ANÁLISE DE NICHOS ECOLÓGICOS DE HORIZONTES ORGÂNICOS EM DIVERSOS ECOSISTEMAS DE SOLO - FITOCENOSE

ANALYSIS OF ECOLOGICAL NICHES OF ORGANIC HORIZONS IN VARIOUS PHYTOCENOSIS-SOIL ECOSYSTEMS

ОЦЕНКА ЭКОЛОГИЧЕСКИХ НИШ НАПОЧВЕННЫХ ОРГАНОГЕННЫХ ГОРИЗОНТОВ В РАЗЛИЧНЫХ ПОЧВЕННО-ФИТОЦЕНОТИЧЕСКИХ ЭКОСИСТЕМАХ

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RESUMO

A resistência dos ecossistemas terrestres às influências climáticas é largamente determinada pela condição de cobertura do solo, onde o horizonte organogênico (serapilheira) desempenha um papel crucial. A interação entre resíduos vegetativos e micro e mesoorganismos é regulada pela temperatura, umidade e parâmetros físico-químicos do ambiente, que juntos formam um nicho ecológico de tal horizonte organogênico. Este trabalho tem como objetivo analisar a formação de horizontes organogênicos do solo em várias combinações de fatores bioclimáticos (nichos ecológicos) e, assim, identificar sua associação com comunidades solo-fitocenóticas - vários ecossistemas terrestres. O estudo utilizou os seguintes métodos: avaliação de especialistas, mapeamento, previsão geográfica, métodos matemáticos (correlação, dispersão, análise de regressão, método de informação estatística para avaliar a conjugação intercomponente de fenômenos e fatores) e o método taxonômico para categorizar os nichos ecológicos do solo. Foram avaliados os parâmetros quantitativos de fatores climáticos do solo (quantidade de serapilheira, t/ha, temperaturas ativas acima de 10 °C, razão de precipitação, potencial redox, mV) que afetam a formação e o desenvolvimento de horizontes orgânicos moídos. Quatro tipos de nichos ecológicos formados em vários ecossistemas da Terra foram identificados. Os resultados podem ser úteis para uma análise comparativa do funcionamento de vários ecossistemas terrestres, a escolha de métodos para a sua reabilitação e previsão de sua evolução na mudança climática.

Palavras-chave: *dinâmica do ecossistema, estabilidade do ecossistema, parâmetros climáticos, cobertura do solo, método estatístico.*

ABSTRACT

The resistance of ground ecosystems to climatic influences is largely determined by the soil cover condition, where the organogenic horizon (ground litter) plays a crucial role. The interaction between vegetative waste and micro- and meso-organisms is regulated by temperature, humidity, physicochemical parameters of the environment, which altogether form an ecological niche of such an organogenic horizon. This paper aims to analyze the formation of ground organogenic horizons in various combinations of bio-climatic factors (ecological niches) and hence identify their association with soil-phytocenotic communities – various ground ecosystems. The study used the following methods: expert assessments, mapping, geographic forecasting, mathematical methods (correlation, dispersion, regression analysis, information-statistical method for assessing the intercomponent conjugacy of phenomena and factors), taxonomic method for categorizing the ground ecological

niches. The quantitative parameters of soil-climatic factors (amount of ground litter, t/ha, active temperatures above 10 °C, precipitation ratio, redox potential, mV) that affect formation and development of ground organic horizons, were assessed. Four types of ecological niches formed in various ecosystems of the Earth were identified. The findings can be useful for a comparative analysis of the functioning of various ground ecosystems, the choice of methods for their rehabilitation and forecasting of their evolution in changing climate.

