Relationship of Tree Stand Heterogeneity and Forest Naturalness

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Abstract – The aim of our study was to investigate if compositional (tree species richness) and structural (vertical structure, age-structure, patterns of canopy closure) heterogeneity of the canopy layer is related to individual naturalness criteria and to overall forest naturalness at the stand scale. The naturalness values of the assessed criteria (tree species composition, tree stand structure, species composition and structure of shrub layer and forest floor vegetation, dead wood, effects of game, site characteristics) showed similar behaviour when groups of stands with different heterogeneity were compared, regardless of the studied aspect of canopy heterogeneity. The greatest difference was found for criteria describing the canopy layer. Composition and structure of canopy layer, dead wood and total naturalness of the stand differed significantly among the stand groups showing consistently higher values from homogeneous to the most heterogeneous group. Naturalness of the composition and structure of the shrub layer is slightly but significantly higher in stands with heterogeneous canopy layer. Regarding other criteria, significant differences were found only between the homogeneous and the most heterogeneous groups, while groups with intermediate level of heterogeneity did not differ significantly from one extreme. However, the criterion describing effects of game got lower naturalness values in more heterogeneous stands. Naturalness of site characteristics did not differ significantly among the groups except for when stands were grouped based on pattern of canopy closure. From the practical viewpoint it is shown that purposeful forestry operations affecting the canopy layer cause changes in compositional and structural characteristics of other layers as well as in overall stand scale forest naturalness.

forest naturalness / tree species richness / vertical canopy structure / age structure / canopy closure

Kivonat – A faállomány heterogenitása és az erdőtermészetesség kapcsolata. Vizsgálatunkban arra a kérdésre kerestük a választ, hogy a természetes fafajú erdők esetében a faállomány egyes összetételi (elegyesség) és szerkezeti (szintezettség, korszerkezet, záródás mintázata) jellemzőinek heterogenitása milyen összefüggést mutat az erdő egyes természetességi kritériumaival és állomány szintű természetességével. Az elemzett kritériumok (faállomány-összetétel, faállomány-szerkezet,

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cserjeszint-összetétel, cserjeszint-szerkezet, gyepszint-összetétel, gyepszint-szerkezet, holtfa, vadhatás, termőhely) természetességi értékei a különböző vizsgálati szempontokból a homogén és a heterogén csoportok esetében nagyon hasonló eredményeket mutattak. A legmarkánsabb elkülönülést a faállományt jellemző kritériumoknál lehetett tapasztalni. A faállomány-összetétel, a faállomány-szerkezet és a holtfa, valamint az erdőállomány természetessége esetében valamennyi csoport szignifikánsan különbözik, egyre magasabb természetességi értékeket mutatva a homogéntől a legheterogénebb csoportig. Ugyanebben az irányban a természetességi érték növekedése szintén e kritériumoknál a legnagyobb. A cserjeszint összetételének és szerkezetének természetessége csak kismértékben, de szignifikánsan nagyobb a heterogénebb faállományú csoportokban. A többi csoportosítási szempont során többnyire csak a homogén és a legheterogénebb csoport mutat szignifikáns különbséget, a köztes heterogenitású csoport általában valamelyiktől nem különül el. A vadhatás természetessége viszont mindegyik csoportosítási szempontnál szignifikánsan alacsonyabb a heterogénebb faállományok esetén, a termőhely természetességének értéke pedig nem különbözött a faállomány eltérő heterogenitású csoportjaiban – a záródás kivételével – egyik vizsgálati szempont esetében sem. Gyakorlati oldalról közelítve megállapítható, hogy a faállományt érintő tudatos erdészeti beavatkozások összefüggést mutatnak a többi állományszint összetételi és szerkezeti jellemzőinek, valamint az erdőállománynak a természetességével is.

erdőtermészetesség / elegyesség / szintezettség / korszerkezet / záródás

1   INTRODUCTION

In the multi-purpose evaluation of forests there is growing focus on forest naturalness and its temporal change as indicators of forest condition (e.g. Scherzinger 1996, Bergstedt 1997, Reif 1999/2000). Naturalness is the most important and widely used criterion for assessing conservation status and serves as a major tool for the analyses that support planning of conservation management (Hoerr 1993, Schmidt 1997). In the last decade a number of proposals were made on how forest naturalness should be evaluated in Hungary (e.g. Bartha et al. 1998, 2003, Mátyás 1996, 1998, Solymos 1998, 2004, Sódor – Madas 1998). However, only Bondor – Halász (1998) published country scale analyses based on the National Forest Database. No separate field measurements have been made for this purpose so far. Lately, some countries and regions managed to carry out the evaluation of forest naturalness using different protocols (e.g. Austria: Grabherr et al. 1998, Germany: Arbeitskreis Forstliche Landespflege 1996, Switzerland: Brassel – Lischke 2001, Baden-Württemberg: Schirmer 1999, Bradenburg: Steinmeyer 2003). These were taken into account when designing the methods for similar analyses of Hungarian forests.

