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BIODIVERSITY AND CLIMATE-REGULATING FUNCTIONS OF FORESTS: CURRENT ISSUES AND RESEARCH PROSPECTS

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The problem of assessing the impact of biodiversity on the climate-regulating functions of forests is fundamental. It is of great applied importance for sustainable forest management in the context of global climate change. On the one hand, climate change affects biodiversity; on the other hand, biodiversity underlies the mechanisms of adaptation of forests and society to these changes, because it is a provider of all ecosystem functions. This article aims to discuss scientific issues currently faced by scientists, such as the relationships between biodiversity and climate-regulating functions of forests, and to outline the perspective of the studies. There are numerous studies that describe the influence of certain plant and animal species – ecosystem engineers – on the ecosystem, including climate-regulating functions of forests. However, we lack estimates of the combined effect of the diversity of biota of different trophic levels and groups on the completeness of the implementation of climate-regulating functions of forests of different types/at different succession stages. We emphasise the importance of accounting for such estimates as taxonomic, including genetic, and the functional and structural diversity of forests. We considered various concepts of forest management, taking into account the conservation and restoration of biodiversity. The most important aspect of this problem is estimates and forecasts of interrelationships (trade-offs and synergies) between climate-regulating and other ecosystem functions of forests characterised by

different levels of biodiversity, with their natural development and with the combined impact of various natural and anthropogenic factors on forests, including climate change, fires, and forest management regimes. Integration of mathematical models is a promising approach to assess and predict the dynamics of relationships between various ecosystem functions of forests.

Key words: *forest ecosystems, taxonomic biodiversity, functional biodiversity, structural biodiversity, ecosystem functions, adaptation to climate change*

INTRODUCTION

Forests fulfill many ecosystem functions and provide numerous ecosystem services to humans. Biodiversity provides ecosystem functions and forest services (TEEB, 2010). Globally, nearly half of all species are predicted to become extinct over the next 100 years due to changing land use, anthropogenic influences on biogeochemical cycles, the spread of invasive species, unbalanced management, and uncontrolled exploitation of natural resources (Louman et al., 2011; Rampino, Shen, 2019). A decline in biodiversity will inevitably lead to disruptions in ecosystems.

In the past 25 years, we have witnessed the development of a new scientific direction, aimed at exploring the links between biodiversity and ecosystem functions (BEF) (Eisenhauer et al., 2019; Van der Plas, 2019). Previously, a large proportion of scientific research was aimed at assessing the impact of abiotic factors (geological, climatic) on ecosystems, although the importance of species diversity for the functioning of ecosystems was shown by Ch. Darwin and A.R. Wallace more than 150 years ago (see Eisenhauer et al., 2019). A meta-analysis of the results of short-term experiments on small, artificially created sites (up to 100 m²) demonstrates the existence of stable relationships between biodiversity changes in experiments and ecosystem functioning (Cardinale et al., 2011; O'Connor et al., 2017). The latest studies have focused on natural ecosystems. Analysis of the results of 259 case studies on over 700 cases of relationships between biodiversity and ecosystem functioning demonstrates that biodiversity

contributes to biomass production and stabilisation of this process over time, as well as successful pollination (Van der Plas, 2019). The number of cases that showed a positive effect of biodiversity on the rate of organic matter decomposition and multifunctionality of ecosystems exceeded the number of cases with a negative effect, but neutral relationships were quite common. It has been emphasised that assessments of links between biodiversity and ecosystem functions focus on taxonomic diversity, although functional diversity is a more informative predictor. It remains unclear how the links between biodiversity and functions change at different spatial levels, although more positive relationships are expected at higher spatial levels (Van der Plas, 2019). The analysis also showed that the relationships between biodiversity and ecosystem functioning are context sensitive, that is, they change depending on natural and climatic conditions, management regimes, and disturbances (Eisenhauer et al., 2019).

Climate change is one of global challenges, and mitigation and adaptation to climate change are of particular importance today (IPCC, 2019). The global loss of biodiversity is associated with forest degradation. This process can negatively affect forest functioning and resilience in a changing climate. The problem of assessing the impact of biodiversity on the climate-regulating functions of different types of forests is fundamental and of great applied importance for sustainable forest management in the context of global changes. On the one hand, climate change affects biodiversity; on the other hand, biodiversity underlies the mechanisms of adaptation of forests and

society to climate change. However, many forest countries, including Russia, have shown a steady trend towards the intensification of forest use, with a consequent decrease in biodiversity (Karpachevsky et al., 2015). In developed countries, this trend is associated with the development of a bioeconomy. It is driven by the increasing demand for forest products and services by the growing population of Earth and per capita consumption (Pülzl et al., 2014).

The assessment of the climate-regulating functions of forests, which include the production of biomass, the regulation of carbon and nitrogen cycles, including the decomposition and mineralisation of organic matter, the formation of natural soil fertility, and water and temperature regimes, are the main issues highlighted in many, including Russian, works dated at the end of the 20th century as well as modern studies conducted within the framework of special scientific programmes and projects (Kazimirov, Morozova, 1973; Kazimirov et al., 1977; Manakov, Nikonov, 1981; Nikonov, Lukina, 1994; Zamolodchikov et al., 2005; Kudeyarov et al., 2007; Bobkova, Osipov, 2012; Osipov, 2013, 2015; Osipov, Bobkova, 2016; Bakhmet, 2018; Lukina et al., 2019, 2020). There are also estimates of the impact of different types of Russian forests on evaporation and water runoff (Karpechko, 2004; Onuchin, 2003; Karpechko et al., 2020; Kondrat'ev et al., 2020) and estimates of greenhouse gas fluxes at the levels of forest biogeocenosis and whole region. (Mamkin et al., 2019; Urban et al., 2019). However, these works did not assess the impact of biodiversity on climate regulation processes and forest functions at different spatial levels and in different time scales. We lack information on the combined effects of biodiversity components of different trophic levels and groups on ecosystem processes and functions (Gamfeldt et al., 2013; Mori et al., 2016; Van der Plas et al., 2016; Pugnaire et al., 2019).

There are few scientific works devoted to assessing the impact of the biodiversity of different types of forests on their climate-regulating functions, taking into account the combined effect of the diversity of biota at different trophic levels, and not only the species diversity of woody plants. Meanwhile, it is precisely these studies that are important for sustainable ecosystem management of forests in a changing climate. The studies in subtropical forests have shown that functional diversity of plants and heterotrophs, which accelerate the decomposition and cycles of nutrients, had a more significant impact on individual ecosystem functions and multifunctionality than the species diversity of woody plants alone (Schuldt et al., 2018). Thus, assessing the links between biodiversity and the climate-regulating functions of ecosystems is a major fundamental problem. Forests, like other ecosystems, are multifunctional, that is, they simultaneously perform many ecosystem functions that shape ecosystem services (Bradford et al., 2014; Byrnes et al., 2014; Manning et al., 2018; Van der Plas et al., 2018). All ecosystem functions are equally important and equitable, but the priority of ecosystem services is determined by humans, and the ecosystem–human relationships are need to be taken into account. The relationships can be either positive (synergy) or negative (conflicts/trade-offs) (Liang et al., 2016; Mori et al., 2017; Manning et al., 2018).

Russia pays much attention to the conservation of the global biodiversity of forests and performance of ecosystem functions by them. This country accounts for more than 20% of all world forest cover, including more than half of Earth's boreal forests. The lands of the forest fund make up more than two thirds of the total land area of the country, and the share of area covered by forests (45.4%) is one of the highest in the world.

Typologies of Russian forests are based on the classification of vegetation (either on the basis of dominant or indicator species) and environmental conditions (types of habitat conditions) (Alekseev, 1925; Braun-Blanquet, Pavillard, 1925, cited in Mirkin, Naumova, 2009; Cajander, 1926; Sukachev, 1972; Pogrebnnyak, 1955; Mirkin, Naumova, 2009). A significant step forward was the unified forest classification, which is based on the dominant approach, supplemented by ecological-cenotic and floristic analysis (Zaugol'nova, Morozova, 2006; Zaugol'nova, 2008). L.B. Zaugol'nova and V.B. Martynenko created an electronic identifier of forest types in European Russia (<http://cepl.rssi.ru/bio/forest/index.htm>). The key allows characterising the typological diversity of forests on the basis of the traditions of Russian forest phytocenology and international approaches to the classification of vegetation.

However, assessing the links between biodiversity and forest functioning requires taking into account the diversity of biota also of other trophic levels and groups. The most important scientific problem, which is currently of great applied importance, is the assessment of the impact of biodiversity on the climate-regulating ecosystem functions of forests. To develop measures to adapt forests to climate change, we need to gain information on the combined effect of the diversity of biota of different trophic levels and groups on the completeness of the implementation of climate-regulating functions of forests and their adaptive potential.

Studies focused on the dependence of the climate-regulating functions of forests, representing different succession stages, on the level of their biodiversity will allow answering the question: is it really only ecosystem engineers, primarily dominant woody plants, that are important for adapting forests to climate change, or is it necessary to maintain

and restore the biodiversity of forest ecosystems in general? Old-growth intact forests in Russia are refugia of biodiversity and a depository of soil carbon (East European ..., 2004; European Russian Forests ..., 2017; Smirnova et al., 2018). The importance of these Russian forests in climate regulation is difficult to overestimate; however, we still lack estimates of the combined effect of biodiversity components of different trophic levels and groups on the climate-regulating functions of old-growth intact forests.

The measures for adaptation to climate change include tree plantations consisting of different species; this approach is reasonable, but clearly insufficient. The climate-regulating functions are most fully implemented in old-growth intact forests, in which natural connections between various components of the biota have been preserved and which can serve as standards for comparisons with forests at different succession stages.

The performance of forest climate-regulating functions at the regional level depends on the forest ecosystem diversity and the contribution of different types of forests. The performance of climate-regulating functions at the ecosystem level is due to intra-ecosystem biodiversity, including the taxonomic and functional diversity of plants, animals, and microorganisms, as well as the structural biodiversity (micromosaics) of forests. This aspect of diversity characterises the diversity of habitats for biota of different trophic levels. For sustainable forest management under a changing climate, it is necessary to assess the relationships (synergy or trade-offs) between climate-regulating and other ecosystem functions of forests with different aspects of biodiversity in the course of natural development and under the combined impact of various natural and anthropogenic factors, including climate change, fires, and forest use regimes.

This article aims to raise a number of questions related to the assessment of the combined effect of the taxonomic and functional diversity of biota of different trophic levels and groups, as well as the structural diversity of forest ecosystems on their climate-regulating functions.

BASIC CONCEPTS OF THE PARADIGM OF FUNCTIONAL DIVERSITY AND BIODIVERSITY – FUNCTIONING LINKS

The need to address the problem of the impact of biodiversity on ecosystem functioning has led to the emergence of a new interdisciplinary research area – functional biodiversity. The functional biodiversity paradigm emphasises the active role of biota and its diversity in creating environmental conditions in ecosystems. Functional biodiversity is the diversity of different biota groups with specific roles in the community. The characteristic functional features of each species determine the biological mechanisms of their joint influence (the effect of the mixed composition of species) on individual functions and on the functioning of ecosystems as a whole (Cadotte et al., 2011; Scherer-Lorenzen, 2013).

