DOI:10.24394/NatSom.2011.19.51

Natura Somogyiensis	19	51-66	Kaposvár, 2011

Climatic conditions and habitats in Belső-Somogy, Külső-Somogy and Zselic as vegetation-based landscape regions II. Temperature and precipitation sensitivity of woodlands

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Salamon-Albert, É., Horváth, F., Ortmann-Ajkai, A.: *Climatic conditions and habitats in Belső-Somogy, Külső-Somogy and Zselic as vegetation-based landscape regions II. Temperature and precipitation sensitivity of woodlands.*

Abstract: In our study climatic sensitivity of significant woody habitats are discussed in the territory of vegetation based landscape regions of South Transdanubia, including Belső-Somogy, Külső-Somogy and Zselic. Selected bioclimatic variables are used to characterize regional and habitat climate surfaces and envelopes by habitat occurrence. Gaussian probability curves were fitted, using long term (1961-1990) data for yearly and quarterly temperature and precipitation variables, representing general and extreme climatic conditions. Studied woodlands are sufficiently integrated into the climate surface and envelopes of the region, according to multipeaks of bioclimatic indices. Among woody habitat types, riverine and swamp woodlands (J) turned to be the most climate sensitive habitats, due to their few peaks with extreme values by numerous bioclimatic indices, especially yearly and quarterly precipitation variables. Mesic deciduous woodlands (K) are no directly climate sensitive on temperature relations, but they are like on the short time quarterly precipitation. Peaks of dry closed deciduous woodlands (L) and other tree dominated habitats (R) are completely fitted to regional climate surfaces and envelopes, so they have no significant climate sensitivity by any analysed bioclimatic variable.

Keywords: habitat distribution modelling (HDM), climate surface, climate envelope, MÉTA database, woodlands, landscape ecology

Introduction

Climate and its change effecting biodiversity is a hot topic of climatic and ecological research, using distribution models, niche theory models and bioclimatic envelope models for predicting distributions or occurrences of species or habitats (Botkin et al. 2007). Key role of climate as determinant of vegetation patterns was recognized already by the very first vegetation scientists, as Humboldt, Bonpland and de Candolle (Guisan and Zimmermann 2000). Climate-vegetation interactions were widely analysed under differ-

ISSN 1587-1908 (Print); ISSN 2062-9990 (Online)

ent spatial scales connected with some vegetation classification according to bioms, continents, countries and regions (OZENDA and BOREL 2000, HOSSEL et al. 2003, PIOVESAN et al. 2005, THOMPSON et al. 2005, ATTORE et al. 2007, THOMPSON et al. 2008). Need for smaller-scale studies are expressed by more and more authors currently (e.g. LINDNER et al. 2010), but conclusions derived from scientific results based on large scale studies have to be applied with caution. Distributions may not match climate exclusively, because of biotic interactions, adaptive evolution, dispersal limitation and historical chance that each or all could exist behind the phenomena (BEALE et al. 2008).

Bioclimatic indices connected to vegetation data are widely used for interpretation of species or habitat distribution or suitability in vegetation science under different climate scenarios (HOSSELL et al. 2003, BEAUMONT et al. 2005, HIJMANS et al. 2005, ATTORRE et al. 2007, CZÚCZ et al. 2009). They were originated from the monthly temperature and precipitation data in order to generate more biologically meaningful variables, representing annual trends, seasonality and extreme or limiting environmental factors (HIJMANS et al. 2005). Climate has been shown to be a significant environmental feature in determining vegetation distribution and classification for European scales, especially in woody habitat types. It is important that we are able to describe current habitat distribution in a reliable way according to climate surface and quantify their climate envelope by a climatic niche concept. It will be reassuming used for analysing and detecting functional landscape diversity and climatic sensitivity of woodlands, to be able to understand the impacts of temperature and precipitation at different scales.

Habitat distribution models often built up on bioclimatic variables as abiotic predictors according to niche stability and evolution (GUISAN-ZIMMERMANN 2000, ZIMMERMANN et al. 2010). Habitat distribution models (HDMs) derived from species distribution modelling (SDMs), can evaluate range of occurrence from environmental point of view, leading towards habitat adaptation under certain climatic conditions. Novel analyses, e.g. connecting distribution models with other ecological phenomena, can provide novel capacities for understanding specific and general drivers of ranges in occurrence.

In this study our aims were to reveal 1) what the climatic range and the character of woodland distributions are, 2) what the relations between regional and habitat climate envelopes are, 3) which climate variables the most significant in woodland habitat distribution and climate sensitivity are.

Material and method

Study area

The study area includes the territory of three vegetation based landscape regions of South Transdanubia: Külső-Somogy, Belső-Somogy and Zselic, covering about 5705 km^2 (570500 ha) in total (Fig 1). Their borders are defined on the basis of present zonal or dominant extrazonal or edaphic vegetation by the knowledge of local expert botanists. It is not derived from any database (MOLNÁR CS. et al. 2008) and differs from the previously used, country-wide, geography-based landscape divisions (e.g. MAROSI and SOMOGYI 1990). Elevation varies in a moderate range from lowlands (96 m a.s.l.) to hills (300 m a.s.l.), average altitude is 161 m a.s.l. Long-term annual precipitation varies between 562 and 753 mm, the average is 674 mm, the annual temperature varies between 9.8 ºC and 11.3 ºC, the average is 10.8 ºC. Studied regions are at the intersection of three climatic areas: from west as the atlantic, from east as the continental and from south as the mediterranean, that can influence the general climatic pattern. According to the main