Keywords: *ecosystem dynamics, ecosystem stability, climatic parameters, soil cover, statistical method.*

АННОТАЦИЯ

Устойчивость наземных экосистем к климатическим воздействиям во многом определяется состоянием почвенного покрова, в функционировании которого важнейшую роль играет поверхностный органогенный горизонт. Интенсивность взаимодействия отмирающего растительного опада с живыми микро- и мезоорганизмами регулируется внешними условиями – температурой, влажностью, физико-химическими параметрами среды, которые в данной работе рассматриваются как экологическую нишу такого органогенного горизонта. Цель статьи заключается в анализе формирования напочвенных органогенных горизонтов при различных сочетаниях биологических и климатических факторов (экологических ниш), что позволило выявить их приуроченность к определенным почвенно-фитоценотическим сообществам – различным наземным экосистемам. В качестве методов исследования использованы методы экспертных оценок, картографирования, географического прогноза, математические (корреляционный, дисперсионный, регрессионный анализ, информационно-статистический метод оценки межкомпонентной сопряженности явлений и факторов), таксономический, позволяющий типизировать основные виды наземных экологических ниш. Оценены количественные параметры почвенно-климатических факторов (величина наземного опада, т/га; сумма активных температур выше 100 °C; коэффициент увлажнения; окислительно-восстановительный потенциал, мВ), оказывающих влияние на формирование напочвенных органогенных горизонтов и появление четырех видов экологических ниш в различных экосистемах Земли.

Ключевые слова: *динамика экосистемы, информационно-статистические методы, климатические параметры, напочвенный органогенный горизонт, устойчивость экосистем, экологическая ниша*

INTRODUCTION

In any ecosystem, the detrital branch is an important link of the circulation: that is the transition from the living (green) organic matter to the mortmass to continue the geosphere cycle.

In phytocenoses, such processes mainly occur within the organic soil horizons, which perform a dual function. On the one hand, the organic matter of litter decomposes, which indicates the final stage of the green cycle. On the other hand, the decomposition products of the litter stimulate the soil formation processes. Such organic soil horizons are an integral part of any soil profile and are usually classified as genetic horizons, in spite of very little thickness in relation to the entire profile. Thus, the forest soil litter, the steppe mat, and the peat horizons can be considered as mega-forms, or large

morphological units that make up the organic profile of soils. The role of litter in soil formation is difficult to overestimate: to a large extent, it determines both the morphological structure and many physicochemical properties of the functioning soil profile. As a rule, any plant succession inevitably leads to the transformation of soil as well. Therefore, the litters should be regarded as relatively independent, spatially defined organomineral horizons where plant litter, meso- and micro-organisms, and soil mineral matter are closely intertwined. Such horizons function in certain conditions that are determined by the external environment parameters where they exist (Kubiena, 1955; Bazilevich, 1965; Bazilevich *et al.*, 1968; Bazilevich, 1986; Bogatyrev, 1993).

Usually, the soil cover is the basic component in the ground ecosystem formation.

Therefore, it can be said that ecosystems are formed under the influence of similar factors: the biological ones (ground plant litter, vital activity of organisms) and the climatic ones (heat supply, wetting, environment acidity, mineral nutrition, etc.) (Bazilevich *et al.*, 1968; Tishkov, 1979; Popova, 2006; Popova, 2012). However, it is the different combinations of these parameters that determine the appearance of specific organic horizons within certain areals. (Chandler, 1941; Karpachevsky, 1983; Bogatyrev, 1993; Bogatyrev, 1996)

If the organic horizon (litter) is regarded as a relatively independent natural object, then the aggregate of external factors affecting its development can be seen as an 'ecological niche', i.e. conditions where such horizon exists. Hence the characteristics of the litter can reveal conditions of the ecosystem functioning. Respectively, the ecosystems can be represented as certain combinations of the ecological niches of different structure, complexity and stability in time and space (Evans, 1956; Orians, 1975; Svirezhev, 1978; Kolomyts, 2003; Popova, 2006).

At present, in connection with the climate change, an important issue is the ecosystem resistance to the external influences (Evans, 1956; Svirezhev, 1978; Holten *et al.*, 1993; Kolomyts, 2003; Popova, 2006). It should be assumed that the ecosystem resistance largely depends on the state of organic horizons, as part of a small biological cycle of matter and energy. The structural-functional and diagnostic properties of such horizons allow assessing the quantitative parameters of the ecosystem resistance in potentially possible variations of hydrothermal conditions and biological factors.

