



THE CONCEPT "COMPLEMENTARITY" AS THE BASIS FOR MODEL AND NATURE RECONSTRUCTION OF POTENTIAL BIOTA IN THE CURRENT CLIMATE

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КОНЦЕПЦИЯ КОМПЛЕМЕНТАРНОСТИ КАК ОСНОВА МОДЕЛЬНЫХ И НАТУРНЫХ РЕКОНСТРУКЦИЙ ПОТЕНЦИАЛЬНОЙ БИОТЫ В УСЛОВИЯХ СОВРЕМЕННОГО КЛИМАТА

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Abstract. From the prospective of ecosystem ecology, the huge role of the concept "complementarity" in perceiving the mechanisms of sustainable existence of the natural (pre-anthropogenic) biota is substantiated. A comparison of structural and functional organization between the paleobiota of Northern Eurasia and its fragments, survived until the present day, the modern biota, was performed in the main types of conservation areas. The incompleteness of the modern biota in natural reservations and its main cause are shown: direct or indirect destruction of key species that determined the possibility of the existence of large groups of subordinate species is described. It has been found out that as the anthropogenic exploration of Northern Eurasia intensifies, the ability of the biota's fragments ("debris") to support ecosystem functions of the biosphere decreases. It is concluded that a fundamentally new direction in the protection of nature is to be developed: "Pleistocene Rewilding" formed on a world-wide basis as a result of the awareness of the need for active restoration of the biosphere functions of the Earth's ground cover.

Key words: complementarity, key species, biota, paleoecology, historical ecology, reserves, Pleistocene Rewilding.

Аннотация. С позиций экологии экосистем обоснована огромная роль понятия «комплементарность» в познании механизмов устойчивого существования природной (доантропогенной) биоты. Проведено сопоставление структурно-функциональной организации палеобиоты Северной Евразии и сохранившихся до настоящего времени ее фрагментов – современных биот – в основных типах заповедников. Показана неполночленность современных биот особо охраняемых природных территорий и ее основная причина: непосредственное или опосредованное уничтожение ключевых видов, определявших возможность существования больших групп подчиненных видов. Установлено, что по мере усиленного антропогенного освоения Северной Евразии фрагменты («осколки») Биоты все в меньшей степени способны поддерживать экосистемные функции биосферы. Сделано заключение о необходимости развития в настоящее время принципиально нового направления в охране природы: «Pleistocene Rewilding», сформированного на мировом уровне в результате осознания необходимости активного восстановления биосферных функций живого покрова Земли.

Ключевые слова: комплементарность, ключевые виды, биота, палеоэкология, историческая экология, заповедники, Pleistocene Rewilding.

*«Far more than any other species in the history of life on Earth, humans alter their environments by eliminating species and changing ecosystem function, thereby affecting the very future of evolution»...
«This is at least in part because the ecological consequences of the historical losses are unknown and even unimagined» [1].*

Formation of the complementarity concept and its concern with the basic concepts of biosystems ecology

The current state of the Biota on Earth raises serious concerns regarding the possibilities of maintaining a stable hydrological regime, climate and other ecosystem functions of the Biosphere, necessary for the survival of mankind [2]. That is why the unique fragments of the Earth's ground cover, which are regarded as natural formations – standards of the full implementation of ecosystem functions, became especially significant.

The history of origin of specially protected natural reservations is long and complex. The objective of SPNR in our country is most clearly formulated in the book: N. F. Reimers and F. R. Shtilmark: Specially protected natural reservation, 1978.

"One way or another, today we can say with all certainty that the core line in the establishment of reserves and national parks has been approved, their main goals have been determined: these are the preservation of the inviolate natural complex for observation, studying and monitoring its changes over time, p. 2" [3]. The above mentioned statement of goals and objectives of SPNR allows us to conclude that the Biota of these "reserved" sites was considered as natural or as capable of restoring the natural state in conditions of the protected regime. These very clear directions have contributed to the widespread dissemination of scientific research in specially protected natural reservations.

However, the emergence and rapid development of historical ecology [4–10] and the great achievements of paleoecology in the reconstruction of the Late Jurassic period of development of Northern Eurasia Biota [11–26] have made and are constantly making significant changes in assessments of the natural state of SPNR. It is established that significant changes in the Biota of Northern Eurasia occurred at the initial stages of development of appropriation, in the era of "mammoth hunters" [18–20, 23–26].

However, so far there is still insufficient information that would allow us to decide for sure which parameters of protected areas should be valued as natural and which are the result of anthropogenic influences preceding the reservation. Under this ideology, another question remains open, which part of the Earth's surface is to be excluded from nature management for the restoration and sustainable maintenance of the ecosystem functions of the Biosphere.

With accumulation of paleoecological and historical data, a concept is being formed that current-

ly there are no territories on the Earth (except for polar deserts), the Biota of which would not have been transformed to some extent by a human, and that these transformations led to changes in climate, hydrological regime, biological productivity and species diversity [4, 7, 9].

