical comparison of the background distribution (Fig. 3: 3 & 6). A maximum distance of four hours is regarded to be a viable maximum travelling distance, leaving four hours for task execution on a day with 12 hours of sunlight. Clearly, different tasks make for varying maximum distances depending on the required time. Furthermore, task execution while travelling may also vary the resulting catchment size (Lyon & Burcham 1998). These variations are not included in this approach.

After modelling the catchments, for all cases (sites and random points) the landform composition within the respective isochrone circular rings (ICR; annulus of the respective one-hour-isochrone bracket) was sampled and added to the GIS-database. ICR represent the areas of accessibility in one-hour brackets, not containing the area of the preceding ICR. For example, the two-hour ICR is only composed of the area accessible *after* one-hour non-stop walking time and *up to* two hours non-stop walking time.

For quantitative analysis, the complement of the Simpson diversity index (1-D; Simpson 1949; Richter 1990; Magurran 2004) was calculated for the individual circular rings (Fig. 3: 8-10). While Simpson's traditional Index ranges from D = 0 = diverse to D = 1 = specialized, the inverted index ranges from D = 0 = specialized to D = 1 = diverse. Therefore, with the complement of the Simpson index, as diversity rises, the value of D rises as well:

$$D = 1 - \sum_{i=1}^{S} \frac{n_i(n_i - 1)}{n(n-1)}$$

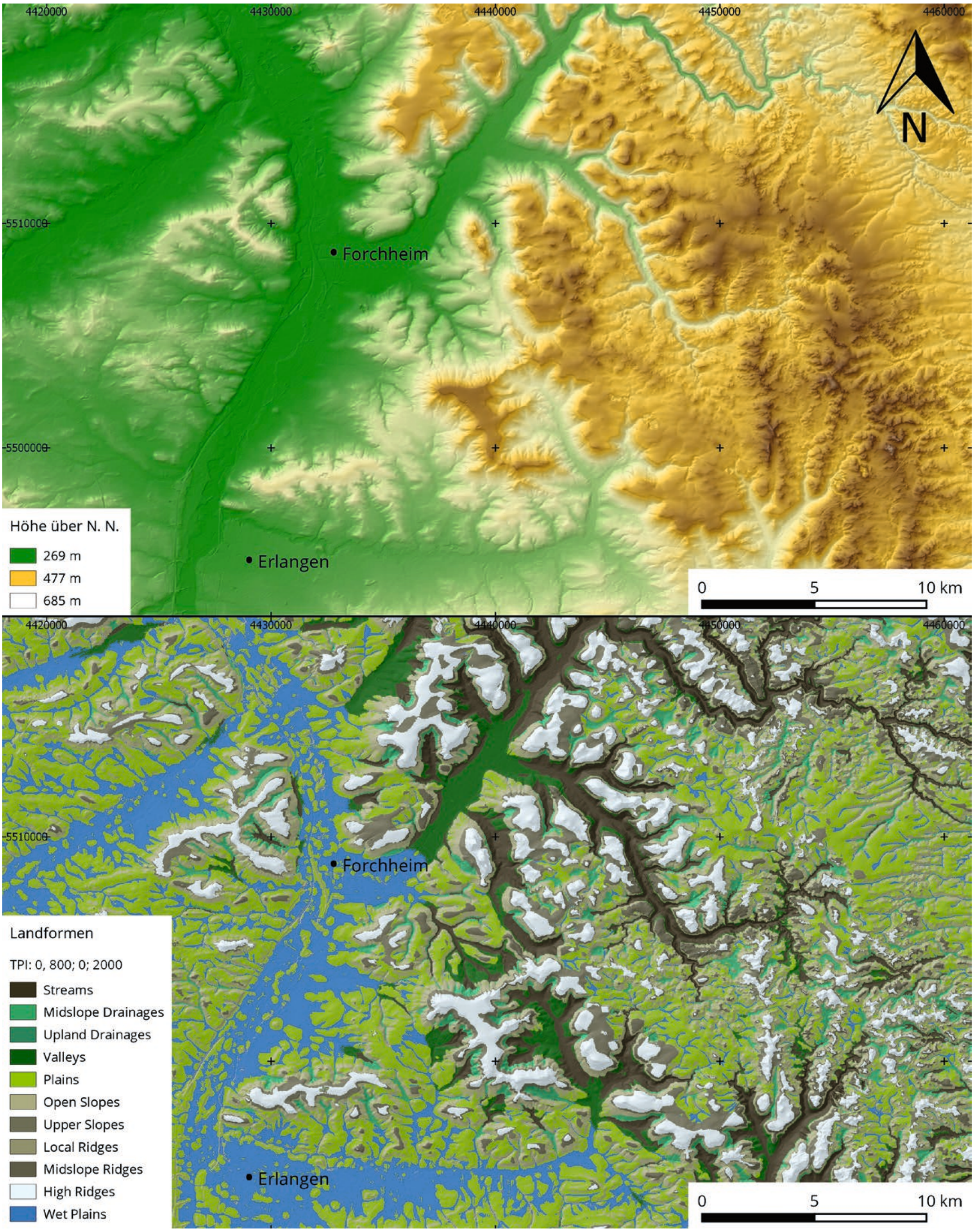

Fig. 4. Comparison of the digital elevation model and the classification results of the TPI-based landform classification; top image – digital elevation model; bottom image – classification results.

Abb. 4. *Vergleich von digitalem Geländemodell und den Klassifikationsergebnissen der TPI-basierenden Landformklassifikation; oben – digitales Geländemodell; unten – Klassifikationsergebnisse.*

The complement of the Simpson diversity index was calculated for the individual circular rings (Fig. 5) of both the sites and the randomly placed points. The respective frequencies of the 0.1-step diversity-classes of sites and random points were compared to one another. Background physiotope diversity was used as comparison for a random choice of the site catchment (Fig. 6 & Tab. 2). For clarifying if choice was

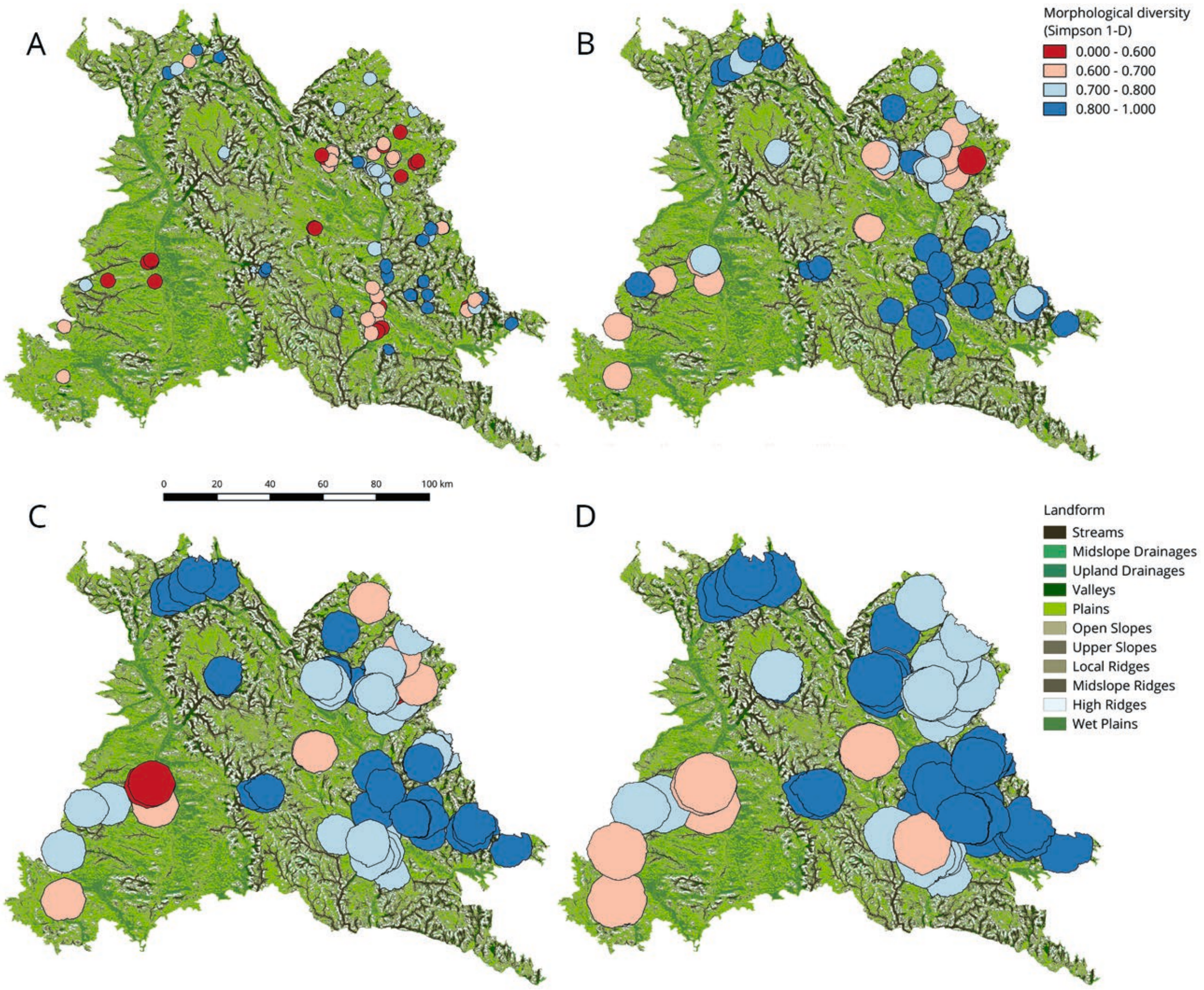

Fig. 5. Catchments and respective physiotope diversity-values for the study area for the one-to-four-hour ICRs; the individual maps can also be found in the supplementary data (SI 1–4); the individual catchment compositions are reflected in supplementary table (SI 13).