By naturalness we mean the uncontrolled prevalence of natural processes and the occurrence of features shaped by them (Peterken 1996). In this interpretation naturalness is not equivalent to originality, which excludes human interference of any sort and thus can only be thought of in a historic context for the forests of Centre Europe (Kowarik 1999). Unfortunately, originality is not a measurable variable for large area and numerous stands. Available historical data are scarce to judge the compositional, structural and functional features of forest communities that could have developed in the absence of any human impact (Peterken 1996, Rose 1992). An alternative approach uses selected attributes (compositional, structural and functional characteristics) to estimate naturalness. This approach contains subjective elements as the measured indicator values depend partially on the judgement of professionals and estimation. It is likewise up to experts to decide which attributes to consider and how to weigh them. These decisions rose as the consensus of numerous researchers with various views (Delphi method, see Grabherr et al. 1998), and the methodology of the measurements and analyses was thoroughly documented. We set the reference forest as one shaped by natural forest dynamics. The attributes of the actual forest were compared to the

corresponding development phase of the natural forest cycle (Leibundgut 1959, Korpel' 1995), and the differences were given in percent values. Naturalness was evaluated as a continuous variable ranging from totally artificial state (0 % naturalness) to natural state (100 % naturalness). Naturalness can be assessed at various spatial scales (stand – landscape – region), each calling for distinct methodology. In the present study we used stand (subcompartment) scale assessment of naturalness in a complex way, which provides data not only on general naturalness of a stand, but also enables independent analyses of different criteria of forest naturalness (composition and structure of canopy and shrub layers, of forest floor vegetation and of regeneration, site characteristics, dead wood and effects of games).

Several studies showed that the naturalness state of the tree stand greatly determines overall species composition, diversity and other community features of forest ecosystems (e.g. McComb – Lindenmayer 1999, Müller-Starck 1996, Peterken 1996, Scherzinger 1996, Frank 2000). Considering either traditional ways of forest use, or ongoing 'modern' forest management still prevalent in the major part of our forest landscape, it is the tree stand that has been mostly affected by human activities (Behre 1988, Bürgi 2003). Although forest management influence almost all components of forest ecosystems (site conditions, herbs, animal communities etc.), it is usually aimed at shaping the tree stand (and using timber).

This present study focuses on the relationships between the tree stand and naturalness criteria. To describe the tree stand we use one compositional (species mixture) and three structural (age structure, vertical and horizontal patterns of canopy) attributes that are both directly affected by and react sensitively to conscious forestry operations. The question at hand is whether the different values of these four stand attributes, and thus the different emerging stand types show correlation with the naturalness of compositional, structural and functional features of the forests stand. This knowledge is indispensable when one plans to improve the naturalness of our forests while still managing them. Our hypothesis is that in naturally heterogeneous tree stands (presence of associate tree species, mixed age structure, several canopy layers, patchy canopy closure) naturalness criteria describing other components and functional features have higher values than in the absence of this heterogeneity. We included only stands containing natural (native and site adapted) tree species. Stands with non-indigenous tree species can be very different in conditions from forests with natural tree species obscuring the features emerging from stand scale heterogeneity and horizontal and vertical structures (age structure, layers, canopy closure) potentially affecting naturalness.

2   MATERIALS AND METHODS

In the framework of our project titled „Assessing forest naturalness in Hungary" (2001-2004) a survey was completed in 3000 subcompartments selected by using stratified random sampling. The sample is representative for Hungarian forests in terms of main forest community types. Each selected subcompartments was in the size-range of 3 to 10 hectares. For the purpose of this analysis we only used those subcompartments, in which canopy trees are higher than 5 meters and are built of native tree species. A further constraint was set stating that the mixing ratio of dominating tree species had to exceed the minimum value established for the potential natural forest community. The minimum values are available in the detailed methodological documentation of the survey (http://ramet.elte.hu/~ramet/ project/termerd/index.htm, Table A1b). 1074 subcompartments matched these conditions and thus became object for detailed analysis for this paper.

For assessing individual stands, we used 57 indicators of forest naturalness that were grouped into sets describing different criteria (tree species composition, tree stand structure, species composition of shrub layer, structure of shrub layer, composition of forest floor vegetation, structure of forest floor vegetation, dead wood, effects of game, site characteristics, see *Appendix*). These indicators describe mainly vegetation characteristics, even the effect of game is assessed by the impact on vegetation and site. Indicators describing site characteristics refer to human impacts. The reason for this bias is the need for indicators that can be estimated fast and reliably (giving robust results) during the field survey. This need resulted in the lack of – otherwise important – zoological indicators in our naturalness assessment.