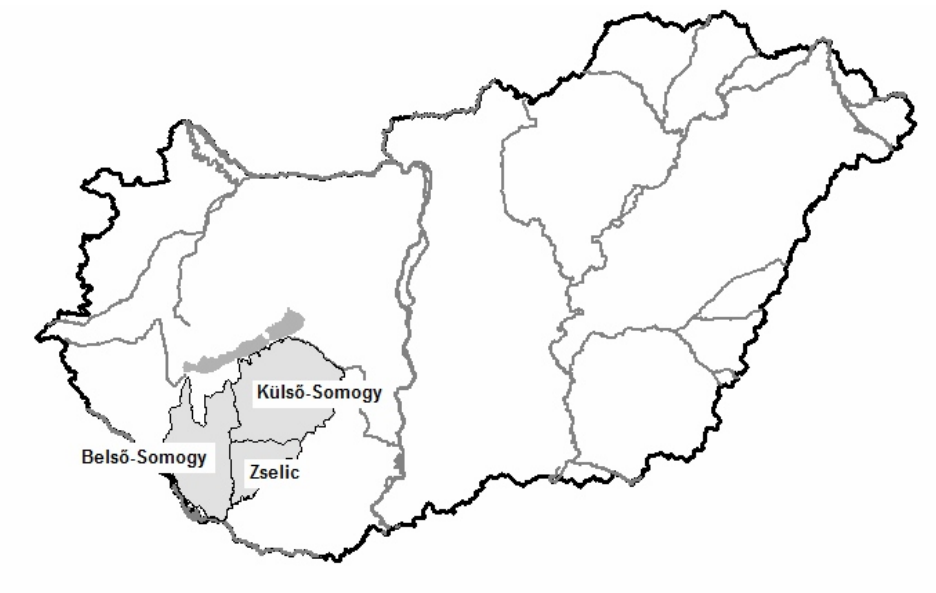

Fig. 1: Study area in South Transdanubia, Hungary, with the three vegetation based landscape regions appearing in Somogy county

geobotanical division of Europe, the regions are rated into the submontaneous oak-hornbeam woodlands and thermophilous oak woodlands with open steppe oak woodlands and riparian vegetation (OZENDA and BOREL 2000).

BIOCLIM variables

For the sake of BIOCLIM calculation, monthly averages of climatic data were used, which were measured at weather stations on global and local scales. Temperature data are from the WorldClim database (http://www.worldclim.org/, HIJMANS et al. 2005), precipitation data are from the local weather stations of Hungarian Meteorological Service (http://vissycd.glia.hu/atlasz.html, MERSICH et al. 2001). Set of selected variables are reported as the regional climatic surface and climatic envelope for potential habitat occurrence (Table 1). Calculation was carried out by the Institute of Ecology and Botany, Hungarian Academy of Sciences (CZÚCZ et al. 2007). Selected variables for the analyses are BIOCLIM-1 the annual mean temperature, BIOCLIM-4 the annual temperature seasonality calculated as the standard deviation of monthly means × 100, BIOCLIM-8 the mean temperature of wettest quarter, BIOCLIM-9 the mean temperature of driest quarter, BIOCLIM-12 the annual mean precipitation, BIOCLIM-17 the precipitation of driest quarter, BIOCLIM-18 the precipitation of warmest quarter, BIOCLIM-19 the precipitation of coldest quarter. Annual data refer to monthly climate measurements from January to December, wettest quarter means data from June to August, driest quarter means data from January to March, warmest quarter means data from June to August, coldest quarter means data from December to February as the periods of three months, ¼ of a year.

Bioclimatic variables were calculated on a long-term (1961-1990) average monthly data and were used for defining climate surface and envelope of the region and climate

Table 1: Basic statistics of the climate surface and the envelope in the landscape regions

Climate SURFACE		range	min	mean	max	std
BIOCLIM-1	Annual mean temperature	1.5	9.8	10.8	11.3	± 0.2
BIOCLIM-4	Temperature seasonality	49	738	764	787	± 12
BIOCLIM-8	Mean temperature of wettest quarter	2.7	17.9	19.4	20.6	± 0.6
BIOCLIM-9	Mean temperature of driest quarter	1.8	1.1	2.1	2.9	± 0.3
BIOCLIM-12	Annual precipitation	191	562	674	753	± 44
BIOCLIM-17	Precipitation of driest quarter	34	100	121	134	± 8
BIOCLIM-18	Precipitation of warmest quarter	57	188	223	245	± 11
BIOCLIM-19	Precipitation of coldest quarter	34	109	130	143	± 8

Climate ENVELOPE		range	min	mean	max	std
BIOCLIM-1	Annual mean temperature	1.5	9.8	10.7	11.3	± 0.2
BIOCLIM-4	Temperature seasonality	47	739	762	786	± 12
BIOCLIM-8	Mean temperature of wettest quarter	2.7	17.9	19.4	20.6	± 0.7
BIOCLIM-9	Mean temperature of driest quarter	1.7	1.2	2.1	2.9	± 0.3
BIOCLIM-12	Annual precipitation	180	570	681	750	± 42
BIOCLIM-17	Precipitation of driest quarter	34	100	122	134	± 8
BIOCLIM-18	Precipitation of warmest quarter	55	190	225	245	± 11
BIOCLIM-19	Precipitation of coldest quarter	33	110	131	143	± 8

envelope of woody habitats. In the first step, scatterplots were constructed from the relative distribution (%) on total area of the region as the regional climate surface, on total area covered by any semi-natural vegetation as the regional climate envelope and on woodland types as the habitat envelope according to bioclimatic variables. Data originated from the linked dataset of habitat occurrence and climatic variables, were sorted for the analyses representing all of the sampling points (MÉTA hexagons) in the three vegetation based landscape regions for the regional climate surface (n=16300) and the envelope (n=9187). In second step, area version of Gaussian function as a nonlinear single or multipeak analysis was executed on each scatterplot, computing Levenberg–Marquardt algorithm as an iterative procedure by Origin 6.1 (OriginLab Inc). Gaussian model describes a bell-shaped curve like a normal probability distribution function. It is characterized by the center of the peak that matematically represents the mean of designated variable and the width of the peak at half height, that is the standard deviation. Representative parameters of distributions were calculated for describing position of the peaks: average (center) and minimum-maximum x-value at half hight (width) of the Gaussian curve. Resulted these parameters, they were statistically compared by a one-way analysis of variance (ANOVA). Pairwise significant differences were counted if $p<0.05$. Climatic sensitivity of a habitat was interpreted as the distribution variability in number and position of the peaks, that were adjusted by ascendent order from lower to higher values of a given bioclimatic variable (e.g. ENV1 to ENV5, see in Table 2). Significant differences to each other and the regional climate envelope were presented by their representative x-value parameters among multipeaks within the envelopes. Peaks are the function of the climate parameter from habitat occurrence point of view. Overlapping peaks without any significant difference are interpreted as a climate gradient, peaks that have significant difference to the others are defined as a regional climate or habitat functional group.

