Adaptive capacity of climate sensitive habitats to climate change in Hungary

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Abstract—Several natural habitats are expected to be sensitive to climate, and their vulnerability to future climate change can be further increased by their insufficient capacity to adapt to the changes. Therefore, it is increasingly pressing to set up methodologies for assessing sensitivity and adaptive capacity of natural ecosystems for enhancing detailed climate change impact, adaptation, and vulnerability assessments. In this paper, we first provide a methodology to quantify the sensitivity of a natural habitat based on habitat distribution models. Next, we selected the 12 most climate sensitive habitats of Hungary as a case study. We also developed a composite adaptive capacity index, which was applied to the selected habitats and used as an input in the climate change impact, adaptation, and vulnerability assessment described. Our adaptive capacity index consists of three main components describing the naturalness, diversity, and connectivity of the studied natural habitats. According to our results, adaptive capacity of the climate sensitive habitats of Hungary is generally lower than it needs to be to cope with the predicted climate change of the 21st century.

Key-words: sensitivity, global climate change, habitat, adaptation, connectivity, naturalness, diversity

1. Introduction

In the assessment of climate change effects, the most widely used methodological framework is the climate change impact, adaptation, and vulnerability (CCIAV) assessment developed by the Intergovernmental Panel on Climate Change (IPCC; *Parry* and *Carter,* 1998; *Carter et al.,* 2007; *IPCC*, 2007), sometimes also named as Climate Impact and Vulnerability Assessment Scheme (CIVAS). According to this framework, vulnerability to climate change is the degree to which geophysical, biological, and socio-economic systems are susceptible to, and unable to cope with, the adverse impacts of climate change. The vulnerability of an object is determined by the potential impact of climate change and by the object's capacity for adaptation (also termed adaptive capacity) to the changing geophysical, biological, and socio-economic conditions. The potential impact is determined by the exposure to the climate change and climate sensitivity.

This paper focuses on compartments of the framework linked to the objects affected by climate change and are independent of the climate change effect itself: sensitivity (S) and adaptive capacity (A). The framework can be applied to several kinds of objects/systems that are exposed to the changing climate. Here we studied habitat types, units of natural and semi-natural ecosystems. Since habitats have several relevant biological and physical properties that influence their S and A, by studying these characteristics we could determine these key elements of vulnerability assessments (*Czúcz et al.*, 2011; *Glick et al.,* 2011). Similarly to the concept of potential impact (*Glick et al.,* 2011), A is not inextricably linked to climate change, the term can be applied to a broader range of stresses (*Yohe* and *Tol,* 2002).

Impacts of climate change, adaptive capacity, and vulnerability can be studied from a variety of approaches. They are explorable both from the perspective of society (*Haddad,* 2005; *Walker et al.,* 2002) and, as in this paper, from the perspective of nature (*Parmesan* and *Yohe,* 2003). Note, however, that the two can not be separated sharply from one another (*Adger et al.,* 2005, *McNeeley et al.,* 2017).

According to *IPCC* (2007, Glossary), S is the degree to which a system is affected by climate variability or change. The effect may be direct or indirect, as well as adverse or beneficial. The S of a system can be characterized by the degree of direct impact (either adverse or beneficial) that is caused by a 'unit change' in the climatic environment (*Czúcz,* 2010). S may depend on innate physiological or biological variables (*Glick et al.,* 2011).

When calculating S of habitats/associations, both species composition and structure should be taken into consideration (*Bartha,* 2004). It can be measured at various scales from global (*Smith* and *Hitz,* 2003) to regional. In this paper, we focus at the national scale identifying the most climate sensitive habitats (*CSH*s) of Hungary based on the predictor selection of potential distribution models that relate the distribution of habitats to environmental variables.

The adaptive capacity indicator framework used in our study unites the indicators or conceptual models of several disciplines. Such frameworks share a common question of interest: how can a system, through its internal reorganization, cope with or mitigate the external effects it is exposed to. Different mechanisms of autonomous or planned adaptation can be triggered or implemented in preparation for or in response to impacts of climate change (*Adger et al.,* 2005). Characteristics of the system that can be estimated from its current state frequently determine its future behavior (*Kelly* and *Adger,* 2000) at various scales from global systems to local populations of a species (*Kimbras,* 2004).

The *A* of habitats to climate change can also be estimated from their current characteristics, including the broader landscape context they are embedded in (*Czúcz et al.,* 2011). *A* in this case corresponds to the feasibility of the implementation of adaptation (*Füssel* and *Klein,* 2006), or more explicitly, *A* is 'the ability of a system to adjust to climate change' in order to 'moderate potential damages, to take advantage of opportunities, or to cope with the consequences' (*IPCC,* 2007, Glossary). For the 'components' of a habitat, i.e., the species constituting it, *A* may be considered a factor of their internal traits (e.g., their ability to migrate, evolve, or modify their behavior) or external conditions (e.g., barriers) (*Glick et al.,* 2011). In the case of ecosystems, adaptation is predominantly autonomous adaptation, which 'does not constitute a conscious response to climatic stimuli but is triggered by ecological changes' (*IPCC,* 2007, Glossary). Consequently, adaptation includes not only genetic evolutionary adaptation (*Glick et al.,* 2011), but also any systemic adjustment processes: local resilience, refugium-based adaptation, and migration-based adaptation (*Czúcz et al.,* 2011).

Based on all these theoretical considerations, we next built a framework for *A* based on the quantification of the most important adaptive processes. Due to the lack of species-level data at such a wide range of habitats, as well as due to the theoretical complexity of integrating them (even if they were at hand) at so large numbers as they occur in natural habitats, we excluded genetic adaptation from this framework. In addition, this mechanism is considered to be of little practical relevance anyway, as the evolution of most macroscopic organisms will not be able to cope with the expected rapid climate change (*Gienapp et al.,* 2008). Accordingly, our framework of *A* relies on the other three adaptive mechanisms: natural capital index naturalness indicator (local resilience), Shannon diversity index (refugium-based adaptation) and connectivity (migration-based adaptation).