Naturalness values are derived during a hierarchical process composed of three levels. At the first level, we evaluate the qualitative or quantitative indicators (observed in the field) by attaching a numerical value (on a ratio scale ranging from 0 to 100) based on how the status of the indicator in question corresponds to that of the hypothetical reference forest. The obtained value may depend on the potential natural forest community (PNFZ) of the stand. At the second level, the naturalness value of a criterion is derived as a weighed sum of the values of corresponding indicators. For each indicator, the applied weight is defined by estimating how important it is in determining the naturalness of the given criterion. To make naturalness values of different criteria comparable, for each criterion the obtained weighed sum is normalized by its possible theoretical maximum in the given PNFC. At the third level, the total naturalness value of the stand (a single number based on all assessed aspects) is calculated. It is derived as a weighed sum of the naturalness values of all the criteria used at the second level. Weight of a criterion may depend on PNFC. Detailed description of the methods used for the field survey and calculations can be found at http://ramet.elte.hu/~ramet/project/termerd/index.htm.

Since we aim to study the effects of four characteristics (tree species mixture, age structure, vertical and horizontal patterns) of the canopy layer on naturalness criteria, for each analysis we separated homogeneous stands from more heterogeneous ones based on the respective characteristic *(Table 1)*. First we analysed the effects of these four characteristics separately, then we formed groups of stands based on different combinations of them. We distinguished three groups of stands based on three tree species composition indicators. We also formed three-level groupings based on age structure, vertical structure and horizontal patterns of canopy closure, respectively using a single indicator for each. Combined effects of canopy heterogeneity were studied by forming two stand-groups based on species mixture, age structure and vertical structuring: 1) pure, even-aged single-storeyed; 2) mixed, uneven-aged, multi-storeyed. We could not include horizontal pattern of canopy closure, since no stand could have been put into the heterogeneous group. Altogether 310 stands could be used for analysing the combined effects of these characteristics.

We compared average values of individual naturalness criteria and total naturalness among the distinguished stand-groups. The criterion on which we based stand grouping was excluded from each analysis, though the calculation of total naturalness was based on all 57 indicators in each case. Differences among groups were tested by ANOVA and Newman-Keuls multiple comparison, or by t-test when only two groups were formed. In cases where parametric tests could not be applied, we used non-parametric alternatives: Kruskal-Wallis test, non-parametric multiple comparison, Mann-Whitney U test (Zar 1999). We used Statistica for Windows 7.0 for our analyses (Statsoft 2004).

Table 1. Stand groups formed by different canopy characteristics (species composition, age structure, vertical structure, pattern of canopy closure) and their combinations

Canopy feature	Selection criteria
Species composition	
Pure	Tree stand is composed of a single tree species.
Mixed 1	Tree stands not belonging to 'Pure' or 'Mixed 2'.
Mixed 2	Numerical value of indicators '*Number of native tree species with cover > 5 %*' and '*Number of and mixing ratio of associate tree species with cover < 5 %*' ≥ 50.
Age structure	
Even-aged	Tree stand contains only a single age class.
Uneven-aged 1	Tree stand contains two age classes.
Uneven-aged 2	Tree stand contains three or more age classes.
Vertical structure	
Single-storeyed	Tree stand is single-storeyed.
Multi-storeyed 1	Tree stand is two-storeyed.
Multi-storeyed 2	Tree stand is three (or more)-storeyed.
Pattern of canopy closure	
Homogeneous	Canopy closure is uniform all over the stand.
Heterogeneous 1	There are a few larger patches with canopy closure different from the rest of the stand.
Heterogeneous 2	There are a several patches with canopy closure different from the rest of the stand.
Combined	
Homogeneous	Pure, even-aged, single-storeyed: tree stand is composed of a single species, of a single age class and is single-storeyed.
Heterogeneous	Mixed, uneven-aged, multi-storeyed: numerical value of indicators '*Number of native tree species with cover > 5 %*' and '*Number of and mixing ratio of associate tree species with cover < 5 %*' ≥ 50; tree stand contains at least two age classes, and is not single-storeyed.

3 RESULTS

3.1 Effects of tree species composition on naturalness criteria and on total naturalness of the stand

As *Table 2* shows, most criteria got higher naturalness values in mixed than in pure stands. There were two exceptions: 1) naturalness of site characteristics was independent form level of mixing; 2) naturalness values based on game effect were significantly higher in pure stands than in the other two mixed stand groups. All three stand groups had significantly different naturalness values for the following criteria: structure of the canopy layer, composition and structure of forest floor vegetation, dead wood. Total naturalness was also different among all three groups. The highest difference was observed for dead wood, where naturalness value of the most heterogeneous group (Mixed 2) was more than two times higher than that of group 'Pure'. Naturalness values of the shrub layer (both composition and structure) were less different among the stand groups, though mixed stands had higher values based on these criteria as well.