The terms ‘ecosystem processes and properties’, ‘ecosystem functions’, ‘functioning’, and ‘ecosystem services’ are key in the concept of functional biodiversity (Naeem et al., 2002; Hooper et al., 2005; de Groot et al., 2010).

Ecosystem processes are physical, chemical, and biological events or actions that link organisms and their environment (Greenfacts <https://www.greenfacts.org/glossary/def/ecosystem-processes.htm>) such as biomass production, litter degradation, nutrient cycles;

Ecosystem functions are the set of physical, biological, chemical, and other ecosystem processes that support the integrity and conservation of ecosystems (Ansink et al., 2008). Functions are intermediate links between processes and services.

Ecosystem services are the benefits that people receive from ecosystems (MEA, 2005), including providing services (fibre, wood, food, etc.), regulating services (erosion control, climate regulation, pollination, etc.), supporting services (soil formation, photosynthesis, etc.), and cultural services (recreational, educational, spiritual and religious, etc.).

Ecosystem functioning comprises events, processes, or properties of ecosystems influenced by biota.

To study the links between biodiversity and ecosystem functions and services, it is important to understand and evaluate the multifunctionality of ecosystems. *Multifunctionality* is the ability of ecosystems to perform simultaneously multiple functions and provide multiple services (Manning et al., 2018). Multifunctionality is divided into two levels: (i) multifunctionality of ecosystem functions, the assessment of which is aimed at fundamental research of biological, geochemical, and physical processes occurring in ecosystems; (ii) multifunctionality of ecosystem services, which is defined as the joint provision of a number of ecosystem services in response to a request from society.

Changes in biodiversity can lead to profound transformations in the functioning of ecosystems. To identify the effects of biodiversity on functions, it is necessary to take into account the influence of environmental factors and specific species. The most pronounced influence on the functioning of ecosystems is exerted by the so-called ecosystem engineers – organisms that create, modify, and maintain habitats, causing changes in the state of biotic and abiotic components that modulate directly or indirectly the availability of resources for other species (Jones et al., 1994, 1997). The ideas about powerful environment transformers – plants – dates back to the works of Braun-Blanquet (Braun-Blanquet, Pavillard, 1925,

cited in Mirkin, Naumova, 2009), who proposed the concept of aedificator (from the French word meaning ‘builder’) in relation to phytocenoses. It was used in works on phytocenology and biogeocenology by V.N. Sukachev. In terms of these works, an aedificator is a plant species, the presence of which in the biogeocenosis noticeably changes the ecological regimes – light, humidity, temperature, chemical composition of soil, water, and atmosphere – and determines the sets of subordinate species (Sukachev, 1928, 1935, 1964). The concepts of keystone species and ecosystem engineers appeared later. Although the scope of these concepts partially overlaps, they are far from identical. Keystone species include species, mainly of high trophic status, that have a disproportionate impact on the environment relative to their abundance (Paine, 1969).

Some species or functional groups make a greater contribution to the relationships between biodiversity and functions than others through specific functional traits that enable those species or groups to use resources more efficiently and to influence processes and functions (Eisenhauer et al., 2019). This phenomenon is called species identity.

THE INFLUENCE OF BIODIVERSITY ON FOREST FUNCTIONING

The question of how changes in biodiversity affect ecosystem processes and functions simultaneously remains unanswered. The existing studies aimed at assessing the impact of biodiversity on forest functioning include comparing monocultures and plantations of several tree species on permanent sample plots, conducting silvicultural experiments, and analysing natural gradients of forest biodiversity and forest inventory results. Studies of forest productivity and nutrient cycles show peculiar relationships between productivity and diversity, with differences between monocultures and mixed stands depending on

the species composition and environmental conditions (Integrating ..., 2016). But we require more in-depth studies of the biological mechanisms of the impact of coexisting species on the functioning of natural ecosystems. It will also be of practical importance for the creation of mixed (multi-species) forests that can fulfil a variety of functions.

The mechanisms by which increased biodiversity influences the functioning of ecosystems include the following (see Eisenhauer et al., 2019): (i) an increase in biotope space and number of ecological niches; (ii) an increase in the efficiency of resource use; (iii) an increase in the relationships between representatives of biota of different trophic levels; (iv) an increase in the effects of complementarity, which is manifested in the fact that a more diverse community consisting of specialised species that differ in structure and functions are able to use the available resources more efficiently than a single species that increases productivity and reduces the level of unused resources; and (v) enhancement of favoured effects, that is, positive influence of one species on the efficiency of another (the so-called nursery plants, or influence through provision of additional nutrients owing to symbiosis, etc.) that can also lead to increased resource efficiency and productivity.

Species richness is one of the main determinants of ecological processes in ecosystems. However, there is a lack of experimental studies on the gradients of the diversity of woody plants in natural conditions. The results of a study in the beech forests of Central Europe showed that an increase in the number of tree species from one to five had variable effects on different ecosystem processes. The diversity of arboreal species is negatively associated with the terrestrial biomass of communities (Jacob et al., 2010), while the relationships with the diversity of the

herbaceous layer (Muller, 2003) and beetles (Sobek et al., 2009) is, on the contrary, positive. It is believed that the species identity of woody plants with special functional features and their abundance are the main determinants of these processes associated with the ‘dilution’ of the influence of beech with an increase in the number of woody species. In addition, the covariance of some soil properties with tree diversity prevents clear recognition of the direct influence of species diversity on processes that are not mediated by environmental conditions. The results of existing studies allow us to conclude that the diversity of woody species partly explains the variation in some ecosystem functions and processes, alongside environmental factors and the influence of specific woody species (identity of woody species) (Pretzsch et al., 2020; Steckel et al., 2020).

Modern studies have shown positive relationships between tree species diversity and productivity and soil carbon stocks (Vesterdal et al., 2013). Many ecosystem functions and services, such as production of woody biomass, accumulation of soil carbon, forest plant species richness of the lower layers, and the presence of deadwood, are positively associated with each other and with the richness of woody species (Gamfeldt et al., 2013; Baeten et al., 2019). Experiments are underway to provide evidence of a link between tree species diversity and ecosystem functioning. They are designed to separate the effects of biodiversity, environmental conditions, and species identity. Such planting experiments are conducted as part of the European TreeDiv-Net programme (see, for example, Verheyen et al., 2016). The results indicate that woody plant diversity may be positively associated with pest resistance, carbon sequestration, and other processes and functions.

The abundance and diversity of plants and animals associated with trees are often positively associated with the diversity of

woody plant species (see, for example, Poeydebat et al., 2020). Ecosystem functions and services are associated not only with environmental conditions, but also with the functional diversity of biota at different trophic levels. The influence of specific species (species identity) is also of great importance. However, from the standpoint of multifunctionality, it is obvious that a single species is not capable of performing many functions simultaneously, and there may be conflicts/trade-offs between individual services.

Biodiversity plays a key role in the sustainability of forests and, therefore, it becomes an essential element of strategies for adaptation to global climate and environmental changes and can be a tool for achieving management goals, such as providing simultaneously a variety of ecosystem services. This strategy should be implemented at the ecosystem level, starting with the creation of mixed-age stands, and at the landscape level through the development of multifunctional management of different types of forests. Forest mosaics with stands of different species can potentially maximise the provision of ecosystem services (Korotkov, 2017). Modern forestry with relatively short rotation plantations must take into account the linkages between biodiversity and functioning.

Given the above considerations, the studies aimed at understanding the role of biodiversity in the functioning of forests are becoming very demanding. There is a need to assess the consequences of species loss on forest functioning in the context of global climate change. Although some results have demonstrated positive relationships between tree species diversity and climate-regulating functions related to productivity and soil parameters (Schuldt et al., 2018), many studies have shown that the effect of individual species (species identity) is stronger than that of diversity (Tobner et al., 2016; Khlifa et al., 2017, 2020).

There are prominent knowledge gaps regarding the combined effects of biota diversity at different trophic levels on forest functions (Gamfeldt et al., 2013; Mori et al., 2016; Van der Plas et al., 2016; Pugnaire et al., 2019). This raises the question of the contribution of certain species and biodiversity in general to the variation of the climate-regulating functions of forests. Studies in subtropical forests showed that the functional diversity of plants and heterotrophs had a more significant effect on ecosystem functions than only the diversity of woody plant species (Schuldt et al., 2018). It is necessary to conduct such studies in boreal and temperate forests.

The results of some studies allow considering in general terms the influence of plants, animals, and microorganisms on ecosystem processes and functions of forests related to climate regulation.

The influence of plants on ecosystem processes and forest functions

Information on the environment-transforming effects of woody plant species continues to accumulate (Korotkov, 1991; Kuuluvainen, 1994; McCarthy 2001; Schliemann, Bockheim, 2011; Yamamoto, 2012; European Russian Forests ..., 2017). The influence of woody plants as ecosystem engineers is manifested at the intra-ecosystem and ecosystem levels. Less disturbed forests create a mosaic of light, temperature, water, and soil regimes of ecosystems (McCarthy, 2001; East European ..., 2004). This mosaic is a consequence of the following processes: (1) the formation of gaps in the forest canopy due to ageing and natural death of one or several nearby growing trees; (2) the formation of microsites created by tree falls, arising when the death of a tree is accompanied by a perturbation of the soil profile; this phenomenon forms specific 'dump' microreliefs, including hillocks, depressions, and deadwood at different decomposition stages (Skvortsova et al., 1983; Ulanova, 2000; The afterlife of a

tree, 2005; Bobrovsky, 2010). The heterogeneity of the environment formed as a result of generation flows in populations of tree species determines the presence in the ecosystems of the least disturbed forests with the maximum possible set of plant, animal, and fungal species and representatives of others kingdoms (East European ..., 2004), which are embedded in the mosaic created by ecosystem engineers. In temperate forests of Russia, elements of microsites created by tree falls can occupy 10–90% of the biogeocenosis area (Karpachevsky et al., 1978; Ulanova, 2000).

With their specific functional features/traits, woody plants are the main contributors in biomass production, nutrient cycles, the presence and abundance of other species, etc. It was shown that 30 years after the creation of single-species plantations of woody angiosperms and gymnosperms, differences in calcium concentration in tree litter had led to profound changes in soil chemistry and fertility (Reich et al., 2005). The abundance of earthworms and their diversity is much higher in forests, the soils of which are rich in calcium. Hence, there is a direct link between vegetation, soil biota, and soil fertility. Changes in the species composition of dominant woody plants in forests, caused by management decisions or climate change, have an impact on certain ecosystem functions and services. The conducted studies were focused on the influence of woody plants on certain climate-regulating functions of forest types, including carbon and nitrogen cycles as well as soil fertility (Cornelissen et al., 2007a; Framstad, 2013; Laganiere et al., 2013; Vesterdal et al., 2013; Mueller et al., 2015; Orlova et al., 2016; Yatso et al., 2016). N.P. Remezov (1953, 1956) discussed the phenomenon of accumulation of biogenic elements in forest soils; he showed that the processes of elution in forests are opposed by the processes of accumulation of nutrients in the upper horizons of soils. Numerous works

in recent decades have shown that plants affect biogeochemical cycles, fertility, and soil acidity (Binkley, Giardina, 1988; Hobbie, 1992; Van Breemen, Finzi, 1998; Augusto et al., 2002; Lukina et al., 2010; Hansson, 2011; Orlova et al., 2013).