The most important goal of this study was to provide inputs for a detailed climate change impact, adaptation, and vulnerability (CCIAV) assessment (*Bede-Fazekas et al.,* 2017, in this issue) by

– creating the methodological basis of sensitivity analysis of natural habitats based on ecological habitat distribution models;

–   selecting the most climate sensitive habitats (*CSH*s) of Hungary as a case study;

–   developing an adaptive capacity index for habitats, based on naturalness, diversity, and connectivity measures;

–   estimating the adaptive capacity of *CSH*s of Hungary.

2. Materials and methods

2.1 Potential natural distribution models

Analysis of *S* and *A* of the habitats was based on previously built habitat distribution models used for modeling the potential natural vegetation of Hungary, as detailed in *Somodi et al.* (2017) and *Bede-Fazekas* (2017). These models were Boosted Regression Tree models (BRT; a.k.a. Gradient Boosting Model, GBM; *Friedman et al.,* 2000; *Friedman,* 2002; *Schapire,* 2003) built for each of the major natural habitat types of Hungary separately. The use of BRT as a predictive ecological model is relatively new (*De'ath,* 2007; *Elith et al.,* 2008), but several studies have pointed out its outstanding predictive power (*Elith et al.,* 2006; *Bühlmann* and *Hothorn,* 2007; *Guisan et al.,* 2007). Training of these models relied on observed vegetation data originated from the Hungarian Actual Habitat Database (MÉTA; www.novenyzetiterkep.hu/english/node/70; *Molnár et al.,* 2007; *Horváth et al.,* 2008) and hydrologic, edaphic (*Pásztor et al.,* 2015), topographic (USGS, 2004), and climatic (*Szalai et al.,* 2013) environmental variables. The predictors were aggregated to the hexagons of MÉTA database using descriptive statistical measures (minimum, maximum, mean, and standard deviation) or extracted to the center of the hexagons [please refer to *Somodi et al.* (2017) and *Bede-Fazekas* (2017) for details].

Based on these distribution models, we made predictions to two future periods (2021–2050, 2071–2100). For both of the prediction periods, two regional climate models provided the climate data with similar temporal (daily) and horizontal (0.1°, approximately 10 km) resolution as that of the reference climate data (1977–2006). The two models, ALADIN-Climate 4.5 (*Csima* and *Horányi,* 2008; hereinafter: Aladin) and RegCM 3.1 (*Torma,* 2011; *Torma et al.,* 2011), are based on the A1B emission scenario of IPCC SRES (*Krüzselyi et al.,* 2011; *Sábitz et al.,* 2015). Scenario A1B describes the radiative forcing of 850 ppm CO_2 concentration by 2100 (*Nakićenović et al.,* 2000). In terms of the forcing, A1B is equivalent to the RCP8.5 scenario by the middle of the century, and runs between RCP6.0 and RCP8.5 by the end of the century (*Burkett et al.,* 2014). While Aladin was developed under an international collaboration by Météo France (*Spiridonov et al.,* 2005), RegCM was built by the US National Center for Atmospheric Research and further improved by the International Centre for Theoretical Physics in Trieste (*Giorgi et al.,* 1993a, 1993b). Finally, *Torma et al.* (2008) adapted

RegCM to the Carpathian Basin. ARPEGE-Climat/OPA and ECHAM5/MPI-OM provided the boundary conditions for Aladin and RegCM, respectively (*Krüzselyi et al.,* 2011).

In case of the reference climate dataset and the four future climate datasets, monthly average of minimum, maximum, and mean temperatures and monthly precipitation sum were calculated from the daily series, and then averaged over the 30-year periods. Future monthly data were bias corrected with additive (temperature) and multiplicative (precipitation) bias terms (i.e., Delta Change method), using the period 1961–1990 for calculation of the bias by comparison of observed and modeled climate. The coarse-resolution monthly climate surfaces were downscaled to the resolution of the vegetation data with regression kriging, a method integrating kriging (*Krige,* 1966) and linear regression, in a way similar to the downscaling of the reference climate data. Kriging is an exact, non-convex, linear, stochastic, and local (in some case with global trend) interpolator, that produce a gradual surface (*Hartkamp et al.,* 1999; *Li* and *Heap*, 2014). Although some types of kriging are univariate, regression kriging is multivariate, since it uses auxiliary variables (*Li* and *Heap*, 2014). From the fine-resolution climate data, seasonal averages/sums and 19 bioclimatic variables (*Nix,* 1986) were calculated. Please refer to *Somodi et al.* (2017) and *Bede-Fazekas* (2017) for further details about the data used, data preprocessing, predictor selection, and building the models of the habitats.

2.2   Sensitivity of habitats

BRT offers the possibility of automatic variable selection based on the frequency of explanatory variables in the subtrees of the model (*Elith et al.,* 2008). It also provides an estimation of variable importance for predictors remaining in the final, simplified model according to a formulae developed by *Breiman et al.* (1984) and *Friedman* (2001) and implemented in the package 'gbm' (*Ridgeway,* 2017) of R statistical environment (*R Core Team*, 2017). Importance is calculated based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged over all trees" (*Friedman* and *Meulman,* 2003).

Since importance is a measure that helps to assess how influential a variable is, climate sensitivity (*S*) of a habitat can be estimated by summation of the relative importance of all the climatic predictors in its final model:

$$S = \sum_{c \in C} \left(\frac{1}{M} \sum_{m=1}^{M} I_c^2(T_m) \right), \tag{1}$$

where *c* is one of the climatic predictors *C*, *M* is the number of trees, and $I_c^2(T)$ is the squared importance of the subtree *T* according to *Breiman et al.* (1984)). A 0.55 minimum of relative importance was chosen to select the most climate sensitive habitats (*CSHs*). The threshold was chosen based on expert decision, so

that the climate predictors have at least 0.5 relative importance, i.e., their importance outweights that of all other variables together. On the other hand, we limited the range of habitats to one fifth of the studied habitats (n = 60). Thus, 12 habitats were selected for further analyses.