Naturalness values based on structure of regeneration were not significantly different between groups 'Mixed 1' and 'Mixed 2', but both had almost twice as high values as group 'Pure'. Tree species composition had even slighter effects on the naturalness based on the composition of regeneration. Multiple comparison could not differentiate the three stand groups.

Table 2. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different species richness

Criteria	Species richness type			ANOVA	Kruskal-Wallis-test
	Pure	Mixed 1	Mixed 2	*(F; p)*	*(H; p)*
Sample size (n) →	*172*	*780*	*122*		
Structure of canopy layer	29.61±0.52[a]	38.06±0.36[b]	43.61±1.15[c]		144.41; p<0.001
Composition of shrub layer	82.98±1.89[a]	85.14±0.82[a]	91.22±1.84[b]		13.79; p<0.01
Structure of shrub layer	73.67±1.69[a]	78.30±0.74[b]	78.20±1.68[b]	3.58; p<0.05	
Composition of forest floor vegetation	56.75±1.71[a]	68.36±0.84[b]	74.08±2.13[c]	23.62; p<0.001	
Structure of forest floor vegetation	53.38±2.36[a]	64.17±0.99[b]	72.10±2.46[c]		32.53; p<0.001
Composition of regeneration	95.41±1.38[a]	97.62±0.44[a]	99.88±0.07[a]		7.09; p<0.05
Structure of regeneration	18.45±1.87[a]	33.19±1.07[b]	34.09±2.70[b]		47.21; p<0.001
Dead wood	10.22±1.19[a]	16.76±0.75[b]	26.25±2.30[c]		52.32; p<0.001
Effect of game	70.62±1.70[a]	63.45±0.89[b]	57.44±2.57[b]		16.82; p<0.001
Site characteristics	81.47±1.03	83.31±0.45	80.67±1.41		3.74; n.s.
Total naturalness of the stand	53.45±0.59[a]	59.63±0.28[b]	64.51±0.74[c]	75.28; p<0.001	

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using p < 0.05. 'n.s.' stands for not significant.

3.2 Effects of age-structure on naturalness criteria and on total naturalness of the stand

As *Table 3* shows, in uneven-aged stands several criteria (composition of the canopy layer and field layer vegetation, dead wood) and total naturalness of the stand got much higher naturalness values than in more even-aged stands. All three stand groups differed with high significance, and mean values also differed considerably, especially for dead wood. Significant, but only slight difference was found among the stand groups in the naturalness values based on composition and structure of the shrub layer, structure of regeneration. Naturalness based on the structure of the field layer vegetation only stand group 'Uneven-aged 2' had significantly higher naturalness value than the other two groups. In our investigation we did not find any statistical relationship between age-structure of the stand and naturalness of the composition of regeneration and of site characteristics. However, we found significant difference between 'Uneven-aged 2' and the other two stand groups when effects of game were considered, but this time, the most heterogeneous group had lower naturalness value than the other two stand groups.

Table 3. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different age structure

Criteria	Age structure type			ANOVA	Kruskal-Wallis-test
	Even-aged	Uneven-aged 1	Uneven-aged 2		
Sample size (n) →	703	266	105	(F; p)	(H; p)
Composition of canopy layer	67.69±0.32[a]	71.10±0.55[b]	74.45±0.88[c]	36.37; p<0.001	
Composition of shrub layer	83.54±0.93[a]	87.57±1.27[ab]	93.27±1.48[b]		13.52; p<0.01
Structure of shrub layer	76.42±0.80[a]	79.18±1.25[a]	80.92±1.70[a]	3.24; p<0.05	
Composition of forest floor vegetation	63.81±0.90[a]	71.36±1.35[b]	78.86±2.20[c]	24.89; p<0.001	
Structure of forest floor vegetation	61.84±1.08[a]	64.10±1.75[a]	71.47±2.66[b]		12.23; p<0.01
Composition of regeneration	97.00±0.54	98.10±0.66	99.52±0.24		3.12; n.s.
Structure of regeneration	28.79±1.10[a]	33.62±1.85[ab]	38.47±2.91[b]	6.38; p<0.01	
Dead wood	13.49±0.68[a]	19.45±1.36[b]	32.19±2.85[c]		61.87; p<0.001
Effect of game	65.62±0.95[a]	62.37±1.54[a]	56.47±2.23[b]	6.81; p<0.01	
Site characteristics	82.49±0.51	84.04±0.72	80.83±1.43		2.62; n.s.
Total naturalness of the stand	57.17±0.30[a]	61.55±0.47[b]	66.88±0.73[c]	87.60; p<0.001	

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using p < 0.05. 'n.s.' stands for not significant.