The mechanisms by which plants influence the soil, which are analysed in the aforementioned works, include chemical weathering of rocks; redistribution of precipitation, light, heat, and nutrients; the input of nutrients via stem and crown waters; the effect on the decomposition and mineralisation of organic matter; the absorption of nutrients; and the creation of microsites by tree falls.

A number of results have been obtained from so-called common garden experiments on plantations formed by various woody plant species aged maximum 50–60 years. The ranking of woody plant species in decreasing acidification ability order is as follows: (*Picea abies*, *Picea sitchensis*, *Pinus sylvestris*) > (*Abies alba*, *Pseudotsuga menziesii*) > (*Betula pendula*, *Fagus sylvatica*, *Quercus petraea*, *Quercus robur*) > (*Acer platanoides*, *Carpinus betulus*, *Fraxinus excelsior*, *Tilia cordata*) (Augusto et al., 2002). These experiments and other studies confirmed the hypothesis that *P. abies* acidifies soils. However, it should be borne in mind that many plantations were formed on former agricultural lands, and the effect of trees on soil properties, including acidity, can change with age, and these changes can be non-linear, as shown for natural old-growth forests (Orlova et al., 2016).

The lower-layer plant species, whose composition changes during successions, also have a significant effect on the ecosystem functions of forests (Maes et al., 2020). An increase in the proportion of herbaceous plants in the composition of communities of taiga forests leads to an increase in the level of accumulation of soil carbon (Lukina et al.,

2020). Functional types or groups of plants are identified based on certain functional features (chemical composition of litter, intensity of water absorption and transpiration, etc.) (Cornelissen et al., 2007b; Hedwall, Brunet, 2016; Vicente-Silva et al., 2016; Zhang et al., 2017; Anderegg et al., 2018).

In some studies, the functional groups of plants are regarded as their life forms (Salemaa et al., 2008). In Russian geobotany, the concept of ecological-cenotic groups is popular, which can in a certain sense correspond to functional groups of plants, because they are formed according to the principle of similarity of ecological and cenotic conditions in which they grow (Smirnova et al., 2004; Smirnov, 2007; Khanina et al., 2015).

The most important functional feature of plants is the litter quality (Cornelissen et al., 2007a). The quality of litter includes two aspects – secondary metabolites and nutrients – and is one of the most important factors determining the rate of litter decomposition (Aerts, 1997; Berg, 2000; Zhang et al., 2008). Litter quality refers to the diagnostic criteria of soil fertility, characterising the relationships between vegetation and soil (Orlova et al., 2011; Freschet et al., 2013, 2020; Orlova, 2013; Lukina et al., 2019); it considerably depends on plant species and individual genotypes (Hättenschwiler et al., 2005; Lang et al., 2009; Makkonen et al., 2012; Sundqvist et al., 2012). This means that the levels of nutrient intake and secondary metabolites in litter depend on the species and, accordingly, the chemical composition of plants and the contribution of various plant species to the composition of the plant community. Secondary metabolites, including phenolic compounds, protect plants (Dixon, Paiva, 1995) and make a significant contribution to the interaction of plants with the environment (Cheynier et al., 2013). We should highlight the prominent role of lignin, a three-

dimensional phenolic polymer (Kovaleva, Kovalev, 2015; Kovalev, Kovaleva, 2016). As a component resistant to degradation, lignin affects the litter decomposition rate and, therefore, affects the mechanisms of interaction with soil biota and nutrient cycles. The rate of litter decomposition depends on the initial concentrations of nitrogen and other nutrients in it, both capable (potassium, phosphorus) and incapable (calcium, manganese) of retranslocation within plants (the latter accumulate in aging organs), and also on several stoichiometric ratios: carbon/nitrogen (C/N), lignin/nitrogen, lignin/cellulose, etc. (Berg, 2000; Osono, Takeda, 2004; Lukina et al., 2017; Artemkina et al., 2018).

The influence of animals on ecosystem processes and forest functions

The role of animals in the functioning of terrestrial ecosystems, including forest ecosystems, has been assessed in many works (Gilyarov, 1951; Dinesman, 1961; Khodasheva, Eliseeva, 1970; Formozov, 1976; Striganova, 1980; Abaturov, 1984; Gilyarov, Krivolutsky, 1985; Mammals ..., 1985; Herbivorous ..., 1986; Toropova, 1994; Edwards et al., 1995; Bobrovsky, 2010; Veen, Olf, 2011; Hornov, 2013; Isaev et al., 2015; Shevchenko, 2016; Isaev et al., 2017; Kurek, 2019; Saikkonen et al., 2019; Evstigneev, Solonina, 2020; Nummi, Holopainen, 2020). These authors have studied the features of the impact of animal species, including ecosystem engineers, on biodiversity and soils. In the studies, animals were combined based on different features – a similar role in the trophic chain (grazing and detrital); behavioural features, that is, individual, reproductive, and social; and their importance in the economy, that is, fur-bearing animals and commercial ungulates. The impact of heterotrophs and their functions in biogeocenoses are diverse; a unified classification of the functional diversity of animals has not yet been developed. Because animals have a marked

impact on the flows of matter and energy, they play a major, yet underestimated, role in the climate-regulating functions of forests.

There are several spatial levels of animal impacts: landscape, biogeocenotic, and intrabiogeocenotic (East European ..., 1994, 2004).

Landscape level

Birds are one of the most prominent vertebrates in many habitats. They are found throughout the world; they are ecologically diverse and better known than other vertebrate groups (Grafius et al., 2017). Birds eat pests, pollinate plants, and disperse seeds (Whelan et al., 2015). Birds provide connectivity to both forests and other landscapes and contribute to the flow of matter and energy. Urban landscapes with high functional connectivity and biodiversity of vegetation are characterised by increased abundance of bird populations (Rosenfeld, 2012). The diversity of birds in forests increases the diversity of biotic connections between community components. However, the functioning of birds is closely related to the structural diversity of forests and the fragmentation of habitats (Galushin et al., 1998; Romanov, Evstigneev, 2016). The modern extinction of avifauna is caused by a decrease in the structural diversity of forests (Fridman et al., 2016).

Large-scale changes in the modern forest biogeocenotic cover are caused by *beavers* (*Castor fiber*). The environment-transforming effects produced by beavers are manifested at all spatial levels (Toropova, 1994; Smirnova, 1998; Wright et al., 2002; East European ..., 2004; Zav'yalov et al., 2005; Aleynikov, 2010; Zav'yalov, 2013; Logofet et al., 2014, 2015). They make huts, burrows, dams, ponds, canals, paths, and glades in the modern forest cover of the valleys of small rivers and streams forming ecosystem complexes that consist of ponds, lowland swamps, waterlogged forests, and damp and fresh meadows. Hydromorphic and

semi-hydromorphic ecosystems fundamentally change hydrological, thermal, and edaphic regimes of the valleys of small rivers and streams. These factors determine the enormous role of beaver landscapes in the optimisation and stabilisation of the local climate and in the formation of a stable hydrological regime of forest areas in general. This affects the realising the productive potential of forests and affects the structure and dynamics of the vegetation and animal populations. Thus, the activity of beavers maintains the main path of vegetation development in wetland and forest communities at the sites of existing settlements as well as in meadow and forest communities at the sites of abandoned settlements (Evstigneev, Belyakov, 1997). The use of the territory by beavers according to the «lea tillage» regulate cycles of vegetation development, which support the cenotic and floristic diversity of the vegetation cover of small river valleys. The mechanism for maintaining this diversity is based on the spatial distribution of vegetation types along the valleys of small rivers. Transformed by beavers ecosystems are actively used by terrestrial, semiaquatic, and aquatic animals (Nummi et al., 2011; Nummi, Holopainen, 2020). For example, beaver ponds serve as watering holes for birds and animals during droughts. In addition, these shallow water bodies provide favourable conditions for spawning of fish and amphibians and for living of teals, mergansers, and mallards (Balodis, 1990). Beaver glades serve as a source of food for wild ungulates, hares, mouse-like rodents, etc. Abandoned huts and beaver burrows can be used as permanent housing or temporary shelter by other animals: desmans, minks, vipers, spindles, forest ferrets, marsh turtles, etc. (Dezhkin et al., 1986).

Biogeocenotic and intrabiogeocenotic levels

According to the concepts developed based on the studies of natural ecosystems, large carnivores affect ecosystem functioning

through trophic cascades by regulating the density of prey populations. However, at present, forest areas have been significantly transformed by humans, and the mechanisms of the influence of the remaining or reintroduced predators on the lower trophic levels are still poorly understood (Kuijper et al., 2016). It is believed that in anthropogenically transformed forests, the potential of such trophic cascades through regulation of population density is limited to unproductive ecosystems, where even a low number of predators can affect the density of prey, or to small areas of landscapes where predators can reach functional density. However, the action of trophic cascades through the behavioural responses of animals may be more significant and more widespread, because even a low density of predators affects the behaviour of ungulates. The effect of this mechanism has been demonstrated by the influence of lynx on roe reindeer in the Swiss Alps (Gehr et al., 2018), as well as the influence of wolf on roe reindeer, red reindeer, and wild boar in the Bialowieza National Park (Kuijper et al., 2013). The latter study was the first to show the influence of large carnivores (wolves) on reforestation and, accordingly, on climate regulating functions. It turned out that in areas with large tree debris (deadwood) that form physical obstacles the intensity of eating the tree seedlings 0.1–2 m high by ungulates decreased because they are more likely to be overtaken by predators (wolves).

Ungulates, bison, representatives of the reindeer family (elk, European reindeer, reindeer, European roe reindeer, etc.), wild boars, badgers, and moles have a significant impact on climate-regulating functions of forests.