This work is devoted to the study of ecological niches of the basic ground ecosystems in the aspect of their differentiation depending on the acting environmental factors (Armand and Vedyushkin, 1989; Armand, 1993; Bogatyrev and Semenyuk, 1996). At that, the ecological niches are studied through the condition of the organic horizons.

The purpose of the study is a structural and functional analysis of formation of the organic soil horizons in order to classify the ecological niches and indicate the ecosystems of basic types in the view of biological (the magnitude of land litter) and climatic (heat supply, wetting, pH of the environment) factors (Svirezhev, 1978; Armand, 1986; Bazilevich, 1986; Bogatyrev and

Semenyuk 1996; Kolomyts, 2003).

The following tasks were solved in accordance with the purpose of the study:

First, a geo-information database of the state of organogenic horizons was created using the authors' own materials, file materials, monographic literature and cartographic data.

Second, the influence of soil-climatic factors on formation and distribution of the organic soil horizons was assessed in various phytocenosis-soil ecosystems.

Third, ecological niches of organic soil horizons were classified based on the assessment of the relationship between the thickness characteristics of the organic soil horizon and environmental factors, and the degree of resistance of the basic ecosystems was determined.

The subject of the study is the phytocenosis-soil ecosystems, which are defined as a biogeocenoses within the boundaries of phytocenosis and characterized by the thickness of the organic soil horizon, consisting of dead remnants of plants, animals and bacteria and being in genetic relationship with both the vegetation cover and the mineral soil mass.

MATERIALS AND METHODS

The study uses the notion 'ecological niche of the organic soil horizon'. It means a certain area of a space of vital factors (biota, heat, moisture, minerals) that affect formation of the organic soil horizons in ecosystems of various types (Bazilevich, 1965; Titlyanova, 1984; Glazovskaya, 1992; Popova, 2012).

The organic soil horizon is regarded as the central biogenic object in a specific soil-cenotic ecosystem, which development and functioning is determined by a number of soil-climatic factors (the size of ground litter, heat supply, moistening conditions, environmental response). Organic soil horizons are characterized by the following properties (Kolomyts, 2003; Popova, 2012):

- *elasticity* is the litter ability to return to its initial state (to restore its structure) at various changes in the effect of factors, to maintain interrelations within the system, i.e. the ability to compensate for the influence of factors;

- *plasticity* is the litter ability to change under the influence of external factors, but to return to the initial state after a certain time;
- *resistance (inertance)* is the litter ability to change within the limits acceptable for a given areal under the influence of factors;
- *ecological optimum* is a combination of the environmental factors that ensures a natural balance, under the conditions of their natural fluctuations.

Relying in the *geo-information method*, this study used the database of the thickness of the organic soil horizons in 300 stakes (Figure 1). The following influencing factors were identified for each stake with litter stocks, known from the previous research (Popova, 2012):

- the amount of ground litter, the zoomass and the number of decomposers (G.I., c/ha);
- environment response (pH);
- redox potential (RP, mV);
- heat supply indexes ($S_{t>10^{\circ}\text{C}}$);
- vegetation wetting indicators (Ku).

The relation between the litter stocks and the influencing factors (G.I., $S_{t>10^{\circ}\text{C}}$, Ku, pH) was estimated by the correlation coefficient in the following form:

$$r_{xy} = \frac{\sum_{i=1}^N x_i y_i - N \bar{x} \bar{y}}{[(\sum_{i=1}^N x_i^2 - N \bar{x}^2)(\sum_{i=1}^N y_i^2 - N \bar{y}^2)]^{1/2}} \quad (\text{Eq. 1})$$

The *dispersion analysis* was used to distinguish the part determined by the influence of the studied environmental factors, from the total aggregate of indicators of the horizon thickness.

To improve the accuracy, the division of places with different litter thickness in the ecosystems of the basic climatic zones was confirmed by the *taxonomic method*. The randomization at a high scale level ensured the representativeness of the samples.