2.3 Adaptive capacity of habitats to climate change

The adaptive capacity (*A*) of the habitats was estimated based on three components: local resilience, refugium-based adaptation, and migration-based adaptation. Two of the three components were first calculated at the resolution of the MÉTA database (consisting of 35 ha 'hexagons', see *Molnár et al.*, 2007; *Horváth et al.*, 2008), while the third one (refugium-based adaptation) was directly computed at the level of the climate grid cells. One of the three indices (migration-based adaptation) was computed habitat-wise, while the other two indices characterize the landscape/environment, and thus, produce the same map for any of the studied habitat types. Components of *A* were only calculated for the 12 selected *CSH*s (see Chapter 3.1. for details). To be compatible with the input data of the habitat distribution models, all the *A* estimation outputs were eventually aggregated (upscaled) to the horizontal resolution of the climate models (0.1°). All the calculations were implemented in the R statistical environment (*R Core Team*, 2017).

Local resilience is best estimated by the naturalness (*N*) of the landscape (*Cook*, 2002, *Czúcz et al.*, 2012). Accordingly, we chose the vegetation-based natural capital index, a habitat-level naturalness metric based on the MÉTA database (*Czúcz et al.*, 2008) to represent local resilience. The natural capital index of a MÉTA hexagon (*N'*) is expressed as the product of ecosystem quality and quantity, while the *N* of an entire grid cell was defined as the maximum of the *N*'s of the hexagons found within the grid cell of interest:

$$N'_i = \frac{1}{\sum_{h \in H} A_h} \sum_{h \in H} (Q_h A_h) \; ; \; N_g = \max_{i \in g} N'_i, \tag{2}$$

where *A* is the area and *Q* is the quality of habitat *h* that is element of the habitat pool *H*, *i* is the studied location (MÉTA hexagon) found within the grid cell of interest *g*.

Refuge-based adaptation is more successful if the landscape is more heterogeneous, and this aspect can be best quantified by landscape diversity indices (*Czúcz et al.*, 2011). We choose the widespread Shannon diversity metric (*Shannon*, 1948) to quantify this aspect based on the habitat data from the MÉTA database. Habitat frequencies (i.e., number of the hexagons where the habitat is present) within the cells of the climate grid were used as input, thus we estimated the habitat diversity (*D*) of a grid cell as

$$D_g = -\sum_{h \in H_g} \left(p_h * \begin{cases} \ln p_h, if\ p_h > 0 \\ 0, if\ p_h = 0 \end{cases} \right), \tag{3}$$

where h habitat is the element of the H habitat pool of the grid cell of interest g, and p is the frequency of the habitat.

Migration-based adaptation relies on the quantification of the connectivity (C) of the landscape. There is a wide variety of landscape connectivity assessment options. A major dichotomy exists along whether the indices reflect structural or functional features of the landscape. Among the former, several measures are based on the presence of corridors, others on distances or graph theory also, accounting for transversability. There are measures based on the amount of habitat in the landscape, too, which can also be extrapolated towards percolation-related measures. Connectivity indices reflecting functional aspects of the landscape often rely on the probability of moving and use matrix permeability as well (*Kindlmann* and *Burel,* 2008).

As our study involves habitats, rather than individual organisms, functional connectivity indices would not be appropriate. The many constituting species are likely to have different functional requirements, e.g., matrix permeability. On the other hand, the structural aspect of connectivity can be useful, because the proximity of similar patches, the presence of corridors, and other landscape elements can undoubtedly enhance the migration process for various constituent species of the habitat, even if to a different degree per species. Therefore, we quantified the migration-based A by an index based on Euclidean distance (*Czúcz et al.,* 2011) accommodated to presence-absence data. Connectivity of a habitat in a MÉTA hexagon (C') is calculated from the frequency of patches of the same habitat type within the search distance from the focal patch weighted by an exponential distance kernel, while the maximum of the C's found within the grid cell of interest results in the C_g of the cell:

$$C'_i = \sum_{j|D_j<D_o} E e^{-\alpha D_j} \; ; \; C_g = \max_{i \in g} C'_i, \tag{4}$$

where js are the patches those D distance to the studied patch is lower than the previously specified D_0 threshold, E is the extent/area of the studied patch (since we used habitat presences, this parameter was set to 1), α is an appropriately chosen dispersal parameter, and i is the studied location (MÉTA hexagon) found within the grid cell of interest g.

The indicator can be fine-tuned with the help of the dispersal parameter, which should reflect the dispersal ability of the modeled species or species groups. The search distance should be large enough to contain the bulk of the quickly decaying exponential kernel. Based on *Czúcz et al.* (2011), we set α to 0.5 km^{-1} and D_0 to 1 km.

Each of the three component indices were rescaled into a 5-grade ordinal scale {0; 1; 2; 3; 4}. The first two were rescaled evenly between their minimum (0 in all cases) and maximum values, while the third was rescaled using the boundaries that emerged from the simulations of *Czúcz et al.* (2011). The maximum of these indices was taken as the *A* of the habitat in question in a specific spatial unit (i.e., cell of the input climate grid):

$$A_g = \max \left[\left(\left\{ \begin{array}{l} 4, \; if \; N_g = \max_{g \in G} N_g \\[2mm] \left\lfloor 5 * \frac{N_g}{\max_{g \in G} N_g} \right\rfloor, else \end{array} \right) ; \left(\left\{ \begin{array}{l} 4, \; if \; D_g = \max_{g \in G} D_g \\[2mm] \left\lfloor 5 * \frac{D_g}{\max_{g \in G} D_g} \right\rfloor, else \end{array} \right) ; \left(\left\{ \begin{array}{l} 4, \; if \; C_g \geq 9.41 \\ 3, \; if \; C_g \in [6.28; 9.41) \\ 2, \; if \; C_g \in [3.14; 6.28) \\ 1, \; if \; C_g \in [1.07; 3.14) \\ 0, \; else \end{array} \right) \right] (5)$$

where *g* is the studied cell of climate grids *G*, *N* is naturalness, *D* is diversity, *C* is connectivity.