European bison (Bison bonasus) was an aedificator of forest ecosystems throughout almost the entire Holocene (Kalyakin, Turubanova, 2004; Croomsigt et al., 2018; Vasile et al., 2018; Lord et al., 2020). This

species, together with other gregarious ungulates, created semi-open and open habitats in forests, formed highly productive pastures, fertilising the soil, and also ensured the stable existence of light-demanding flora (Smirnova, 2004; Shevchenko, 2016). Currently, the bison populations are small and protected by humans. Even the few existing bison populations markedly change the structure of forest communities. Bison eats herbaceous and woody plants; breaks down small trees; and creates trails, wallows and sites. A variety of microsites, differing in ecotopic conditions, ensures coexistence in a community of species that differ in environmental needs and life forms. For example, trees and shrubs damaged by bison often die, and gaps appear that provide sufficient light to support some meadow plant species in forests (Korochkina, 1969a; Kazmin, Smirnov, 1992). The high food plasticity of bison, oriented to the dominant plants of the vegetation cover, prevents competitive grasses from occupying the entire living space, freeing up habitats for other plants (Korochkina, 1969b; Tolkach, 1980). Bison creates disturbances of the ground cover; they support populations of weakly competitive juvenile plants in communities (Evstigneev, Solonina, 2016). One bison produces approximately 5,000 kg of excrement each year (Kholodova, Belousova, 1989). In this regard, bison grazing in forest biogeocenoses leads to a significant increase in the diversity of dung beetles and, consequently, to an increase in the content of nitrogen and available compounds of mineral nutrients of plants in the soil (Nemtsev et al., 2003; Barber et al., 2019).

Representatives of the reindeer family (*Cervidae*), which include elk (*Alces alces*), red reindeer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), and European roe reindeer (*Capreolus capreolus*), among others, also have a powerful environment-transforming effect on forest ecosystems, but

not always as powerful as that of bison. Bison grazing affects the abundance and species composition of the undergrowth of trees and shrubs as well as the species composition and cover of shrubs, grasses, mosses, and lichens; these effects determine the direction of the successions of modern forest communities (Korochkina, 1973; Vereshchagin, Rusakov, 1979; Gusev, 1983, 1986; Abaturov, Smirnov, 1992). For example, moderate grazing of reindeer in taiga forests increases the diversity of mosses, lichens, and vascular plants in the ground cover; the diversity of soil invertebrates; and the temperature of the soil (Suominen, Olofsson, 2000; Saikkonen et al., 2019). On the contrary, reindeer overgrazing decreases the cover and species diversity of vascular, primarily bushy, plants, mosses, and lichens, which are the most preferred food for reindeer in the winter (Hansen et al., 2007). Reindeer overgrazing can also reduce bird diversity due to destruction of nests (Rooney, 2001). Reindeer grazing has a significant effect on the undergrowth of woody plants, which defines the modern boundaries of the forest and tundra in Fennoscandia (Bognounou et al., 2018). The observed negative effects of the high density of herbivorous mammals emphasise the importance of predators as regulators at the highest trophic level for maintaining balance in ecosystems.

Wild boars (Sus scrofa) searching for soil invertebrates and underground plant organs disturb the ground vegetation cover (Sablina, 1955; Vereshchagin, Rusakov, 1979; Siemann et al., 2009; Gornov, 2013). In this case, soil disturbances are formed in different-sized areas. The soil exposed and mixed by wild boars is characterised by increased aeration, humidity, temperature, and high microbiological activity (Zlotin, Khodasheva, 1974; Gusev, 1986; Zav'yalova, 1997; Wirthner, 2011; Gornov, 2014). Boar excavations change the hardness of the soil, decreasing its density (Antonets, 1998). The

special ecological conditions of the pores determine the dynamic processes in the communities (Evstigneev et al., 1999; Gornov, 2011, 2013). The following features of wild boars' behaviour are important for the successional development of the ground vegetation: (i) formation of excavations, which are characterised by a bare substrate that is necessary for seed and vegetative reproduction of plants; and (ii) use of the territory according to the «lea tillage» system, in which excavations remain undisturbed for some time (Evstigneev et al., 1999). The latter is associated with a decrease in their feeding capacity. It is known that the invertebrate biomass in recently disturbed sites decreases 2–4 times (Gusev, 1986; Pakhomov, 2003) whereas the herbaceous plant's biomass decreases 2–5 times (Smirnova, 1987). The invertebrate population usually recovers within 2–3 years (Gusev, 1986; Pakhomov, 2003) whereas vegetation recovers within 1–2 years (Kozlo, Stavrovskaya, 1974; Gornov, 2011). These recovery periods determine the cyclical development of vegetation spots on the disturbed areas and their spatial redistribution in the communities. Boar excavations are inhabited by numerous spiders, millipedes, carabids, earthworms, and other invertebrates. Their biomass and diversity are higher in these excavations than in the surrounding areas (Pakhomov, 2003).

An increase in the density of large phytophages in forest ecosystems affects not only grazing but also detrital food chains. The growing number of detritus as a result of the decomposition of excrement and animal corpses increases the diversity and density of coprophages and detritus feeders (earthworms, arthropods etc). The organisms intensify humus formation and increase soil fertility and plant productivity throughout the growing season (Van Klink et al., 2020).

Badgers (Meles meles) markedly change the structure of forests. First, as a result of

burrowing activity, these animals produce two types of soil disturbances. The first type involves the release of soil material during the cleaning of old burrows and the construction of new burrows. The individual earth mounds (butane) are 2–23 m². At the same time, badgers rise to the surface from 0.7 to 8.1 m³ of soil (Soloviev, 2007). On butanes, the availability of nutrients is significantly changed because the material ejected from the deep horizons of the soil is rich in potassium, calcium, magnesium, and available phosphorus but depleted in carbon and nitrogen (Kurek et al., 2014; Kurek, 2019). The second type of disturbances arise as a result of the trophic activity of badgers. In search of invertebrates and small vertebrates, as well as succulent underground parts of plants, badgers disturb the ground vegetation. The burrowing activity creates a mosaic of ground vegetation. The mosaic is represented by different microgroups: (i) a predominance of vegetatively immobile annuals and reactive juveniles, (ii) dominance of vegetatively mobile perennials of the reactive group, as well as with a significant participation of phytocenotically tolerant plants, and (iii) dominance of vegetatively mobile competitive perennials (Evstigneev, Solonina, 2020; Kurek, 2019). O.I. Evstigneev and O.V. Solonina (2020) consider this sequence of microgroups, which replaces each other in time, as a micro-succession. Competitive species are the driving force behind the development of microgroups. They gradually replace reactive and tolerant plants and can become dominant species of the herbaceous cover for a long time. However, the use of sites by badgers in a «lea tillage» system periodically interrupts these unidirectional micro-successions. The disturbances that badgers create and cyclical micro-successions maintain a multi-species composition in the herbaceous cover. The mechanism for maintaining this diversity works due to the

spatial redistribution of microgroups with the dominance of plant species of different strategic types. Currently, due to overhunting, the badger has become an extremely rare and endangered species. A similar impact in forests is produced by foxes (Kurek et al., 2014). However, their burrowing activity is less intense than that of badgers (Formozov, 2010).

Moles (Talpa europaea) are insectivores that improve soil quality. By tunneling and moving soil material, they improve aeration and promote the penetration of humus both into deeper soil horizons and to the surface, increasing the availability of nutrients for plants. These underground mammals have low mobility; they live in a fairly constant environment characterised by the absence of light and stable temperature and humidity (Lacey et al., 2000). They are expected to be less susceptible to seasonal climatic fluctuations, unless these fluctuations lead to severe drought or freezing, which will dramatically increase soil hardness and reduce the availability of forage resources (soil animals) (Feuda et al., 2015). The burrowing activity of moles results in significant transformations of the horizontal structure of forests at the intrabiogeocenotic level. Moles make two types of passages in the soil: superficial and deep. When constructing deep passages, moles throw out the soil mass (Sklyarov, 1953). They create molehills, which are relatively small. The burrowing activity of moles results in the changes in microrelief. Moreover, the material inside the soil is mixed and the area of contact between the soil and air increases. The volume of soil involved in the release is approximately 10 m³ per hectare (Abaturov, 1984; Pakhomov et al., 1987). Molehills provide favorable conditions for many plant species, including trees (Tikhomirova, 1967; Zenyakin, Onipchenko, 1997). Over time, they are colonised by ants and other invertebrates (Tikhomirova, 1967). Mole tunnels attract vertebrates (amphibians,

reptiles, small mammals) and invertebrates (earthworms, ground beetles, molluscs, spiders, etc.). In burrows, animals search for food, hide from enemies, and, in some cases, procreate (Nakonechny, 2013).

Birds and mammals are an active part of biocenoses, which determine the species composition of communities through the dissemination of diaspores: seeds, fruits, vegetative primordia, etc. (Levina, 1957; Udra, 1988; Ndiade-Bourobou et al., 2010; Holbrook, 2011; Evstigneev et al., 2017). The distance of dissemination of zoochorous plant species diaspores are determined by the biology and behaviour of animals – dissemination agents. There are three types of zoochoria: endozoochory, synzoochory, and epizoochory (Levina, 1957). Endozoochory is the spread of diaspores passed through the digestive tract of animals and then discarded with droppings. Synzoochory is the spread of diaspores associated with their dissemination by animals with the aim of storing them in pantries or eating them in nests. Epizoochory is the spread of diaspores attached or adhered to the body of animals. For example, bison, bears, elks, roe reindeer, capercaillies, and fieldfares spread diaspores mainly in endo- and epizoochoric ways. Squirrels, mice, voles, jays, nutcrackers, woodpeckers, nuthatches, and tits disseminate diaspores mainly in a synzoochoric manner. The survey works by Evstigneev et al. (2013, 2017) showed that massive dissipation of plant diaspores by animals are of great importance for the formation of phytocenoses, whereas single cases of dissipation over a long distance is of great importance for the expansion of the habitat of plant populations. Massive dissipation of diaspores of zoochoric plant species is implemented within the individual habitats of animals, whereas single cases of dissipation is implemented in the course of distant movements of animals (migrations). Thus, species diversity and high numbers of

animals and birds contribute to the formation of diaspora flows both at the intercenotic and intracenotic levels. A decrease in the species diversity and number of animals limits the participation of zoochoric plant species in successions and weakens the intercenotic flows of diasporas.

Insects play a major role in the functioning of forest ecosystems. Given that insects and plants are the two largest taxa on Earth, it seems likely that interactions among these species will be crucial in shaping the response of many ecosystems to future climate changes. Insects affect nutrient cycles in ecosystems (Brussaard, 1998) accelerating them by the rapid transformation of phytomass to simple organic compounds, and regulating soil fertility. Insects influence the functioning and dynamics of plant populations and thus regulate their impacts on ecosystem processes (Brussaard, 1998). At a low population density, phytophagous insects remove 5%–7% of the phytomass of the leaf apparatus of trees; this action maintains the viability of plants. During outbreaks of mass reproduction and in cases of tree damage and death, there is renewal and transformation of the species composition. At the same time, caterpillar excrement acts as a fertiliser that contributes to the enhanced growth of herbaceous plants and reforestation. All of these processes affect the carbon cycle in forests. In many cases, phytophagous insects act in the forest ecosystem as components that determine the direction of successional processes, contributing to both acceleration and deceleration of forest ecosystem successions (Chernyshev, 1996).