The *information-statistical method* was used to assess the inter-component contingency of various factors and litter stocks in areals and to identify the types of ecological niches (Puzachenko, 1988; Kerzhentsev, 1999; Kolomyts, 2003; Popova, 2012). The ecological niches of the organic soil horizons were classified

according to the following parameters:

- intervals of litter stocks in the areals/sub-areals – the dependences of the horizon thickness on the amount of ground litter;
- niche volume per each gradient of the factor ($V, rel.$) – the number of gradations of the described factor, covered by this niche;
- niche capacity per each gradient of the factor ($P, rel.$) – the maximum value of the normalized *frequency (ratio of the indicator to the relative value)* for the considered factor (biological or climatic); such maximum value corresponds to the ecological optimum of phenomena.

The first parameter indicates the width of the homeostasis region, i.e. the range that the organic soil horizon occupies in the space of values of the considered factor. The second parameter indicates the degree of concentration of the organic soil horizon in that factor gradation where the litter occurs with the greatest probability, and which is accepted as optimal.

It was believed that the relation between the factor and the phenomenon is significant if >1 . Gradations of the factor with the highest coefficient values form an ecological optimum of the niche, while the remaining gradations refer to the part influenced by random factors (the 'blurred' part of the niche). Hence *the ecological optimum of the niche characterizes the statistical norm, which corresponds to the equilibrium requirement*. Consequently, it can be assumed that when within its ecological optimum, the ecosystem is in a fairly balanced state, but the 'blurred' parts of the ecological niche characterize deviations from equilibrium, and in this respect they are of prognostic interest as values of the probabilistic 'normal' states of the ecosystem in case of the future shift of a certain parameter.

The *information-statistical method* was used to characterize and typify the ecological niches by estimating the ratios of litter stock indicators in areals with inter-component contingency of various factors. The algorithm was as follows:

- (1) Determination of the number of intervals, that all values of the litter stocks of the considered areal are divided into, by the expression adopted in the probability theory:

$$K = 1 + 3.2 \lg N \quad (\text{Eq. 2})$$

where N is the number of points in the areal. The number of intervals in each areal is 5 at $N = 30$.

- (2) Building the matrices of joint occurrence of phenomenon A (litter stocks) in different intervals with the gradations of factors—G.I. (c/ha), $S_{>10^{\circ}\text{C}}$, Ku, pH. Determination of possible combinations of the litter stocks (A) with the gradations of factors (B).
- (3) Calculation of the probabilities (frequencies) of the joint occurrence P_{ij} , where i is the repeatability of phenomenon A, and j is the repeatability of gradations of factors B.
- (4) Determination of the total frequencies of occurrence of the litter stocks (A) for different gradations of factors (B) in each interval—by adding in columns. Determination of the total values of one factor gradation for the whole areal—by adding in rows.
- (5) Determination of conditional probabilities (Pa_i/Pb_j) of the fact that the litter stocks in each interval have definite values for specific factor gradations.
- (6) The coupling coefficient Ca_i/Cb_j was determined for each interval of litter stocks in the areal and specific factor gradations. The coefficient > 1 indicates that the coupling between the litter stocks and the factor is significant.
- (7) The number of coupling coefficients > 1 characterizes the volume of the ecological niche of the areal ($V, rel.$). The niche volume (V) shows how many factor gradations have a significant effect on litter stocks in the areal.
- (8) To determine the niche capacity ($P, rel.$), the normalized partial coupling coefficients were calculated for each factor gradation in each litter stock interval, using the formula

$$C = a_i/b_j / C(a_i/Cb_j) \quad (\text{Eq. 3})$$

The following methods were also used in developing the theoretical and methodological basis for this study: expert assessments, mapping, geographic forecasting, mathematical methods (correlation, dispersion, regression analysis, information-statistical method for assessing the inter-component contingency of phenomena and factors), and taxonomic method.