As a result of awareness of the biotic losses that preceded the foundation of SPNR, the idea is formed that the solution of the problems of the sustainable existence of the Earth's ground cover should be based not only on preserving the "fragments" of natural biodiversity, but also on its restoration [1, 2, 9, 10]. At the current level of knowledge, the tasks of restoration of natural biota cannot be limited to the reintroduction of individual species; they should be focused on the possibly complete restoration of pre-anthropogenic Biota at model ranges in SPNR and similar organizations.

As an example of such activity it is reasonable to consider Pleistocene Park of Zimov:

A theoretical basis for assessing the degree of preservation of the Biota in protected areas has changed with the paradigm shift in ecology. The classical concepts of "gap-mosaic", "mosaic-cycle concept", "natural disturbance", "key species" and "ecosystem engineer", "facilitation model", "potentielle naturliche" had a significant impact on the formation of modern concepts of the potential ground cover of protected areas vegetation [27–36]. All these concepts are to some extent devoted to the manifestations of mutualistic relationships between organisms and populations, since, according to the views of many researchers, it is precisely these relationships that are characteristic of "climax" (according to Y. Oduma) ecosystems [37]. While in recent decades, the term "complementarity", widely used in chemistry, molecular biology and genetics, is widely used in ecology, precisely in this respect.

Analyzing the ecological works of the previous time, we can distinguish two lines of research basically devoted to complementarity (without using this term):

1) *alteration of groups of individuals or populations of different species in time in the process of using the same environmental resources.* The earliest known studies in our country are devoted to changes in time and intensity of growth and production processes in broadleaf trees [38]; changes in the necessity of photosynthetically active radiation (PAR) for different broad-leaf tree species as the undergrowth develops [39, 40] changes in the rate of growth processes in sinusia of Ephemeroids and summer-growing herbs in broad-leaf forests [41, 42];

2) *the creation by individuals and populations of certain types of favorable conditions (resources,*

habitats) necessary for the sustainable existence of individuals and populations of other species.

This type of relationship is reflected in all the above mentioned classical concepts of the modern ecology of ecosystems; the most striking examples are given in describing studies of animal populations considered as the key species: "key species", "ecosystem engineer" [28, 29, 32–35].

Accumulation of the studies devoted to complementarity in ecology of biosystems, rethought in accordance with the concept of the "key species", we consider as the basis for verbal reconstructions of the potential ground cover of the analyzed territories [2, 43].

Reconstructions of Pre-anthropogenic Ecosystems of Northern Eurasia

By now in paleoecology, archeology and historical ecology a great number of evidences, which as a whole enable the composition and the structure of natural ecosystems of Northern Eurasia to be reconstructed at the end of the Pleistocene (Late Würm), has been accumulated. Reconstruction of pre-anthropogenic landscapes of that period was made by the explorers of the second half of the XX century in accordance with synthesis of paleoecological data on the composition and structure of tundra-steppes of the Late Würm [11–16, 19–21, 24–26, 44–49], paleodatings of that period and actual studies of savannas of the Paleotropics [32–36].

At the early stage of reconstruction ecological parallelism of fauna of the tundra-steppes of Northern Eurasia and African savannas has been revealed and demonstrated [21]. The researchers outlined it as a "biotic pyramid" which consisted of the species' groups, preferring this or that habitat conditions.

At the first level: the species that live in open grass spaces; the model group in Northern Eurasia: horses (*Equus*), zebras (*Hippotigris*) in African savannas. A great share in their food makes cereals (*Gramineae*) capable of growing upon biting off due to the development of intercalary meristems that make this group of plants most evolutionally significant in formation of pasture ecosystems.

At the second level: the species that inhabit the forest-meadow-steppe complexes of communities; and eat trees and grasses. As models the most powerful key species of herbivores are designated: in Northern Eurasia – mammoths (*Mammuthus*), in African savannas – elephants (*Loxodonta*).

From the third to fifth levels: the carnivores that dwell in open grass spaces and the forest-meadow-steppe complexes of communities. Among them at the third level there are little and medium-sized predators (polecats (*Mustela*), Arctic foxes (*Vulpes lagopus*), gluttons (*Gulo gulo*), wolves (*Canis lu-*

pus) and so forth); at the fourth level – lions (*Panthera leo*) that live both in Northern Eurasia and African savannas; at the fifth one – scavenging hyena (*Crocuta*), the model species that inhabit both territories.

According to the view point of the authors cited "...ecological parallels in the structure of mammoth fauna in Eurasian tundra-steppes and African savannas are the result of similar requirements to landscape conditions". In this case the type of food is included in the attributes of landscape conditions [21].

Based on investigations performed by paleontologists [36–43]: verbal reconstruction of the ground cover of tundra-steppes of the Late Würm of Northern Eurasia – "mammoth ecosystems" – has been created. In-depth investigations of the conditions transforming activity of ecologically similar "key species" of African savannas played a significant role in this reconstruction. The following fragments taken from the article of P. V. Puchkov (1992, № 1, p. 28) describe major features of the landscapes of that period.