Based on data of above-mentioned climate GIS databases, distribution maps were prepared in order to connect regional spatial and habitat occurrence data, using ArcMap 9.2 ESRI (Figs 4 to 6). Number and limits of ranges in bioclimatic data displayed on maps, corresponded to those of Gaussian multipeaks. In the case of BIOCLIM-1 that has only one Gaussian peak, was decided to display two ranges separated by natural break option of ArcMap, reflecting to altitudinal zones of the surface. In the thematic maps darker colors show the higher, lighter colors show the lower values of bioclimatic indices.

MÉTA habitats

MÉTA project (2002-2006) was a systematic habitat mapping of the Hungarian vegetation on landscape scale integrated with spatial and geographical information (BÖLÖNI et al 2007, MOLNÁR et al 2007, HORVÁTH et al. 2008). MÉTA quadrats (35 km^2 per each) are the organisational and constructing units, divided into hexagons (35 hectares per each) per each for higher resolution, as the basic units of MÉTA tables and databases (HORVÁTH and POLGÁR 2008). In our study, woody habitat types and selected bioclimatic variables were assigned to finer spatial scale for 16300 hexagons of 163 MÉTA quadrats.

In total 57 MÉTA habitat types were identified in the vegetation based regions, including woody habitats with natural, semi-natural and managed status (SALAMON-ALBERT et al. 2008, 2010). In our study we focused on significant woody habitat groups of the landscape, using the binary data of occurrence for the analyses. Main woody habitat groups in the regions are: riverine and swamp woodlands (signed by J, n=1943), mesic deciduous woodlands (signed by K, n=3848), closed dry deciduous woodlands (signed by L, n=906) and other tree dominated habitats (signed by R, n=4708). Riverine and swamp woodlands are abundant in Belső-Somogy, mostly streamside alder groves (signed by J5, 8.7%) and alder swamps (signed by J2, 2.4%). Mesic deciduous woodlands are the most widespread as the original zonal vegetation in the study area by hornbeam-pedunculate oak forests (signed by K1a, 8.0%) that dominate in Belső-Somogy, by hornbeam-sessile oak forest (signed by K2, 4.3% and 8.1%) occur in Külső-Somogy and Zselic, by beech forests (signed by K5, 5.4%) that are also important in Zselic. Closed dry deciduous woodlands (L) are sporadic and marginal in Külső-Somogy, most of them are disappeared nowadays, their actual coverage is about 3.0%. Other tree dominated habitats (including RA, RB and RC habitat types) that are mostly plantations, dominate in Belső-Somogy and Külső-Somogy (12.0%, 14.0%), far less widespread in Zselic (7.0%). English nomenclature of habitats is by MOLNÁR ZS. et al (2008).

Results

There was a strong superimposition between data of the climate surface and the envelope (Table 1), and also there was no significant difference between their peak distribution by any BIOCLIM variable. Natural and semi-natural habitats occupy territories by their climate envelope according to the climate surface of the region. Due to the previous facts, our results are introduced as the similarity or dissimilarity of woodland habitat distribution to the regional climate envelope.

Climate envelope as the functional effectuation of climate niche concept, had variable ranges according to nature of the variable. Among temperature variables, BIOCLIM-4 the temperature seasonality had the widest range and deviation, BIOCLIM-1 the mean temperature of the year has the narrowest one. Among precipitation variables, BIOCLIM-12 the annual sum of precipitation has the widest range and deviation, BIOCLIM-19 the precipitation in the coldest quarter has the narrowest ones. Ranges in precipitation vari-

