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MULTILEVEL ANALYSIS OF LANDSCAPE STRUCTURE FOR LAND USE DECISIONS

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Abstract

The success of land use depends greatly on how correctly the hierarchy of ecological processes is taken into consideration. Relief is believed to be a critical factor of landscape spatial pattern. The purpose of this research is to identify hierarchical levels of relief which control the correlated response of plant and soil cover. We apply multi-level modeling of relationships between landscape components which relies on step-by-step examination of equations relating the property of the focus landscape unit to relief parameters of a hypothetical higher-level unit. Relief indices were tested as indicators of moisture and nutrients redistribution in landscape. The results of case studies in three forest regions of Russia revealed different dominant space scales for the response of nutrition-sensitive and moisture-sensitive plant species and soils horizons to relief properties. Land use decisions should be based on landscape maps that consider hierarchical levels of relief, imposing restrictions on focus landscape properties and processes.

Key words: landscape, components, interaction, hierarchy, characteristic space scale, multiple regression, resonance

Introduction

Landscape is a multidimensional system in which processes of various spatio-temporal scales operate simultaneously. Each landscape unit is nestled into higher-order systems which impose constants on its structure and functioning (Turner et al., 2001; Wu, David, 2002). Landscape management and decision-making is realized usually at the level of landscape units with linear dimension about hundreds of metres. While affecting any property of landscape in some manner, we assume that it will cause a desirable chain of consequences among other properties. The success of desirable effects depends greatly on how correctly the hierarchy of ecological processes and relations is taken into consideration (Marceau, 1999).

The hierarchy of landscape structure and land-use decisions is a problem of crucial importance for landscape ecology. Direct and indirect linkages between ecosystem components manifested in matter and energy circles and their hierarchy is declared to be one of the most critical focuses of ecosystem science (Pickett, Cadenasso, 2002). The present-day level of explaining mechanisms of relief and plant cover interactions as well as contributions of natural anthropogenic factors is insufficient. Complexity and multidimensionality of a landscape require the necessity to relate numerous biotic and abiotic attributes to a reasonable number of classes. The theoretical framework of landscape ecology to date does not provide a well-developed methodology for analyzing pattern and dynamics in landscapes with strong topography, or, more generally speaking, landscapes with a strong underlying physiographic structure; at the same time, landscape ecological research has a good potential to fill this gap by quantifying the effect of topography on different aspects of landscape pattern (Dorner et al., 2002). We evidence rapid growth of a number of publications that focus on the relationship between properties of landscape units and that of higher-order systems characterized by means of remote sensing and digital terrain models (e.g. Myster et al., 1997; Burrough et al., 2001; Musio et al., 2007). Mechanisms of interactions between hierarchical levels of landscape organization, and characteristic space scales of interactions between landscape components need to be investigated more deeply. For example, Saunders et al (1998) evaluated correlations between pairs of soil, plant cover and temperature attributes and tested hypotheses concerning the dominant scale of their variability. As a result, a bimodal structure of correlations was revealed and interpreted as a discrete characteristic of interactions and the existence of several scales of interaction. Burnett, Blaschke (2003) applied multiscale segmentation to study flow gradients among landscape units. Borcard, Legendre (2002) proposed a method of detecting and quantifying spatial patterns over a wide range of scales.

To adapt land use to natural units, one should identify ecological gradients and boundaries which control concerted spatial changes of landscape properties under impact. Spatial structure differs in landscapes of different origin; individual components of landscape (plant cover, soil, deposits, water etc.) respond to gradients in different ways. Identification of holistic separate units requires gaining insight into the correlated response of landscape properties to environmental gradients.

Relief is believed to be one of the most critical factors in the landscape spatial pattern. A number of relief attributes have been proposed to describe ecological processes, such as moisture distribution, illumination, chemical and mechanical migration matter, and groundwater level etc. (Krcho, 1973). Relief has a close connection to tectonic and geological features of the territory and it preserves information about palaeogeographical events. Hierarchical levels of relief can be related to hierarchical levels of climate, hydrology, and soil and plant cover. The most intriguing question is how to identify hierarchical levels of relief which are the most relevant in explaining spatial variance of individual landscape properties and how to find sets of properties responding to the same level of relief.

Moisture-related properties of landscape are connected to climatic changes. If they are also related to relief, the forecast of climate-induced changes can be elaborated separately for different classes of landforms. Nutrient supply in landscape also undergoes changes due to climatic trends. This kind of unit-referenced forecast will provide information concerning properties of landscape components (e.g. plant species abundance), and under which relief conditions they are most likely to be changed in correspondence with climatic trends. At the same locations hydrology-independent properties (e.g. plant species mainly sensitive to mineral nutrition) would resist a new level of heat and moisture supply. This example is the particular case of the more generalized problem of research – how to delineate areas with different rules of relationships between landscape components. Resilience of the landscape unit to local impact is influenced by a spatio-temporal scale of exterior impact, either natural or anthropogenic.

In the research we focused on the following questions:

- In which space scale landscape attributes vary in concordance with each other?
- Which processes are responsible for spatial variability of various landscape attributes?
- What is the typical size of holistic landscape units which control processes in the investigated lower-order units?
- Which hierarchical levels of landscape organization, and how many of them, should be considered in land-use decision-making which is expected to affect a particular landscape attribute?

Materials and Methods

The study areas are located in different subzones of the forest landscape zone in European Russia (Fig. 1).