3.3 Effects of vertical structure of the canopy on naturalness criteria and on total naturalness of the stand

Vertical structure had similar effects on naturalness to that of age structure. It had no effects on the naturalness based on the composition of regeneration and on site characteristics, and a slight negative relationship was shown with effects of game. For all other criteria significantly higher naturalness values were found in stand groups with more complex vertical canopy structure (*Table 4*). Naturalness values differed greatly among the stand groups when composition of the canopy, dead wood and total naturalness were considered. For other criteria (composition and structure of the shrub layer and field layer vegetation, structure of regeneration) we found much slighter difference, and in several cases multiple comparison did not differentiate between stand groups 'Single-storeyed' and 'Multi-storeyed 2', mostly as a result of small sample size in the latter.

Table 4. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different vertical structure

Criteria	Vertical structure type			ANOVA	Kruskal-Wallis-test
	Single-storeyed	Multi-storeyed 1	Multi-storeyed 2	(F; p)	(H; p)
Sample size (n) →	697	343	34		
Composition of canopy layer	66.89±0.31[a]	73.24±0.46[b]	75.55±1.58[b]	75.77; p<0.001	
Composition of shrub layer	83.14±0.94[a]	89.36±1.05[b]	94.65±2.32[ab]		15.52; p<0.001
Structure of shrub layer	76.36±0.81[a]	79.20±1.04[ab]	85.10±2.77[b]	4.49; p<0.05	
Composition of forest floor vegetation	63.17±0.91[a]	74.17±1.15[b]	77.94±4.03[b]	29.75; p<0.001	
Structure of forest floor vegetation	61.18±1.10[a]	67.01±1.45[b]	70.63±4.67[ab]		10.26; p<0.01
Composition of regeneration	96.88±0.56	98.61±0.44	99.71±0.29		3.12; n.s.
Structure of regeneration	28.12±1.10[a]	35.77±1.60[ab]	39.66±5.64[b]	9.31; p<0.001	
Dead wood	14.03±0.70[a]	20.72±1.28[b]	33.78±5.38[c]		36.63; p<0.001
Effect of game	65.55±0.92[a]	60.82±1.42[a]	61.58±4.16[a]	4.27; p<0.05	
Site characteristics	82.36±0.52	83.64±0.66	80.55±2.26	1.56; n.s.	
Total naturalness of the stand	57.03±0.30[a]	62.67±0.38[b]	68.68±1.57[c]		141.78; p<0.001

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using $p < 0.05$. 'n.s.' stands for not significant.

3.4 Effects of horizontal structure of canopy closure on naturalness criteria and on total naturalness of the stand

As *Table 5* shows, the three stand groups formed by horizontal canopy structure differed considerably in the naturalness values based on structure of the shrub layer, on dead wood and on total naturalness of the stand, by having much higher naturalness values in stands with heterogeneous canopy closure than in stands with more uniform canopy. The two heterogeneous stand groups got higher naturalness values than the uniform group when composition of the canopy, structure of regeneration and field layer vegetation layer were considered. Regarding the naturalness of composition of the field layer vegetation, stand group 'Heterogeneous 2' got higher values than the other two groups. Stand groups based on horizontal structure of canopy closure did not differ significantly in the composition of the shrub layer and regeneration. Similarly, only slight differences were found between these groups in naturalness values based on effects of game and site characteristics, but lower values were characteristic of stand groups with more heterogeneous canopy closure pattern.

Table 5. Naturalness values (mean ± standard error of the mean) of criteria in stand groups with different canopy closure patterns

Criteria	Canopy closure pattern type			ANOVA	Kruskal-Wallis-test
	Homogeneous	Heterogeneous 1	Heterogeneous 2		
Sample size (n) →	650	295	129	*(F; p)*	*(H; p)*
Composition of canopy layer	68.29±0.33[a]	70.31±0.55[b]	71.18±0.81[b]	8.96; p<0.001	
Composition of shrub layer	85.21±0.92[a]	84.34±1.35[a]	89.53±1.86[a]		6.99; p<0.05
Structure of shrub layer	75.37±0.81[a]	78.23±1.29[b]	86.90±1.32[c]		42.83; p<0.001
Composition of forest floor vegetation	64.72±0.91[a]	68.66±1.42[a]	75.96±2.04[b]	13.41; p<0.001	
Structure of forest floor vegetation	58.51±1.13[a]	69.01±1.57[b]	74.71±2.13[b]		50.59; p<0.001
Composition of regeneration	97.26±0.53	97.81±0.65	98.18±1.09	0.38; n.s.	
Structure of regeneration	28.07±1.12[a]	35.31±1.80b[b]	35.36±2.64[b]	7.78; p<0.001	
Dead wood	13.24±0.67[a]	18.80±1.24[b]	30.11±2.75[c]		39.80; p<0.001
Effect of game	65.62±0.96[a]	61.46±1.50[a]	60.94±2.27[a]	3.83; p<0.05	
Site characteristics	83.53±0.50[a]	81.76±0.79[a]	80.78±1.20[a]		6.58; p<0.05
Total naturalness of the stand	57.24±0.30[a]	60.78±0.46[b]	65.40±0.76[c]	65.17; p<0.001	

Groups were compared by using ANOVA or Kruskal-Wallis test. Superscript letters indicate group membership by Newman-Keuls and non-parametric multiple comparisons using p < 0.05. 'n.s.' stands for not significant.