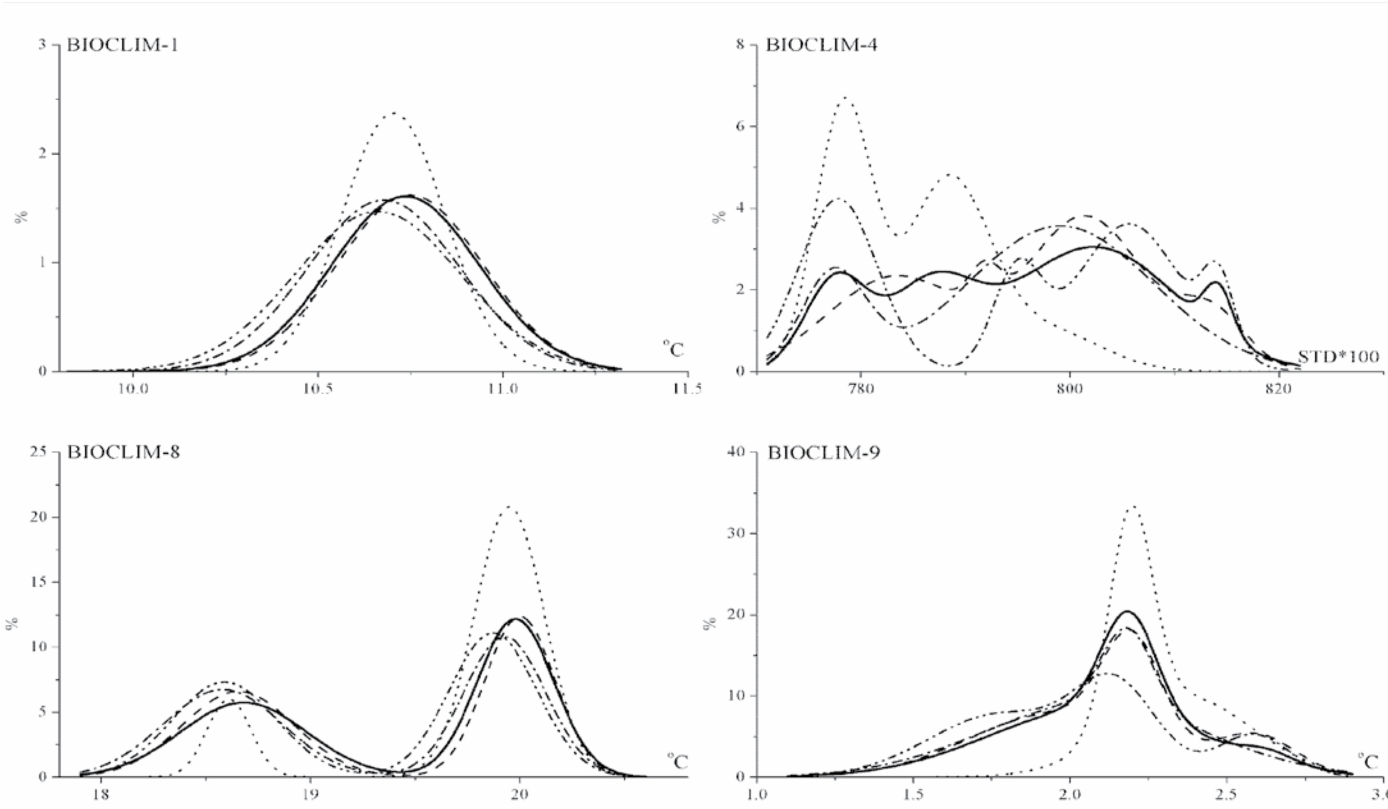

Fig. 2: Gaussian curves of woodland distribution on relative occurrence by temperature variables in the landscape regions.
Signs: – regional climate envelope, ··· riverine and swamp woodlands (J), – · – mesic deciduous woodlands (K),
– · · – closed dry deciduous woodlands (L), – – other tree dominated habitats (R).

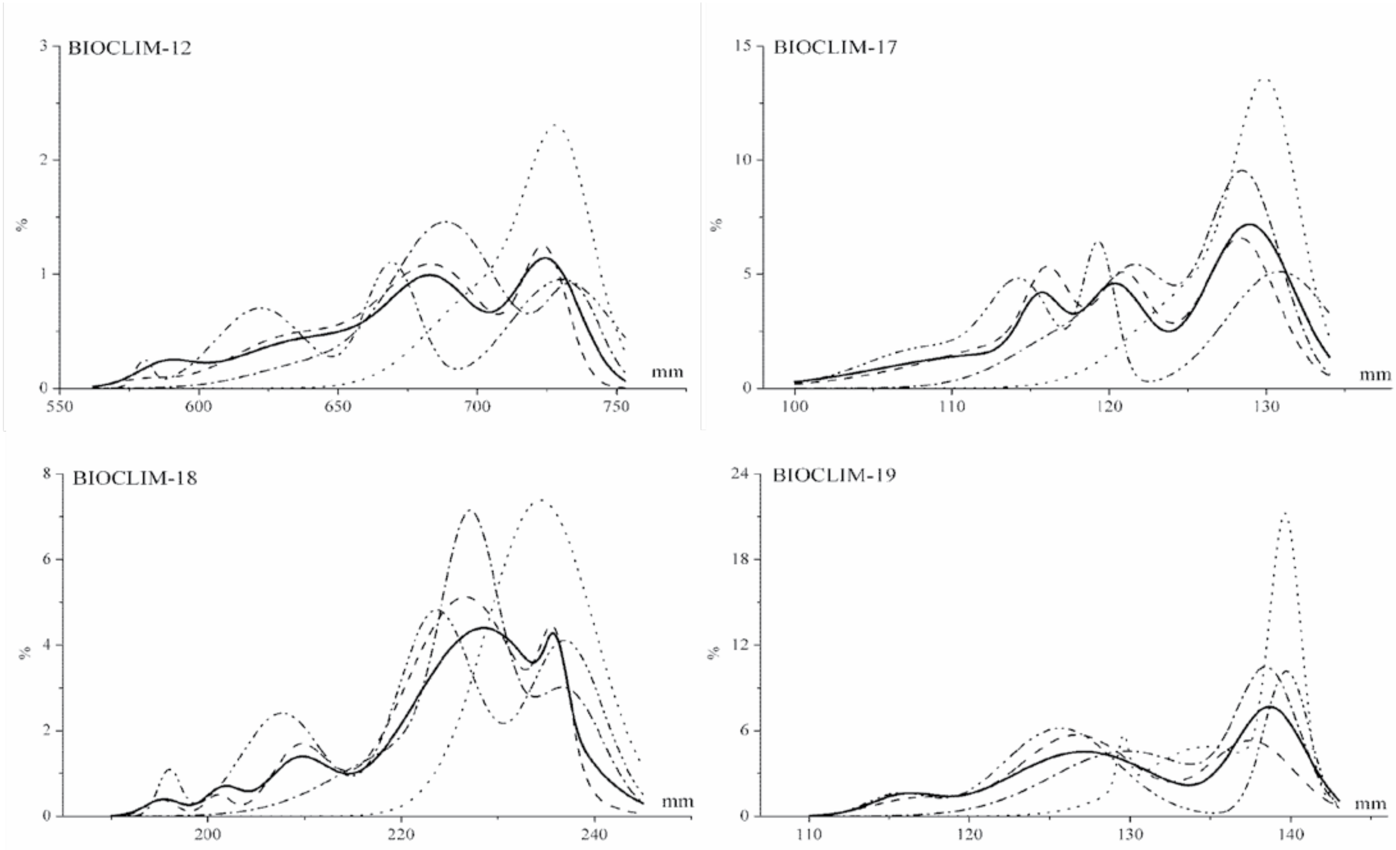

Fig. 3: Gaussian curves of woodland distribution on relative occurrence by precipitation variables in the landscape regions
Signs: – regional climate envelope, ··· riverine and swamp woodlands (J), – · – mesic deciduous woodlands (K), – · · – closed dry deciduous woodlands (L), – – other tree dominated habitats (R).