RESULTS AND DISCUSSION

3.1. Quantitative parameters of ecological niches

The determined quantitative parameters of the environmental factors that influence formation of the organic horizons made it possible to build a *correlation matrix* and identify the relation patterns in various terrestrial ecosystems.

Eleven gradations of litter stocks were identified: >0.6 ; $0.6-1.2$; $1.3-1.6$; $1.7-2.6$; $2.7-6.0$; $6.1-12$; $13-14$; $15-21$; $22-47$; $48-97$; $98-225$ t/ha. They are referred to as 'areals' in this paper. Breakdown of points into areals was confirmed using the taxonomic method. The following were selected as basic conditions:

First, an areal should be a relatively dense accumulation of points in comparison with other areas of space. Such accumulation of points determines the litter stocks at different points, depending on the influencing factors: the amount of ground litter, the sum of active temperatures, the wetting factors and pH of the environment. All other areas of space must contain either few points, or contain none. In the first case, the points can be classified as extreme, requiring a separate detailed consideration. To quantify the above density concept, it is necessary to obtain both the mean values of the litter stocks and the influencing factors for the selected areals, and the value of the dispersions describing how close the points of the areal are located to the centre (mean value) in the space: the denser and more compact the areal is, the less the dispersions should be.

Second, the areals should be separable from each other – they can be relatively close to each other or separated by wide empty sections.

Third, the set of points should be divided into areals, based on the above rules. At that, one more option was adopted in addition to the requirements for the closeness of points within the areals, density and their remoteness from each other: the divided areals must have the same number of points ($N = 30$). This rule was implemented by analyzing the graphs of the dependencies of litter stocks on the influencing factors. Then, the most informative and clear graph of areal division was determined. This graph reflected the dependence of litter stocks on the wetting factor, since the features of

distribution of 330 points on the plane 'litter stocks – wetting factor' made it possible to highlight the areals most clearly (Figure 2). The graph 'litter stocks – amount of ground litter' was also rather indicative (Figure 3).

The first 120 points arranged along the abscissa axis, which made it possible to distinguish areals by density and separation from each other. It was impossible to identify areals from these 120 points with respect to the ordinate axis. The remaining 210 points arranged along the ordinate axis, which allowed identifying the remaining areals.

In the process of classification, a situation occurred that 60 points with litter reserves of 11.9–21.1 t/ha could not be divided into separate areals in the plane 'amount of ground litter' with respect to the ordinate axis, since the points arranged in a very compact manner (Figure 3).

Due to this, there were considered options for classification in the planes 'litter stocks – sum of active temperatures' and 'litter stocks – environment response'. It appeared that the most expedient was the classification of these areals in the plane 'litter stocks – heat supply (the sum of active temperatures)' and these 60 points were divided into two areals (Figure 4).

Since the data samples in the areals should be a source of information on litter stocks, influencing factors and their interaction, it is important that such samples correctly reflected the properties of the resultant feature – the litter stocks and the factors. For this, the samples should be representative. The method of ensuring the sample representativeness is randomization, i.e. random sampling of data. The randomness of data in the samples was provided by using random numbers.

For each areal there were estimated the mean value of litter stocks and influencing factors and the dispersion (mean deviation squares of random values—litter stocks and influencing factors—from the estimated mean in the areal), which made it possible to assess the compactness of areals.

The estimates of the arithmetic mean are used as the estimates of mean. The analysis of errors of mean (arising from the fact that the estimate of mean was obtained from a finite number of data) brought a conclusion that the obtained estimates of mean with a small error characterize the true mean value.

The boundaries of the intervals were determined, and it became possible to state that the true mean values in 95% of cases fall into this interval, and respectively the sample means (estimates of mean) are in this confidence interval.

The compactness (density) of areals was estimated as a ratio of estimates of dispersion of litter stocks and the influencing factor in which plane the distribution to the areals was conducted.

The compactness analysis showed that three areals were loose. These were the areals with litter stocks 0.02–0.6; 0.6–1.2; 51.4–96.5 t/ha. The points with litter stocks in them are rather scattered in relation to their center (mean). It was suggested to allocate the so-called extreme points in these areals.