In a balanced forest ecosystem, *saproxyllic insects*, whose cycles are associated with deadwood of varying degrees of decomposition, regulate the density of woody plant populations based on the feedback principle, and also participate in food chains (Rafes, 1968; Demakov, 2000). The state of

xylobiont populations is closely related to the state of tree stands, which are their food base and habitat and, therefore, some species can be indicators of the state of forest ecosystems (Lachat et al., 2012). In recent decades, the biology and ecology of key xylobiont insects from different functional groups have been studied in more detail to elucidate the mechanisms by which they maintain a stable state of forest ecosystems organised and supported by the life of their populations (Isaev, Girs, 1975; Isaev et al., 1981; Rozhkov, 1981, Lee et al., 2018). Large xylobiont species maintain a high biodiversity of other groups of invertebrates living together in wood (Buse et al., 2008a, 2008b). However, their interspecific relationships in forest ecosystems and changes in behavioural reactions under the influence of biotic and abiotic environmental factors remain understudied.

Coprophagous insects such as the dung beetle provide ecological functions and services through the physical management of the ecosystem (Nichols et al., 2008; Simmons, Ridsdill-Smith, 2011). In addition to consuming animal faeces, dung beetles scatter and bury them in the soil through burrowing and thus control a number of ecological processes, including nutrient cycling, soil aeration, and seed burial (Nichols et al., 2008; Simmons, Ridsdill-Smith, 2011). In this respect, dung beetles are considered ecosystem engineers (Boze et al., 2012) because their activities in the soil physically alter the environment in such a way that they increase the availability of resources for other organisms (Jones et al., 1994, 1997). There are examples of the activity of dung beetles promoting plant growth by mobilising nutrients in the soil (e.g., Bang et al., 2005; Nichols et al., 2008). This is due to the fact that beetles improve soil fertility by increasing nitrogen availability (Yokoyama et al., 1991). Dung beetles improve soil hydrological properties by increasing water infiltration and

soil porosity while reducing surface water runoff (Brown et al., 2010). In the future, these ecosystem engineers should be able to alleviate water stress in plants, especially during droughts caused by changing rainfall patterns (Jonson et al., 2016).

Ants (Formicidae) produce special aboveground and underground structures – anthills (Zakharov, 1978). There are more than 10,000 ant species (Bolton, 1994), but with the use of DNA methods, estimates of species diversity are constantly changing (Schlick-Steiner et al., 2006). Ants are also referred to as ecosystem engineers changing the flow of energy and matter in terrestrial ecosystems (Finer et al., 2013). The overwhelming majority of ant species build nests in mineral soil and, therefore, they have a significant effect on soil properties (Hölldobler, Wilson, 1990). Building organic mounds on the soil surface makes ants susceptible to disturbances (Jurgensen et al., 2008). Forest fires and the use of heavy machinery for logging or preparing the soil for tree planting have led to the destruction of mounds and have had a negative impact on ant activity. The absence or low frequency of forest fires in Central and Northern Europe over the past centuries has led to an increase in the number of ants (Niklasson, Granstro, 2000). Wood ants (*Formica rufa* group) are key species in the European and Asian boreal and mountain forests (Hölldobler, 1960; Laine, Niemelä, 1980). They transfer organic matter from forest litter to their nests and from nests back to forest litter as well as from tree crowns to nests (Punntila and Kipelainen, 2009). Much attention has been paid to how ants of the genus *Formica* build mounds in boreal forests. Wood ants affect the abundance and distribution of many forest invertebrates and vertebrates in forests, forest litters, soils, and trees.

Inhabited anthills are characterised by a thin herbaceous cover; increased soil porosity,

aeration, and temperature; and high microbiological activity (Dymina, 1985; Zryanin, 2003; Golichenkov et al., 2011; Dauber, Wolters, 2000), which affects the climate-regulating functions of forests. During humidification periods, anthills are well drained, whereas in dry periods they are strongly dried out (Kurkin, 1976). Anthill building contributes to the survival of the young generation of many plant species, including weakly competitive ones (Evstigneev, Rubashko, 1999; Dmitrienko, Ludwig, 2005). That is why special vegetation microgroups forming on anthills are floristically different from the surrounding cover. For example, in connection with the activity of *F. rufa*, the following microsites were distinguished: (i) dome of an active anthill, (ii) earthen rampart of an active anthill, (iii) dome of an abandoned anthill, and (iv) the shaft of an abandoned anthill (Rubashko et al., 2010). The appearance of these microsites increases the capacity of the habitat and the floristic diversity of the territory.

Invertebrates – soil saprophages

Matter and energy flows in forest ecosystems largely depend on the activity of the complex of invertebrate – saprophages associated with litter and soil. The diversity and structure of the saprophage complex provide a number of the most important ecosystem functions: they determine the direction and rate of litter decomposition and regulate soil fertility (Striganova, 1980; Ernst et al., 2009; Yang, Chen, 2009; Yatso, Lilleskov, 2016). Saprophages among soil invertebrates account for $\geq 80\%$ of the total zoomass (Striganova, 2003).

The flow rate of dead organic matter entering the soil reaches at least 95% of the total amount of organic matter assimilated by producers (Begon et al., 1986). The source of carbon for soil saprophages is plant litter (including leaves, stems, and roots), root exudates of plants, and soil algae (Gleixner,

2013; Goncharov, 2014). In turn, the structure and functions of the complex of destructive saprophages depend on soil type, plant community composition, and climatic features.

All groups of soil saprophages have a significant effect on the cycles of carbon and nutrients and the formation of soil fertility. The example of earthworms, which often prevail among soil saprophages by biomass in deciduous forests, shows that their activity contributes to (i) fixation of soil carbon in the form of humus compounds (Kozlovskaya, Belous, 1967; Six et al., 2004; Jastrow et al., 2007; Schmidt et al., 2011; Lubbers et al., 2017); (ii) horizontal mosaic distribution of carbon in the soil due to horizontal migrations of worms in soil, movement of soil particles, and the formation of water-resistant coprolites, that is, a mixture of a mineral substrate and organic matter in which the carbon content increases by 30%–50% compared with the content in mineral soil horizon (Kurcheva, 1971; Tiunov, 2007; Kutovaya, 2012); and (iii) vertical mosaic distribution of carbon in the soil due to the transfer of organic matter from the upper to the lower soil horizons due to deep vertical migrations; this function is performed by the anecic earthworm group that was also shown by us on the example of old-growth mountain coniferous-broadleaf forests (Shevchenko et al., 2019).

However, there is still no unambiguous assessment of the effect of earthworm activity on soil carbon dynamics. Several studies have shown that carbon stocks decrease as a result of the activities of earthworms (Alban, Berry, 1994; Burtelow et al., 1998; Bohlen et al., 2004), while other studies have indicated that earthworms contribute to the accumulation of carbon in soils (Pulleman et al., 2005; Novara et al., 2015). Such opposing conclusions are probably due to the fact that in most works the complex of earthworms is considered holistically and does not take into account the role of individual functional types and groups:

earthworms feeding on litter are primary humus formers (epigeic, epi-endogeic, and anecic) and endogeic worms feed in the soil, that is, secondary humus consumers (Perel', 1979). In this regard, we face the need of differentiating the influence of different groups of earthworms in terms of soil carbon accumulation.

Initially, Bouché (1972) identified seven ecological categories of earthworms. They were subsequently combined into three main ones: epigeic, endogeic, and anecic. T.S. Perel' (1979) singled out the morpho-ecological group represented by epi-endogeic earthworms.

Epigeic species are small, reaching 5 cm in length; these pigmented earthworms live in litter and rotting wood. They provide the primary decomposition of litter leached and secondary decomposition of polyphenolic, and other chemically resistant compounds preliminarily destructed by microorganisms. In the course of grinding plant material, the specific surface of the substrate increases hundreds of times together with its accessibility to microorganisms (Tiunov, Kuznetsova, 2000; Tiunov 2003, 2007). The succession of saprophages from the size group of the mesofauna (collembolans, oribatids) is accelerated simultaneously during the decomposition of organic substrates (Chernov, 1977). This results in the acceleration of tree litterfall decomposition, ammonification processes, nitrification, and consumption of ammonium and nitrates by plant roots (Kurcheva, 1971; Striganova, 1980; Byzov, 2005).

Epi-endogeic species include pigmented medium-sized earthworms (5–15 cm); they live in the forest litter and in the soil at shallow depths, recycle poorly decomposed tree litterfall, and actively mix it with the soil.

Endogeic species include unpigmented medium-sized earthworms (5–15 cm); they live in the soil, most often to a depth of 30–40

cm. They actively loosen the soil during horizontal and vertical migrations, feed on plant residues that have passed through the digestive tract of epigeic and epi-endogeic species, and get mixed with soil particles.

Anecic species include large earthworms (> 15 cm); only the anterior part of their bodies is pigmented. They live in the soil and, as a result of vertical migrations, they mix the soil layers and dig 1–8 m long passages, thus making the soil porous and filled with air and water that defines its fertility. Anecic earthworms are ecosystem engineers (Wright, Jones 2006; Tiunov, 2007; Zhang et al., 2016; Le Bayon et al., 2017). They affect both physical and chemical properties of the soil. The systems of cavities and passages dug by them exist much longer than the organisms that dig them and have a long-term effect on subsurface processes. These earthworms feed on plant debris on the soil surface, so the biomass of anecic earthworms largely determines the rate of litter decomposition in forests.

A global meta-analysis showed that the presence of not only epigeic and anecic earthworms, but also endogeic species decrease the content of organic matter in the litter horizon, with the strongest effect exerted by anecic earthworms (Huang et al., 2020). Moreover, even earthworms of the same group can have different impact on soil characteristics (Van Groenigen et al., 2019).

Assessment of the functional diversity of soil saprophages is very important because the completeness of the implementation of ecosystem functions of forest communities depends on the diversity of functional groups. However, until now, the isolation of functional groups has not been justified clearly even within such a group of macrosaprophages such as earthworms, although it is obvious that worms of different ecological categories (Bouche, 1972) or morpho-ecological groups (Perel', 1979) have different effects on soil properties (as shown above). Since 2000, the

term 'functional group' has become synonymous with the designation of the main ecological categories (groups) of earthworms. At the same time, some authors consider this approach to be incorrect and argue that the ecological groups of earthworms are not identical to functional groups (Bottinelli, Capowiez, 2020). The main arguments are: (i) the classification of ecological groups is based on the morphology and anatomy of earthworms and reflects, first of all, how the worms have adapted to the environment, but not how they affect it; and (ii) the number of functional groups of worms is probably greater than the number of ecological groups, because the impact on soil properties even within the same ecological group often differs (Van Groenigen et al., 2019).

Consequently, the question of the functional classification of large soil saprophages remains open. To elucidate the influence of invertebrates on soil properties, we need to use a combination of methods: direct measurements of the influence of individual species, which requires the development of standard research protocols and the formation of open databases (Bottinelli, Capowiez, 2020); molecular genetic research, because until now a number of even widespread saprophages with pronounced polymorphisms has no definite systematic status (Shekhovtsov et al., 2020); and a stable isotope method to study trophic relations in the soil, including in the field – this method opens up large horizons in ecosystem ecology (assessment of trophic niches, food resources, substance flux). However, the use of a larger number of isotope pairs (in addition to carbon and nitrogen isotopes) is still methodologically restricted: some isotopes are poorly fractionable, namely sulphur isotopes, and we still lack data on hydrogen isotopes (Tiunov, 2007; Potapov et al., 2014; Makarov et al., 2019, etc.). The latest studies are focused on isotopic composition of nitrogen and carbon

of amino acids of dipteran larvae (Pollierer, 2020), epigeic and endogeic earthworms (Potapov et al., 2019) that makes it possible to differentiate their trophic resources. In particular, these studies indicate major roles of plant litter in the nutrition of epigeic earthworms, and of soil organic matter and microorganisms in the nutrition of endogeic earthworms (Potapov et al., 2019).