Table 2: Width at half height and the center of the multipeaks for the regional climate envelope (ENV1 to ENV5) and woody habitat groups (J1 to R5). Significant differences are signed by different small letters

	BIOCLIM-1		BIOCLIM-4		BIOCLIM-8		BIOCLIM-9		BIOCLIM-12		BIOCLIM-17		BIOCLIM-18		BIOCLIM-19	
	width	center	width	center	width	center	width	center	width	center	width	center	width	center	width	center
ENV1	0.4	10.7	5.1	778 *a*	0.6	18.7 *a*	0.7	2.1 *a*	19	588 *a*	14	113 *a*	4	195 *a*	4	116 *a*
ENV2			8.3	787 *a*	0.4	20.0 *b*	0.2	2.2 *a*	59	643 *b*	3	116 *a*	4	202 *a*	9	127 *b*
ENV3			15.9	802 *b*			0.2	2.6 *a*	31	685 *b*	4	120 *a,b*	6	209 *a,b*	4	139 *c*
ENV4			2.5	814 *b*					23	725 *b*	6	129 *b*	14	229 *c*		
ENV5													2	236 *c*		
J1	0.3	10.7	5.3	778 *a*	0.2	18.6 *a*	0.1	2.2 *a*	41	704 *a*	9	126 *a*	11	234	0	130 *a*
J2			8.0	788 *a*	0.3	19.9 *b*	0.4	2.4 *a*	23	730 *a*	4	130 *a*			8	135 *a,b*
J3			9.8	798 *b*											2	140 *b*
K1	0.4	10.7	6.1	777 *a*	0.6	18.6 *a*	0.2	2.2 *a*	43	642 *a*	8	119 *a*	15	221 *a*	9	130 *a*
K2			17.8	799 *b*	0.4	19.9 *b*	0.7	2.1 *a*	38	689 *a,b*	4	122 *a*	6	227 *a,b*	4	139 *a*
K3									19	734 *b*	5	129 *a*	7	237 *b*		
L1	0.4	10.7	7.5	778 *a*	0.5	18.6 *a*	0.5	1.8 *a*	5	580 *a*	8	109 *a*	2	196 *a*	4	116 *a*
L2			4.5	795 *b*	0.4	19.9 *b*	0.3	2.1 *a*	32	622 *a*	4	114 *a*	8	208 *a*	7	126 *b*
L3			10.1	806 *b,c*			0.2	2.6 *b*	19	669 *b*	2	119 *a,b*	8	224 *b*	3	140 *c*
L4			3.0	814 *b,c*					37	730 *c*	7	131 *b*	8	237 *c*		
R1	0.4	10.7	13.1	783 *a*	0.5	18.6 *a*	0.6	2.0 *a*	20	580 *a*	16	118 *a*	3	195 *a*	5	117 *a*
R2			2.7	792 *a,b*	0.3	20.0 *b*	0.2	2.2 *a,b*	43	634 *b*	2	116 *a,b*	2	201 *a,b*	7	127 *b*
R3			11.1	802 *b,c*			0.3	2.6 *b*	39	684 *b,c,d*	3	121 *a*	6	210 *b*	5	138 *c*
R4			6.5	814 *c*					16	724 *d*	4	128 *a,c*	12	227 *c*		
R5													3	236 *c*		

ables for driest and coldest quarter are similar due to the remarkable seasonal overlapping (see Material and Method).

Analysing habitat distribution of woodlands occurrence by temperature variables, there are four peak pattern types, including 1, 2, 3 or 4 multipeaks (Figure 2, Table 2). BIOCLIM-1 has one bell-shaped distribution curve, the same as in regional climate and habitat envelopes, forming one regional climatic functional group. Among distribution curves riverine and swamp woodlands (J) has the narrowest width at half height with the highest relative proportion. Maximum frequency in occurrence all of woody habitats is manifested at exactly equalled mean annual temperature compared to the one of the regional climate envelope.

BIOCLIM-4 has a four-peaked distribution as the regional climate envelope, containing two climate functional groups (ENV1-2, ENV3-4) in its range. All woody habitats completely seize the range of this bioclimatic variable, but the exception of riverine and swamp woodlands. Among habitats mesic deciduous woodlands (K) have a two-peaked distribution, assuming at the medium regional values. Riverine and swamp woodlands (J) has a three-peaked distribution at the lowest values of annual seasonality range. Closed dry deciduous woodlands (L) and other tree dominated habitats (R) both have a four-peaked distribution, properly fitted to multipeak of regional climate envelope by the annual temperature seasonality.

BIOCLIM-8 has a significantly different two-peaked regional climate envelope, containing two regional climate functional groups (ENV1, ENV2). All woody habitats completely seize the range of this bioclimatic variable and they are also completely divided by the differentiation of regional climate envelope, resulting similar width and proportion within the groups. The only exception are the riverine and swamp woodlands, that have a narrowest width at lower temperatures and a higher proportion at higher temperatures of the mean temperature of wettest quarter.

BIOCLIM-9 has a three-peaked regional climate envelope, showing only one climate functional group (ENV1-3) in its range. Most of woody habitats completely seize the range of this bioclimatic varible. Riverine and swamp woodlands (J) as an exception, having a two-peaked distribution and it is shifted toward the highest temperatures with the highest proportion at medium regional temperature range. Mesic deciduous woodlands (K) have also a two-peaked distribution, normally fitted to higher temperatures of regional climate envelope. Closed dry deciduous woodlands (L) and other tree dominated habitats (R) both have a three-peaked distribution, properly fitted to the multipeak of regional climate envelope by the mean temperature of driest quarter.

Analysing habitat distribution of woodlands occurrence by precipitation variables, there were three peak pattern types, including 3, 4 or 5 multipeaks (Fig. 3, Table 2). BIOCLIM-12 has a four-peaked regional climate envelope, insisting two climate functional groups (ENV1, ENV2-4). Most of woody habitats (K, L, R) completely seize the range of annual precipitation, but the exception of riverine and swamp woodlands. J habitats exclusively occur at high yearly precipitation (>650 mm), including two peaks as one habitat functional group. Mesic deciduous woodlands have a three-peaked distribution, by two significantly different habitat functional groups (ENV1 and 3, ENV2). Closed dry deciduous woodlands (L) and other tree dominated habitats (R) both have a four-peaked distribution, properly fitted to multipeak of regional climate envelope by the annual precipitation.