To isolate such extreme points and confirm the fact that they differ from the bulk of the values of litter stocks, culling of points in the areals was carried out. The rules justifying culling were developed with reference to the case when the data sampling (litter stocks or influencing factors in the areal) is described by the normal (or close to it) distribution law.

The assumption of the normal distribution of values in the samples characterizing both litter stocks and influencing factors was checked for all areals. The need for such a check was also connected with the fact that all subsequent mathematical operations—correlation analysis, showing how justified the choice of factors is; dispersion analysis, showing how much variation in environmental factors in the areal affects variation in litter stocks; and regression analysis that predicts litter stocks – require the normal distribution of values in the samples.

The hypothesis on the normality of distribution of values in the samples was checked on the basis of the Wilk-Shapiro test, specially adapted for the case when the sample size is $N < 50$. The results of the check showed that, at the risk of making a mistake in 10% of cases, it can be argued that all the samples are distributed normally. This is also confirmed by the variation coefficient (Table 1).

The arithmetic mean values of litter stocks were used in the study to characterize the main geographic areals (Table 2).

The parameters of areals were considered depending on the environmental factors: with

litter stocks from 0.3 to 141.4 t/ha, the sum of active temperatures above 10°C from 0.1 to 10,000°C, wetting coefficient from 0.1 to 1.4, soil solution reaction from 4.0 to 7.0 (Figure 5).

3.2. Types of ecological niches

Next, ecological niches of litter were typified.

3.2.1 Type I – unstable ecological niche

This type has $V = 0.1 - 0.2$; $P = 0.9 - 1.0$ and includes niches for sub-areals in terms of ground litter, heat supply and soil solution reaction. It is characterized by absolutely minimal resistance of the organic soil horizon. Having an extremely narrow ecological niche and a very wide variety of its states in the zone of ecological optimum, the litter quickly loses balance even with a slight change in any factor of the external environment. The organic soil horizon of this type can be used as a primary indicator of changes in the landscape-ecological state of various ecosystems.

Thus, it can be assumed that the sub-areals and gradations of the environmental factor that are within the ecological optimum, reflect a decrease in stability of litter and the ecosystem functioning as a whole.

This ecological niche is typical for the deserts of tropical and equatorial belts with litter stocks of less than 0.3 t/ha and the deserts of arctic belt with litter stocks of 3.3 t/ha.

3.2.2 Type II – ecological niche with poor resistance

This type has $V = 0.3 - 0.5$; $P = 0.6 - 0.8$ and includes niches for sub-areals, where the leading factors are the amount of ground litter, wetting factors and soil solution reaction. Such niches are widespread, but the main states of the organic soil horizon are concentrated in a bottleneck of the ecological optimum, so the resistance is poor. The litter of this type can retain its qualitative certainty in various conditions due to elasticity near the ecological optimum and, to a lesser extent, plasticity in the range of blurred branches of the ecological niche. In general, this litter is characterized by an insignificant number of ecological optimums, which increases the ecosystem functioning stability of the terrestrial version of the landscape sphere.

In terms of *ground litter*, this type of ecological niches includes the following areals

among the areals with different litter stocks:

- Sub-areal with litter stocks of 64.3–71.3; 71.3–78.3 t/ha (suffrutescent tundra);
- Sub-areal with litter stocks of 0.6–0.9 t/ha (savanna).

A sub-interval, where heat supply is the limiting factor ($S_{>10^{\circ}\text{C}}$), was not found among the main areals. Probably, such parameters as mean July temperatures and radiation balance of dryness could point to the bottlenecks (limiting resistance) of the ecological niches.