Abb. 5. *Catchments und dazugehörige Diversitätswerte der ein bis vier Stunden Isochronen für das Arbeitsgebiet; die einzelnen Karten finden sich ebeno in den Zusatzdaten (SI 1-4); die einzelnen Catchment-Zusammensetzungen sind in der Zusatztabelle (SI 13) wiedergegeben.*

governed by other decisions than chance it was tested for independence using the χ^2-test (Tab. 2). This approach aims towards analysing, whether relatively high or low levels of potential physiotope diversity were preferred along the range of available diversity levels and whether these conditions differ significantly from the general landform setup provided by the landscape. Comparisons were processed on the level of the entire study area as well as the individual environmental landscape units (Fig. 7).

Results

Quantitative Results on Geotope Composition

For the one-hour ICR physiotope diversity values ranged from 0.48 to 0.85 (Mean (MN): 0.7, Median (MD): 0.68) for the sites and 0.40 to 0.87 (MN: 0.71, MD: 0.75) for the background diversity range. Values towards zero would reflect a completely flat landscape over extended areas. Within the study area (and indeed most of Europe) these conditions are absent. Therefore, a minimal topographic diversity always can be expected. All further diversity ranges are represented in table 2.

The individual ICR diversities and the background diversity range were tested for independence with the χ^2-test and a threshold p-value of 0.05 for discerning for random ($p > 0.05$) and independent ($p \leq 0.05$; $p \leq 0.05$ = significant; $p \leq 0.01$ = high significance; $p \leq 0.001$ = highest significance) distribution. The test-statistics (p) for the individual ICR are reported in table 2.

In the one-hour ICR ($p = 0.021$) and the two-hour ICR ($p = 0.026$) significantly independent distributions could be observed. Given the available range of diversity provided by the landscape, components of relative low variability dominated the dataset (cf. Figs. 5 & 6). This situation changes with increasing distance to the site. While the three-hour ICR ($p = 0.438$) does not provide independent values, the four-hour ICR ($p = 0.044$) shows the significant dominance of relatively diverse landscape components (cf. Fig. 5).

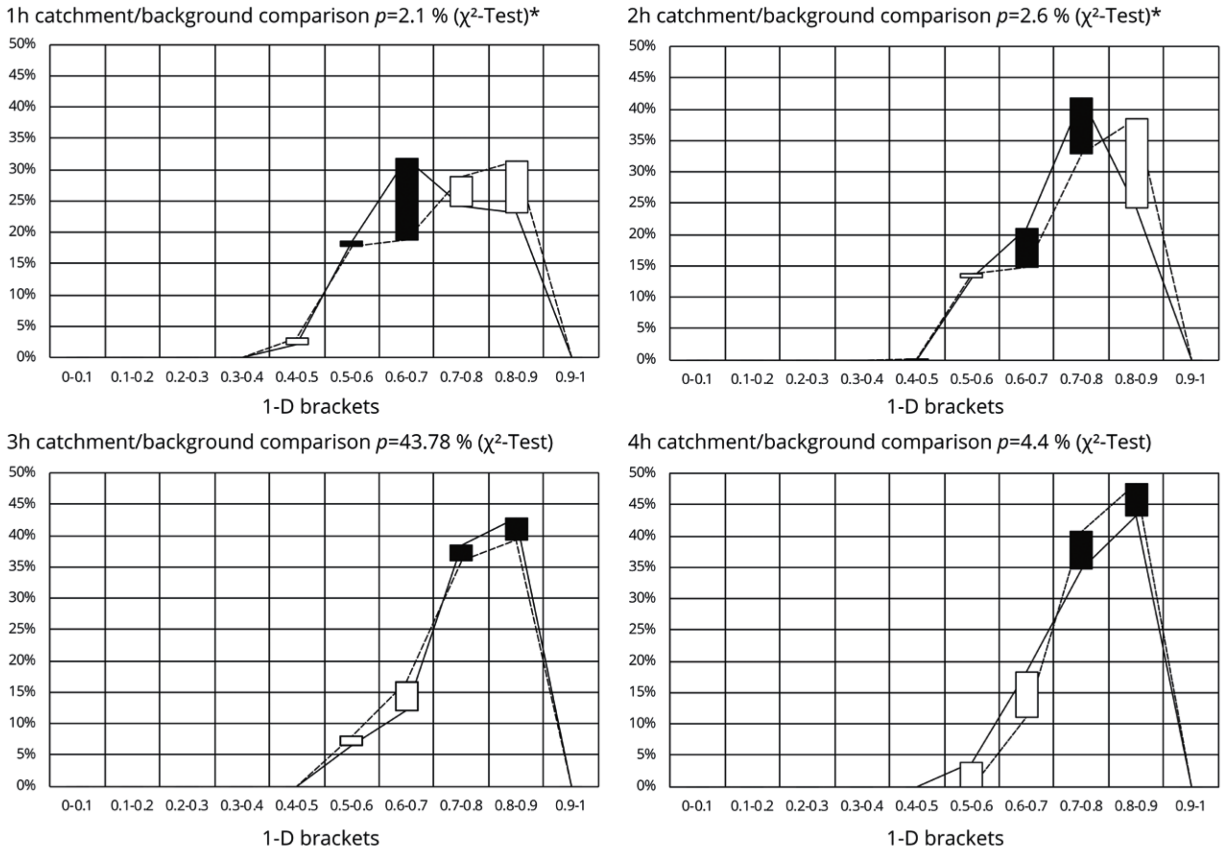

Fig. 6. Comparison of background physiotope diversity and site diversities in the study area for the one-to-four-hour ICRs. The solid line represents the diversity-distribution of Late Palaeolithic sites in the study area, the dashed line represents the background distribution of 1,000 randomly placed control-points in the study area; white blocks represents negative deviation of the site-dataset from the background distribution, black blocks represent positive deviation of the site dataset from the background distribution.

Abb. 6. *Vergleich der Hintergrunddiversität und den Fundstellendiversitäten im Arbeitsgebiet für die ein bis vier Stunden Isochronen. Die durchgezogene Linie repräsentiert die Diversitätsverteilung für die Spätpaläolithischen Fundstellen im Arbeitsgebiet, die gestrichelte Linie zeigt die Hintergrundverteilung für 1.000 zufallsverteilte Kontrollpunkte im Arbeitsgebiet; die weißen Blöcke zeigen die negative Abweichung des Fundstellendatensatzes von der Hintergrundverteilung, die schwarzen Blöcke zeigen die positive Abweichung des Fundstellendatensatzes von der Hintergrundverteilung.*

In general, this image remains valid, even when the individual environmental landscape units are considered (Fig. 6). However, regional variations are present, too. In the case of the Upper Palatinate Forest (Fig. 1: b. D63) the dominance of relatively homogenous landscape elements prevails throughout all isochrones. In the Franconian Thuringian Range (Fig. 1: b. D48), independent low diversity values are only present in the four-hour isochrone although a p-value of 5.3 % in the case of the two-hour isochrone shows a clear tendency. In the Upper Palatinate Valley (Fig. 1: b. D62) the one-and two-hour isochrones show independent and relatively low diversity values. In the case of the Keuper-Lias Land (Fig. 1: b. D59), independent values could not be observed. The Franconian Alb (Fig. 1: b: D61) did not provide statistically reliable results due to the low number of sites in this area. It must be noted that in no case a statistically independent preference of relatively high levels of physiotope diversity can be observed.