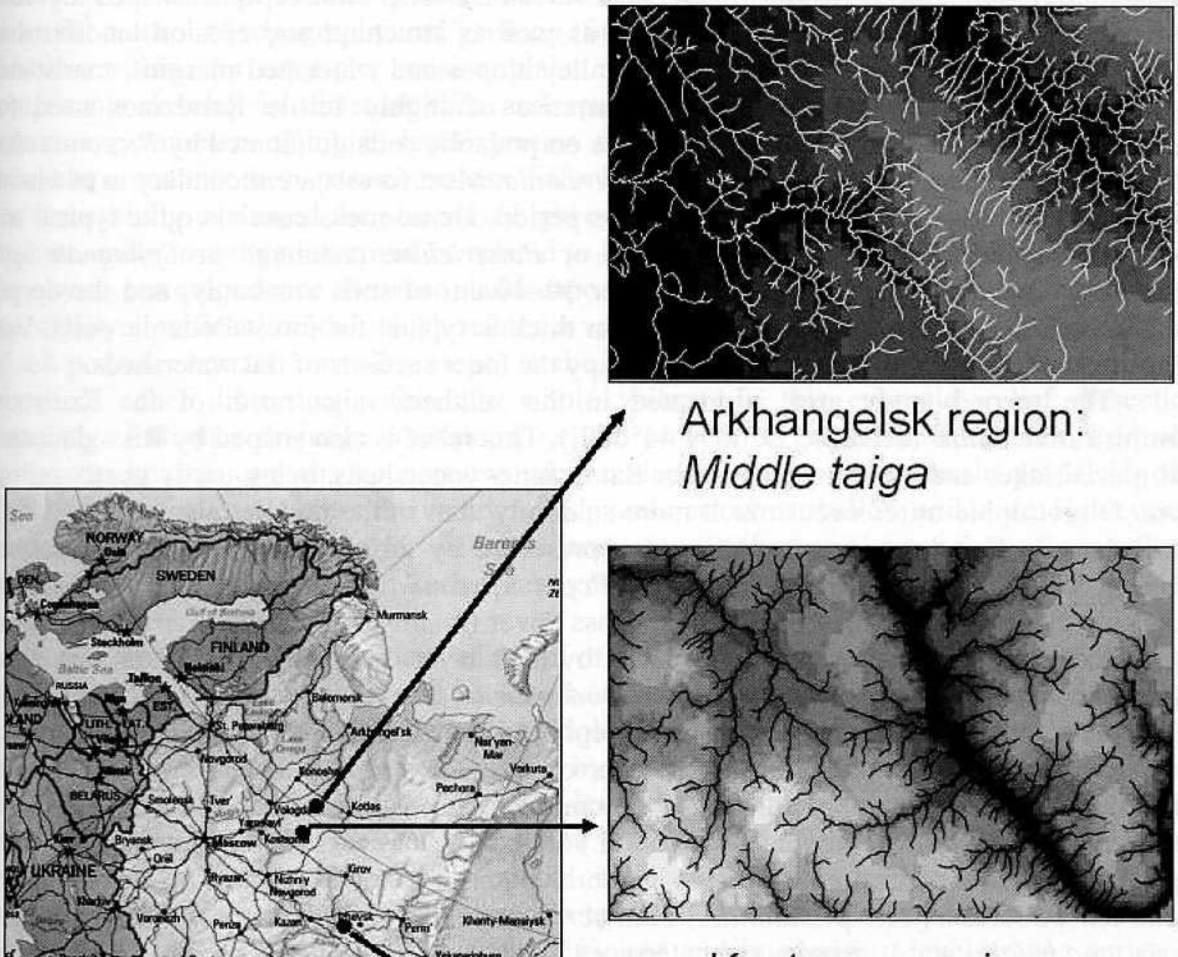

Fig.1. Location of study areas and digital elevation models

The northenmost study area is located south of the Arkhangelsk administrative *oblast* (region) in middle taiga (center – 60°54′N 43°14′E). The landscape is shaped by Riss morainic and Würm limnoglacial landforms as well as structural and erosion landforms in near-surface Permian marlstones. On steep valley slopes and watershed margins, marlstones are exposed and they determine the occurrence of highly fertile Rendzines used for agriculture. Watersheds are covered by forests on podzolic soils dominated by *Picea excelsa*, *Pinus sylvestris*, *Betula pendula* and *Populus tremula*. Most forests are secondary to extensive ploughing and clearcutting in the 1930–1970s period. Dense moss cover is quite typical and dominated by either *Pleurozium schreberii* or *Polytrichum commune* or *Sphagnum spp.* dependent on drainage conditions. The upper 30–40 cm of soils are sandy, and the deeper horizons are loamy. A peat horizon 10–30 cm thick is typical for forest Podzolic soils. Vast oligotrophic *Sphagnum*-dominated mires occupy the inner sections of flat watersheds.

The second study area is located in the southern taiga north of the Kostroma administrative *oblast* (center – 59°00′N 44°01′E). This relief is also shaped by Riss glaciation and glacial lakes and currents. It is rather flat in inner watersheds, being partly gently rolling plain. Oligotrophic mires occur much more seldomly than in the middle taiga and they have smaller sizes. The dominant vegetation is represented by forests with *Picea excelsa*, *Abies sibirica*, *Tilia cordata*, *Betula pendula* and *Populus tremula.* Most forests are secondary to extensive clearcutting in the 1950–1980s. Moss cover (mainly *Pleurozium schreberii*) occurs sporadically and in most areas it is replaced by herb layer dominated by *Oxalis acetosella, Maianthemum bifolium and Aegopodium podagraria.* The marginal parts of watersheds adjusting to the Unzha river valley are deeply dissected and well-drained; exposures of Jurassic carbonate clays and marlstones occur on steep slopes. The soil texture is similar to that in the Arkhangelsk study area, but the humus horizon is thicker and the podzolic one is thinner. Upper elevations (about 200 m a. s. l.) are covered by loess-like loams resulting in a higher occurrence of nutrient-sensitive nemoral plant species which are more typical for broad-leaved forests (*Acer platanoides, Tilia cordata, Ulmus glabra, Asarum europaeum, and Paris quadrifolia* etc.). Sandy river terraces with well-developed eolian landforms are occupied by pine forests of deep Podzols.