In terms of *wetting conditions*, the following intervals were identified:

- sub-areal with litter stocks of 12.2–15.2 t/ha (forest steppes);
- sub-areal with litter stocks of 11.8–13.2; 13.2–14.6; 16.0–17.4; 17.4–18.8 t/ha (broadleaved woodlands);
- sub-areal with litter stocks of 147.9–180.9; 213.9–246.9 t/ha (swamps of western Siberia);
- sub-areal with litter stocks of 7.4–9.4 t/ha (subtropical forests);
- sub-areal with litter stocks of 4.9–5.9 t/ha (arctic tundra).

In terms of *soil solution acidity*, the following sub-areals were identified:

- sub-areal with litter stocks of 1.9–2.4; 2.4–2.9; 2.9–3.4 t/ha (savannas);
- sub-areal with litter stocks of 0.9–1.2 t/ha (dry steppes);
- sub-areal with litter stocks of 1.9–2.9; 4.9–5.9 t/ha (arctic tundras);
- sub-areal with litter stocks of 0.092–0.128 t/ha (deserts).

Type II ecological niches are the least numerous, because they have a significant number of states with parameters that have little influence on the litter formation. Consequently, such niches can be found only in those ecosystems where only the studied factors affect formation of the organic soil horizon and the influence of other environmental factors is dramatically reduced. The indicators of climatic and biological niches of some areals are in a border state with other niches, which is found in almost all ecosystems.

The organic soil horizons of the broadleaved woodlands with litter stocks of 15 t/ha and the savannas and the sparse forests with litter stocks of 16 t/ha belong to this type of

ecological niches.

3.2.3 Type III – ecological niche with poor resistance and increased plasticity

This type has $V = 0.5 - 0.7$; $P = 0.4 - 0.6$ and includes niches, where ground litter, wetting conditions and soil solution reaction play a leading role. Such ecological niches of the organic soil horizon differ from those of previous type by a combination of a poorly manifested ecological optimum with average values of the volume of the niche itself. In this case, litter resistance is also dramatically reduced, but when conditions change, it is able to maintain its state due to manifestation of plasticity and, much less, elasticity. This litter has a high level of homeostatic nature and resistance, which is an indicator of terrestrial landscape functioning.

This type of ecological niches includes organic soil horizons of the suffruticous steppes and the forest tundra with litter stocks of 85 t/ha, the coniferous and mixed temperate forests (taiga) with litter stocks of 33 t/ha, and the subtropical forests with litter stocks of 10 t/ha.

3.2.4 Type IV – resistant, homeostatic ecological niche

This type has $V = 0.6 - 0.9$; $P = 0.1 - 0.4$ and includes niches, where the leading role is played by heat supply, wetting conditions and soil solution reaction. With such a niche structure, the organic soil horizon is the most stable, for it has the maximum possible homeostatic nature, which provides it with a high level of resistance.

The litter can vary its structural variables without qualitative transformations in the widest possible range of factor gradations, so it is most tolerant to changes in climatic and biological gradients. Extreme changes in the environmental factors are necessary to bring litter of the fourth type beyond the boundaries of the homeostasis region. In the niche itself, all factor gradations are relatively balanced, which indicates of highly developed mechanisms for adapting the ground organic horizon to changes in this factor. This type of ecological niches includes organic soil horizons of the forest-steppe ecosystems with ground litter stocks of 12.1 t/ha.

CONCLUSIONS

Based on the extensive factual material, the authors developed a comprehensive method of identifying the ecological niches of the organic

soil horizons in the aspect of their differentiation, depending on the active environmental factors. A new concept of *ecological niche of the organic soil horizon* is proposed with reference to the assessment of soil-climatic factors (the amount of ground litter, t/ha; the sum of temperatures above 10°C; wetting factor; redox potential, mV) that influence formation and development of the organic soil horizons. The parameters of ecological niches of the organic soil horizons were analysed, and four main types of ecological niches were identified.