ICR	Background diversity range	ICR diversity range	p	Independent distribution
1h	0.401-0.869	0.477-0.848	0.021	Yes
2h	0.477-0.870	0.559-0.854	0.026	Yes
3h	0.518-0.867	0.546-0.861	0.438	No
4h	0.546-0.884	0.602-0.858	0.044	Yes

Tab. 2. Physiotope diversity ranges of the study area (background diversity range) the individual ICR diversity ranges, the associated test-statistics and the resulting independencies.

Tab. 2. *Physiotop-Diversitätsbereiche im Arbeitsgebiet für die Hintergrundverteilung, die einzelnen Isochronen, die Teststatisiken und die daraus resultierenden Abhängigkeiten.*

Qualitative Results on Geotope Composition

We indicated that different physiotopes provide a range of topographically controlled abiotic conditions, which determine biocoenosis presence and distribution. Within the study area, an important gradient for biocoenosis distribution in relation to foraging behavior is water retention and distribution. In landscapes that are morphologically diverse, the gradient of surface wetness is relatively pronounced

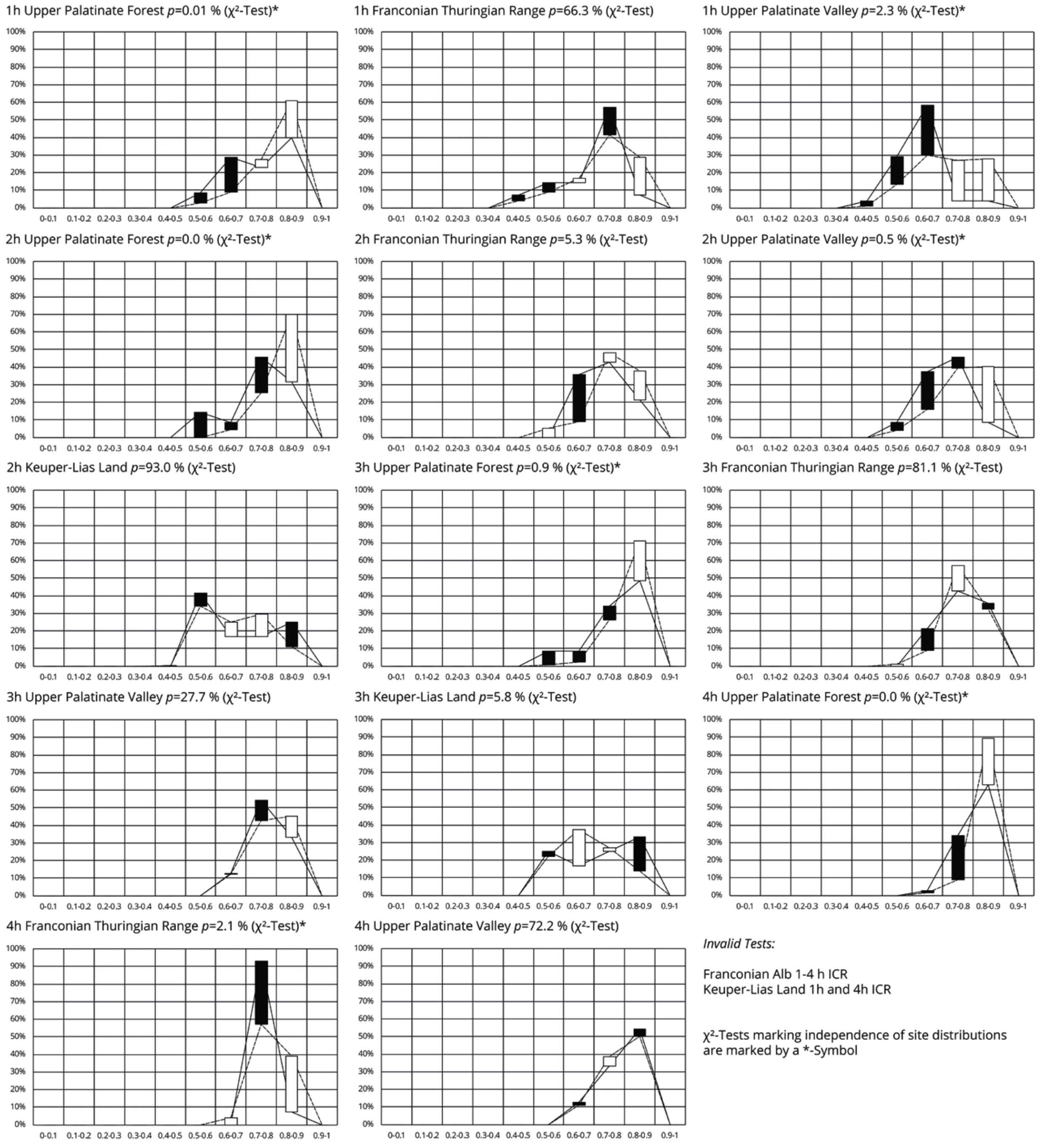

Fig. 7. Comparison of background physiotope diversity and site diversities for the individual environmental landscape units for the one-to-four-hour ICRs. Cases, where the χ^2-Test was not applicable due to small site numbers were omitted. The solid line represents the diversity-distribution of Late Palaeolithic sites in the study area, the dashed line represents the background distribution of 1,000 randomly placed control-points in the study area; white blocks represents negative deviation of the site-dataset from the background distribution, black blocks represent positive deviation of the site dataset from the background distribution.

Abb. 7. *Vergleich der Hintergrundverteilung und der Fundplatzdiversitätsverteilungen für die einzelnen Naturräumlichen Einheiten und die ein bis vier Stunden Isochronen. Fälle, in denen der* χ^2*-Test wegen zu geringen Fallzahlen nicht durchführbar war, wurden nicht dargestellt. Die durchgezogene Linie repräsentiert die Diversitätsverteilung für die Spätpaläolithischen Fundstellen im Arbeitsgebiet, die gestrichelte Linie zeigt die Hintergrundverteilung für 1.000 zufallsverteilte Kontrollpunkte im Arbeitsgebiet; die weißen Blöcke zeigen die negative Abweichung des Fundstellendatensatzes von der Hintergrundverteilung, die schwarzen Blöcke zeigen die positive Abweichung des Fundstellendatensatzes von der Hintergrundverteilung.*

and, according to the few palynological samples for the Allerød and Dryas III presented above, of great importance for Late Glacial plant society distribution (Stalling 1987). Positive or negative correlation of the relatively specialized catchments may reflect choices of foragers for specific biocenoses.

A cluster analysis (CLA, Morisita Similarity Index, PAST statistics 3.0) of the catchment compositions for the one-hour isochrone of all 95 archaeological sites shows the specific composition of four different clusters on the similarity level of 0.8 and 0.72 (Fig. 8) which are statistically independent (χ^2-test, Tab. 3). We chose Morisita's index due to its particular suitability for species dispersion analysis (Morisita 1959). Values towards zero reflect no overlap between samples, while values towards one represent a total congruence of datasets. Four major clusters can be observed in the dataset. These units show statistically independent landform compositions, which are analysed in a second step (Tab. 3).

To analyse the different factors determining the four individual clusters, the groups A through D were analysed in a correspondence analysis (CA; Software: CAPCA; Fig. 9 & Tab. 4). In this CA, we employed the individual sites as units, while the landforms were regarded as variables. Cluster A is associated with the dry conditions of the *plains*, cluster B also yields primarily dry conditions in a moderately hilly landscape. Cluster C and D are associated with wet conditions in a flat (C), respectively very heterogeneous (D) landscape. In fact, factors with the highest **inertia** in the CA are the *wet plains*, the *valleys* and the *canyons*.

With increasing catchment size, the clear association of the clusters, determined in the CLA for the one-hour isochrones, dissolves and the clear association of sites with specific habitats is less pronounced (in this situation, spatial autocorrelation is a factor which has to be considered; anyhow, we feel it reflects the factual broadening of options for foragers with increasing catchment size). This supports the impression, which was obtained from the quantitative analysis of the catchment compositions.