The southernmost study area is located in the mixed forests subzone in Udmurtia Republic (center – 52°28′N 56°38′E). The peculiarity of this region is the absence of morainic deposits and landforms. An erosion-shaped undulating hilly plain built of gently inclined strata of Permian carbonate red clays and marlstones prevails. Most of the area has a thin cover of loess-like loams (30–50 cm) above loams, These are replaced, mainly on valley slopes, by a cover of sands. The highly fertile soils on loess-like loams and carbonate loams determine an intensive agriculture with remnant forest patches among fields. Inner parts of wider watersheds are covered by mixed forests with a dominance of *Picea excelsa*, *Abies sibirica*, *Quercus robur, Tilia cordata*, *Populus tremula and Ulmus glabra.* Pine forests were planted in the 1970s to stop erosion on valley slopes with sandy cover above bedrocks. Nemoral species dominate the herb layer, while moss layers rarely occur. Bogs are very small and also occur rarely. The climate is more continental and less humid than the two regions previously described.

The study areas have obvious climatic differences, but at the same time they have much in common: e.g. dominant elevations 120–200 m a. s. l., carbonate bedrocks close to the surface with local exposures, a two-layered soil texture, a combination of flat and deeply dissected areas, well-manifested humidity and fertility gradients, and a prevalence of secondary forests with remnant patches of zonal ones. Each study area embraces about 400 km^2 and is provided in 170–180 integrated field descriptions distributed in accordance with landforms proportions.

Methods to delineate holistic landscape units differ depending on the purposes of research. The concept of strictly deterministic relationships between landscape components under the control of topography and geology (Solnetsev, 1948) were relevant for agricultural planning within, for example, erosion plains. However, it is well known that landscape components develop in different time and space scales. Hence, we face the necessity to determine parameters of higher-level systems separately for certain landscape properties. It should be noted that these parameters can differ between geographical regions. Given that one has successfully evaluated the size of a higher-level controlling system, the variance of the attribute under investigation could be related to the gradient of differing ecological processes. To reveal correspondence between landscape property and process we need to build a statistically significant model which relates a value of the landscape attribute (e.g. thickness of soil podzolic horizon on valley slope) to the characteristics of a higher-level unit (e.g. the degree of relief dissection within the whole valley). In this example, relief dissection parameters influence drainage conditions, i.e. the process of groundwater transfer. Podzolic horizon thicknesses can vary between two similar slope units depending on the properties of a higher-level unit, e.g. whether the valley is deep and narrow or shallow and wide. However, a hierarchy cannot be the same for different landscape attributes. The number of controlling higher-order levels can vary for soils, plant cover, groundwater and even for their specific attributes.

To solve the problem of determination of hierarchy for various landscape attributes we applied multilevel modelling of relations between landscape components. This methodology relies upon step-by-step examination of multiple regression equations which relate attributes of the focus landscape unit to parameters of a hypothetical higher-level unit (Khoroshev et al., 2007). Hypotheses for dimensions of higher-level unit are formulated based on the varying extent and resolution for which the calculation is performed. Parameters of the model which provide the best results indicate the spatial scale of the process that determines spatial variability of the focus attribute (*resonance* level). The most relevant statistical model is chosen based on the maximum r-square coefficient and minimum p-level among series of equations. Two interpretations of a high-quality model are possible. The first one involves the direct cause-effect relationship between dependent and independent variables. For example, the productivity of a herb layer in the forest is directly affected by canopy cover since the latter controls light conditions. The second interpretation involves indirect linkage via dependence on some third variable. For example, species composition in tree and herb layers can correlate due to the spatial variance of groundwater level even if they are not in a direct cause-effect relationship. One of the most crucial methodological challenges in the study of intercomponent relationships is how to distinguish direct and indirect linkage in pairs of landscape attributes. The answer to this question will determine the success of forecasts of the future landscape state under either anthropogenic pressure or natural environmental changes.

Each landscape component is controlled by numerous factors of spatial differentiation. The same factor (e.g. moisture gradient) can control various components (e.g. trees, herbs or soil horizons). If some combination of spatial parameters provides a significant multilevel model of relationships between relief, soils and plant cover, then sites with similar relief properties can be interpreted as elements of some holistic landscape unit within which landscape attributes vary in strict concordance with each other. A set of units that follows the same regularity in relationships between components is interpreted as an area with manifestation of a single driving force. To determine such areas, we performed analysis of residuals from multiple regression equations. The units with close to zero residuals belong to the mosaic area with non-random variability of components controlled by some strong driving force. Units with a high deviation of residuals from zero are believed to be indifferent to the driving force analyzed. The residuals can be either random or following another rule. Hence, two groups of units can be in close neighbourhood but indicate a prevalence of different driving forces. If a relief controls the groundwater level, then moisture-sensitive herb species will have higher or lower abundance in accordance with the relief conditions. If a relief is determined by geological or tectonic phenomena, then nutrition-sensitive plant species will be distributed in space in accordance with the relief. Since different driving forces affect a landscape property simultaneously, it is possible to identify intersecting areas of their manifestation