3.5 Combined effects of canopy characteristics

As *Table 6* shows, when stand groups were formed by combinations of the studied stand characteristics, several criteria (composition and structure of forest floor vegetation, structure of regeneration, dead wood, total naturalness of the stand) got significantly and much higher naturalness values in stands that were heterogeneous regarding several canopy features (i.e. mixed, multi-aged, multi-storeyed). Similar trend but much less difference was shown when composition of the shrub layer was considered.

We found no difference between the two stand groups in the naturalness of the following criteria: composition of the shrub layer, composition of regeneration, site characteristics. Naturalness value based on the effects of game was significantly lower in the stands with more heterogeneous canopy.

Table 6. Naturalness values (mean ± standard error of the mean) of criteria describing the combined canopy types

Criteria	Combined stand type		T-test	U-test
	Homogeneous	Heterogeneous 1	$t; p$	$Z; p$
Sample size (n) →	155	55		
Composition of shrub layer	83.38±2.00	92.43±2.56		2.32; p<0.05
Structure of shrub layer	74.72±1.77	81.23±2.44	1.97; n.s.	
Composition of forest floor vegetation	55.52±1.79	77.94±3.21	6.29; p<0.001	
Structure of forest floor vegetation	53.34±2.51	74.43±3.45		4.31; p<0.001
Composition of regeneration	95.55±1.40	99.91±0.10		1.02; n.s.
Structure of regeneration	19.07±2.03	34.01±3.62	3.72; p<0.001	
Dead wood	10.24±1.28	29.26±3.87		5.58; p<0.001
Effect of game	70.91±1.83	57.58±3.98		2.81; p<0.001
Site characteristics	81.23±1.12	80.38±2.02	0.38; n.s.	
Total naturalness of the stand	53.43±0.62	66.74±1.14	10.74; p<0.001	

Groups were compared by using t-test and Mann-Whitney U-test. 'n.s.' stands for not significant.

3.6 Comparison of different groupings

As *Table 7* shows, the naturalness values of the assessed criteria showed similar behaviour when groups of stands with different heterogeneity were compared regardless from which of the 5 canopy characteristic was used for stand grouping. The greatest difference was found in the naturalness of criteria describing the canopy layer (composition, structure, dead wood) and of the total naturalness of the stand. For these criteria naturalness values increased significantly – and also in the highest degree – from homogeneous to more heterogeneous stand groups for all studied canopy characteristics. The greatest differences were found in dead wood, where the naturalness values obtained for the most heterogeneous groups were almost always twice as high as those for the homogeneous ones. Naturalness of the composition and structure of the shrub layer is slightly but significantly higher in stands with heterogeneous canopy layer. Regarding other criteria, significant differences were found only between the homogeneous and the most heterogeneous groups, while groups with intermediate level of heterogeneity did not differ significantly from one extreme. Between-group differences in naturalness values were higher for criteria describing composition and structure of the forest floor vegetation than those of shrub layer with higher values for the more heterogeneous stand groups. Naturalness values of forest floor vegetation differed among all three stand groups when species richness and age structure of the canopy served the basis for grouping, whereas stand groups of intermediate heterogeneity did not differ from one extreme. Naturalness of the composition of regeneration was insensitive for

canopy characteristics except for species richness of the canopy, where more heterogeneous stand groups had slightly higher values. On the contrary, structure of regeneration got higher naturalness values in the most heterogeneous stand groups for all the five respects than in the homogeneous groups. Stand groups of intermediate heterogeneity either did not differ from others (age structure, vertical structure), or they only differed from the homogeneous groups (species richness, canopy closer). The criterion describing effect of game got lower naturalness values in more heterogeneous stands regardless from which canopy characteristics was used for stand grouping. This relationship was the strongest when groups based on combined canopy characteristics and on tree species composition. Naturalness of site characteristics did not differ significantly among the groups except for when stands were grouped based on pattern of canopy closure, where it slightly decreased with increasing heterogeneity.