Discussion

Both the values for quantitative and qualitative physiotope distribution describe a relatively clear picture of resource exploitation *opportunities* in the catchments of the Late Palaeolithic sites in Northern Bavaria. In general, there is a significant congruence of site location and physiotope diversity in the associated catchments. Based on the model, the sites were placed in areas, which provided relatively low levels of geomorphological diversity in the vicinity and a greater bandwidth of options at a greater distance from the site. This is reflected by the data for quantitative distribution of physiotope composition throughout the several ICRs (Tab. 2). These variations could reflect variability of exploitation options and potentially associated risk management strategies. The comparably low near-field diversity of physiotopes provides high volumes of specific sets of resources, potentially providing high return-rates. This picture

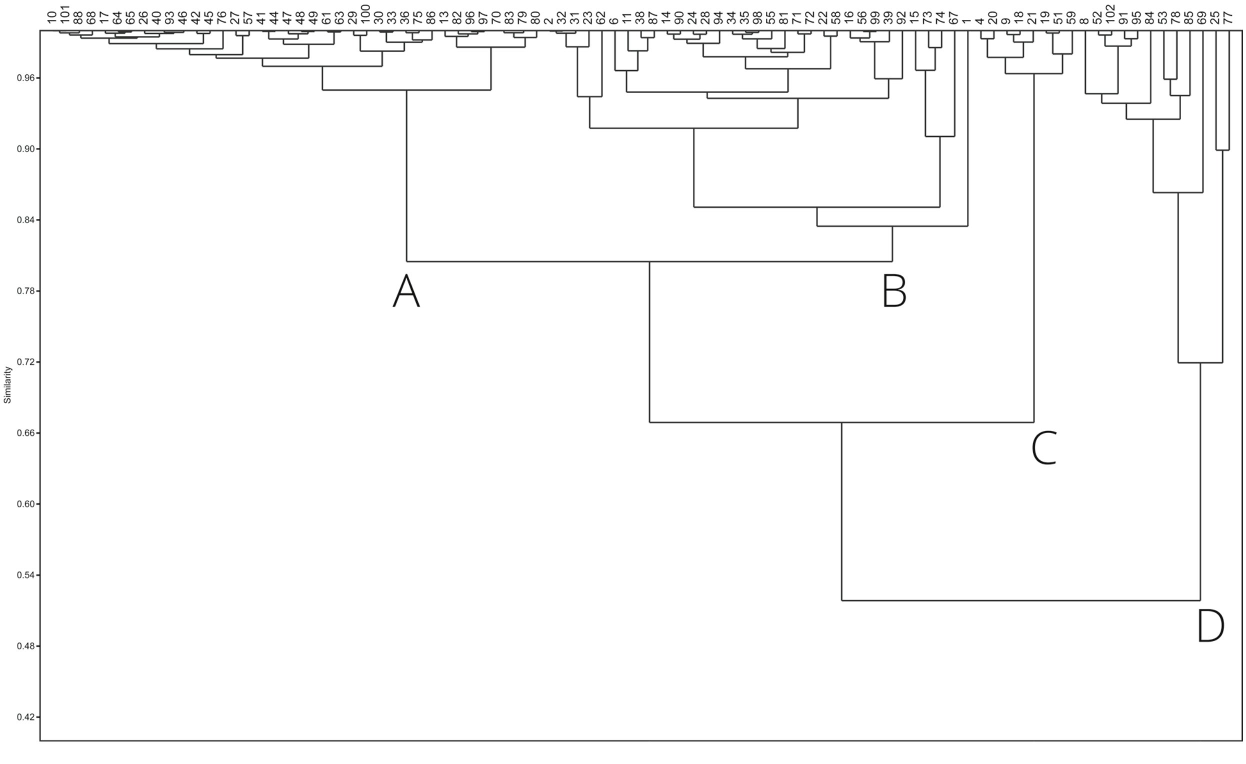

Fig. 8. Results of the cluster analysis for the landform composition of the one-hour catchments of the sites in the study area; four major clusters were set on the similarity level of 80 % (A–C) and 72 % (D Morisita Similarity Index, PAST statistics 3.0); the site numbers are solved in supplementary table (SI 14).

Abb. 8. *Ergebnisse der Clusteranalyse für die Landformzusammensetzung der Einstundencatchments der Fundstellen im Arbeitsgebiet; vier Hauptcluster wurden auf dem Ähnlichkeitsniveau von 80 % (A-C) sowie 72 % gesetzt (D Morisita Similarity Index, PAST statistics 3.0); Die Fundplatznummern sind in der Zusatztabelle (SI 14) aufgelöst.*

Cluster	A	B	C	D
A	-	< 0.1%	< 0.1%	< 0.1%
B	< 0.1%	-	< 0.1%	< 0.1%
C	< 0.1%	< 0.1%	-	< 0.1%
D	< 0.1%	< 0.1%	< 0.1%	-

Tab. 3. χ^2-test statistics for the different clusters provided by the cluster analysis regarding the one-hour ICR composition of landforms (Fig. 8).

Tab. 3. *χ^2-Teststatistik für die verschiedenen Cluster wie sie in der Clusteranalyse für die Einstundenisochronen in Bezug auf die Landformzusammensetzung modelliert wurden (Fig. 8).*

persists at a distance up to two hours. At a greater distance from the centre, the resource options change to greater variability, potentially allowing the access to a greater number of different organic resources (cf. Fig. 10). This is associated with the opportunity of risk-reduction. Fundamentally, the near-field provides high risk-high gain landscape compositions, the far field provides low risk, low gain instead.

At first glance, the analysis of the individual landscape units shows a greater variability in composition than the entire study area. In all cases where an *independent* composition of landforms in the catchments could be observed (Fig. 7), low levels of relative physiotope diversity were favoured. In cases where a *dependent* distribution could be observed, the general landscape setup was already comparatively homogeneous (cf. Fig. 7: 2 h & 3 h Keuper Lias Land, 1 h & 2 h Franconian Thuringian Range). Therefore, the tendency for diversification, which is visible on the large scale, cannot be observed that clearly but is present, nevertheless. It has to be underlined, that the general landscape setup in the far-field catchments increases in relative physiotope diversity (We are aware that this is also the result of spatial autocorrelation resulting in greater diversity with increasing annulus area. However, this still results in a *de facto* increase in options for prehistoric foragers). This holds particularly true for examples like the Upper Palatinate Forest and the Upper Palatinate Valley which show a diversification of the background distribution with increasing distance.

Qualitatively, the predominant *types* of physiotopes determining the geomorphological composition of the individual catchments are associated with the topographically controlled accumulation of water. In the correspondence analysis, wetland-physiotopes provide the highest inertia, particularly given their low mass in the dataset (cf. Tab. 4). While the immediate vicinity of the Late Palaeolithic sites typically provides specialized physiotope compositions of wetlands and watercourses, regions in greater distance are diverse and provide an greater variety of different physiotopes.

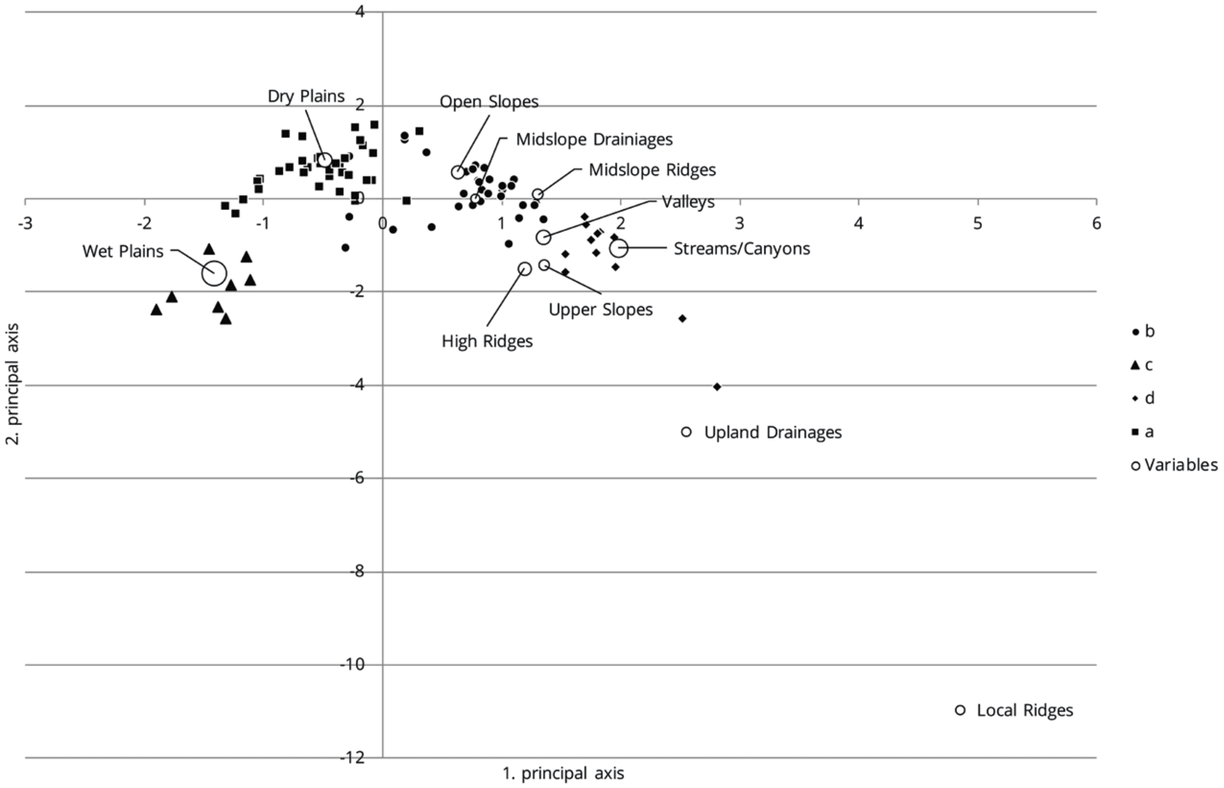

Fig. 9. Results of the correspondence analysis for the landform composition of the one-hour catchments of the sites in the study area (Software: CAPCA); the analysis for the individual ICRs is shown in the supplementary data (SI 5–12).