The research procedure consisted of the following stages:

1. Field investigation: Principal landscape attributes were described and measured, namely: landforms, plant species abundance for different layers (trees, mosses, herbs etc.), soil horizons thickness and Munsell colors, and soil texture.
2. A digital elevation model (DEM) in the scale of 1:200 000 with a resolution of 400 m was designed. By choosing a rather coarse resolution we assume that landscape units associated with relief mesoforms will be the focus level. Finer landscape details are deliberately eliminated from consideration. Each field description corresponds to a typical unit for the particular relief mesoform.
3. Morphometric properties of landforms were evaluated by means of neighbourhood statistics (standard deviation of elevations, sum of talweg lengths, vertical and horizontal curvature) for each sample plot in the square neighbourhood with linear dimension consequently 1.2, 2.0, 2.8, 3.6, 6.0 km. Arcview Spatial Analyst and FRACDIM software were applied. Below, for simplicity, we refer to these neighbourhoods as "*2.0 km level*", "*6.0 km level*" etc. In this way, each landscape unit provided by field description (a total of about 170 in each study area) was characterized by 20 relief indices. These latter were considered to indicate restrictions imposed by higher-level units on the focus-level unit.
4. Initial variables (attributes of landscape components) were transformed by means of multidimensional scaling to: i) reduce dimensionality, ii) to receive normal distribution of values, and iii) to reveal independent virtual factors of spatial differentiation. Virtual factor values, which reflect concerted changes of variables in space, were interpreted based on field data as factors of spatial differentiation, or ecological gradients, namely: factors of humidity, mineral nutrition, light availability, recovery succession, intensity of podzolization, and intensity of peat accumulation etc. (below referred to as "*factors*")
5. Non-linear second-order multiple regression models of relations between each factor of landscape differentiation (y) and relief morphometric attributes ($x1$, $x2$, $x3$, $x4$) were designed for each square neighbourhood separately:

$$y=a+b_1x_1+b_2x_1^2+b_3x_2+b_4x_2^2+b_5x_1x_2+...+b_mx_nx_k+\varepsilon).$$

We evaluated the degree to which each landscape property is controlled by the integrated effect of the independent morphometric relief parameters of the hypothetical higher-order unit. The value and sign of b parameters indicate individual contributions of independent variables x to the explanation of the dependent variable y, i.e. a particular ecological gradient.

6. The quality of models for different square neighbourhoods was compared based on *r-square* (i.e.the proportion of variance explained) and *p-level*. Square neighbourhood was assumed as the scale parameter which characterizes the size (extent) of a hypothetical higher-order landscape unit.

7. The resonance level (single or multiple) of interaction between relief and landscape attribues was determined. *Resonance effect* is understood as the agreed spatial variability of a set of landscape attributes under a certain combination of scale parameters. It is indicated by the highest r-square among statistically significant models for different neighbourhoods. This means that if relief morphometric parameters within certain a square neighbourhood vary significantly, the dependent landscape attribute(s) will vary in strict concordance.

8. Resonance levels were compared for different landscape properties. The one characteristic for most factors (ecological gradients) was considered to be the level of the holistic geosystem which requires consideration when making land use decisions. Relief classification approximates obtains holistic landscape content.

9. Relief classification based on morphometric attributes of relief in the square neighbourhood was performed using the k-means method.

10. Discriminant analysis was applied to determine what number of relief classes is necessary in order to reflect plant and soil cover variability. Relief classes were used as a grouping variable and the total set of factors - as independent variables. The analysis was performed several times separately for each neighbourhood and for the different number of classes. The percentage of correct classification was used as an indicator of discrimination quality, i.e. as an indicator of holistic content of a corresponding number of relief classes

Results

In the Udmurtia mixed-forest landscape the most statistically significant equations (Table 1) show the best quality for the square neighbourhood with a linear dimension of 6 km (i.e. within the area extending for 3 km either side of the focus landscape unit). Therefore the properties of the focus landscape unit are controlled by properties of some higher-order unit with an average size of 6 km. This reflects the geomorphological specifics of the territory. Here, more or less parallel wide river valleys which fall within a system of neotectonic joints alternate with watersheds with an average size of 6 km. Broad-leaved trees prevail on the watersheds while coniferous ones are on the valley slopes (D1tr). Herbs preferring loamy soils prevail on these watersheds while sand-preferring ones are on the valley slopes (D3h). Humus horizons are thicker on the watersheds while thick litter without humus horizon is more typical for valley slopes (D3hor). Detailed analysis of the correlated spatial behaviour of these factors shows evidence that 6 km is the dominant scale for factors which reflect a contrast of nutrient-rich and nutrient-poor habitats. This kind of contrast is manifested both in plant communities and soil processes. Another kind of spatial pattern is created by relief properties at the 1.2 km level. This finer scale level is indicative for identification of small second-order streams, narrow local watersheds, isolated wateshed hills, small depressions, wide and narrow sections of big valleys, and individual ravines etc. The humus and podzolic horizons thickness (D2hor) is highly dependent at the 1.2 km level since it is insensitive to coarser scale contrasts. The deeper the dissection goes in the near neighbourhood, the thicker the podzolic horizon and the thinner the humus one become

At the same time, factors of an obviously anthropogenic nature have no dominant scale and consequently no statistically significant relations with relief. Factor D4h values and D4hor are related to the proportion of non-forest species closely linked to the presence of former arable horizons in the forest soils. Since relief does not impose strict limits for agriculture, former arable soils can occur both on watersheds and valley slopes. Meadow species are able to penetrate to the marginal sections of forest patches located on any landform. Hence, relief cannot be treated as a significant control over these properties of soil and plant cover.