3. Results

3.1 Sensitivity of habitats

Based on the relative importance of climate-related predictors compared to other predictors retained in the habitat models (*Table 1*), the twelve most climate sensitive habitats are mixed coniferous forests (N13), mixed forests of slopes and screes (LY2), annual salt pioneer swards of steppes and lakes (F5), beech woodlands (K5_K7a), oligotrophic reed and *Typha* beds of fens and floating fens (B1b), closed lowland steppe oak woodlands (L5), closed steppes on loess, clay, tufa (H5a), steppe oak woodlands on foothills and on loess (L2x_M2), Turkey oak woodlands (L2a_L2b), forest steppe meadows (H4), willow mire shrubs (J1a), and oak-hornbeam woodlands (K1a_K2_K7b). In all of the other studied habitats, the relative importance of climate variables were lower than the previously selected 0.55 threshold.

Table 1. Sensitivity analysis of the modeled habitats ordered according to the relative importance of climate variables in their final models (sensitivity, *S*). Number and relative frequency of climate predictors are also shown. Horizontal line indicates the 0.55 threshold of relative importance, which separates the most climate sensitive habitats from the other ones. Habitats are encoded according to *Bölöni et al.* (2011).

| Habitat code	Descriptive habitat name	Number of climate variables	Frequency of climate variables	Relative importance of climate variables
N13	Acidofrequent coniferous forests	2	1.00	1.00
LY2	Mixed forests of slopes and screes	2	0.67	0.75
F5	Annual salt pioneer swards of steppes and lakes	4	0.67	0.67
K5_K7a	Beech woodlands	7	0.44	0.62
B1b	Oligotrophic reed and *Typha* beds of fens, floating fens	6	0.60	0.61
L5	Closed lowland steppe oak woodlands	7	0.50	0.60
H5a	Closed steppes on loess, clay, tufa	7	0.41	0.60
L2x_M2	Steppe oak woodlands on foothills and on loess	7	0.47	0.60
L2a_L2b	Turkey oak woodlands	7	0.44	0.59
H4	Forest steppe meadows	7	0.47	0.58
J1a	Willow mire shrubs	6	0.46	0.58
K1a_K2_K7b	Oak - hornbeam woodlands	7	0.47	0.55
J6	Riverine oak-elm-ash woodlands	7	0.58	0.54
M7	Continental deciduous rocky thickets	1	0.50	0.53
LY4	Mixed relic oak forests on rocks	6	0.50	0.53
F2	Salt meadows	6	0.46	0.52
F1a	Artemisia salt steppes	5	0.50	0.52
J5	Riverine ash-alder woodlands	7	0.50	0.52
B6	Salt marshes	6	0.40	0.52

Table 1. continue

Habitat code	Descriptive habitat name	Number of climate variables	Frequency of climate variables	Relative importance of climate variables
F4	Dense and tall *Puccinellia* swards (alkaline vegetation)	5	0.50	0.52
J2	Alder and ash swamp woodlands	6	0.50	0.51
M6	Continental deciduous steppe thickets	4	0.44	0.50
B4	Tussock sedge communities	3	0.43	0.49
H2	Calcareous rocky steppes	6	0.40	0.47
LY3	Limestone beech forests	4	0.50	0.46
G2	Calcareous open rocky grasslands	3	0.38	0.42
L1_M1	Downy oak woodlands	7	0.47	0.41
L4a_L4b	Acidofrequent oak woodlands	5	0.38	0.39
H3a	Slope steppes on stony ground	5	0.42	0.39
G3	Siliceous open rocky grasslands	3	0.43	0.37
M5	Poplar-juniper steppe woodlands	3	0.38	0.34
B1a	Eu- and mesotrophic reed and Typha beds	6	0.33	0.31
H5b	Closed sand steppes	6	0.43	0.31
J3_J4	Riverine willow shrubs and willow-poplar woodlands	7	0.50	0.30
LY1	Forests of ravines (mesic rocky forests rich in *Acer pseudoplatanus*)	2	0.40	0.29
G1	Open sand steppes	6	0.43	0.28
M3	Open salt steppe oak woodlands with openings	1	0.14	0.17
H1	Closed rocky grasslands, species rich *Bromus pannonicus* grasslands	0	0.0	0.00
M4	Open sand steppe oak woodlands with openings	0	0.0	0.00

All seven climate predictors were included in the final models of K5_K7a, L5, H5a, L2x_M2, L2a_L2b, H4, and K1a_K2_K7b. The model of B1b and J1a lacks one climate predictor only: isothermality and precipitation of the coldest quarter, respectively. F5 has four climate predictors, while N13 and LY2 have two climate predictors. The model of LY2 includes one non-climatic predictor only (standard deviation of topographic position index), while the model of N13 is completely climate-dependent.