BIOCLIM-17 displays a four-peaked regional climate envelope, containing two climate functional groups (ENV1-3, ENV4). Some of woody habitats (L, R) completely seize the range of this variable, but the exception of riverine and swamp woodlands and mesic deciduous woodlands at the range of higher precipitation. J habitats exclusively

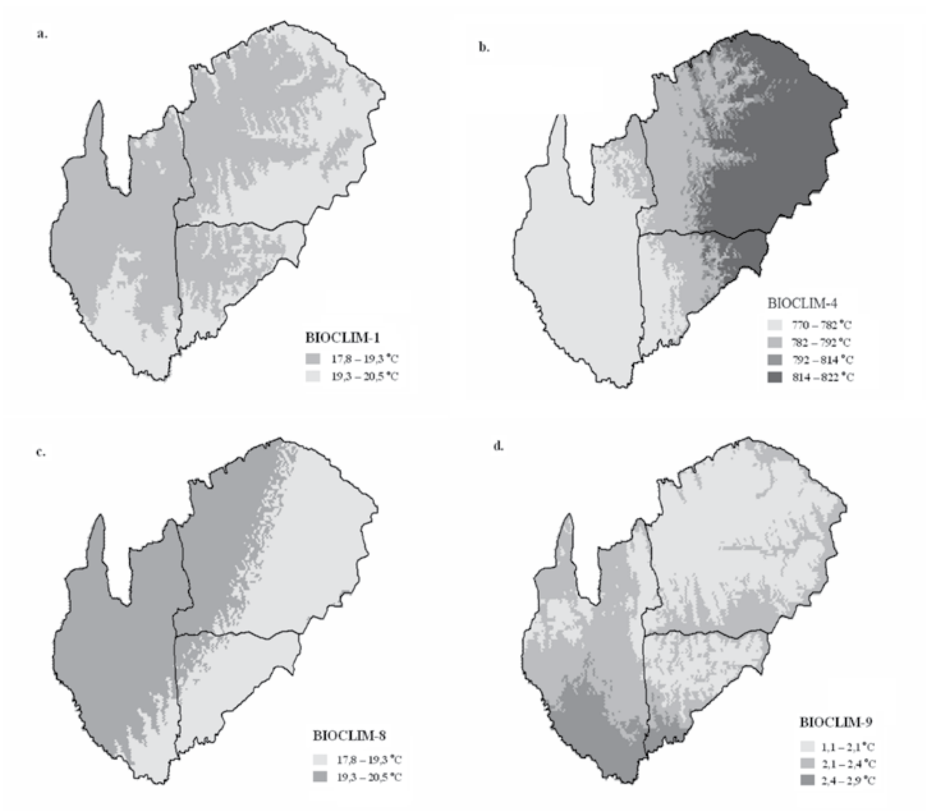

Fig. 4: Spatial patterns of temperature variables as the regional climate surface

a) BIOCLIM-1 the mean annual temperature, b) BIOCLIM-4 the temperature seasonality, c) BIOCLIM-8 the mean temperature of wettest quarter, d) BIOCLIM-9 the mean temperature of driest quarter. More sign and abbreviation see in Material and methods

occur at high precipitation (>110 mm), including two peaks as one habitat functional group. Mesic deciduous woodlands (K) have a three-peaked distribution, clustered into one habitat functional group also. Closed dry deciduous woodlands (L) and other tree dominated habitats (R) both have a four-peaked distribution with two habitat functional groups, properly fitted to multipeak of regional climate envelope by the precipitation of driest quarter.

BIOCLIM-18 displays a five-peaked regional climate envelope, containing two climate functional groups (ENV1-3, ENV4-5). Most of woody habitats (K, L, R) completely seize the range of this variable, but the exception of riverine and swamp woodlands with the absence at lower precipitation values. J habitats exclusively occur at medium and high precipitation values (>210 mm), including one peak as one habitat functional group. Mesic deciduous woodlands (K) have a three-peaked distribution, clustered into two habitat functional groups (K1-2 and K3). Closed dry deciduous woodlands (L) have a four-peaked, other tree dominated habitats (R) have a five-peaked distribution, properly fitted to multipeak of regional climate envelope by the precipitation of warmest quarter.

BIOCLIM-19 has a three-peaked regional climate envelope, showing three climate functional groups (ENV1, ENV2, ENV3). Most of woody habitats completely seize the range of this bioclimatic variable, with the exception of riverine and swamp woodlands (J) and mesic deciduous woodlands (K). J habitats have a three-peaked distribution but it is shifted toward the medium and high precipitation range (>120 mm). Mesic deciduous woodlands (K) have a two-peaked distribution, fitted to the second and third peak of regional climate envelope. Closed dry and deciduous woodlands (L) and other tree dominated habitats (R) both have a three-peaked distribution, properly fitted to the multipeak of regional climate envelope by the precipitation of coldest quarter.

Spatial pattern and distribution of regional climate surface (Fig 4) contrasted to multipeaks of climate envelopes (Fig. 2 and 3, Table 2) also had to be analysed to get better understanding habitat differentiation affected by bioclimatic factors. BIOCLIM 1 the mean annual temperature, shows the smallest variation with a fine scale pattern on the climate surface. Moreover this bioclimatic index had no distinctive power among vegetation types. BIOCLIM-4 the temperature seasonality, showed a distinct SW-NE spatial gradient, similar to that of many other bioclimatic indices in South Transdanubia (SALAMON-ALBERT et al. 2010b). This bioclimatic index had a strong distinctive power within and between vegetation types, especially for J and K habitats. BIOCLIM-8 the mean temperature of wettest quarter, separated three NW-SE zones, represented with higher values in Külső-Somogy, with lower ones in Zselic and Belső-Somogy occurs as a transitional zone. This bioclimatic index had a significant distinctive power within and between vegetation types, as well as the climate surface. BIOCLIM-9 the mean temperature of driest quarter, showed a most variable spatial pattern: although values of bioclimatic indeces were corrigated with elevation, valleys of medium-sized water courses (e.g. Kapos, Koppány) were distinguished by higher temperature values. This bioclimatic index had a moderate distinctive power within and between regional and habitat climate envelope.