Table 1. Udmurtia study area : Proportion of variance explained (r-square*100) by multiple regression equations, where Factor value at the focus landscape unit is the dependent variable and morphometric attrubutes of relief in square neighborhood are independent variables. Bold italic letters are used for statistically significant equations

Factors of landscape components spatial differentiation		Linear dimension of square neighborhood, km				
	Herbs abundance	***1.2***	***2.0***	***2.8***	***3.6***	***6.0***
D1h	Boreal vs. Nitrophilous dpecies	10	8	7	10	9
D2h	Tilia-related vs. Pinus-related species	***20***	***22***	***22***	***24***	***34***
D3h	Loam preferring vs. Sand preferring species	10	12	***14***	***20***	***27***
D4h	Forest species vs. Meadow species	12	13	12	12	9
	Trees abundance					
D1tr	Coniferous vs. Broad-leaved	***28***	***28***	***27***	***28***	***48***
D2tr	Pinus vs. Abies, Populus, Tilia	***18***	***22***	***20***	***20***	***34***
D3tr	Deciduous vs. Coniferous	***30***	***29***	***35***	***32***	***36***
D4tr	Picea, Abies, Populus vs. Pinus, Betula	11	***14***	***14***	***18***	***14***
	Low shrubs abundance					
D1low	Rubus saxatilis vs. Vaccinium vitis-idaea	12	11	11	11	12
D2low	Vaccinium myrtillus vs. Vaccinium vitis-idaea	4	6	9	9	9
	Shrubs abundance					
D1bush	Corylus vs. Frangula	12	***15***	***18***	***21***	***16***
D2bush	Corylus vs. Juniperus	10	***19***	***22***	***22***	***34***
D3bush	Daphne vs. Padus	***14***	10	10	9	***17***
D4bush	Rubus vs. Viburnum	10	11	10	12	***17***
	Soil Munsell color					
D1col	Leaching intensity	***20***	***14***	11	***22***	***19***
D2col	Humus accumulation intensity	***19***	***19***	***17***	***18***	***21***
D3col	Humus and Fe transfer	9	7	9	10	11
D4col	Humus accumulation intensity	7	***14***	13	9	15
	Soil horizons thickness					
D1hor -	Podzol vs. Peat	7	4	3	6	12
D2hor-	Humus vs. Podzol	***20***	11	12	13	10
D3hor	Humus vs. Litter	***19***	***24***	***22***	***18***	***27***
D4hor	Arable horizons	11	13	13	11	9

Table 1. continued

Soil texture						
D1text	Change at 30 cm depth	6	11	10	12	10
D2text	Peculiarity of 30-40 cm layer	4	8	6	4	5
D3text	Change in 0-30 cm layer	14	12	8	13	***18***
D4text	Multiplicity of strata	***16***	***14***	10	5	7

Thus, sensitivity of a large set of landscape attributes to relief morphometry at the 6 km level support the hypothesis that holistic landscape systems exist and their delineation can be based on relief classification. Now, the intriguing question arises of how many relief classes are necessary to identify holistic landscape systems. The results of discriminant analysis (Fig. 2) show that the 2.8 km level is the least informative and has no holistic landscape content, but relief classification in the space with a linear dimension of 6.0 km is the most adequate level that provides perfect discrimination of plant cover and soils attributes. The 4 and 12 relief classes make sense for landscape mapping based on relief properties in a 6 km wide neighbourhood, whereas the 8 relief classes provide almost the same discrimination as 12 classes do (64 and 63% of correct classification respectively). Hence, it is more reasonable and informative to divide the 4 main classes into 12 subclasses at the lower hierarchical level. By doing this, we find rationales for relief-related classification of landscape units at two hierarchical levels.