Table 7. Effects of different canopy characteristics on naturalness

| Criteria | Studied aspect of canopy heterogeneity | | | | |
	Species richness	Age structure	Vertical structure	Pattern of canopy closure	Combined
Composition of canopy layer	n.e.	⇒	⇒	⇒	n.e.
Structure of canopy layer	⇒	n.e.	n.e.	n.e.	n.e.
Composition of shrub layer	→	→	⇒	→	→
Structure of shrub layer	→	→	→	⇒	n.s.
Composition of forest floor vegetation	⇒	→	⇒	⇒	⇒
Structure of forest floor vegetation	⇒	⇒	→	⇒	⇒
Composition of regeneration	→	n.s.	n.s.	n.s.	n.s.
Structure of regeneration	⇒	→	⇒	⇒	⇒
Dead wood	⇒	⇒	⇒	⇒	⇒
Effect of game	⇐	←	←	←	⇐
Site characteristics	n.s.	n.s.	n.s.	←	n.s.
Total naturalness of the stand	⇒	⇒	⇒	⇒	⇒

Legend: n.e. = not evaluated,
n.s. = not significant,
⇒ = considerable increase from homogeneous to heterogeneous,
→ = slight increase from homogeneous to heterogeneous
⇐ = considerable decrease from homogeneous to heterogeneous,
← = slight decrease from homogeneous to heterogeneous.

We found more pronounced between-group differences in naturalness when tree species composition, age structure and canopy closure were used for grouping, whereas differences among groups based on vertical structure and combined canopy characteristics – having only limited number of stands in the most heterogeneous group – were less noticeable.

4   DISCUSSION

While interpreting the findings of this work one has to consider that significant relationships between grouping variables (this time canopy characteristics) and naturalness criteria do not necessarily indicate causal relationship. An illustrative example is the naturalness based on dead wood, which shows strong positive relationship with tree species composition, age structure, vertical structure and horizontal patterns of canopy closure. It is obvious that naturalness of dead wood is not affected by canopy heterogeneity, rather, both are affected by the intensity (or lack) of forest management. On the contrary, naturalness of criteria describing sub-canopy layers (shrub, forest floor, regeneration) is more directly affected by the heterogeneity of the canopy layer, which is the target of purposeful forestry operations. Shrub layer might be an exception since it is often the object of direct forestry operations (e.g. complete removal), however, in such cases canopy layer also bears the signs (homogeneous character) of intensive management.

Forest floor vegetation has a much more stronger reaction (both in composition and structure) to changes in canopy heterogeneity than shrub layer and regeneration. The reason for this lies in the fact that forest floor species can react much faster to changes in canopy closure than woody species, resulting in a much stronger relationship with structural characteristics of the canopy layer. Based on this, we assume that effects of forest management (either increasing or decreasing heterogeneity) get manifest faster in the composition and structure of forest floor vegetation than those of the shrub layer and regeneration. We found that the naturalness of shrub layer composition showed more direct relationship with canopy heterogeneity than that of shrub layer structure. As a possible explanation, we assume that management-induced changes in the canopy layer have a more pronounced manifestation in composition (appearance of non-indigenous or nitrophilous species) than in changes of horizontal patterns of cover.

There is no straightforward explanation of our findings regarding the effects of game (i.e. stands with more heterogeneous canopy tended to have lower naturalness value). We assume no direct relationship between canopy structure and naturalness based on game effects. Instead, more heterogeneous stands tend to occur at such places (under special site conditions), where game density is generally higher because the these sites are difficult to access, have lower economic importance hence receive less intensive human impact. Examples include forests of rocky spots, riverine willow–poplar galleries and calciphile, thermophilous oak thickets and forests. In our naturalness assessment this criterion has the least representative data, since its evaluation in the field is rather difficult and suffers the most from subjectivity. Of the indicators we used, extent of damage in the litter layer (cf. *Appendix*) can be estimated relatively reliably, whereas it is hard to decide if the complete lack of a layer (shrub, regeneration or herbs) is caused by browsing game, or by site conditions (e.g. lack of light). Complete lack of certain layer is a typical phenomenon in stands with extremely homogeneous canopy.

While interpreting our findings, it is important to emphasize that – mainly as an effect of varying intensity of their use – potential natural forest communities are not equally represented within the stand groups formed by different aspects canopy structure. Although we made serious efforts to make our full sample (almost 2900 subcompartments) representative of Hungarian forests, the obtained ratios have changed while we selected stands for this study. However, naturalness values of different forest communities are comparable, since their different characteristics were taken into consideration during the assessment.

Complexity and hierarchical nature of our scheme for naturalness assessment is exemplified by the fact that stand groups formed by different levels of canopy heterogeneity differed the most in the total naturalness of the stand, while naturalness of individual criteria

behaved individually among the stand groups. Total naturalness of the stand – based on evaluation of many indicators – proved to be a sensitive indicator of changes in the forest canopy. As a result, it can also be used for studying ecological, economic or other aspects of forest management, as an overall indicator of management intensity and for assessing if management follows close to nature principles.