Abb. 9. *Ergebnisse der Korrespondenzanalyse für die Landformzusammensetzung der Einstundencatchments der Fundstellen im Arbeitsgebiet (Software: CAPCA); die Analyse der einzelnen Isochronenringe ist in den Zusatzdatensätzen (SI 5–12) wiedergegeben.*

	1. Principal axis	2. Principal axis	3. Principal axis
Cumulative explanation %	60.8	17.8	9.5

Landform type	Mass %	Inertia %
Streams/canyons	6.3	18.0
Midslope drainages	2.7	2.2
Upland drainages	0.0	0.7
Valleys	4.4	13.1
Dry plains	41.9	11.7
Open slopes	18.7	7.3
Upper slopes	1.5	5.2
Local ridges	0.0	0.5
Midslope ridges	3.7	5.0
High ridges	4.2	8.0
Wet plains	16.8	28.3

Tab. 4. Statistical values to the correspondence analysis of the one-hour catchments of the sites in the study area; all further ICR values can be found in the supplementary data (SI 5–12).

Tab. 4. *Statistische Werte der Korrespondenzanalyse für die Einstundencatchments der Fundstellen im Arbeitsgebiet; alle weiteren ICR Werte können in den Zusatzdaten (SI 5–12) nachgelesen werden.*

This indicates that, given their low mass, the greatest pull within the geomorphic context was exerted by wetness-related physiotopes and the associated biocoenoses. Fishing and the hunting of waterfowl or larger forest animals approaching the watering places can be named here as potential targets. In the forests of the Late Glacial, wetlands could be focus areas with increased prey predictability reducing risk and increasing chances for hunting success (Jochim 1976: 54).

Bioeconomic requirements of foragers are part of a set of determinants (e.g. also the exploitation of abiotic resources or the pursuit of social and cultural agendas) for site placement in the landscape. Optimal foraging theory argues, that risk and cost minimization (Jochim 1976), among other factors, could govern the decisions which influence site location in relation to resource patches (Pyke 1984; Harris 2001). Heterogeneous distribution of key biocoenoses therefore could determine a non-random settlement pattern regarding biomass accessibility. In contrast, uniform distribution would not necessarily require for the placement of settlements in specific locales, since target resources are spread evenly in the landscape and hard to predict (Jochim 1976; Binford 1980). Typically, this continuum is linked to the effective temperature and primary production (Kelly 1983: 290; Binford 2001: 84). However, the continuum can also be analysed with geomorphology as the determinant of biotic resource patch distribution. While climatically driven change happens on a chronological scale, topographically controlled variations of the environment predominantly occur on a spatial scale. Environments, which are characterized by high production of primary biomass (typically regions with a relatively high effective temperature), are traditionally regarded to represent a relatively uniform distribution of biotic resources (Binford 1980; Kelly 1983, 1995). This is believed to result in a settlement pattern, which focuses on residential mobility to facilitate optimal resource exploitation (Kelly 1995: 116-130). The Late Glacial Interstadial Complex represents, compared to the preceding Glacial Maximum, conditions of relatively high primary net production. However, the topographically induced variability of biocoenosis distribution and the preference of specific environmental conditions by Late Glacial foragers suggest a stronger patterning of bioresources. This could reduce the level of expected residential mobility and emphasize ephemeral special task camps, which are only rarely detected in the archaeological record (Werner & Schönweiß 1974; Heinen 2005).

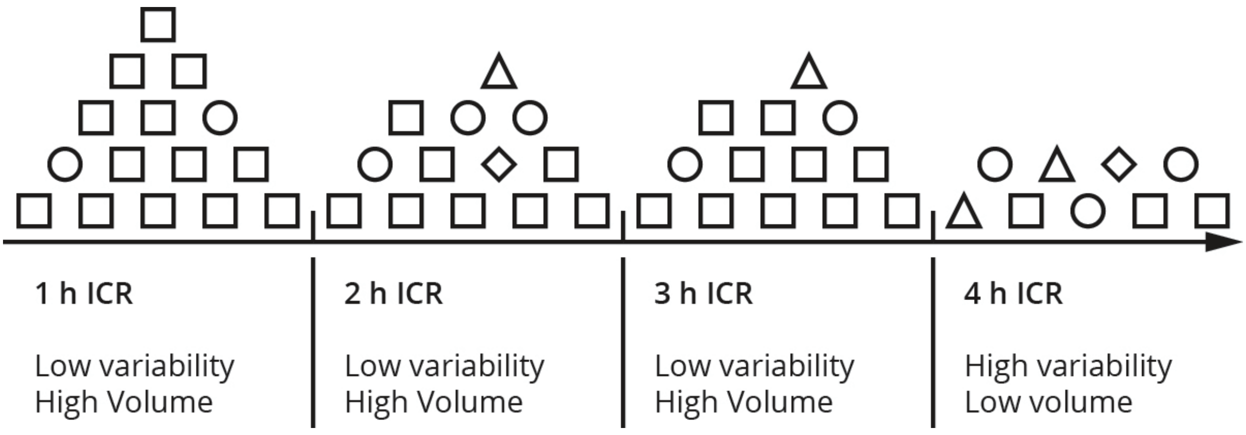

Fig. 10. Variability of the physiotope framework with increasing distance to the site and its implications on the potential resource exploitation strategy.

Abb. 10. *Variabilität des Physitioprahmens mit zunehmender Distanz zur Fundstelle und die daraus resultierenden Implikationen für potentielle Strategien zur Ressourcennutzung.*

Association with certain habitats of specific biocoenoses describes the ecological niche of the Late Glacial foragers in Bavaria and their potential adaption to exploiting specific sets of resources (on ecological niche modelling and species distribution modelling: Banks et al. 2008; Banks et al. 2011; Svenning et al. 2011; Franklin et al. 2015). PPG shows that sites are placed in environments, which provide a relatively low variability of habitats. This suggests a focus on both a high volume and low variability of resources. Regarding risk-management, these results could indicate the exploitation of a specialised potential resource spectrum. Although Tallavaara et al. pointed out, that hunter-gatherers "*appropriate only a small fraction of the production*" (2018: 1), Hahn also stressed the dramatic influences of predatory interference in local environments (Hahn 1995). He estimated, that even a brief stay of a relatively small group of foragers would have had a catastrophic effect on the locally available biomass (Hahn 1995: 91-94). The selection of large-volume environments could reduce this impact to some degree.

Beyond general specialization, the presence of landscape elements with a tendency for water-accumulation characterises the economic options around sites in the Central Uplands. Wetland conditions promote the presence of marshes, small ponds, lakes, and watercourses like streams and rivers. Hunting prey, like waterfowl, and aquatic resources, especially fish, can be linked to these habitats (Brouwer Burg 2013). Although the wetland physiotopes appear to be dominant in the vicinity of the sites, other biotic resources were accessible in the close and the extended catchments. There, greater variability of physiotopes allowed for the exploitation of biocoenoses that relate less closely to high levels of humidity. These are, among others, the dry highlands, which can provide more open landscapes and other species societies. Archaeological data can hardly shed light on this question in the study area. It is only at the site of Steinbergwand near the town of Ensdorf (Amberg-Sulzbach district, Bavaria), that we get a brief glimpse of the exploitation of fauna by late glacial hunter-gatherers in the study area (Gumpert 1933). Here, Late Palaeolithic (ABP) tools were found in a layer also containing macrofossils of horse and deer, which can suggest the exploitation of closed, transitional and open environments. The question, whether the physiographic pattern surrounding archaeological sites traces down to the level of organic remains in the archaeological record remains subject to further investigation. The approach presented here focuses on modelling the qualitative and quantitative variability of physiotopes (not specific floral or faunal elements!) in the context of prehistoric settlement leading to different possibilities in the respective catchments.