All studied precipitation indices (Fig 5) show a distinct SW-NE change direction, similar to that of many other climatic indices in Southern Transdanubia, reflecting a gradient from a wettest, slightly atlantic-submediterranean climate to a driest subcontinental one. Belső-Somogy and Zselic can be characterized by atlantic climate character, mostly with regionally high precipitation. Transitional regions, the zones of more rapid climate change, are in Külső-Somogy, indicating that this area represents a regional-scale ecotone between Transdanubia, belonging to the mesophilous forest zone and the Great Hungarian Plain, belonging to the forest steppe zone (BORHIDI 1961, OZENDA and BOREL 2000).

Distribution of semi-natural woodland habitat types of riverine and swamp woodlands (J2-J6), mesic deciduous woodlands (K1a-K5) and closed dry deciduous woodlands (L1-L2x) differentiates well in the three vegetation based landscape regions (Fig 6). Zselic is covered with mesic deciduous woodlands, especially with oak-hornbeam woodlands (K2) and beech woodlands (K5). Belső-Somogy mostly characterized by azonal riverine and swamp woodlands, including alder and ash swamp woodlands (J2), riverine ash-alder woodlands (J5) and riverine oak-elm-ash woodlands (J6). They are developed on sandy soils with locally favourable and extreme groundwater conditions, originated from the precipitation. In the transitional-positioned Külső-Somogy all three woodland categories of semi-natural habitat groups and types are to be found.

Riverine and swamp woodlands (J habitats by Fig 6b) show the highest diversity in Belső-Somogy. The riverine ash-alder groves (J5) in the valleys and the alder and ash swamps (J2) at the lower end of the valleys, where streams leave the hills and slow down in the lowlands, are dominant. Ash-alder groves occur sporadically in valley between

Fig. 5: Spatial patterns of precipitation variables as the regional climate surface
a) BIOCLIM-12 the annual precipitation, b) BIOCLIM-17 the precipitation of driest quarter, c) BIOCLIM-18 the precipitation of warmest quarter, d) BIOCLIM-19 the precipitation of coldest quarter. More sign and abbreviation see in Material and methods

hills in both other small regions; presumably they must be more abundant before anthropogenic landscape management. Riverine oak-elm-ash woodlands (J6) is rare, already extirpated from widening valleys fit for cultivation.

Mesic deciduous woodlands (K habitats by Fig 6c) are widespread in all three vegetation based landscape regions, that are clearly distinguished by their subtypes. Lowland pedunculate oak-hornbeam woodlands (K1a), with dominance of Quercus robur, demanding more temperate conditions, and it is most abundant in Belső-Somogy. Zselic is the real home of sessile oak-hornbeam woodlands (K2) and beech forests (K5). Külső-Somogy has a very fragmented forest cover (SALAMON-ALBERT et al. 2010a), but all three types of mesophilous forests occur here, implying a diversely forested landscape before human extension.

Closed dry deciduous woodlands (L habitats by Fig 6d) exist here on the edge of their climatic zone (BORHIDI 1961, OZENDA and BOREL 2000), all their types occur in Külső-Somogy. The zonal turkey oak-sessile oak woodlands (L2a) are the most widespread, the more continental closed thermophilous oak woodlands (L1) occur in the most continental northeastern part, corresponding to high values of seasonality and low values of

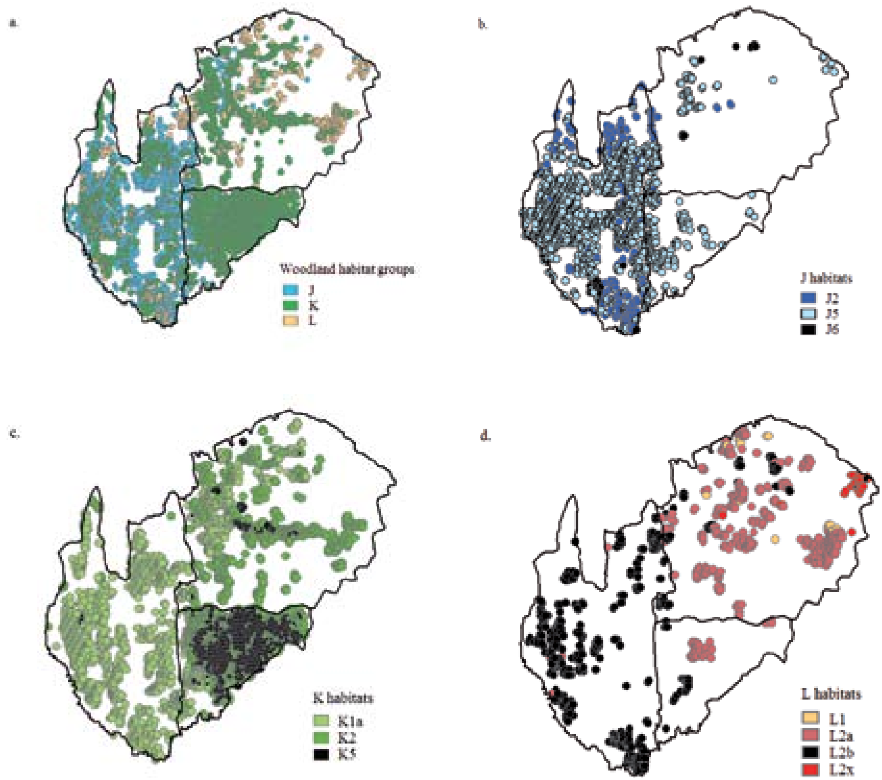

Fig. 6: Spatial distribution of semi-natural woodlands and their habitats in the vegetation based landscape regions

a) woodland habitat groups (J, K, L), b) habitats of riverine and swamp woodlands (J2-J6), c) habitats of mesic deciduous woodlands (K1a-K5), d) habitats of dry closed deciduous woodlands (L1-L2x). More sign and abbreviation see in Material and methods

precipitation indices. Closed and mixed steppe oak woodlands on foothills (L2x) occur only in the most eastern part, on hillsides facing the Great Hungarian Plain. Turkey oak-pedunculate oak woodlands (L2b) developed on soils with changing water level, dominate in Belső-Somogy. Although it is grouped to dry closed deciduous woodlands (L), this is not a dry woodland, but a habitat bound to sandy soils with changing water supply, similarly to azonal riverine and swamp woodlands (J).