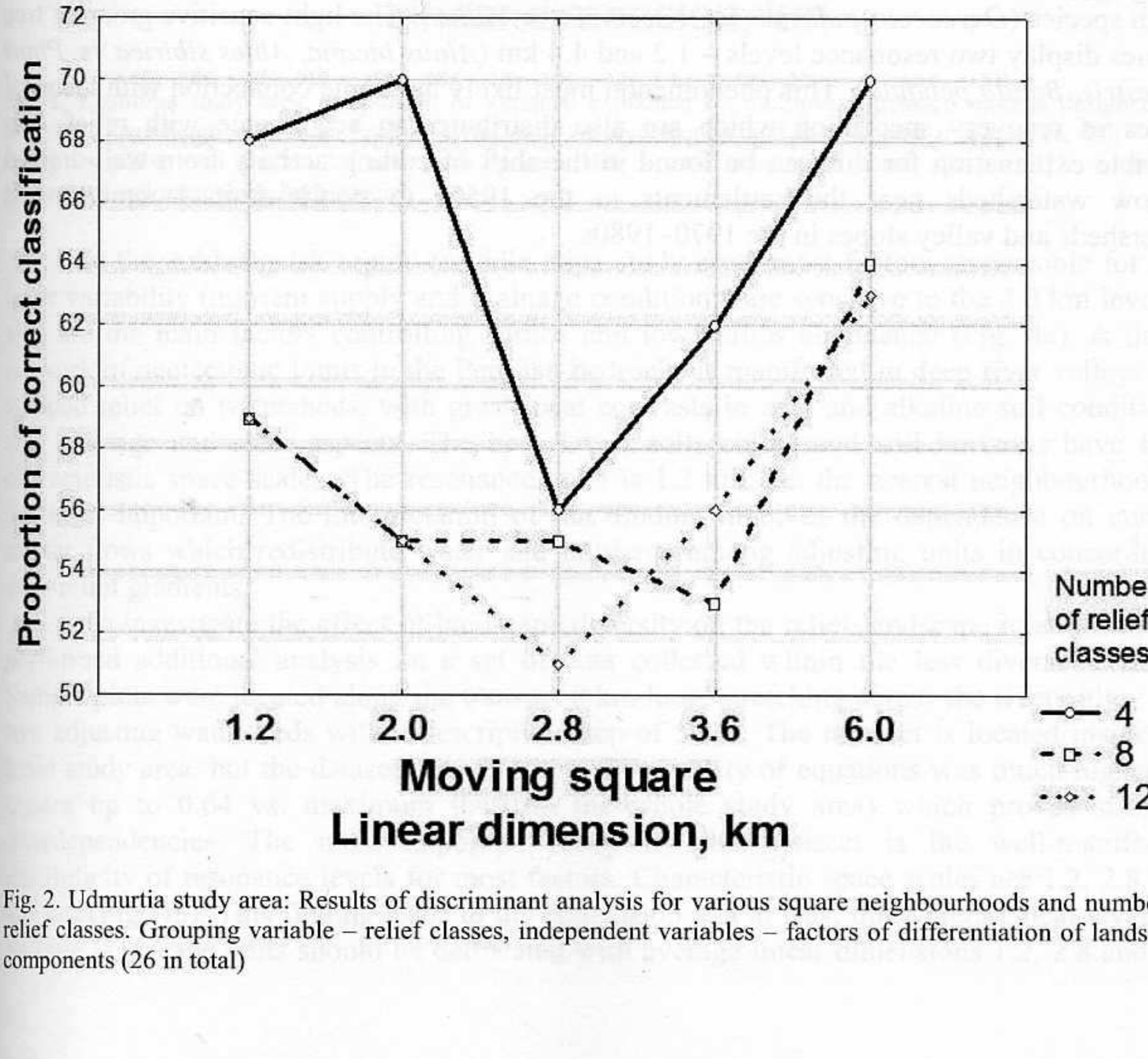

Fig. 2. Udmurtia study area: Results of discriminant analysis for various square neighbourhoods and number of relief classes. Grouping variable – relief classes, independent variables – factors of differentiation of landscape components (26 in total)

Following the same methodology, we tested how moisture-sensitive and nutrients-sensitive landscape properties respond to various hierarchical levels of relief in the southern and middle taiga landscapes.

In the Kostroma region (southern taiga study area) most attributes of tree, herb, moss and shrub layers turned out to be insensitive to relief at the 1.2–2.8 km levels but much more sensitive at the 3.6–6.0 km level (Fig. 3). The most widely occurring resonance level of interactions between plant cover and relief is in the 4.4 km neighbourhood. Relief classification based on attributes at this level successfully identifies groups of landforms with various degrees of Riss glaciation and fluvio-glacial current heritage. Additionally, groups of well-drained morainic hills, flat outwash plains and terraces, deeply dissected marginal parts of watersheds with Jurassic bedrocks exposures can be delimited at this level more precisely. These kinds of landscape elements differ in drainage conditions and nutrients supply resulting in plant cover contrasts. The values of the factors which vary in concordance with relief at the 4.4 km level are interpreted as follows: the ratio of oligotrophic and mesotrophic low shrub species (e.g. *Andromeda palustris* vs. *Rubus saxatilis*) and tree species (e.g. *Alnus incana* vs. *Abies sibirica*), the proportion of nutrient sensitive tree species (*Tilia cordata* vs. *Pinus sylvestris*), and the total amount of shrub species (more on nutrient-rich loess-like loams and less on poor eolian sands). However, some properties are insensitive to the 4.4 km level while being in resonance with the 2.0 km level, and this reflects the current system of low-order river valleys and local erosion-shaped watersheds. Such fine-scale resonance relationships are characteristic for the ratio of hydrophyte and mesophyte herb species (e.g. *Carex rostrata* vs. *Asarum europaeus*), the radial redistribution of ferrum-related soil color indices (Chroma at 10 cm depth vs. Chroma at 40 cm depth), and the ratio of hydrophyte and mesophyte low shrub species (*Oxycoccus palustris* vs. *Vaccinium myrtillus*). The light-sensitive group of tree species display two resonance levels – 1.2 and 4.4 km (*Alnus incana, Abies sibirica* vs. *Pinus sylvestris, Betula pendula*). This phenomenon most likely has some connection with the seral stages of recovery succession which are also distributed in accordance with relief. The possible explanation for this can be found in the shift of cutting activity from well-drained narrow watersheds near the settlements in the 1950s to poorly-drained remote wide watersheds and valley slopes in the 1970–1980s.