"...In Pleistocene phytocenoses of "mammoth and other ecosystems" were characterized by higher, than in Holocene, productivity and mosaic structure, higher specific weight of valuable for large phytophags plant associations and in landscapes with canopy cover of the bigger role of park forests and savannas as compared to continuous forests...".

"...Main Pleistocene plant communities often resembled not current "climax" zonal formations, but areas of their contact (ecotones) and communities at different stages of plant succession. As a result, there is the increased local diversity of the biota and higher, than in the Holocene, density and diversity of large mammals...".

"...phytocenoses with the mentioned features were present on all continents with different types of the climate, without losing these characteristics in all Pre Würm climatic alterations (except areas covered with glacier or turned into deserts).

Factors that improved the habitat for big animals were big themselves, especially the biggest animals...". "Activity of the giants controlled climatogenic changes in cenoses, making them less harmful to some animals...". "This activity was a protective mechanism for communities from climatogenic transformations, the efficiency of which was observed by the absence of uncompensated mass extinctions of megafauna in Pre Würm shifts of arid and Pluvial periods, glaciations and interglacial stages".

"...Eliminating the giants from the ecosystem at the end of the Würm (or a persistent decline of their population) as a result of hunting activities

caused deterioration of the habitat intolerant for a number of animals who died off after the giants".

These paleoreconstructions of the ground cover of Northern Eurasia, made in the 90s last century, have constantly been reported based on the found bone remains of the animals with radiocarbon dating and plant pollen that allow us to create a detail view of prehistoric landscapes at one or another time period of the Biota [44–49]:

Also, the results of studies on Paleolithic settlements in the Late Würm give an idea on the Biota of prehistoric landscapes. For instance, in Sungir [50], the Late Paleolithic settlement, in the coldest period of the Late Würm the list of bone remains included more than 20 species. Among them are: mammoth (*Mammuthus*) horse (*Equus*), bison (*Bison*), reindeer (*Rangifer tarandus*), brown bear (*Ursus arctos*), wolf (*Canis lupus*), cave lion (*Panthera leo spelaea*), piping hare (*Ochotona*), hare (*Lepus*), ground squirrel (*Citellus*), Arctic lemming (*Dicrostonyx torquatus*), marten (*Martes martes*), Arctic fox (*Vulpes lagopus*), glutton (*Gulo gulo*), saiga (Saiga); grouse (Lyrurus), and so on. Interestingly, the jungle fowl (*Gallus gallus*) was also found at the same time, it is the species that nowadays inhabits only South-East Eurasia.

The list of plants included: alder (*Alnus*), oak (*Quercus*), linden (Tilia), hazel (*Corylus*), birch (*Betula*), spruce (Picea) pine (*Pinus*) and dwarf birch (*Beula nana*); representatives of cereals (*Gramineae*), composite families (*Compositae*), iris families (*Iridaceae*) and many other flowering plants, as well as ferns (*Polypodiopsida*) and green mosses (*Bryophyta*) [50].

Importance of paleoreconstructions for solution of current problems of nature conservation

From the viewpoints of current ecology, paleoreconstructions of "mammoth ecosystems" of Northern Eurasia are of great value, since they characterize the state of the Biota on the area before the start of anthropogenic transformations. Undoubtedly, it is necessary to assess the extent of anthropogenic transformation of natural Biota in order to improve methods of its preservation, restoration and proper use.

Main achievements of paleoecology in the late 80s – early 90s of the XX century, that enable the importance of a concept of complementarity to be assessed for creation of model reconstructions of natural canopy, are as follows:

1) the authors applied a concept of "complementarity" in ecology (without using this term) and instantiated it perfectly by comparing the composition and structure of the ecosystems of "mammoth

tundra-steppes» and African savannas of Paleotropics at population and ecosystem levels. It should be emphasized that a significant increase of paleodata obtained by now on the composition and structure of Late Würm ecosystems of Northern Eurasia ("mammoth tundra-steppes") makes it quite reasonable to compare their composition with those typical of ecosystems of African savannas preserved until now [11–15, 19–26];

2) in the analyzed works, main ideas on key species of animals have been given; the main ways of transformation of their habitat, developing necessary living conditions for relevant species, have been shown. In these works it has been shown that the presence of a group of key species, first of all, the strongest transformers such as elephants, mammoths, is an absolutely necessary condition for stable existence of the Biota as a whole and, therefore, for complete realization of its ecosystem functions [8–12, 36, 37, 48, 49, 54–57].