Conclusion

The modelling of physiotope diversity in the catchments of Late Palaeolithic sites in Northern Bavaria showed a distinct pattern for the placement of sites. Regarding physiotope diversity, Late Palaeolithic hunter-gatherers preferred landscapes on the lower end of the diversity-spectrum. Sites were generally placed in locations which provide low levels of physiotope diversity in the vicinity and morphologically diverse landscapes at a greater distance. The applied methodology allows for the contextualisation of site and landscape based on the principles of physiographic plant geography. While specific biological communities could not be determined this way it still allows to quantify topographic composition of the accessible landscape.

The preference of relatively specialized environments can reflect the focus on a specific set of organic resources. An association with wetland components possibly points in the direction of biological communities related to such conditions.

It merits further investigation, how these patterns change in both space and time and how they can translate to the archaeological record. As part of a subsequent research project, this question will be covered on a larger synchronical and diachronical scale in the DFG-funded project "GEOPAL - Geotope reconstruction and Bioeconomic Potential in Palaeolithic site territories" (DFG-GZ: SA 3428/2-1).

Acknowledgements: Funding: This work was supported by the Deutsche Forschungsgemeinschaft (DFG); grant number: DFG-GZ: UT 41/5-1; project title: „GIS-basierte Rekonstruktionen spätpaläolithischer Landnutzungsmuster der nordostbayerischen Mittelgebirgszone"). Special thanks go to the Bavarian Heritage Administration (Bayerisches Landesamt für Denkmalpflege, BLfD) for supporting the research into the Late Glacial archaeological landscape of Northern Bavaria. We also thank the reviewers for their helpful constructive criticism. We also want to thank Dr. Christian Hoggard for redacting the text.

Literature cited

Baales, M. (1999). Neue Untersuchungen zum Spätpaläolithikum des Neuwieder Beckens: Einige Aspekte des Federmesser-Fundplatzes Kettig, Kr. Mayen-Koblenz. *In*: E. Cziesla, T. Kersting & S. Pratsch (Eds.), *Den Bogen spannen... Festschrift für Bernard Gramsch zum 65. Geburtstag*, Beier & Beran, Weissbach, 55-66.

Baales, M. (2001). From lithics to spatial and social organization: interpreting the lithic distribution and raw material composition at the Final Palaeolithic site of Kettig (Central Rhineland, Germany). *Journal of Archaeological Science* 28 (2): 127-141.

Baales, M. (2002). *Der Spätpaläolithische Fundplatz Kettig. Untersuchungen zur Siedlungsarchäologie der Federmesser-Gruppen am Mittelrhein*, Habelt, Bonn.

Baales, M., Mewis, S. & Street, M. (1996). Der Federmesser-Fundplatz Urbar bei Koblenz. *Jahrbuch des Römisch-Germanischen Zentralmuseums Mainz* 43: 241-279.

Banks, W., Aubry, T., d'Errico, F., Zilhão, J., Lira-Noriega, A. & Peterson, A. T. (2011). Eco-cultural niches of the Badegoulian: unraveling links between cultural adaptation and ecology during the Last Glacial Maximum in France. *Journal of Anthropological Archaeology* 30 (3): 359-374.

Banks, W., d'Errico, F., Townsend Peterson, A., Vanhaeren, M., Kageyama, M., Sepulchre, P., Ramstein, G., Jost, A. & Lunt, D. (2008). Human ecological niches and ranges during the LGM in Europe derived from application of eco-cultural niche modelling. *Journal of Archaeological Science* 35: 481-491.

Barka, I., Vladovic, J. & Malis, F. (2011). Landform classification and its application in predictive mapping of soil and forest units. *GIS Ostrava* 1: 23-26.

Beck, M., Beckert, S., Feldmann, S., Kaulich, B. & Pasda, C. (2009). Das Spätpaläolithikum und Mesolithikum in Franken und der Oberpfalz. *Bericht der Bayerischen Bodendenkmalpflege* 50: 269-291.

Beven, K. J. & Kirkby, M. J. (1979). A physically-based variable contributing area model of basin hydrology. *Hydrology Science Bulletin* 24 (1): 43-69.

Binford, L. (1980). Willow smoke and dog's tails: Hunter-gatherer settlement systems and archaeological site formation. *American Antiquity* 45 (1): 4-20.

Binford, L. (2001). *Constructing Frames of Reference*, University of California Press, Berkeley, Los Angeles, London.

Bolus, M. (1992). *Die Siedlungsbefunde des späteiszeitlichen Fundplatzes Niederbieber (Stadt Neuwied)*, Habelt, Mainz.

Bosinski, G. (2007). *Gönnersdorf und Andernach-Martinsberg. Späteiszeitliche Siedlungsplätze am Mittelrhein*, Gesellschaft für Archäologie an Mittelrhein und Mosel, Koblenz.

Bosinski, G. (2008). *Urgeschichte am Rhein*, Kerns Verlag, Tübingen.

Brouwer-Burg, M. (2013). Reconstructing "total" paleo-landscapes for archaeological investigation: an example from the central Netherlands. *Journal of Archaeological Science* 40 (5): 2308-2320.

Burkert, W. & Floss, H. (2006). Lithic Exploitation Areas in the Upper Paleolithic of West and Southwest Germany - A Comparative Study. *In*: G. Körlin & G. Weisgerber (Eds.), *Stone Age - Mining Age*, Deutsches Bergbau-Museum, Bochum, 329-343.

Burnett, M. R., August, P. V., Brown, J. H. & Killingbeck, K. T. (1998). The Influence of Geomorphological Heterogeneity on Biodiversity I. A Patch-Scale Perspective. *Conservation Biology* 12 (2): 363-370.

Conrad, O., Bechtel, B., Bock, M., Dietrich, H., Fischer, E., Gerlitz, L., Wehberg, J., Wichmann, V. & Böhner, J. (2015). System for Automated Geoscientific Analyses (SAGA). *Geoscientific Model Development* 8 (7).

De Reu, J., Bourgeois, J., Bats, M., Zwertvaegher, A., Gelorini, V., De Smedt, P., Chu, W., Antrop, M., De Maeyer, P., Finke, P., Van Meirvenne, M., Verniers, J. & Crombé, P. (2013). Application of the topographic position index to heterogeneous landscapes. *Geomorphology* 186: 39-49.

Eberhardt, H., Keefer, E., Kind, C.-J., Rensch, H. & Ziegler, H. (1987). Jungpaläolithische und mesolithische Fundstellen aus der Aichbühler Bucht. Auswertung von Oberflächenfunden aus dem südlichen Federseegebiet. *Fundberichte aus Baden-Württemberg* 12: 1-51.

Fahlke, J. (2009). *Der Austausch der terrestrischen Säugetierfauna an der Pleistozän/Holozän-Grenze in Mitteleuropa*, Universitäts und Landesbibliothek, Bonn.

Floss, H. (1994). *Rohmaterialversorgung im Paläolithikum des Mittelrheingebietes*, Dr. Rudolf Habelt GmbH, Bonn.

Franklin, J., Potts, A. J., Fisher, E. C., Cowling, R. M. & Marean, C. W. (2015). Paleodistribution modeling in archaeology and paleoanthropology. *Quaternary Science Reviews* 110: 1-14.

Frenzel, B. (1983). Die Vegetationsgeschichte Süddeutschlands im Eiszeitalter. *In*: H. Müller-Beck (Ed.), *Urgeschichte in Baden-Württemberg*, Theiss, Stuttgart, 91-166.

Gelhausen, F. (2011). *Siedlungsmuster der Allerødzeitlichen Federmessergruppen in Niederbieber, Stadt Neuwied*, Gesellschaft für Archäologie an Mittelrhein und Mosel, Mainz.

Geyer, L. (2013). *Die magdalénienzeitlichen Funde von Barbing A*, Lkr. Regensburg, Verlag Dr. Faustus, Erlangen.

Giesler, R., Högberg, M. & Högberg, P. (1998). Soil chemistry and plants in Fennoscandian boreal forest as exemplified by a local gradient. *Ecology* 79: 119-137.

Guisan, A. & Zimmermann, N. E. (2000). Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147-186.

Guisan, A., Weiss, S. & Weiss, A. (1999). GLM versus CCA spatial modeling of plant species distribution. *Plant ecology* 143: 107-122.

Gumpert, K. (1933). Eine paläolithische und mesolithische Abri-Siedlung an der Steinbergwand bei Ensdorf in der Oberpfalz. *Mannus. Zeitschrift für Vorgeschichte* 25 (2): 176-206.