3.2 Adaptive capacity of habitats to climate change

Since the country-wide landscape-level habitat diversity (*D*) can be of relatively broad interest (see Chapter 4.2.), we detail this intermediate result (*Fig. 1*). *D* is relatively low in the lowlands (both in the northwest of Hungary and in the Hungarian Plains) except in Nyírség (eastern Hungary) and near to the lower section of River Tisza. Extremely low *D*s occur sporadically, evenly distributed across the country. *D* takes its highest value in the mountain regions, including the Northern Mountains (northern and northeast Hungary) and the Transdanubian Mountains (northern part of Transdanubia). In summary, pattern of *D* shows tendency to be high in territories that are (1) forested or accommodate woody natural vegetation, (2) less disturbed by agriculture, (3) situated in higher altitudes. Note that the latter may be a proxy for the former ones.
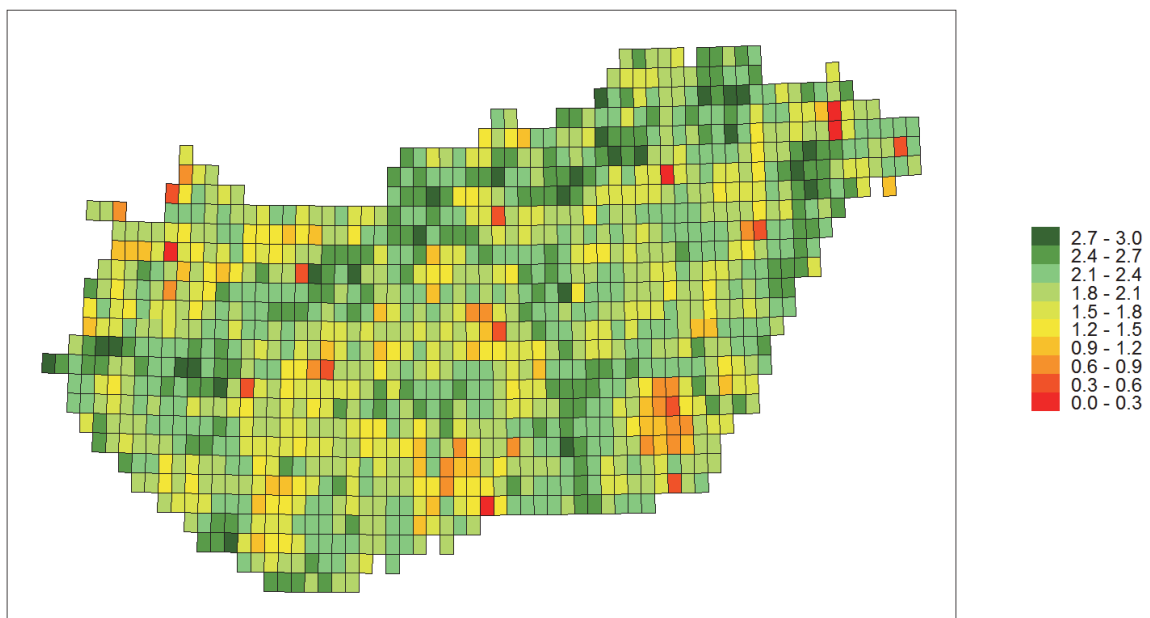
Fig. 1. Shannon diversity (*D*) of climax and subclimax habitats of Hungary calculated at the resolution of the input climate grid (0.1°). *D* increases from red to green.

Many of the *CSH*s are zonal and widespread types and thus have relatively high *A*, which has the potential to greatly mitigate the potential impact of climate change. Most widespread zonal habitats, such as oak-hornbeam woodlands (K1a_K2_K7b), beech woodlands (K5_K7a; *Fig. 2*), and others which form larger blocks in the current landscape have high *A* in the center of the blocks, which decreases towards the edges and reaches low *A* values. Turkey oak woodlands (L2a_L2b), however, are so widespread that this pattern does not apply to them and have high *A* even at the edges of its current patches, which ensures the best *A* among the *CSH*s (*Fig. 3*). There are habitats with variable pattern, but typically medium to high *A*: floating fens, oligotrophic reed and *Typha* beds of fens (B1b), closed lowland steppe oak woodlands (L5), closed steppes on loess (H5a), semi-dry grasslands, forest-steppe meadows (H4), mixed forests of slopes and screes (LY2).
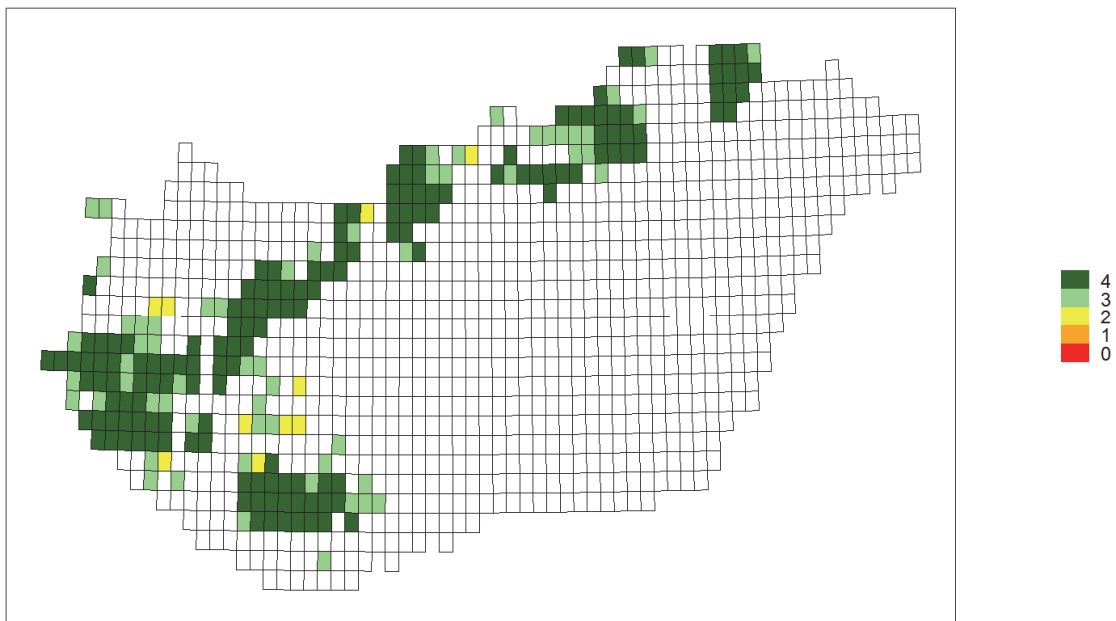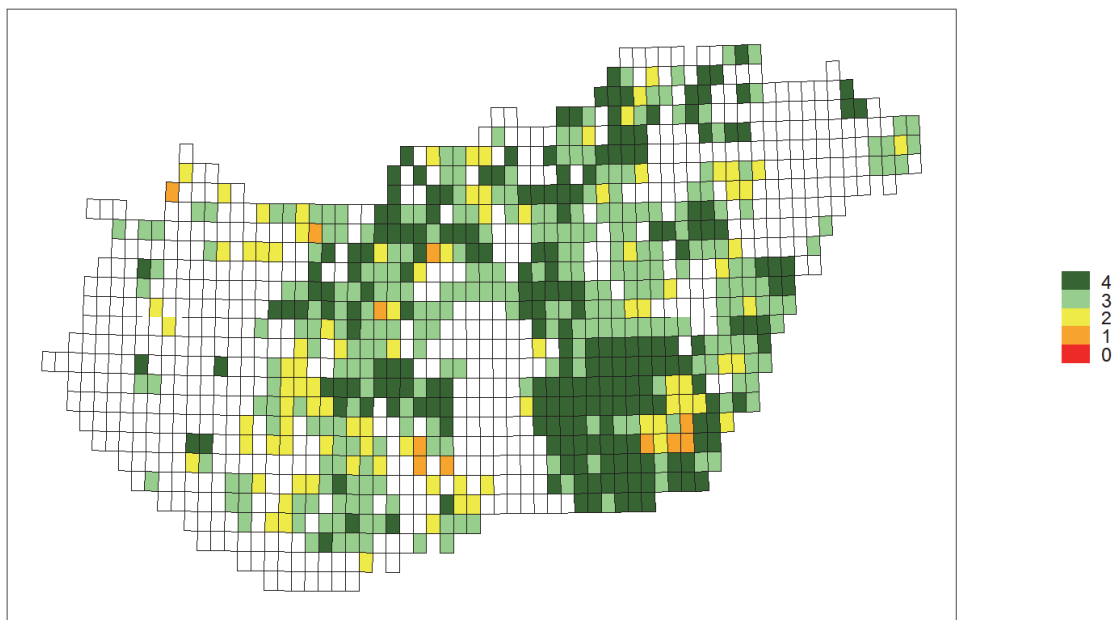