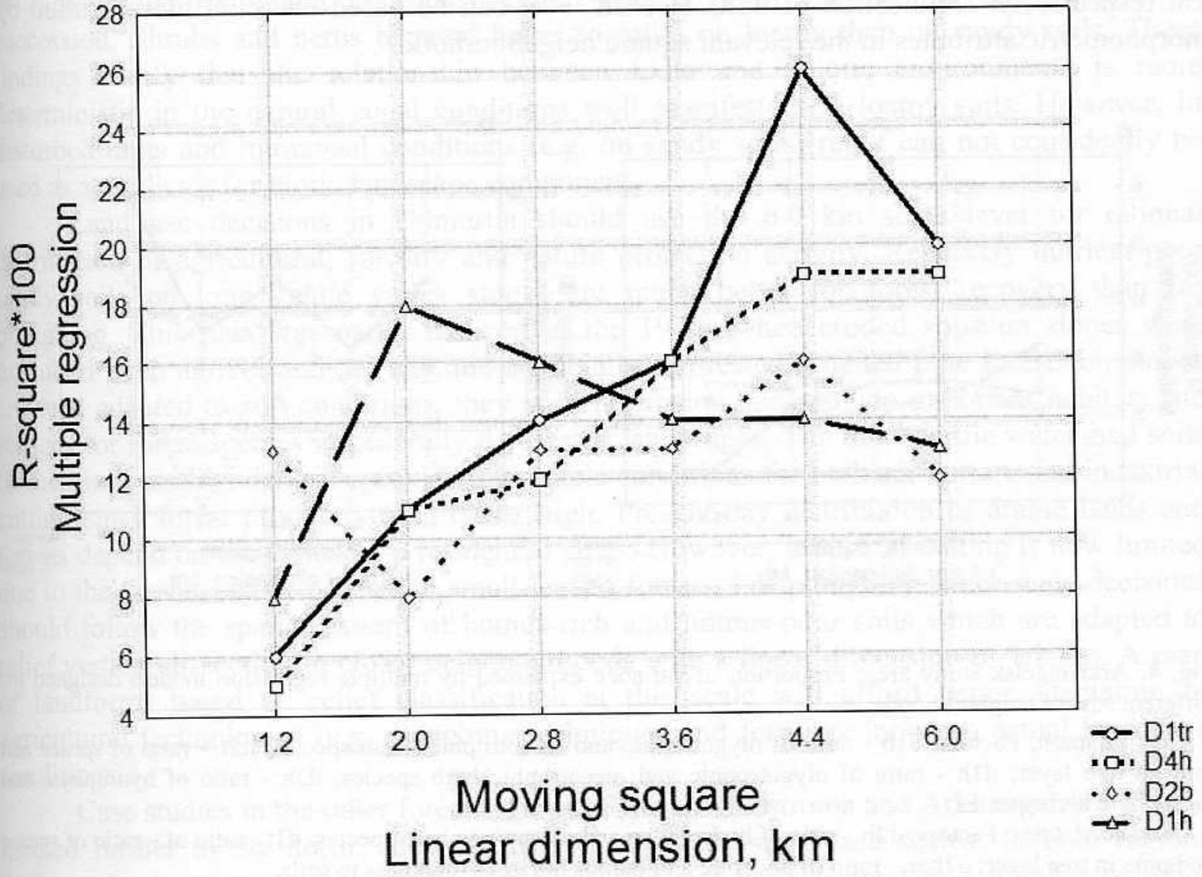

Fig. 3. Kostroma study area: Proportion of variance explained by multiple regression models designed for different square neighbourhoods. Factors: d1tr - ratio of olygotrophic and mesotrophic tree species; d4h – ratio of light-sensitive and shadow-tolerant herb species; d2b - total amount of shrub species; d1h – ratio of hydrophyte and mesophyte herb species

In the Arkhangelsk region (middle taiga study area) most factors responsible for tree layer variability (nutrient supply and drainage conditions) are sensitive to the 2.0 km level as also are the main factors controlling shrubs and low shrubs abundance (Fig. 4a). A dense network of neotectonic joints in the Permian bedrocks is manifested in deep river valleys and stepped relief on watersheds, with great local contrasts in acid and alkaline soil conditions, and drainage and solar aspects. The herb layer, soils colors and soil horizons have finer characteristic space scales. The resonance level is 1.2 km, i.e. the nearest neighbourhood is the most important. The interpretation of this finding involves the dependence on current matter flows which redistribute water and nutrients among adjusting units in concordance with relief gradients.

To investigate the effect of landscape diversity on the relief-landscape relationship we performed additional analysis on a set of data collected within the less diverse territory. Sample plots were located along the transect 8 km long, stretching across the river valley and two adjusting watersheds with a description step of 50 m. The transect is located inside the main study area, but the datasets are different. The quality of equations was much higher (r-square up to 0.64 vs. maximum 0.40 on the whole study area) which proves stronger interdependencies. The most important result for the transect is the well-manifested multiplicity of resonance levels for most factors. Characteristic space scales are 1.2, 2.8 and 6.0 km (Fig. 4b). This finding leads to the conclusion that at least three hierarchical levels of holistic landscape units should be delineated with average linear dimensions 1.2, 2.8 and 6.0

km respectively. Delineation of units at each level can be based on relief classification by morphometric attributes in the relevant square neighbourhood.