Discussion

Previous studies suggest, that precipitation must have a more significant role in the existence of woody habitat types in the landscape region, opposite to temperature variables (SALAMON-ALBERT et al. 2010a). According to our current results, temperature variables are valid in narrow ranges and had poorly differentiated multipeak distributions and climate functional groups as well. Among them temperature seasonality is an exception, with its four-peaked distribution and three-grouped regional climate function. Precipitation variables are valid in a wider range with strong differentiation in multi-peaks and climate functional groups.

By our statistical analyses, studied semi-natural woodland groups are sufficiently integrated in the climate surface and envelopes of the region, but in very different way, according to type of bioclimatic index. Some temperature and precipitation variable is a sensitive predictor in occurrence of woodland habitats in the region on the given scale. Climate sensitivity of woodlands is interpreted by distribution variability of multipeaks, and by the values of bioclimatic variable belonging to.

All studied precipitation indices and also some temperature ones showed a characteristic southwest-northeast gradient as the regional climate surface and envelope. Same gradient was expressed in most of woodlands as a habitat climate envelope, e.g. closed dry deciduous and mesic deciduous woodlands, especially also in other tree dominated habitats.

Occurrence and pattern of riverine and swamp woodlands were no tightly attached to regional climate surface and envelope, but especially in the high values of precipitation indices, due to lagged effect of rainwater being reflected to groundwater level. It may be explained that azonal water-dependent vegetation are indirectly dependent on precipitation on a longer time scale (CZÚCZ et al 2007, 2009). Opposite this fact, they were continuously displayed by certain ranges of certain bioclimatic variables, e.g. temperature seasonality and precipitation of coldest quarter. Riverine and swamp woodlands forming an azonal, groundwater-dependent habitat group, showed no climatic delimitation by annual mean temperature (BIOCLIM-1) and mean temperature of wettest quarter (BIOCLIM-8). They have a moderate climate delimititation by temperature seasonality (BIOCLIM-4), mean temperature of driest quarter (BIOCLIM-9) and precipitation of coldest quarter (BIOCLIM-19). Strong climate delimitation was resulted by annual precipitation (BIOCLIM-12), precipitation of driest (BIOCLIM-17) and warmest quarter (BIOCLIM-18).

Mesic deciduous woodlands as a habitat group were not nearly or moderately delimitated by the regional climate surface and envelope in general. Gaussian distributions come up with two multipeaks by temperature variables, and with 3 ones by precipitation indices. They showed no climatic delimitation by annual mean temperature (BIOCLIM-1), temperature seasonality (BIOCLIM-4), mean temperature of wettest (BIOCLIM-8) and driest quarter (BIOCLIM-9) and annual precipitation (BIOCLIM-12). They are under moderate climate delimititation by precipitation of driest (BIOCLIM-17), warmest (BIOCLIM-18) and coldest quarter (BIOCLIM-19). Strong climate delimitation was not resulted by any bioclimatic variable. It can be interpereted with multifarious occurrence of K habitat types in different range of bioclimatic variables. It is summarized, that mesic deciduous woodlands are more differentiated by precipitation indices than temperature variables. Group of mesic deciduous woodlands are the dominant elements in the vegetation based landscape regions, they are abundant in the west and disappear towards east, showing a good gradient and differentiation by their habitat types. Among three main K habitats, beech forests (K5) are the most sensitive indicators of climate variables, due to their occurrence in the eastern subcontinental part of the region, sporadically in Külső-Somogy and en masse in Zselic.

Dry closed deciduous woodlands (L) are mostly fitted to regional climate envelopes, showing similar number and position of multipeaks, according to high variability in their habitat types. There is a peak at low precipitation values of BIOCLIM-18, where this woodlands are absent, due to extremities in precipitation of warmest quarter or lack of habitat type or previous landscape management. Habitat types of dry closed deciduous woodlands are the most sensitive indicators of these regional-scale climatic gradient, occurring here on the western border of their climatic range. Their Gaussian distribution curves show the most distinct peaks, especially to regional climate envelopes.

Other tree dominated habitats (R) are also completely fitted to regional climate envelopes, both by number and position of multipeaks. The only one exception is the first peak of temperature seasonality (BIOCLIM-4), where this woodlands are missing. This climate function of other tree dominated habitats may represent a result of landscape management, or it can suggest their deriving from numerous woody or probably non-woody habitat types.

Acknowledgements

Data for the analyses were delivered from MÉTA workgroup, Institute of Ecology and Botany of the Hungarian Academy of Sciences (Vácrátót, Hungary). The project was financed by the grant of OM-NKFP/2002: „Magyarország természetes növényzeti örökségének felmérése és összehasonlító értékelése". Further participating botanists are Bauer N., Bódis J., Botta-Dukát Z., Börcsök Z., Csiky J., Dávid J., Filotás Z., Fridrich Á., Hegedős L., Horváth A., Juhász M., Kádár G., Király G., Kovács T., Lelkes A., Lőrincz P., Mányoki G., Pándi I., Pfeiffer N., Szabó A., Szalóky I., Szeglet P., Toldi M., Varga A., Wágner L., Zsidákovits J. contributed to field data collection. Special thank to Bálint Czúcz, who consent to apply climatic datatsets developed for MÉTA database.

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