3) in the works analyzed, verbal reconstructions of pre-anthropogenic landscapes have been given: unified forest-meadow-steppe complexes with all their population formed by the giants, large phytophags of the mammoth complex. These reconstructions put in doubt the ideas on the "natural zones" of Northern Eurasia, such as continuous closed forests, steppes and deserts [8–12, 36, 37, 48, 49, 52–59];

4) these works represent scientific foundations of modern environmental activities in national parks (Pleistocene Rewilding), where experiments are carried out to restore the Pleistocene megafauna and possibly complete restoration of the ecosystems in late Pleistocene as a whole [1];

5) a crucial role of the BIOTA in the development of conditions for life on the Earth is defined in these works, so it is possible to explain a "paradox of prehistorical pastures", i.e. maximum, in comparison to the modern one, productivity of the pastures of the late Würm in climatically unfavorable (according to the viewpoints of many researchers) conditions. It also became possible to explain "the mixed character of flora and fauna" in the Würm, based on data on climate and land forming role of the giants, phytophags, of the mammoth complex [57–59].

6) these works represent data on "mammoth ecosystems" widely spread in Pleistocene and characterized by high productivity, a great number and variety of key animal species, and contributed to support the ideas proposed by the prominent geologists I. G. Pidoplichko [51, 52], and V. G. Chuvardinsky [53] "about the absence of continuous continental glaciers at the end of Cenozoic epoch". Currently, these ideas are supported by a great number of radiocarbon datings from the found

mammoth and related species [54–55], that lived (according to the concepts of glaciologists) many kilometers below the surface of an ice sheet.

Failure to take into account the global by their significance ideas on the composition, structure and functioning of the Würm (pre-anthropogenic) landscapes interferes adequate development of the Biota in reserve systems, despite numerous measures taken for a partial restoration (reintroduction) of their natural biodiversity [63].

It is necessary to understand clearly that the basis for restoration of natural diversity of the protected areas should be an idea on the prevailing role of pre-anthropogenic Biota in the maintenance of optimal hydrological regime and climate, maximum productivity and biodiversity [2].

Current zoning of Northern Eurasia as a result of transformation of late Pleistocene complex of the key species

Significant changes in flora and fauna over most of Northern Eurasia occurred gradually, their modern composition has completely formed in the Late Holocene [4, 5, 51, 55, 59, 65–73].

The End of Pleistocene and Ancient Holocene (Late and final Paleolithic Age)

This period was characterized by mixed flora and fauna, large phytophags dominated, limited expansion of the tree types and the dominance of grasses, that allowed the researchers to make a direct comparison between the productivity of the "mammoth" pastures and modern African savannas [13–15, 23, 41]. The maps of selected areas of the key species show that ground cover was not divided into zones as the modern ones, considered as elements of natural zonality [4, 59, 61, 62].

Early Holocene (Mesolithic period). To the end of this period key species of the mammoth complex were almost entirely eliminated, hunting for smaller animals and fishing were developed. Degradation of the mammoth complex resulted in transformation of pasture ecosystems of flat interfluvies into detrital-based ecosystems [4, 59, 61, 62].

Middle Holocene (Neolithic and Bronze Ages). During that period the areas of large phytophags: aurochs (*Bos primigenius*), bisons (*Bison bonasus*), Asiatic wild asses (*Equus hemionus*) and horses (*Equus*) reduced significantly [64–66]. However, canopy cover had many open spaces, sufficient for coexistence of such animals as reindeer (*Rangifer tarandus*), elk (*Alces*), bison (*Bison bonasus*), and saiga (*Saiga tatarica*). At the same time, a new powerful factor of the influence on the ground cover was developed, by its strength it could be compared with effects of the key species used in production system [67]. In osteological material

domesticated animals play a key role in it [68, 69]; pollen of the cultivated cereals appears in the spore pollen spectra [70, 71]. By the end of the Middle Holocene steppe zone was formed as a result of livestock grazing, and autumn and spring burnings that benefited the growth of young grass.

Late Holocene (Iron Age). Delineation of "natural" zones ": forests, steppes and semi-deserts is in its final stage and carried out in accordance with the land use: reindeer herding in the north; slash-and-burn farming and livestock grazing over most of modern forest belt; agriculture and cattle breeding in the south in the modern belt of steppes and semi-deserts [5, 68, 69, 71].

The most significant features of Late Holocene for modern times:

1) the formation of the forest belt and its delineation by the anthropogenic effect from livestock grazing and forest clearance; a decline in species diversity [61, 62];

2) large-scale deforestation for slash-and-burn agriculture, podsolization, ploughing of the meadow-steppe areas [4–10];

3) anthropogenic climate changes: The "Little Ice Age" as a result of great plowing: XII–XIII centuries in the West Europe and XVI–XVIII centuries in the East Europe [4, 5, 72, 73];

4) "choleric" (unpredictable) climate [72–74] as a result of extirpation of the most part of natural Biota and large-scale replacement of natural vegetation with farmlands.

Thus, within the Holocene period key species of animals in Northern Eurasia, giant phytophags of the mammoth pastures and the population of predators regulating them, were liquidated [4, 5, 7, 59–62], and unified biotic complexes decomposed into the fragments controlled by a man, in fact the only key type of the Earth.

It is possible to assume that liquidation of the huge part of key herbivores which during pasturing stimulated transpiration activity of the cereals (the main group of pasture ecosystems species), using their properties to grow repeatedly after biting, changed substantially the ratio of natural grass and forest ecosystems and it could significantly affect changes in the hydrological regime of the Earth.