Fig. 2. Adaptive capacity (*A*) of beech forests (K5_K7a) in its existing stands. *A* increases from 0 to 4 (red to green).

An important aspect of the *A* of closed steppes on loess, clay, tufa (H5a) is that there is a high *A* area in the southeast of Hungary, while its *A* is low in the southwest (*Fig. 4*). It is also worth to note that relatively lower *A* areas of mixed forests of slopes and screes (LY2) appear aggregated north to Lake Balaton and in the Mecsek Mountains, which points out areas likely to become vulnerable. In this analysis, willow mire shrubs (J1a) appears to be one of the types that has the lowest *A* overall, which coincides with its ecology. This habitat typically appear in small depressions in the landscape surrounded by other vegetation or even agricultural land. So neither its *C* nor characteristics of its surroundings (*D, N*)

predestine for high A. Closed lowland steppe oak woodlands (L5) also has low A values, which can be attributed to the fragmentedness of this type. Opposed to J1a, L5 would not be fragmented under natural conditions, but as it is a habitat of the lowlands, it became a frequent victim of human landscape transformation.
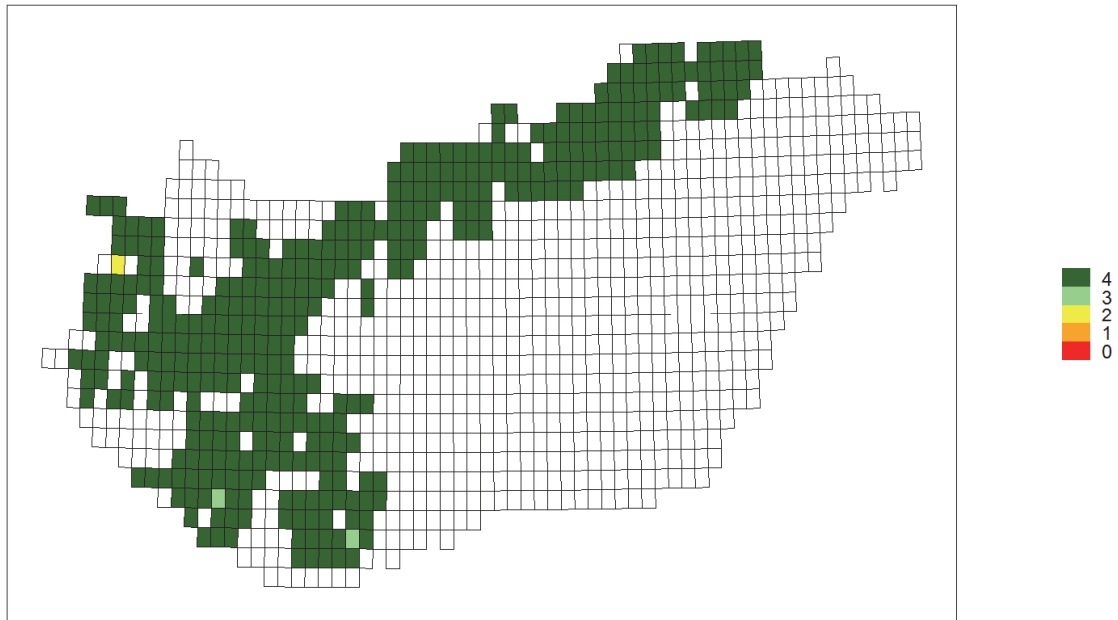
Fig. 3. Adaptive capacity (*A*) of turkey oak woodlands (L2a_L2b) in its existing stands squares. *A* increases from 0 to 4 (red to green).

Fig. 4. Adaptive capacity (*A*) of closed steppes on loess, clay, tufa (H5a) in its existing stands. *A* increases from 0 to 4 (red to green).