Hahn, J. (1995). Die Buttentalhöhle. Eine spät-jungpaläolithische Abristation im Oberen Donautal. *Fundberichte aus Baden-Württemberg* 20: 13-158.

Hahne, J. (1991). Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im nördlichen Bayern (Rhön, Grabfeld, Lange Berge). *Flora* 185: 17-32.

Hahne, J. (1992). Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im nordöstlichen Bayern (Bayerisches Vogtland, Fichtelgebirge, Steinwald). *Flora* 187: 169-200.

Harris, M. (2001). *The rise of anthropological theory: A history of theories of culture*, AltaMira Press, Walnut Creek.

Heinen, M. (2005). *Sarching '83 und '89/90. Untersuchungen zum Spätpaläolithikum und Frühmesolithikum in Südost-Deutschland*, Welt und Erde, Loogh.

Heinen, M. (2008). Wirklich einzigartig! Der spätpaläolithische Fundplatz Wesseling-Eichholz. *Archäologie im Rheinland 2007*: 46-49.

Higgs, E. S. & Vita-Finzi, C. (1972). Prehistoric Economies: A Territorial Approach. *In*: E. S. Higgs (Ed.), *Papers in Economic Prehistory. Studies by Members and Associates of the British Academy Major Research Project in the Early History of Agriculture*, Cambridge University Press, Cambridge.

Hiltermann, H. (1982). Ökologische Regeln und Erfahrungen von August Thienemann. *Osnabrücker naturwissenschaftliche Mitteilungen* 9: 99-104.

Hobohm, C. (2011). Landschaft und Biodiversität: Welche Faktoren bestimmen die Vielfalt der Gefäßpflanzen von Landschaften? *Berichte der Reinhold-Tüxen Gesellschaft* 23: 37-58.

Hörmann, K. (1913). Der Hohle Fels bei Happurg. *Abhandlungen der Naturhistorischen Gesellschaft Nürnberg* 20: 21-63.

Hunter, M. L., Jacobson, G. L. & Webb, T. (1988). Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation biology* 2 (4): 375-385.

Ikinger, E.-M. (1998). *Der endeiszeitliche Rückenspitzen-Kreis Mitteleuropas*, Lit, Münster.

Jennes, J. (2005). *Topographic Position Index* Extension for ArcView 3.x. Software. www.jennessent.com (2. 1. 2015).

Jennes, J. (2006). *Topographic Position Index*. www.jennessent.com/arcview/TPI_jen_poster.htm (2. 1. 2015).

Jochim, M. (1976). *Hunter-Gatherer Subsistence and Settlement. A Predictive Model*, Academic Press, New York, San Francisco, London.

Jochim, M. (1998). *A Hunter-Gatherer Landscape. Southwest Germany in the Late Palaeolithic and Mesolithic*, Springer, New York, London.

Jochim, M., Herhahn, C. & Starr, H. (1999). The Magdalenian Colonization of Southern Germany. *American Anthropologist* 101 (1): 129-142.

Kaulich, B. (1996). Hohler Fels, Petershöhle und Hunas. Drei altsteinzeitliche Höhlenfundstellen im Herzen der Hersbrucker Alb. *In*: K. Heinlein (Ed.), *Schichten einer Landschaft*, Bund Naturschutz, Nürnberg, 13-23.

Kaulich, B. (2003). Das Abri bei der Troglauermühle, Gde. Falkenberg, Lkr. Tirschenreuth. Spätpaläolithikum, Metallzeiten und Mittelalter an der Waldnaab - Ein Vorbericht. *Beträge zur Archäologie in der Oberpfalz* 6: 9-26.

Kaulich, B. (2004). Das Abri bei der Troglauermühle, Gde. Falkenberg, Lkr. Tirschenreuth. *Beiträge zur Archäologie in der Oberpfalz* 6: 9-26.

Kaulich, B. (2005). Steinbruch contra Steinzeitmensch: Erbendorf "Birkäcker", Lkr. Tirschenreuth - spätpaläolithischer Fundplatz endgültig zerstört. *Beiträge zur Archäologie in der Oberpfalz* 7: 7-16.

Kegler, J. (2002). Die Federmesserzeitliche Fundschicht des Paläolithischen Siedlungsplatzes Andernach-Martinsberg, Grabung 1994-1996. *Archäologisches Korrespondenzblatt* 32: 501-516.

Kelly, R. (1983). Hunter-gatherer mobility strategies. *Journal of Anthropological Research* 39 (3): 277-306.

Kelly, R. (1995). *The foraging spectrum. Diversity in Hunter-Gatherer Lifeways*, Smithsonian Institution Press, Washington, London.

Knipping, M. (1989). *Zur spät- und postglazialen Vegetationsgeschichte des Oberpfälzer Waldes*, Borntraeger, Berlin, Stuttgart.

Kortfunke, C. (1992). *Über die spät- und postglaziale Vegetationsgeschichte des Donaumooses und seiner Umgebung*, Borntraeger, Berlin, Stuttgart.

Kratochwil, A. (1999). Biodiversity in ecosystems: some principles. *In*: A. Kratochwil (Ed.), *Biodiversity in ecosystems: principles and case studies of different complexity levels*, Kluwer Academic Publishers, Dordrecht, Boston, London, 5-38.

Küster, H. (1992). *Postglaziale Vegetationsgeschichte Südbayerns: Geobotanische Studien zur prähistorischen Landschaftskunde*, Akademie Verlag, Berlin.

Lang, G. (1962). Die spät- und frühpostglaziale Vegetationsentwicklung im Umkreis der Alpen. *Eiszeitalter und Gegenwart* 12.

Leser, H. (1996). *Landschaftsökologie*, Ulmer, Stuttgart.

Lyon, L. & Burcham, M. (1998). *Tracking elk hunters with the Global Positioning System*, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden.

MacMillan, R. A. & Shary, P. A. (2009). Landforms and Landform Elements in Geomorphometry. *In*: T. Hengl & H. I. Reuter (Eds.), *Geomorphometry: concepts, software, applications*, Elsevier, Amsterdam, Boston, Heidelberg, London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney, Tokyo.

Magurran, A. (2004). *Measuring Biological Diversity*, Blackwell Publishing, Malden, Oxford, Carlton.

Maier, A. (2015). *The Central European Magdalenian. Regional Diversity and Internal Variability*, Springer, Dordrecht, Heidelberg, New York, London.

Meynen, E., Schmithüsen, J., Gellert, J., Neef, E., Müllerminy, H. & Schultze, J. (1962a). *Handbuch der Naturräumlichen Gliederung Deutschlands, Bd. 1*, Bad Godesberg.

Meynen, E., Schmithüsen, J., Gellert, J., Neef, E., Müllerminy, H. & Schultze, J. (1962b). *Handbuch der Naturräumlichen Gliederung Deutschlands, Bd. 2*, Bad Godesberg.

Möbius, K. A. (1877). *Die Auster und die Austernwirtschaft*, Verlag von Wiegandt, Hempel & Parey, Berlin.

Moník, M. & Pankowská, A. (2020). Settlement Patterns of the Late Palaeolithic in Bohemia and Moravia. *In*: S. Grimm, M.-J. Weber, L. Mevel & I. Sobkowiak-Tabaka (Eds.), *From the Atlantic to beyond the Bug river. Finding and Defining the Federmesser-Gruppen/Azilian*, Proceedings of Session A5b (Commission "The Final Palaeolithic of Northern Eurasia") of the XVIIth UISPP Congress, Burgos, September 2014, Verlag des Römisch-Germanischen Zentralmuseums, Mainz, 79-89.

Mischka, D. (2007). *Methodische Aspekte zur Rekonstruktion prähistorischer Besiedlungsmuster. Landschaftsgenese vom Ende des Neolithikums bis zur Eisenzeit im Gebiet des südlichen Oberrheins*, Rhaden/Westfalen.

Morisita, M. (1959). Measuring of the dispersion and analysis of distribution patterns. *Memoires of the Faculty of Science* 2: 215–235.

Neef, E. (1968). Der Physiotop als Zentralbegriff der komplexen physischen Geographie. *Petermanns Geographische Mitteilungen* 112: 15-23.

Neef, E. (1981). *Das Gesicht der Erde*, H. Deutsch, Zürich, Frankfurt a. Main.

Parker, K. & Bendix, J. (1996). Landscape-scale geomorphic influences on vegetation patterns in four environments. *Physical Geography* 17 (2): 113-141.

Parkington, J., Cable, C., Carter, P., Deacon, H., Deacon, J., Humphreys, A., Inskeep, R., Isaac, G., Jacobson, L. & Brooker, M. L. (1980). Time and Place: Some Observations on Spatial and Temporal Patterning in the Later Stone Age Sequence in Southern Africa [with Comments and Reply]. *The South African Archaeological Bulletin*: 73-112.