Examples of complementarity in the reserves (specially protected natural reservations)

Most of the natural reserves in Northern Eurasia within the current forest belt do not include all or include some key species of animals, and forests are partially transformed because of different agricultural activities (selective fellings, livestock grazing in the forest) and fires. The longest life span of the trees in the main part of nature reserves

is no longer than the few hundred years, the time within which one or seldom two generations of trees live.

Current knowledge allows addressing the challenges of restoration of biological and structural diversity of the Biota of nature reserves in nowadays conditions as much as possible based on the studies on paleohistory, historical ecology, the estimates of whether landscape particular features of the area meet the requirements of sustainable existence of preserved and/or reintroduced types of plants and animals, the keystone species rank first. On the whole, in order to perform this task, it is necessary to maximize the area and broaden landscape diversity of the reserves and take active measures on restoration of the Biota that has been planned regarding the management and use of Biosphere reserves activity [63].

Natural forest reservations

Complementary relationships in the forests developed without human interference and natural disturbances within the life time of several generations of trees are described in the concept of "gap-mosaic", mosaic of renewal of gaps formed because of the death of one or several old trees [4, 5, 27–29]. A gap-mosaic of natural forests creates:

1) *mosaic regime for PAR (Photosynthetically active radiation)*, which implies that heliophilous and shadow types of the trees are able to live in the same community;

2) *mosaic regime of humidification* formed by different distribution of precipitations; in closed forest area considerable part of moisture remains on tree crown, flowing down the stems. In the gaps it falls on young undergrowth and grass canopy, infiltrates faster into the soil, establishing a mosaic of the areas with different soil moisture, thereby contributing to diversity of the types of ground vegetation.

A mosaic of renewal of gaps and their spontaneous development were described in mixed coniferous-broad-leaf forests and taiga east European forests. For example, in mixed coniferous-broad-leaf forests in the gaps of 20 meters in diameter and longer three stages of the development of grass canopy are clearly defined. At the first stage, within the first years upon the development of the gap, tall grasses are dominant, where *Urtica dioica* is a key species, and restoration of both coniferous and broad-leaf types of the trees are suppressed. At the next stage, within the first-second decades the dominance of tall herbaceous vegetation is still observed, but species composition becomes more variable. Such types of grasses and subshrubs like *Calamagrostis arundinacea*, *Aconitum excelsum*, *Rubus idaeus*, etc. prevail. At the next stage, that lasts several decades in the areas where vegetative young undergrowth of linden (*Tilia cordata*) or

birth (*Betula pubescens*) is dominant, typical Nemoral species (*Aegopodium podagraria*, *Asarum europaeum* etc.) grow as tall as possible. In the areas where fir and spruce grow, typical boreal species (*Oxalis acetosella*, *Trientalis europaea* L.) are present. Mapping of the areas of 1–1,5 ha showed that gaps, being at the first stage, occupied 6–8 % from total area, at the second stage – 50–60 %, at the third stage – 20–30 % (gaps where the forest contains more linden) and 10–15 % (gaps where the forest contains more fir and spruce), respectively [4, 5, 33–35, 75, 77].

Change of plants species composition in the gaps points to the first variant of complementarity – alternativeness in time of the groups of individuals or populations of different types during the use of the same resources of the habitat or spatial-temporal distribution in the use of resources.

The death of an old big tree is followed by breaking the trunk at the bottom or "fall" – drawing a part of the root system with stoolbed that creates new structures, the elements of treefall microsites complexes (TMC): stumps, pits and fallen logs [24, 74–77].

This is an example of complementarity of the second type – *creation by the same species and populations of favorable conditions (resources, habitats) required for sustainable existence of other species and populations*. Every element differs in ecological regimes: temperature, humidity, density and soil space, chemical composition and others, that determine the existence of specific sets of the species of the living organisms in TMC of each type [78–85]. Microsites appeared due to the fact that the mounds of big trees form a patchwork of many different types of soil cover. So, the results of studies carried out in nature reserve "Kaluzhskie zaseki" ("Kaluga Forest Reserve") showed that pits are characterized by chronic soil moisture and local gleization. As a result, grass species seen in flood – plain sticky alder forests (*Ranunculus repens*, *Lysimachia nummularia*, *Chrysosplenium alternifolium*, *Filipendula ulmaria*, *Cardamine pratensis*), are dominant in these pits, and among the tree undergrowth the species such as *Ranunculus repens*, *Lysimachia nummularia*, *Chrysosplenium alternifolium*, *Filipendula ulmaria*, *Cardamine pratensis*, which are able to grow in chronic moisture, prevail. Stumps are characterized by maximum soil dryness and only here it is possible to see *Carex pilosa*, that dominate in the dryer broad leaf forests. Decomposed fallen logs are an optimal substrate for mosses, many types of the grasses, bushes and trees of pioneer strategy (*Impatiens noli-tangere*, *Urtica dioica*, *Sambucus racemosa*, *Salix caprea*, *Populus tremula* etc.).