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Appendix.   Criteria and indicators used for assessing forest naturalness

Criteria	Indicators	Scale type	Potential values
A. Composition of canopy layer	Number of natural tree species with cover > 5%	ratio	Positive integers
	Presence of natural dominants*	binary	yes; no
	Number of associate tree species with cover < 5%	ratio	positive integers
	Proportion of associate tree species with cover < 5%	ratio	positive integers
	Proportion of non-indigenous tree species	ratio	positive integers
	Proportion of cultivars of native tree species	ratio	positive integers
	Proportion of native tree species, not suited to the site	ratio	positive integers
B. Structure of canopy layer	Age-structure of the canopy layer*	ordinal	1; 2 ;3 or more age classes
	Difference between maximum and minimum canopy closure	ratio	positive integers
	Mean canopy closure*	ratio	positive integers
	Cover of clearings (non-wooded areas)*	ordinal	0; ≤20; >20
	Cover of patches with canopy closure < 50%*	ordinal	0; ≤20; >20
	Cause of canopy openness	nominal	forestry; natural
	Pattern of canopy closure	nominal	several patches with different canopy closure; a few larger patches with different canopy closure; uniform canopy closure
	Vertical structure of the canopy	ordinal	1; 2; ≥3
	Transition between the canopy and shrub layers	ordinal	continuous; locally continuous; non-continuous
	Number of old/veteran trees	ratio	positive integers (no/ha)
	Pattern of old/veteran trees	nominal	not present; large patches; small patches; random; uniform
	Relative abundance of trees with unusual crown or stem shape	ordinal	0; ≤10; >10
C. Composition of shrub layer	Authenticity of species composition	binary	yes; no
	Proportion of non-indigenous and/or aggressive tree and shrub species in the shrub layer	ordinal	0 - <10; 10-50; >50
	Proportion of nitrophilous tree and shrub species in the shrub layer*	ordinal	0 - <10; 10-50; >50
D. Structure of shrub layer	Cause of the absence of shrub layer	nominal	Not absent; human impact; natural
	Signs of shrub removal	binary	visible, not visible;
	Difference between maximum and minimum cover of shrub layer	ratio	positive integers
	Mean cover in the shrub layer*	ratio	positive integers
	Spatial pattern of shrubs	nominal	small patches; large patches; random; uniform or missing
E. Composition of forest floor vegetation	Proportion of weeds and/or nitrophilous herb species	ratio	positive integers
	Presence of subordinate associate herbs	ordinal	present in great numbers, present, sparse, missing

Criteria	Indicators	Scale type	Potential values
F. Structure of forest floor vegetation	Difference between maximum and minimum cover of herbaceous species*	ratio	positive integers
	Mean cover in the herb layer*	ratio	positive integers
	Spatial pattern of herbs	nominal	small patches; large patches; random; uniform or missing
	Mean cover of bryophytes*	ratio	positive integers
G. Composition of regeneration	Proportion of non-indigenous and/or aggressive species in the regeneration	ratio	positive integers
H. Structure of regeneration	Difference between maximum and minimum cover of regeneration	ratio	positive integers
	Mean cover of regeneration of native trees	ratio	positive integers
	Proportion of viable, several-years-old regeneration	ratio	positive integers
I. Dead wood characteristics	Relative abundance of standing dead trees and snags	ratio	positive integers
	Number of large standing dead trees and snags	ratio	positive integers (no/ha)
	Cover of lying dead wood (∅ > 5 cm)	ordinal	<1; 1-5; >5
	Decay status of dead wood	nominal	Not present; all decay classes are evenly represented; mostly soft, well-decayed; mostly solid, less decayed
	Number of large lying dead logs (∅ >30 cm)	ratio	positive integers (no/ha)
K. Effects of game	Extent of stripping damage (%)	ordinal	0 - <10; 10-50; >50
	Extent of browsing in the shrub layer	ordinal	none, rare, abundant, on all individuals
	Extent of browsing in the herb layer	ordinal	none, rare, abundant, on all individuals
	Extent of damage in the litter layer (%)	ratio	positive integers
	Shrub layer completely eliminated by game	binary	yes; no
	Herb layer completely eliminated by game	binary	yes; no
	Regeneration completely eliminated by game	binary	yes; no
J. Site characteristics	Signs of secondary erosion*	binary	visible; not visible
	Extent of erosion	ordinal	0; <10; 10-50; >50
	Type of erosion*	nominal	gully, rill, sheet, partial, none
	Humus form*	nominal	mor; moder; mull
	Proportion of area with compacted soil	ordinal	0; ≤10; >10
	Mixing soil horizons*	binary	present; missing
	Damage to the soil surface	binary	present; missing
	Presence of microhabitats	ordinal	none; few; many

Detailed description of field sampling and calculation is available at http://ramet.elte.hu/~ramet/project/termerd/index.htm.

* – Applied rules of evaluation (attaching numerical value) depend on potential natural forest community dependent