In a broad sense, forest ecologists increasingly agree that all diversity levels of soil invertebrates – taxonomic, phylogenetic, ecological, and functional – serve as the basis for the multifunctionality of ecosystems (Tresch et al., 2019) and that increased functional diversity of soil biota complements enhances ecosystem functions; in other words, synergy effects outweigh trade-off effects (Bender et al., 2016).

Diversity in the soil biome makes a significant contribution to the inverse relationships between soil functions and climatic parameters (Wall, 2012). Assessment of the role of the biodiversity of soil fauna in adapting forests to climate change is considered in the context of ecological soil engineering (Bender et al., 2016) and the need to form and maintain climate-smart soils (Paustian et al., 2016).

It is crucial to study soil biodiversity effects on greenhouse gas emissions from soils as well as carbon storage in soils to assess carbon cycles. Soil fauna activities can trigger feedback mechanisms that either enhance or mitigate the impact of climate change (Lubbers et al., 2013; Crowther et al., 2016). It is also assumed that the diversity of soil macrosaprophages (earthworms, isopods, molluscs, and millipedes) can serve as an important mechanism for limiting greenhouse gas emissions from soil (Lubbers et al., 2020). Greater functional diversity of soil macrofauna leads to an intensification of litter decomposition and the fixation of carbon in the soil in the form of humic compounds as a result

of the trophic activity of soil saprophages, as well as bioturbation, which is realised primarily by earthworms. In the absence of macrofauna, especially earthworms, litter is decomposed by the representatives of saprotrophic meso- and microfauna; however, this leads to intensification of carbon dioxide emission from the soil surface, and only the activity of earthworms reduces these losses (Frouz et al., 2013).

The diversity of soil macrofauna has a significant impact on the biogeochemical cycle of nutrients (Coulis et al., 2015; Filser et al., 2016; Sauvadet et al., 2017) and plant productivity (Van Groenigen et al., 2014). The biodiversity of soil macrofauna directly correlates with the diversity of vegetation (Tresch et al., 2019) and affects the diversity of soil microorganisms, namely bacteria and fungi (Cao et al., 2018).

As a result of the interaction between macrofauna and microbial community, nitrogen cycles are significantly affected by soil invertebrates. Forty percent of all nitrogen absorbed by plants is processed by soil saprophages. Digestive enzymes of the intestines of earthworms activate mineralization processes in soil – ammonium transforms into nitrites and nitrates (Bityutskiy et al., 2007). In addition, the annual death of earthworms in soils alone increases the nitrogen pool by 24 g/m², which is comparable to the annual dose of mineral nitrogen fertilisers (100–200 kg nitrogen per hectare). Earthworm biomass, which contains 65%–75% protein, quickly decomposes in soil, but nitrogen is not washed out as quickly as it is bound by microorganisms (Lee, 1985; Makeshin, 1997). Earthworms decrease emissions of nitrous oxide (N₂O), a gas with a strong greenhouse effect (Drake, Horn, 2006; Nebert et al., 2011).

Earthworms decrease the C/N ratio threefold compared to tree litterfall. This is associated with the direct and indirect

influence of earthworms on the mineralisation and humification of organic matter (Striganova, 1968). There is experimental evidence of a significant decrease in the C/N ratio under the influence of different morpho-ecological groups of earthworms; this decrease is not limited to forest soils. For epi-endogeic earthworms, this fact was established in vermicompost (Talashilkar et al., 1999); for endogeic earthworms, this fact was established in agricultural fields (Sandor, Schrader 2007; McDaniel et al., 2013). According to our published data (Geraskina, 2020), the influence of different morpho-ecological groups of earthworms on the nitrogen content and the C/N ratio is multidirectional in the horizons of their activity – the nitrogen content increases whereas the C/N ratio decreases.

The role of earthworms as ecosystem engineers is also significant regarding regulation of the water regime. During horizontal and vertical migrations, they form up to 50% of the pore space of the soil (biopores). This area affects water migration and gas diffusion in the soil and outside of it (Lee, Foster, 1991; Lubbers et al., 2011) and prevents surface runoff and water erosion of soil by increasing the vertical transport of atmospheric waters (Schneider et al., 2018).

Influence of fungi on ecosystem processes and forest functions

Fungi are one of the main components of forest ecosystems and contribute significantly to the overall biodiversity. Most of mycobiota are soil dwellers (Carlile et al., 2001). The mycelial structure helps them search for new nutrient substrates in this heterogeneous environment with maximum speed and efficiency (Carlile et al., 2001; Gadd, 2007; Chernov, Marfenina, 2010). This adaptation has allowed fungi to become one of the main components of microbial cenoses in the soil; they perform various ecological functions (decomposition of almost any organic

compounds, formation of symbiosis with plants, participation in soil formation, etc.).

According to some estimates, the total number of fungal species can reach several million, but no more than 10% of these species have been described and documented (Hawksworth, Lücking, 2017). Despite the fact that most fungal species are unknown, the main functions that they perform in biocenoses have been identified. Fungi play an important role in the life of forest ecosystems: they are the main agents for processing organic matter in the soil and forest litter, forming ectomycorrhiza on tree roots, phytoparasites, or antagonists of parasites (Frąc et al., 2018). Mycorrhizal mycobiota support almost all vascular plants (including trees), saprotrophic fungi decompose organic residues (including wood lignin), and entomopathogenic fungi control the number of invertebrates. An one third of all microbial biomass is represented by ectomycorrhizal fungi in forest soils; together with colonised roots, they secrete half of all soluble soil organic matter (Högberg, Högberg, 2002).

Soil fungi are divided into three functional groups: biological and ecosystem regulators and species involved in the decomposition of organic matter and transformation of compounds (Swift, 2005; Gardi, Jeffery, 2009). Fungi regulate not only diseases and the number of parasites, but also the growth of other organisms (Bagyaraj, Ashwin, 2017). Thus, mycorrhizal fungi have a positive effect on plant growth, activating the absorption of mineral nutrients. In addition, fungi are involved in the nitrogen cycle (Kurakov, 2003) and production of hormones; they play an important role in the stabilisation of organic matter and the decomposition of plant debris (Jayne, Quigley, 2014; Baum et al., 2015; El-Komy et al., 2015; Treseder, Lennon, 2015). The functioning of soil fungi depends on the diversity and composition of plant communities. On the other hand, fungi affect

plant growth through mechanisms such as mutualism and parasitism, and through the effect on the cycles of mineral nutrients and their bioavailability (Wardle, 2002; Wagg et al., 2014; Hannula et al., 2017).

The prokaryotic (bacteria and archaea) soil component has been studied much more thoroughly than the fungal component, despite the fact that mycobiota account for most (up to 98%) of the entire microbial biomass (Ananyeva et al., 2010; Polyanskaya et al., 2020). However, unlike bacteria, whose taxonomic position (especially in the case of high taxonomic ranks) cannot always be associated with specific ecological functions, relationships between the taxonomic position of fungi and their functions in forest ecosystems can be established. Specifically, representatives of the taxon Glomeromycetes are the main generators of endomycorrhiza of herbaceous plants. Most representatives of the order Boletales form ectomycorrhiza with trees. The large genera *Penicillium*, *Aspergillus*, and *Trichoderma* are saprotrophs that decompose cellulose and starch. The genera *Armillaria*, *Phellinus*, *Cronartium*, and *Laetiporus* are tree parasites. Members of order Polyporales are wood destructors of living and dead trees. (Frąc et al., 2018). The overall diversity (alpha diversity) of fungi is related to the state of ecosystems and responds to soil degradation and deforestation, among other factors (Chaer et al., 2009).

In recent decades, the biodiversity of soil fungi has been actively determined using molecular biological methods, primarily metabarcoding and metagenomics (Semenov, 2019). High-throughput sequencing of fungal phylogenetic markers in DNA preparations extracted from soil allows a much more complete variety of fungi to be covered than microscopic and fungal cultivation methods. Constantly updated taxonomic databases (such as SILVA) allow for the most complete

assessment of the taxonomic structure of the fungal community based on genetic information.

Functionally, fungi are closely related to earthworms. The influence of earthworms on fungi is multifaceted: trophic – selective consumption of fungi; phoric – the transfer of spores and mycelium fragments in horizontal and vertical directions along the soil profile; metabolic – the effect of biologically active compounds of the earthworm digestive tract on the viability of fungi (there are known effects of both inhibition and activation of the development of fungal spores); and metabiotic – the creation of fundamentally new ecological niches for fungi during the burrowing activity of large saprophages (creation of pores, cavities, changes in the chemistry of the environment, isolation of coprolites, etc.). At the same time, the pool of fungi determines the activity of earthworms due to the trophic value of fungal biomass and the fungal production of biologically active substances (Byzov, 2005; Spurgeon et al., 2013; Kurakov et al., 2016; Cao et al., 2018).

Overall, fungi in forest ecosystems have a direct effect on climate-regulating functions through the conversion of carbon compounds, including mineralisation of lignin, cellulose, and soil organic matter, and an indirect effect through the redistribution of nutrients and regulation of the activity of plants and invertebrates. Thus, the assessment of not only the taxonomic, but also the functional diversity of biota of different trophic levels and different trophic groups is one of the most important scientific problems. Indeed, if it is not solved, it will be impossible to assess the impact of biodiversity on the climate-regulating functions of forests and to develop approaches to adapting forests to climate change.

Structural biodiversity

One of the most important aspects of forest diversity is structural diversity. The structural diversity of forest ecosystems reflects the

diversity of habitats and, accordingly, the general level or the potential of forest biodiversity and the prospective for the implementation of ecosystem climate-regulating functions. Researchers have used different approaches and criteria to assess the structural diversity of forests: deadwood decomposition stages, the ratio between dead and living trees, the size (diameter) of trees, the proportion of old trees, and the richness of tree species in the dominant canopy and undergrowth, among others (Storch et al., 2018).

In our studies, we have interpreted structural diversity as a mosaic of forest cover. The basic concepts of the mosaic nature of forest biogeocenoses and their individual components widely known in Russia and abroad include the concept of elementary soil areals by V.M. Friedland (1986), the concept of forest parcella by N.V. Dylis (1969), the concept of coenobiotic microgrouping by L.G. Ramensky (1938), and the concept of tessera by H. Jenny (1958) and by L.O. Karpachevsky (1977).