It should be noted that even with rich diversity of the elements of gap mosaic in the nature reserves under study; species diversity is considerably reduced when local livestock grazing takes

place without following the rules of the reserve regime [76, 77].

Mounds form a patchwork/a mosaic of habitats in the soil cover too that greatly contribute to ecological diversity of soil Biota [80–85]. Complementarity in the Biota of forest soils is studied using the activity of "ecosystem engineers": earthworms of various groups [86] who make a mosaic structure of soil habitat more intricate:

1. Epigeic species dwell in the leaf litter and decaying wood; these species provide primary destruction of the tree waste subjected to leaching or preliminary degradation of polyphenol and other chemically stable compounds by microorganisms.

2. Epi-endogeic species inhabit the leaf litter and soil near the ground surface; they digest partly decayed wastes, actively mixing it with the soil.

3. Anecic species live deep in the soil, due to vertical migrations they intermix soil layers, forming pathways 1 to 8 m, making porous air-water structure of the soil that determines its fertility. They eat plant residues on the soil surface, hence, anecic earthworms together with epigeic and epi-endogeic species are assigned to primary humus forming species.

4. Endogeic species live within the soil, frequently up to 30–40 cm soil depth. They actively slide through the soil during horizontal and vertical migrations. They eat plant residues passed through the alimentary canal of epigeic and epi-endogeic species and mixed with soil particles. In fact, endogeic species belong to the secondary humus forming species.

Spatial and temporal distribution of environmental transforming activity of the earthworms of different functional groups provides necessary conditions for other groups of soil inhabitants: plants, animals, mushrooms and other organisms: mushrooms, invertebrates (availability of the elements of mineral nutrition, porous structure of the habitat).

In turn, fallen logs, especially during the last stages of decaying or with developed moss cover, make favorable conditions for survival of earthworms during droughts. Epigeic species live usually in fallen logs, epi-endogeic species and anecic species may live there for only short period of their life cycle, endogeic species can use this habitat as a temporal habitat [87–91].

With earthworms, other species of mesofauna (insects, spiders, mariapods etc.) favorably develop on the decaying fallen logs [78–79, 83, 90].

Forest natural reservations with reintroduced bisons

A bison, along with the wild ox, tarpan and other hoofed animals, was a part of fauna of "Pleisto-

cene landscapes"; its area occupied a great part of the Holartic [17, 51]. In ecological structure of key species of "mammoth fauna" it is at the first level together with a large group of phytophages [21], in the nutrition of which herbal forage, primarily cereals, which have the ability to grow after biting due to the activities of intercalary meristem, is dominant.

In Late Pleistocene bison's area covered west, central and east Europe and the Caucasus; in the north it reached the Baltic, in the south – Black and Azov Seas [64, 92, 93]. Until XVI–XVIII centuries bisons were typical foresters which were killed a lot during hunting [94–102]. Total elimination of bisons and other powerful phytophages by the XVI–XIX centuries resulted in great changes of the living soil cover: large zoogenic mosaics disappeared, forest vegetation of the shadow type started to dominate. Heliophilous flora and fauna were displaced from the forest to anthropogenic habitats: margins, grasslands, haymaking places, waysides. As a result, at one time unified living cover disintegrated to the fragments which are considered nowadays as independent communities or ecosystems.

Since 1927 bisons have started to breed in nature reserves and national parks; at present the largest plain herd lives in the nature reserve "Belovezhskaya Pushcha" ("Belovezha Forest"), and the mountain ones – in the "Caucasian nature reserve".

Analysis of the lists of bison feed makes it possible to reconstruct the habitat of landscapes, required for its existence.

In all studied nature reserves total share of the number of species of trees and bushes in bison food is no more than 20 %, grasses – 80 % and higher, among them meadow, steppe-meadow, nemoral and wetland species prevail, with 60 % belonging to the photophilous types. Comparison of the lists of forage grasses for bisons with that one's of grasses of hayfield meadows and pastures of domestic animals revealed their significant ecological and ecological-coenotic similarity [103–114].

As shown by the experience of reintroduction of bisons in drinking places, pathways, stopping places of these animals, due to the destruction of woody vegetation, there are communities of meadow-forest edge and meadow-steppe species [112–115]. The area of such zoogenic openings with meadow flora ranges from 0,1 to 3–5 ha. The use of stopping places within one to two decades leads to a strong compaction of the soil and the development of cespitose cereals. Simultaneously, damage of large trees and use of young growth as food causes the death of trees and shrubs. Large gaps appeared in the forests, con-

nected the wide pathways to the places of watering and feed sites [116–118].

Information on the areas' dimensions, required for sustainable existence of the populations of this species, is still insufficient due to short periods of observation and small areas of nature reserves. Bisons' migrations during a day can be several tens kilometers long. As a result, the forest is penetrated by a network of roads and clearings, which serve as channels for migration of meadow and forest edge flora and fauna [98, 103–105, 112, 119, 120]. The area of gaps with meadow and meadow-steppe flora ranges from 0,1 up to 3–5 ha. The use of stopping places within one- two decades results in strong compaction of the soil and development of cespitose cereals. At the same time damage of large trees and the use of young growth as feed causes the death of trees and shrubs. Large gaps appear in the forests, connected by wide pathways to the place of watering and feed sites [116–120].