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4. Discussion

4.1 Sensitivity of habitats

Sensitivity (S) of the studied habitats to climate, both in case of highly and hardly sensitive ones, is generally well justified. Note, however, that our results can only be interpreted in the context of Hungary, since the training database of the habitat models our work was based on was limited to Hungary. Although our S measure is not able to separate the different aspects of climate, according to a research on the predictor selection of the predictive habitat models used in our sensitivity analysis, S of the habitats of Hungary is generally related to drought (*Bede-Fazekas,* 2017). This finding is in accordance with the literature (e.g., *Ladányi et al.,* 2010; *Rasztovits et al.,* 2012, 2014).

S of habitat N13 (mixed coniferous forests) is outstanding, although more pronounced dependence of edaphic parameters would have been expected (*Bölöni et al.,* 2011). It can be assumed that a more balanced model, and therefore lower S, should have emerged if areas outside Hungary were taken into account. Among the *CSH*s, S of only B1b (oligotrophic reed and *Typha* beds of fens and floating fens) seems to be overestimated if the ecological demands of the habitat cited in the literature (*Bölöni et al.,* 2011) are taken into account. Our findings on the high S of B1b, LY2 (mixed forests of slopes and screes) and L5 (closed lowland steppe oak woodlands) contradict the results of *Czúcz* (2010). Hence, previous findings of *Czúcz* (2010) about the higher S of zonal forests and lower S of grasslands and shrublands are just partially confirmed by our results. However, our results, in general, correspond to the conclusion of *Czúcz* (2010): those habitats that are distributed in the mountain regions depend more on, and therefore are more sensitive to climate than the ones located in the lowlands.

Among those habitats whose S is lower than 0.35 (*Table 1*), the model of M5 (poplar-juniper steppe woodlands) and H5b (closed sand steppes) might underpredict their S. It should be noted, however, that their reliance on sandy soils may elucidate the relatively low importance of climatic predictors. Our results on the hardly sensitive habitats, except for H1 (closed rocky grasslands, species rich *Bromus pannonicus* grasslands), are in line with the findings of *Czúcz* (2010).

4.2 Adaptive capacity of habitats to climate change

A system will be less vulnerable, i.e., it can survive in the long term against the environmental adverse effects, if it has low S while high A (*Smit et al.,* 1999). Although it may seem that average A of the habitats of Hungary is relatively high, we must draw attention to the fact that the rescaling of the adaptation components applied in Eq. (5) stretches the scale and masks the absolute values. Based on a closer investigation of the values of N, D (for Hungary), and C (for the habitats of Hungary), we must conclude that, in average, A is much lower than what would be necessary to be able to cope with the predicted climate change in an

autonomous way. According to *Glick et al.* (2011), *A* of a habitat is equal to its ability to accommodate or cope with climate change impacts with minimal disruption. Hence, habitats of Hungary need external support to increase their *A* and their adaptive capacity. Although no components that would describe capacities for planned adaptation (i.e., economic resources, or critical infrastructure) are incorporated in our composite index, further research on the *A* of habitats can benefit from exploring the possible interventions for enhancing the resilience of natural ecosystems.

Although the habitats occurring at higher elevations are more climate sensitive (*Czúcz,* 2010), historical anthropogenic impacts have transformed the lowland vegetation to a far greater degree (*Molnár et al.,* 2012; *Nogués-Bravo et al.,* 2008; *Mezősi et al.,* 2017), which, in turn, could significantly decrease the *A* of the habitats. This effect was only indirectly studied in this paper through the following relationships: 1) *N* is lower for historically degraded habitats; 2) *D* is lower where humans had historically extirpated natural habitat types (*Luoto et al.,* 2003); and 3) *C* is lower where humans had made the landscape more fragmented. Anthropogenic effects can cause change in the abiotic environment as well (e.g., level of groundwater). Hence, some habitats may be present at, or extinct from, a certain location induced by non-natural processes. The predictive habitat models used in our research could not separate the results of these processes from the natural patterns and impacts, which has to be taken into account when interpreting our results.

One of the three component indices that make up the *A* composite index, the landscape-level habitat diversity (*D*) can be of particular interest even out of the context of vulnerability assessments. This index (1) was computed at the climate grid resolution, (2) is not habitat specific, and (3) has not yet been calculated for Hungary in this way. Therefore, although it is only an intermediate result, it can still be of relatively broad interest. The habitat diversity of the country is used to be characterized only by proxies based on species number, which have a high (yearly) temporal resolution, but a very low (national) spatial resolution (e.g., *Hungary,* 2015). Our estimation is the first attempt to characterize the country-wide fine-resolution habitat diversity pattern (*Fig. 1*), a task urged earlier (*Molnár* and *Horváth,* 2008) and incorporated in the Hungarian biodiversity monitoring system (*Fekete et al.,* 1997). However, we want to stress that diversity measures are highly dependent on scale (*Tóthmérész,* 1995), thus the current estimation is only to be interpreted in the frame of the current study. Pattern of *D* suggests that territories less disturbed by agriculture are more diverse in terms of habitats. Impacts of agriculture on the diversity has been previously proven for Hungary (*Fésüs et al.,* 1992) and globally (*Glick et al.,* 2011) as well. *D* shows some similarities to *N* in terms of their pattern (*Czúcz et al.,* 2008). Shannon diversity of habitats of Hungary is low similarly to the natural capital index (naturalness) of the country (*Czúcz et al.,* 2008, *Hungary,* 2015). *N* is also correlated with

shape- and size-related landscape indices (*Szilassi et al.,* 2017), therefore with connectivity, as well.

There is a general agreement that *A* is high in the center of large homogeneous landscape blocks and decreases towards the edges. This is certainly the consequence of the way how the *C* component of *A* was defined, which can exhibit much larger values at the core of such blocks. This pattern is scale-dependent (*Hernando et al.,* 2017) and have been found by several other studies (e.g., *Riitters et al.,* 2000; *Saura* and *Pascual-Hortal,* 2007).