Pyke, G. H. (1984). Optimal foraging theory: a critical review. *Annual review of ecology and systematics* 15 (1): 523-575.

Richter, J. (1990). Diversität als Zeitmaß im Spätmagdalénien. *Archäologisches Korrespondenzblatt* 20: 249-257.

Sauer, F. & Riede, F. (2019). A critical reassessment of cultural taxonomies in the Central European Late Palaeolithic. *Journal of Archaeological Method and Theory* 26 (1): 155-184.

Sauer, F. (2016). Raw material procurement economy and mobility in Late Palaeolithic Northern Bavaria. *Quartär* 63: 125-135.

Sauer, F. (2018). *Spätpaläolithische Landnutzungsmuster in Bayern*, OPUS FAU, Erlangen.

Sauer, F. (2020). Landform-Based Modelling of Potential Bilogical Diversity. Inferring Ecological Variability in Site Catchments from Digital Elevation Data. *In*: S. Grimm, M.-J. Weber, L. Mevel & I. Sobkowiak-Tabaka (Eds.), *From the Atlantic to beyond the Bug river. Finding and Defining the Federmesser-Gruppen/Azilian*, Proceedings of Session A5b (Commission "The Final Palaeolithic of Northern Eurasia") of the XVIIth UISPP Congress, Burgos, September 2014, Verlag des Römisch-Germanischen Zentralmuseums, Mainz, 67-78.

Schaefer, M. (1999). The diversity of the fauna of two beech forests: some thoughts about possible mechanisms causing the observed patterns. *In*: A. Kratochwil (Ed.), *Biodiversity in ecosystems: principles and case studies of different complexity levels*, Kluwer Academic Publishers, Dordrecht, Boston, London, 39-58.

Schmeidl, H. (1971). Ein Beitrag zur spätglazialen Vegetations- und Waldentwicklung im westlichen Salzachgletschergebiet. *Eiszeitalter und Gegenwart* 22: 110-126.

Schönweiß, W. & Sticht, E. (1968). Das Endpaläolithikum von Plankenfels/Ofr. *Archiv für Geschichte von Oberfranken* 48: 71-86.

Schönweiß, W. (1974). Fränkisches Epipaläolithikum - Die Atzenhofener Gruppe. *Bonner Hefte zur Vorgeschichte* 8: 17-108.

Schönweiß, W. (1982). Die spätpaläolithische Fundlandschaft der Bibertmündung bei Altenberg. *Abhandlungen der Naturhistorischen Gesellschaft Nürnberg* 39: 47-58.

Schönweiß, W. (1989). Ein Schlagplatz der Federmesserkultur im Fichtelgebirge. *Archäologisches Korrespondenzblatt* 19: 325-331.

Schönweiß, W. (1992). *Letzte Eiszeitjäger in der Oberpfalz. Zur Verbreitung der Atzenhofener Gruppe des Endpaläolithikums in Nordbayern*, Grafenwöhr.

Schönweiß, W. (1993). Leupoldsdorf 2 – Das Frühmesolithikum Nordbayerns – Bergbau und Rohstoffgewinnung am Feuerberg bei Wunsiedel. *Archiv für Geschichte von Oberfranken* 73: 11-54.

Schönweiß, W. (1997a). Neufunde der Endeiszeit aus der nördlichen Oberpfalz. *Oberpfälzer Heimat* 41: 7-23.

Schönweiß, W. (1997b). Endpaläolithikum und Frühmesolithikum aus Uckersdorf, Lkr. Schwandorf. *Beiträge zur Archäologie in der Oberpfalz* 1: 97-111.

Schwabe, A. (1999). Spatial arrangements of habitats and biodiversity: an approach to a sigmasociological view. *In*: A. Kratochwil (Ed.), *Biodiversity in ecosystems: principles and case studies of different complexity levels*, Kluwer Academic Publishers, Dordrecht, Boston, London, 75-106.

Simpson, E.H. (1949). Measurement of diversity. *Nature* 163: 1476-4687.

Smith, T. & Smith, R. (2009). *Ökologie*, Pearson Studium, München.

Sørensen, R., Zinko, U. & Seibert, J. (2006). On the calculation of the topographic wetness index: evaluation of different methods based on field observations. *Hydrology and Earth Sciences* 10: 101-112.

Stalling, H. (1987). *Untersuchungen zur spät- und postglazialen Vegetationsgeschichte im Bayerischen Wald*, Schweizerbart, Göttingen.

Stojakowits, P., Friedmann, A. & Bull, A. (2014). Die spätglaziale Vegetationsgeschichte im oberen Illergebiet (Allgäu/Bayern). *Eiszeitalter und Gegenwart* 63 (2): 130-142.

Summerfield, M.A. (1991). *Global Geomorphology*, Longman, Singapore.

Süß, E. & Thomann, E. (2009). *Vorgeschichtliche Funde aus dem Landkreis Schwandorf*, Nabburg.

Svenning, J.-C., Fløjgaard, C., Marske, K.A., Nógues-Bravo, D. & Normand, S. (2011). Applications of species distribution modeling to paleobiology. *Quaternary Science Reviews* 30 (21): 2930-2947.

Swanson, F., Kratz, T., Caine, N. & Woodmansee, R. (1988). Landform effects on ecosystem patterns and processes. *BioScience*: 92-98.

Tagil, S. & Jenness, J. (2008). GIS-based automated landform classification and topographic, landcover and geologic attributes of landforms around the Yazoren Polje, Turkey. *Journal of Applied Sciences* 8: 910-921.

Tallavaara, M., Eronen, J. & Luoto, M. (2018). Productivity, biodiversity, and pathogens influence the global hunter-gatherer population density. *Proceedings of the National Academy of Sciences* 115 (6): 1232-1237.

Thannheiser, D. (1992). Landschaftsökologische Studien in der kanadischen Arktis. *Naturschutzforum* 5/6: 201-217.

Tourneau, G. (1933). Eine mesolithische Wohngrubensituation bei Pottenstein in der fränkischen Schweiz. *Bayerische Vorgeschichtsblätter* 11: 70-74.

Uthmeier, T., Ickler, S. & Kurbjuhn, M. (2008). Site Catchment Analysis in the Late Middle Palaeolithic of Crimea: a GIS Based Approach. *In*: V. Chabai, J. Richter & T. Uthmeier (Eds.), *Kabazi V: Interstratification of Micoquian and Levallois-Mousterian camp sites, Part II.* , Kerns, Simferopol, Köln, 481-508.

Valde-Nowak, P., Kraszewska, A. & Stefański, D. (2012). Arch-backed and Tanged Point Technocomplexes in the North Carpathian zone. *Recherches Archéologiques Nouvelle Serie* (5-6): 69-85.

van Wagtendonk, J.W. & Benedict, J.M. (1980). Travel time variation on backcountry trails. *Journal of Leisure Research* 12 (2): 100-106.

Vermessungsverwaltung, Bayerische (2012). Digitales Geländemodell DGM 25 (Datensatz).

Vita-Finzi, C., Higgs, E.S., Sturdy, D., Harris, J., Legge, A.J. & Tippet, H. (1970). Prehistoric Economy in the Mount carmel Area of Palestine: Site Catchment Analysis. *Proceedings of the Prehistoric Society* 36: 1-37.

Weiss, A.D. (2001). *Topographic Position and Landform Analysis.* www.jennessent.com/downloads/tpi-poster-tnc_18x22.pdf (7. 2. 2015).

Weißmüller, W. (1987). Eine Freilandfundstelle des mittleren Jungpaläolithikums (Périgordien-Gravettien) am Südrand der Straubinger Senke bei Salching, Ldkr. Straubing-Bogen, *Quartär* 37/38: 109-134.

Weißmüller, W. (1995). *Sesselfelsgrotte II. Die Silexartefakte der Unteren Schichten der Sesselfelsgrotte. Ein Beitrag zum Problem des Moustérien*, Franz Steiner, Saarbrücken.

Werner, H. & Schönweiß, W. (1974). Eine epipaläolithische und mesolithische Wohnanlage von Sarching, Ldkr. Regensburg. Eine Fundstelle der "Atzenhofener Gruppe" im Donautal? *Bonner Hefte zur Vorgeschichte* 8: 109-120.

Zimmermann, R. & Thom, B. (1982). Physiographic plant geography. *Progress in Physical Geography* 6 (1): 45-59.

Zipf, G.K. (2012). *Human Behavior and the Principle of Least Effort*, Martino Fine Books, Mansfield Centre.

Inhalt - *Contents*