Constant presence of bisons and other big phytophages determined in preagricultural period principally other structure of ground cover: native forest areas with typical for them mosaic of restoration of gaps and windfall-soil complexes interchanged with zoogenic clearings, ecotone communities were presented very widely. Animal pathways served as migration channels for photophilous flora and fauna [120–122].

Hoofed mammals (moose deers, roe deers, deers, etc.), preserved to the present time in the woods, due to the smaller sizes and preference for woody forage, do not act as so powerful habitat transformers as bisons and similar species, though they introduce mosaic in wood canopy [120–125]. For example, moose deers, roe deers and deers, selectively eating crown shoots at the young growth of trees and shrubs, control the density and species composition of the trees undergrowth, contributing to the development of grasses [124–127].

An estimate of habitat transforming activity of the kept until now hoofed mammals [120–125] shows that formed by them mosaics are small as compared to that ones of bisons, and unable to keep photophilous flora in the forests. An absence of natural mechanisms of maintaining such flora in the forests results in the fact that forest nature reserves formed at long-developed areas to preserve biodiversity, lose photophilous flora faster than the areas with traditional land use [84, 85].

Liquidation of bisons and reduced number of smaller phytophages in the forests affect negatively the quantity and diversity of populations of soil biota. As seen from the studies the absence of bisons' excrements hinders development of the group of soil earthworms, the secondary humus

formation species, supporting not only soil resources, but also porous structure of the soils.

Experiments conducted in the US on fertilization of high-grass prairie with liquid bisons' excrements showed a significant increase in the composition of cereals, the preferred feed of bisons [127].

Experiments on introduction of bisons into nature reserves and a comparison of the development of soil biota at places of bisons and livestock grazing at forest and meadow grasslands show that some elements of complementary relations were successively kept at domestication of animals. Thus, according to multiple investigations on meadows and pastures with moderate grazing biomass of the earthworms was several times higher than on the meadows and forests without any grazing [128–130]. Upon grazing cessation on meadows in the Central Alps abundance and biomass of soil-litter species decreased, abundance of native soil species reduced significantly, and an increase in the number of small litter *D. octaedra* was not sufficient for decomposing the litter [130].

Increased number of worms in the soil in the pastures, especially actual soil and hole species, prevents soil compaction that occurs during grazing [131]. Direct link between biomass of the earthworms and the content of organic substances in the soil was defined in the mountain beech forests in Northern Germany [132]. Increased number of earthworms in the meadows, with grazing of bisons, is shown in the reserve "Kaluzhskie Zaseki" ("Kaluga Forest Reserve") [133]. In the nature reserve "Orlovskoe Polesye" ("Orel woodlands") diversity and biomass of the earthworms are higher than in the areas of forests affected by bisons as compared to forest sites without bisons' grazing. In this case litter earthworms and soil-litter earthworms are directly involved in decomposition of manure (unpublished date).

Forest natural reservations with reintroduced beavers

Since total account of the key species is of great importance in paleoreconstructions, it is necessary to mark the difference in the composition of ecological groups of the "mammoth ecosystems" in Pleistocene of Northern Eurasia and African savannas.

It implies absence of the representatives of beavers' family (Castoridae) in the latter. Paleodata show that starting from the Oligocene the beavers were spread along the whole Holartic [134]. Modern species, *Castor fiber*, was spread at the end of the Pleistocene from Atlantic seaboard up to the Baikal region and Mongolia beavers were preserved for the last millennium on separate sites in

the forests of Eastern Europe [135–139]. Recently, due to successive reacclimation and subsequent migration, populations of the beavers are restored on a great part of prehistoric area, and, therefore, importance of this species is gradually increasing in transformation of the forest landscapes [130–141]. Significance of complementary relationship of the beavers with other species is so great that it can be compared with relations of the elephants and mammoths with subordinate ones; the areas transformed by them got the name: "beavers' landscapes" [142–143].

Influence of the beavers on hydrological regime of the area and geochemistry of ecotopes

Among all effects of the beavers on the habitats the most prominent are reclamation ones. Beavers' dams on creeks and little rivers transform hydrological mode of the area: creeks and small rivers turn into cascade of ponds; water level increases significantly; the level of soil-ground waters increases and becomes stable; the amplitude of their alterations while changing dry and humid years reduces. Flood control of the small rivers runoff during building of the dams by the beavers increases bottom land of the valley of the tributaries of small rivers that lead to stabilization of the temperature mode, atmospheric pressure, humidity. Possibility of nature fires is greatly decreased or disappears in actual fact [144–146]. Populations of various water basins by the beavers, their active building activity affect the population of small rivers and biogeochemical processes in aquatic ecosystems [147–149]. The studies showed that as a result of flooding in the upper 15 cm soil layer the content of calcium, magnesium, iron and sulphate increased by 82–169 %, total nitrogen, and ammonium nitrate – by 72–295 %, total phosphorus – by 43 %, potassium – by 20 %. The soils formed upon ponds shoaling are much richer as compared to the forest ones [144–151].