According to V.M. Friedland (1986), sporadically spotted homogeneous elementary soil areals are widespread in the forest. The background of these soils is complicated by spots of limiting structural elements, which are not considered elementary soil-geographical objects. Because they owe their origin to biota, they are formed by recent disturbances, including windfalls; they exist due to woody plants. The entire complex of limiting structural elements and homogeneous background represents the forest soil cover in successional development, whereas homogeneous soil background reflects only a part of the soil forest cover.

N.V. Dylis (1969) substantiated the identification of the level of a parcella in forests as an intrabiogeocenotic unit. The concept of a parcella was further developed, including in the works of CEPF RAS employees (East European ..., 1994, 2004; Smirnova, 1998). In forests with a pronounced

mosaic structure, parcellas are represented by gaps, which are formed at the site of the fall of one or several trees and are at different overgrowth stages. The elements of such a mosaic differ based on environmental conditions, including light, temperature, precipitation, and element cycles (Muscolo et al., 2014). At present, large areas are dominated by forests in which this mosaic is not expressed; the belowcrown and between-crown spaces are often distinguished with only some elements of microsites created by tree falls.

There is an entire class of forest gap mosaic models. Their development presumably began in 1969, and the JABOWA model is considered to be the parent. These models are popular among ecologists because they allow assessing and predicting all stages of the development of woody plants; the dynamics of their productivity due to changes in the light availability, soil temperature, precipitation; and the impact of global changes on forests (Bugmann, 2001; Chumachenko, Smirnova, 2009; Zhu et al., 2014), including the carbon balance (Chambers et al., 2013). A number of modern experimental studies have focused on assessing the effect of gap sizes in forests on soil biota, which regulates nitrogen and carbon cycles. Researchers have concluded that an optimal microclimate and substrate formed at the border of the gaps increases the microorganism biomass and activity. The biomass of microbes and fungi that form endomycorrhiza and determine soil respiration negatively correlate with gap sizes (Scharenbroch, Bockheim, 2007; Schliemann, Bockheim, 2014).

In gaps of Norwegian old-growth spruce forests, soil waters were characterised by higher C/N ratios compared to soil waters under the forest canopy. Large wood residues formed as a result of tree felling serve as a source of dissolved organic matter (Nygaard et al., 2018). It is estimated that 20%–40% of

organisms in forest ecosystems live off the decaying wood of living, weakened, or dead trees for their life cycle (Bauhus et al., 2018). It is recognised that deadwood not only serves as a habitat, but also plays an important role in the carbon and hydrological cycles, in the cycles of mineral nutrients, and is a key structural component influencing ecosystem processes. Deadwood at different decomposition stages serves as an important habitat for many species and groups of soil fauna. The underestimation of deadwood can lead to incorrect estimates of not only the taxonomic, but also the functional diversity of soil fauna (including earthworms), insects, and other invertebrates, especially in boreal forests (Goncharov, 2014; Geraskina, 2016; Ashwood et al., 2019; Jacobsen et al., 2020).

Parcellas are not homogeneous: there are mosaics of different types of trees at different ages. The soil and plant components of the gap parcella are also mosaic – it is possible to identify the trunks of previously felled trees overgrown with mosses and shrubs, spots of mounds and depressions, green moss, lichen, small grasses, tall grasses, fern components of biogeocenoses, and undergrowth of woody plants, all of which have a specific effect on soils (Lugovaya et al., 2013; Geraskina et al., 2020).

A tessera is another unit of cover. H. Jenny (1958) identified a tessera as a landscape element, including soil, vegetation, and soil biota. For a tessera, he suggested taking a unit of those area and shape, which are convenient for certain purposes. L.O. Karpachevsky (1977) regarded a tessera as a soil component of a parcella. Within a tessera, he distinguished microzones: near-trunk, middle, and edges of the crown. L.G. Ramenskiy (1938) identified coenobiotic microgroups related to the plant component resulting from the specific effect of certain plants on environmental conditions. These plants, 'having settled and occupied a certain area, so strongly influence the regimes

of the air and soil environment that they largely displace some other species and get along with the species for whom these newly created conditions are favorable' (Ramenskiy, 1971).

Thus, for V.M. Friedland, an elementary soil areal reflects only a part of the soil forest cover. For L.G. Ramenskiy, a microgroup refers only to the plant component, and for L.O. Karpachevsky, a tessera includes only the soil component. For N.V. Dylis, a parcella includes atmosphere, vegetation, soil, and soil biota. However, L.O. Karpachevsky (1977) was the first to prove that the soil component of a parcella can be divided into microzones. Therefore, we can conclude that the parcella is not an elementary unit of biogeocenosis. In addition, in modern forests, the parcel structure is far from always expressed, because most of the forests have been significantly transformed. The tessera defined by H. Jenny includes all elements of the biogeocenosis, but it has artificial boundaries.

In our opinion, an elementary unit of the forest biogeocenotic cover, as an elementary provider of ecosystem functions, must meet three requirements (Orlova, 2013). Specifically, this unit must: (i) be indivisible, the smallest, and basic; (ii) include all interrelated components of the biogeocenosis (atmosphere, soil, vegetation, soil biota); and (iii) form a base level in the hierarchy of spatial units of the forest biogeocenotic cover. To study the vegetation–soil relationships that regulate ecosystem functions, it was proposed to consider the elementary biogeoaerial as an elementary unit of the biogeocenotic cover, at the level of which these relationships are formed (Orlova, 2013). Areas, forms, boundaries, as well as the name of the elementary biogeoaerial are determined by the dominant plant species – that is, by plant component – which corresponds to the concept of coenobiotic microgrouping by L.G. Ramenskiy. We consider the elementary biogeoaerial to be a structural and functional

unit of the forest biogeocenotic cover. It is an elementary provider of ecosystem functions, including the climate-regulating functions of forests. To assess the structural diversity of forests in each study object, it is advisable to single out the dominant elements of the forest cover mosaic in the canopy (in the belowcrown space of different tree species) and in between-crown space and/or gaps, including different felling stages. The hierarchy of spatial units of the forest biogeocenotic cover, in our opinion, can represent the following series: elementary biogeocoenoses (EBGA) – biogeocenosis – geochemically coupled biogeocenoses – drainage basins (see also Orlova, 2013).

Thus, assessing the impact of structural diversity on the climate-regulating functions of forests is a scientific problem of great practical importance. Analysis of the current state of the problem indicates that it is necessary to assess more thoroughly the impact of the structural diversity of forest ecosystems on the climate-regulating functions.

RELATIONSHIPS BETWEEN CLIMATE-REGULATING FUNCTIONS: ASSESSMENT BY ENVIRONMENTAL MODEL COMPLEXES

It is important to assess not only the climate-regulating functions of forests with different levels of biodiversity, but also the relationships between these functions. The modern computer simulation methods allow assessing individual ecosystem functions. These models differ at the spatial level: local individual-based models (Seidl et al., 2012), landscape models (Scheller et al., 2007), and regional and national models (Kurz et al., 2009; Beringer et al., 2011; Kuz'mina et al., 2017). However, these tools focus on individual ecosystem functions of forests (Rämö, Tahvonen, 2017; Pukkala, 2018), and only the approach developed in the last decade is based on the integration of models within decision support systems (Wikström et al.,

2011; Borges et al., 2014) and allows their comprehensive assessment. Modern experimental studies often involve simulation models of forest ecosystems to compare different forest management strategies (Shanin et al., 2011; Söderbergh, Ledermann, 2003). Such models are usually developed as the basis for decision support systems in the forestry sector. These models are multifunctional and include empirical stand growth models, individual-based models, biogeochemical models, matrix models of carbon balance, dynamic global vegetation models, and landscape and regional models.

Trade-offs and synergies between the climate-regulating functions of different types of Russian forests can be forecast using the existing Russian models applicable to forest ecosystems: FORRUS-S, EFIMOD-ROMUL-SCLISS, ILHM, ILLM, and COSMO.

The *FORRUS-S simulation model* (Chumachenko et al., 2003) belongs to the class of ecological and physiological models simulating the processes of establishment, growth, and death of trees. It is designed to predict the dynamics of wood and non-wood resources, the recreational potential of forests, and biodiversity dynamics.

The *EFIMOD Forest Ecosystem Model System* (Komarov et al., 2003) is an individual-based system that includes the ROMUL soil organic matter dynamics model (Chertov et al., 2001) and the SCLISS statistical soil climate generator (Bukhovets, Komarov, 2002), and it is associated with the BioCalc phytodiversity assessment model (Khanina et al., 2007). The model system is individual-based; there are two aspects of interaction between neighboring trees: shading and competition for available soil nitrogen. The system consists of a number of blocks: a model of the growth of biomass for an individual tree, a spatial model of the stand with a detailed imitation of competition between trees, and a ROMUL soil organic matter dynamics model (Komarov et

al., 2017; Chertov et al., 2017a, 2017b), which describes the dynamics of mineralisation and humification of organic matter depending on its chemical composition and hydrothermal conditions in the soil. A new submodel for calculating the production of tree biomass (Shanin et al., 2019) makes it possible to take into account the influence of a complex of factors associated with climate change (changes in air temperature, soil moisture, concentration of carbon dioxide in the air). In addition, new submodels of competition for light (Shanin et al., 2020) and soil nitrogen in forms accessible to plants (Shanin et al., 2015) make it possible to more accurately analyse the spatial structure of the stand. The model also provides tools that allow simulating various kinds of disturbances (fires, selective and clear cuttings, etc.).

The *Hydrological model for the formation of runoff from the catchment or ILHM (Institute of Limnology Hydrological Model)* (Kondrat'ev, Shmakova, 2005; Kondrat'ev, 2007) is intended to calculate hydrographs of meltwater and rainwater runoff from a catchment area, as well as the water level in a reservoir.

The *Model for the formation of biogenic load on water bodies or ILLM (Institute of Limnology Load Model)* (Kondrat'ev, 2007) was designed to solve problems related to the quantitative assessment of runoff and removal of nutrients from the forest catchment under influence of different forest management regimes and climate change.

The *Climatic version of the COSMO model* is intended to assess the impact of changes in forest cover in the central regions of the European territory of Russia on regional meteorological conditions (Kuz'mina et al., 2017).

Trade-offs and synergies between the functions/services of an ecosystem can be assessed using the integrated platforms presented above and other mathematical

models. The existing approaches for simulation modelling will make it possible to assess the relationships (synergy and/or trade-offs) between the climate-regulating functions of forests and to predict the dynamics of these functions in the natural development of forests characterised by different levels of biodiversity, and with the combined impact of climate change, fires, and management regimes on forests.

There are two main approaches to measure multifunctionality. The first approach implies averaging or summing functions: the sum of the standardised values of each measured function is used (Mouillot et al., 2011; Maestre et al., 2012). The second approach is threshold; it takes into account the number of functions that crossed a threshold or a range of thresholds, usually expressed as a percentage of the highest level of functions observed in a particular study (Gamfeldt et al., 2008; Byrnes et al., 2014). This approach can be improved by using weights that determine the importance of a particular function (Lukina et al., 2020). Trade-offs and synergies between functions can be analysed based on the magnitude and sign of the coefficient of the correlation between their normalised values.