Although genetic diversity can facilitate evolutionary adaptation of a habitat (*Glick et al.,* 2011), our suggested composite *A* index did not contain genetic adaptation-related measures, since they are hardly interpretable in the context of habitats. Although species-level genetic *A* can, in theory, be integrated in a habitat-level index, it seems unfeasible due to its data intensity and unsoundness in methodological terms. Nonetheless, as diversity of functional traits can assist adaptation (*Bussotti et al.,* 2015), species diversity or functional diversity within a habitat may serve as a proxy for genetic diversity, and therefore genetic *A*, of the habitat.

Component indices of *A* can also be used in other research areas. The natural capital index, measurement of *N*, can provide comprehensive and substantial information on the state of an ecosystem, and on quantitative and qualitative changes in ecosystem services (*Kelemen,* 2013). The Shannon index, measurement of *D*, is widely used in subdisciplines of ecology (e.g., *Pakeman,* 2001), and found to perform excellently in some comparative research, (e.g., *Morris et al.,* 2014). However, a study focusing on *D* should apply a multiscale approach rather (*Podani et al.,* 1993; *Tóthmérész*, 1995; *Bartha*, 2008; *Güler et al.,* 2016). All the indices of migration-based adaptation, e.g., dispersal potential index (*Glick et al.,* 2011) beyond *C*, can describe the permeability of the landscape, and therefore, function as landscape evaluation measures.

4.3 Discussion of the research and application

There is a great need for CCIAV assessments on natural habitats (*Bede-Fazekas,* 2017). To our knowledge, only one CCIAV assessment on habitats of Hungary were done (*Czúcz,* 2010). Our research fills the scientific gap, since it is more detailed and based on updated input data and ecological models. Note, however, that our findings are limited to *CSH*s of Hungary, while *Czúcz* (2010) conducted his research on all the climax and subclimax habitats of the country. The *S* and *A* analyses presented in this paper provide inputs for a CCIAV assessment on habitats of Hungary (*Bede-Fazekas et al.*, 2017, in this issue). Our results can, however, provide input for other CCIAV assessments, whose method or exposure data differ from those of *Bede-Fazekas et al.* (2017). The three adaptation capacity indicators we implemented to habitats and presented in this paper now fill the gap to which *Molnár* and *Horváth* (2008) have drawn attention.

Since most of the zonal habitats of Hungary can be found among the *CSH*s, studying the *A*, potential impact and vulnerability give a reliable overview about the ecological impacts of climate change on Hungary. In studies describing the ecological impacts of climate change, species distribution models are much more frequently applied than habitat distribution models (*Ferrier* and *Guisan,* 2006). Species data are widely available, and the interpretation of the results is also relatively straightforward. Nevertheless, if such simple impact models need to be integrated into a more integrative vulnerability assessment framework, then individual species will become too particular. We think that in such cases, habitats can serve as an efficient proxy for species, since species' *S* are likely to be influenced, in many cases, by *S* of their habitats (*McCarty,* 2001). Moreover, vice versa, *S* of a habitat is usually determined by *S* of its component species (*Glick et al.,* 2011). Applying habitat distribution models in CCIAV assessments thus seems to be an efficient strategy, which means an important motivation for additional methodological research in the field of habitat distribution models.

The database that our research produced (*NATéR,* 2017) may serve as a basis for a wide variety of applications. *S* and *A* of natural habitats may provide an important and easily interpretable input for numerous disciplines. Our results might be integrated in further research conducted in the field of forestry or agronomy. Forestry studies deal typically with smaller entities, i.e. species, than our research. Hence, cooperation may result in more detailed *S* studies. There are several policy sectors, where the intermediate results of a CCIAV assessment on natural ecosystems, including *S* and *A*, can provide relevant and easily interpretable inputs (*European Environment Agency,* 2005, *Glick et al.,* 2011). Major applications of the results of our case study are expected in the field of landscape evaluation, nature conservation, restoration prioritization, forestry planning, landscape design, and landscape rehabilitation. Our methodological results can be implemented in further CCIAV assessments and may induce or facilitate further theoretical research on the sensitivity and adaptive capacity calculations based on habitats. We see a great need for the development and testing of complex adaptability indicators. It may also be necessary to develop suitable sensitivity metric for each ecological modeling approach beyond BRT.

Our research bears a number of development potential. A more detailed sensitivity analysis can be carried out by studying the predictor selection of the distribution models and interpreting those climatic variables that have the highest relevance for a certain habitat (*Bede-Fazekas,* 2017). Further research is needed to analyze not only the patterns but also the specific values of *A* in each grid cell, especially those that are outliers.

5. Conclusion

In this paper we focused on providing inputs, i.e., sensitivity (*S*) of habitats and their adaptive capacity (*A*), for a detailed climate change impact, adaptation, and

vulnerability (CCIAV) assessment (*Bede-Fazekas et al.*, 2017, in this issue). We have methodologically established the measurement of *S* of natural habitats when distribution model of the habitat is based on the boosted regression trees (BRT) algorithm. *S* is suggested to be calculated from the relative importance of climatic predictors among all of the studied predictors. We selected the most climate sensitive habitats (*CSH*s) of Hungary as a case study and found that mixed coniferous forests and most of the zonal forests are highly sensitive to climate, similarly to annual salt pioneer swards of steppes and lakes, closed steppes on loess, clay, tufa, forest steppe meadows, willow mire shrubs, and some other grassland or shrubland habitats.

We developed an *A* index for habitats, based on naturalness (natural capital index), diversity (Shannon diversity index), and connectivity measures and estimated the *A* of *CSH*s of Hungary. According to our results, willow mire shrubs and closed lowland steppe oak woodlands are those *CSH*s that have the lowest capacity to adapt to climate change, while Turkey oak woodlands may be the most adapted habitats among the studied ones. Shannon diversity of Hungary is relatively low in the lowlands and takes its highest value in higher altitudes, including the Northern Mountains and the Transdanubian Mountains. In summary, adaptive capacity of the climate sensitive habitats of Hungary is generally lower than it needs to be to cope with the predicted climate change of the 21st century.

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