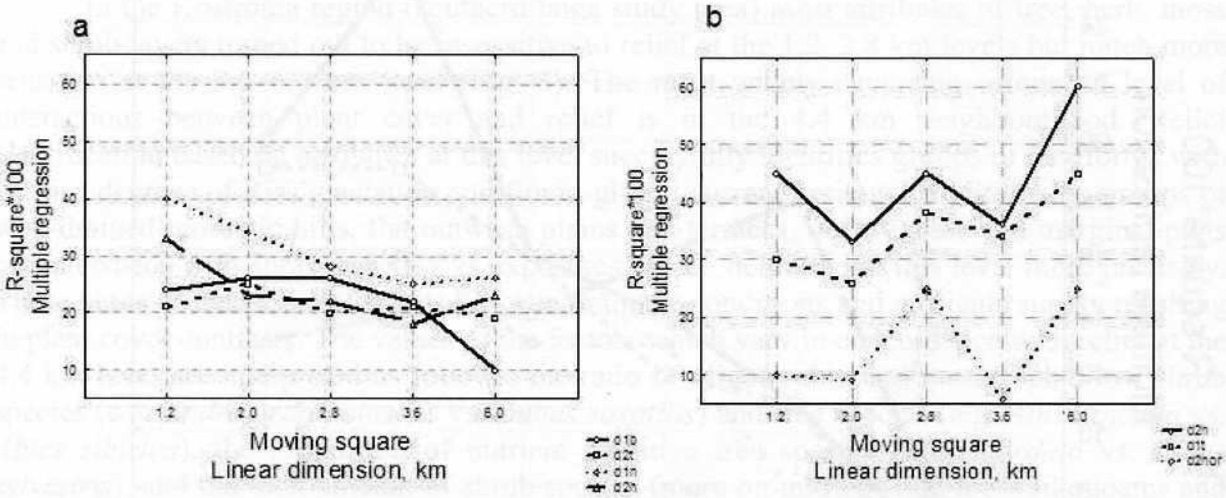

Fig. 4. Arkhangelsk study area: Proportion of variance explained by multiple regression models designed for different square neighborhoods.

a - main dataset. Factors: d1b - ratio of olygotrophic and mesotrophic shrub species; d2t – ratio of spruce and pine in tree layer; d1h - ratio of olygotrophic and mesotrophic herb species; d2h - ratio of hydrophyte and mesophyte herb species.

b - transect dataset. Factors: d2h - ratio of hydrophyte and mesophyte herb species; d1t - ratio of – ratio of spruce and pine in tree layer; d2hor – ratio of podzolic and humus horizons thickness in soils.

Discussion and conclusion

The chosen resolution of digital elevation model (400 m) and corresponding level of focus landscape units dictate a rather coarse resonance level of interactions between landscape components and relief properties. In most cases, higher-order landscape units which drives spatial variability at the focus level have a larger size than the simple closest neighbourhood (i.e. more than 8 adjusting pixels-units). In the Arkhangelsk region, the most "powerful" higher-order units have a linear dimension of about 2.0–2.8 km, whereas in the Kostroma region it is 4.4 km and in Udmurtia 6 km. Finer-scale interactions certainly have no less significance, but higher DEM resolution is needed to reveal them (and this identification is planned as the next step of our research). The results obtained for the resolution at 400 m show that soil properties are less sensitive to relief than plant cover. The most likely explanation for this is that soil is controlled by finer details of landforms, e.g. alternation of shallow narrow depressions and low hills, which cannot be depicted by the chosen resolution but have a great affect on the intensity of podzolization, peat accumulation, and gley process etc.

Concordance of response of various landscape components to the same hierarchical level of relief shows a characteristic space scale of processes which control matter redistribution in landscape. Thus, land use decisions, e.g. forest or agriculture planning, should rely on landscape maps based on relief classification in moving window with region-specific linear dimensions as evaluated above.

The residual analysis perfomed in the Udmurtia study area showed that it is possible to delineate areas where the model of dependence between tree layer and relief is most relevant. The highest quality of the model is achieved for landscape units with dominance of *Picea abies and Abies sibirica*, high crown closure, low rate of litter decomposition and the absence of *Pinus sylvestris* which is usually either planted or prevails at the initial stages of succession. Shrubs and herbs respond better to relief on loamy than on sandy soils. These findings testify that the relationship between biota and abiotic environments is more deterministic in the natural zonal conditions well manifested on loamy soils. However, in disturbed units and intrazonal conditions (e.g. on sandy soils) relief can not confidently be used as a predictor for biotic landscape components.

Land use decisions in Udmurtia should use the 6.0 km scale level for rational distribution of agricultural, forestry and nature protection activity. Relatively nutrient-poor sandy soils on long gentle valley slopes are much better for forest recovery than for ploughing. This idea was partly realized in the 1970s when eroded soils on slopes were excluded from agricultural activity and artificially reforested. Planted pine forests on slopes are well adapted to soil conditions, they prevent erosion and provide important habitats and refuges for forest species in generally deforested landscapes. The more fertile watershed soils formed in loess-like deposits provide favourable conditions for both agriculture and industrial cutting since forest productivity is rather high. Present-day distribution of arable lands and forests depend on the distance to residential areas. However, industrial cutting is now limited due to the prevalence of premature small-leaved forests. For ploughing, finer-scale decisions should follow the spatial pattern of humus-rich and humus-poor soils which are adapted to relief vertical dissection in closer neighbourhoods with a linear dimension of 1.2 km. A map of landforms based on relief classification at this scale will afford better adaptation of agricultural technologies (e.g. ploughing techniques and fertilizer input) to actual landscape conditions.

Case studies in the other forest regions of Russia (Kostroma and Arkhangelsk regions), located further to the north, showed different characteristic space scales. In both regions different landscape components are less correlated and they respond to a number of relief hierarchical levels. Although phytocoenotic layers are more strongly inter-related here than in the mixed forest zone, they are less connected to soils and relief. Hence, land use decisions and strategies for biodiversity preservation should be multi-scale, and they require careful consideration of scale-specific processes which control plant cover layers and soils.

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