Influence of the beavers on area topography

Activity of the beavers is one of the most significant zoogenic factors of relief formation in the bottomlands of small rivers. Influence of the beavers on relief manifests at digging the holes, construction of lodges, dams, channels and tunnels [141, 142, 144–146, 150–154]. In some beavers' settlements there can be dozens of holes of different types with total length of hundreds of meters. This changes temperature and water modes of the soils, affects on the trend and the rate of soil formation processes, favoring formation of micro- and nanorelief [136, 142, 143, 151–158].

Influence of the beavers on vertebrates and invertebrates

Beavers dams on small rivers, the channels dug by the beavers, their ways on water are used as transport highways by terrestrial, near water and aqueous animals. Beavers' ponds during drought serve as drinking places for birds and animals; "beavers felling areas" and sapwood trees give additional food for hoofed, hares, murine rodents; in winter some mammals concentrate around "beavers felling areas". Created by beavers' activity special "beaver" landscape is mastered by birds which previously lived here: teals, harles, and mallard ducks. Shallow waters and ponds at watersheds form conditions for fish spawning and amphibians. Lots of animals use homes (lodges) and multiple ways and holes of the beavers as permanent dwellings and temporal refuge from enemies and unfavorable conditions [138, 158–161]. The studies made at shallow Kiev water storage basin showed that activity of beavers led to increased species composition of zooplankton. 16 indicator species, positively responding to the beavers' activity in the basin, were determined. Total mass of zooplankton in beavers' ponds was 2–345 times higher than in the control. Frequency of total biomass increase of zooplankton in beavers' ponds on small rivers made up 3–127 times as compared to the control [147, 149].

Formation of beaver landscapes

All the diversity of habitats formed as a result of the topical and trophic activity of beavers is accumulated in a complex of ecosystems, which includes flooded or swamped forest, a pond, a grassy swamp, a swamp with undergrowth of trees and shrubs [162–170]. This system of habitats is the result of the environment transforming (topical and trophic at the same time) activity of one beaver family. Flooded forest is being formed during the first year after the dam was built. Usually black alder dies the next year after flooding. After the forest stand dies, a pond with aquatic and coastal-aquatic plants is formed, where the same species dominate as in the flooded forests. If the dam is not repaired by beavers, the duration of the pond stage is 2–5 years. Ponds exist much longer on the rivers with superficially incised bed, the maximum longevity of the pond on the Rechitsa River in the Bryansk Forest conservation area is 8 years. After the beavers abandon the pond, the dam is destroyed. The pond becomes shallow and turns into a low-lying grassy swamp. The duration of the grassy swamp stage is 5 or more years. As the grassy swamp continues to shrivel bushes begin to appear in it. The duration of this stage is 20–30

years. As undergrowth of trees and shrubs continue to develop on the territory of the former pond, black alder forests are formed. The formation of the tree layer lasts at least 40-50 years. The entire development cycle is approximately 60-80 years. Complexes of ecosystems in the valleys of small rivers occupy areas of dozens and hundreds of thousands of square meters; they are maintained under the condition of continuous habitat of beavers and the use of the territory by a "lea tillage system". The studies conducted in the Bryansk Forest Preservation area [166–170] provide the necessary basis for determination of the size, composition and structure of the landscape elements that are necessary and sufficient for the restoration of local beaver populations, one of the most important for the realization of ecosystem functions of the keystone species of North Eurasia Biota.

Conclusion

The review of the work devoted to the concept of complementarity helped to realize its integrating role in the reconstruction of the potential ground cover (potential biota) of the Earth on the basis of generalization of palaeodata, historical data and modern ecological studies of complementary relationships in the context of the preserved keystone species of Northern Eurasia Biota.

Comparison of the main features of the paleo-landscape Biota and the landscapes of modern

preservation areas (PAs) Biota demonstrates the functional incompleteness of the latter. Unified Pliocene-Pleistocene complexes have fallen into pieces of different degree of anthropogenic transformation; moreover, the destruction of the largest phytophages in most of Northern Eurasia played the largest role in the primary transformation of the Earth's ground cover.

As the anthropogenic development of Northern Eurasia took place, the fragments ("debris") of the Biota became less able to maintain the ecosystem functions of the Biosphere, and the new direction "*Pleistocene Rewilding*", formed on a world-wide basis as a result of the awareness of the need for active restoration of natural Biotas and, in the first place, their keystone species, is of vital importance so far. Realization of this new direction, which is essential for the nature of Northern Eurasia, is possible only if there is institutionally-based recognition of the fact that the preserved areas are in need of substantial assistance in fitting with modern equipment, in qualified specialists, and the organization of biosphere polygons for experimental research.

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Smirnova, O. V.

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