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Figure 1. Stakes with known litter stock (Popova 2012)

Figure 2. Dependence of litter stocks (c/ha) on wetting conditions (Ku) (Popova 2012)

Figure 3. Division of 330 points with known litter stocks into areals in the plane: litter stocks (c/ha) – amount of ground litter (c/ha) (Popova 2012)

Figure 4. Division of 330 points with known litter stocks into areals in the plane: litter stocks (c/ha) – heat supply ($S_{>10^{\circ}\text{C}}$) (Popova 2012)

Figure 5. Characterization of the ecological niches of areals with known litter stocks and parameters: sum of active temperatures above 10°C ; wetting coefficient; environment response. The figures indicate litter stocks (Popova 2012) and the letters stand for climates: A – tropical semi-deserts, B – tropical deserts, C – savannas, D – subtropical steppes, E – subtropical hard-leaved forests, F – moist subtropical forests, G – deserts of the subtropical belt, H – semi-deserts of the moderate belt, I – deserts of the moderate belt, J – grassland steppes, K – broadleaved woodlands, L – arctic tundra, M – forest tundra, N – swamps

Table 1. Indicators of density of the main geographical areals

Areal of litter stocks (c/ha)	Factors	Compactness	Variation coefficient (%)	Estimate of median
2.6	Litter stocks (c/ha)	1.1	68	0.55
	Ground litter (c/ha)		58	2
	Sum of active temperatures (°C)		26	5050
	Wetting coefficient		44	0.2
	Environment response		5	8.2
12.8	Litter stocks (c/ha)	1.3	26	13
	Ground litter (c/ha)		16	17.5
	Sum of active temperatures (°C)		27	2200
	Wetting coefficient		27	0.4
	Environment response		3	7.2
16.3	Litter stocks (c/ha)	0.04	36	15.5
	Ground litter (c/ha)		44	76
	Sum of active temperatures (°C)		6	9450
	Wetting coefficient		42	0.35
	Environment response		3	5.8
19.2	Litter stocks (c/ha)	0.08	38	20
	Ground litter (c/ha)		11	240.5
	Sum of active temperatures (°C)		25	9800
	Wetting coefficient		44	2.65
	Environment response		6	4.9
33	Litter stocks (c/ha)	147.5	46	35.5
	Ground litter (c/ha)		38	3
	Sum of active temperatures (°C)		26	345
	Wetting coefficient		9	2
	Environment response		3	5.7
101.3	Litter stocks (c/ha)	4.43	31	100
	Ground litter (c/ha)		8	192.5
	Sum of active temperatures (°C)		20	6350
	Wetting coefficient		10	1.6
	Environment response		4	4.2
121	Litter stocks (c/ha)	4.0	22	120.5
	Ground litter (c/ha)		21	64.5
	Sum of active temperatures (°C)		26	2550
	Wetting coefficient		12	0.7
	Environment response		5	6.4
151	Litter stocks (c/ha)	22	25	152.5
	Ground litter (c/ha)		10	47
	Sum of active temperatures (°C)		27	2600
	Wetting coefficient		6	1.05
	Environment response		15	6.05
329	Litter stocks (c/ha)	306	29	305
	Ground litter (c/ha)		20	30
	Sum of active temperatures (°C)		22	1600
	Wetting coefficient		15	1.3
	Environment response		16	4.4
849	Litter stocks (c/ha)	4337	17	952
	Ground litter (c/ha)		24	9
	Sum of active temperatures (°C)		39	600
	Wetting coefficient		15	2.2
	Environment response		7	5
1414	Litter stocks (c/ha)	54435	36	1134
	Ground litter (c/ha)		10	24
	Sum of active temperatures (°C)		16	961
	Wetting coefficient		10	1.75
	Environment response		14	4.8

Table 2. *Characteristics of litter stocks in areals*

Limits of fluctuations in litter stocks in the areal (t/ha)	Estimate of arithmetical mean (t/ha)	Estimate of median (t/ha)
0.02–0.6	0.3	0.06
0.6–1.2	1.3	1.3
1.3–1.6	1.7	1.6
1.7–2.6	2.0	20
2.7–6.0	3.3	3.6
6.0–12.3	10	10
12–14	12	12
14–21	15	15.3
25–47	33	31
52–97	85	95
97–225	141	113