APPROACHES TO CONSERVATION AND RESTORATION OF BIODIVERSITY

Global climate changes will continue. They are difficult to predict or even unpredictable; therefore, mitigation of the effects of climate change and adaptation to them becomes the most important strategic goal of states. An approach to preserve the remaining intact or almost intact forests with their existing levels of biodiversity and to restore biodiversity (rewilding) in those disturbed forests, where possible, will contribute to the adaptation of forests to climate change and mitigation of its impact, because owing to biodiversity, these ecosystems are self-regulating.

Due to long-term nature management and past anthropogenic impacts, self-regulated

ecosystems cannot always be restored, especially in cases of endangered species, namely large herbivores (Smirnova, Toropova, 2017; Cromsigt et al., 2018; Vasile et al., 2018; Smirnova, Geraskina, 2019; Lord et al., 2020) or soil fauna (Bulavintsev, 1979; Butt, 2008; Moradi et al., 2018; Geraskina, 2019). In these cases, another approach is acceptable – human intervention. Obviously, long-term land use that disrupted natural processes and ecosystem dynamics on Earth, which was determined by biodiversity, has led to the formation of anthropogenic landscapes that can function sustainably only with human participation. At the same time, moderate anthropogenic disturbances have resulted in landscape mosaics of species habitats; periodic disturbances are crucial to preserve these landscape mosaics (Feurdean et al., 2018). Therefore, we share a concept that takes into account both approaches: restoration of biodiversity, where possible, and human intervention, where necessary (Van Meerbeek et al., 2019).

The scientific literature also discusses a binary approach to biodiversity conservation and the use of forest ecosystem services: segregation or integration (Krauss, Krum, 2013; Abruscato et al., 2020). To develop strategies and measures for the conservation and restoration of forest biodiversity as a mechanism for forest climate-regulating functions, the key issue is the choice of management approaches that allow preserving biodiversity and providing all forest ecosystem services, including supportive (soil formation, conservation and maintenance of biota habitats, etc.), regulatory (regulation of climate, hydrological regime, etc.), productive (provide wood, fibres, non-wood products), and cultural (educational and scientific purposes, recreation, health rehabilitation, aesthetic pleasure). Although the Russian forests are divided according to their intended purposes (production, protection, reserve), not

only in reserve, but in all protective (not only protected areas) and production forests, forests of high conservation value should be preserved and allocated (Jennings, 2005; Yanitskaya, 2008). In our opinion, the most acceptable tactic is the joint use of elements of both approaches in the same territory/in the same zone. However, such planning at different spatial levels requires special studies aimed at justifying the approaches, the application of which will allow conserving and restoring biodiversity at different levels for adaptation to climate change.

The genetic diversity of plants plays the most important role in the preservation and restoration of forests and their adaptation to climate change. The European Forest Genetic Resources Programme (EUFORGEN) was launched in 1994 based on a resolution adopted in 1990 at the first Ministerial Conference on the protection of forests in Europe (<http://www.euforgen.org>). This programme promotes the conservation and sustainable use of forest genetic resources in Europe as an integral part of sustainable forest management and implementation of relevant provisions of the Convention on Biological Diversity. The forests of Russia are characterised by a poor species composition of forest stands but significant intraspecific variability, which is formed under conditions of ecologically heterogeneous vast areas of forest-forming species (CPSR, 2017). A unique feature of the Russian forest fund is the preservation of vast areas of boreal forests with a native or intact population genetic structure. For the study, conservation, and rational use of forest genetic resources in Russia, it is necessary to implement the programme on forest genetic resources developed by Russian geneticists (CPSR, 2017; Concept ..., 2020). This endeavour requires, along with other tasks, the study of natural mechanisms for maintaining the optimal (adequate to forest growing conditions) genotypic composition of

populations and the influence of various natural and anthropogenic factors on it. It is also necessary to conduct experimental, analytical, and simulation studies to substantiate the maximum permissible volumes and rules for the placement of plantation forests, which guarantee the preservation of the population structure and genetic potential of forest-forming species. We also need to systematise Russian and international achievements in the field of forest genetics, genomics, breeding, and biotechnology to modernise and integrate programmes for forest varietal seed production and plantation forestry. Finally, methods for clonal micropropagation of valuable tree species should be developed.

Due to overhunting and poaching, many animals have been extinguished or have become extremely rare in forests. In this regard, developed and implemented programmes are aimed not only at their protection, but also at their reintroduction. A successful example is the restoration of beaver populations. A nature conservation ideology is based on the restoration of highly productive ecosystems characteristic of this region by the gradual return of preserved large animals to their original ranges, where they were previously completely exterminated by humans. Rewilding is a new strategy for conserving natural resources; it has gained immense popularity in the modern world. It is aimed at restoring natural processes with minimal human intervention (Donlan et al., 2006; Zimov et al., 2012; Van Klink, 2020). The restoration of European bison populations in forest ecosystems is one of the most striking modern examples of reintroduction, and bison populations are now being restored in several countries (Cromsigt et al., 2018; Vasile et al., 2018; Lord et al., 2020). There are several examples of the recovery of populations of large animals in Russia. The Russian Ministry of Natural Resources is actively working on

the resettlement of bison. The participants of this programme specifically include protected natural areas such as Bryansky Les (Bryansk region) and Kaluzhskiye Zaseki (Kaluga region), as well as the national parks Orlovskoe Polesie (Oryol region), Smolenskoe Poozerie (Smolensk region), and Ugra (Kaluga region). The total number of bisons in these territories at the end of 2018 was more than 650. The goal of the Pleistocene Park project in the Republic of Sakha (Yakutia) is to create a highly productive ecosystem imitating the mammoth steppes that dominated Eurasia in the late Pleistocene (pleistocenepark.ru). The park is inhabited by bison, Yakut horses, moose, musk oxen, reindeer, and other ungulates. Experimentation has led to the dominance of grasses and cereals in many plots and an increase in the soil carbon content (Zimov, 2005).

However, modern forest ecosystems are highly fragmented and disturbed by long-term (since the beginning of the Holocene) anthropogenic impact (Smirnova et al., 2020) as a result of the loss of biota groups that formed various functional blocks that regulated, among other things, the density of ecosystem engineers. Therefore, these ecosystems are subject to opposite effects – biodiversity decreases rather than increases and habitat degrades. Overgrazing of reintroduced reindeer has resulted in soil depletion and loss of land cover biodiversity in Norway (Hansen et al., 2007). Incompleteness of the coprophage complex and grazing of reintroduced bison do not increase soil fertility; indeed, bison excrement accumulates and remains for a long time at the initial decomposition stages in the Orlovskoye Polesie National Park (Geraskina et al., 2018). An increase in the density of beavers in North America has led to large-scale environment-transforming effects and a decrease in the diversity of grasses and trees. Therefore, they are called ecosystem pests (Hacker, Coblenz,

1993). The literature indicates that even the unintentional settling of ecosystem engineers such as earthworms (European species) in the forests of North America, where they form highly dense populations, decreases the biological diversity and density of other groups of meso- and microfauna. According to the authors, this is due to habitat homogenisation (Migge-Kleian, 2006; Ferlian et al., 2018) and a decrease in the biodiversity of the vegetation cover. The consumption of forest litter by worms is a serious obstacle to the development of undergrowth of tree species (Hale et al., 2006; Frelich et al., 2019). The above examples of the negative impact of ecosystem engineers on biological diversity may indicate a strong disturbance of forest ecosystems, the absence of important functional biota groups that regulate the density and behaviour of animals at different trophic levels, as well as a low level of structural diversity of ecosystems, that is, a weakly expressed mosaic of habitats for different species and groups of animals in managed forests.

Restoration of biological, including structural, diversity in modern forests is possible due to the inclusion in forestry practice of some measures aimed at enhancing the heterogeneity of the forest: staggered and hollow felling combined with planting multi-species forest trees with multi-chess placement of planting material and thinning. Sanitary felling with the preservation of undergrowth of coniferous and broad-leaf tree species can be conducted in the drying-out foci of forest stands (Methodical ..., 1989; Korotkov, 2016, 2017; Zagidullina, Drobyshhev, 2017). Gaps in the forest canopy can be created by ringing the bark of trees (injection of arboricides is also possible), causing them to dry out, as well as by artificial fallouts, when the formation of gaps is combined with the formation of microsites created by tree falls, which enhance the heterogeneity of the soil cover (East European ..., 1994). It is also important to

preserve – and maintain through haymaking – in-forest clearings for moderate grazing of livestock or wild animals. These actions markedly increase biodiversity and also create favourable conditions for the development of light-demanding species of trees and shrubs at the forest edges. Therefore, the breeding and cultivation of forest trees should be aimed at the formation of a group-glade type of plantations (groups of trees alternate with glades and blanks) (Korotkov, 2016, 2017).

A combination of forestry practices should aim to restore the species and structural diversity, as well as the diversity of habitats. The latter endeavour, now called retention forestry, includes the preservation of some deadwood and stumps to ensure the existence of fungi, different groups of invertebrates, and hollow-nesting birds, among others, and making gaps for light-demanding flora, pollinating insects, birds, and mammals. It is considered to be the most promising forestry methodology (Storch et al., 2019; Augustynczyk et al., 2020; Gustafsson et al., 2020).

CONCLUSION: SCIENTIFIC ISSUES AND KNOWLEDGE GAPS

Assessment of the combined effect of diverse biota of different trophic levels on the climate-regulating functions of forests of different types, taking into account their structural diversity, is a fundamental scientific problem of great practical importance. Such assessments are essential for the conservation and restoration of biodiversity, which underpins the mechanisms of adaptation of forests and society to climate change.

The suitable object for assessing the impact of biodiversity on climate-regulating functions is intact old-growth forests, in which the natural mechanisms of the joint functioning of many species are still preserved.

To assess the impact of biodiversity on the climate-regulating functions of forests, it is necessary to undertake the following tasks:

- **Design and develop functional classifications of biota of different trophic levels and to assess their functional diversity in different types of forest biogeocenoses, landscapes (geochemically coupled biogeocenoses), and whole catchment.**

Because the level of functional biodiversity determines the completeness of the implementation of climate-regulating ecosystem functions, the functional classification of biota belonging to different trophic levels is crucial. Thus, the classification of plants by the quality of litter makes it possible to assess the influence of plants on such climate-regulating functions as the regulation of the cycles of carbon, nitrogen, and other elements of mineral nutrition, and the formation of soil fertility. At the same time, as our studies (Lukina et al., 2018) have shown, to assess the influence of woody plants on the climate-regulating functions of forests, including their water regime formation function, we need to take into account characteristics of woody plants such as density and the length of crowns. These properties determine the amount of precipitation penetrating under the canopy and the volume of soil water. To assess the impact of plants on ecosystem functions, it is necessary to develop classifications using the corresponding specific properties/traits of plants.

The question of the functional classification of vertebrates remains open. However, it needs to be addressed to clarify the influence of different functional groups on the functioning of forests and, therefore, on the possibility of adapting forest ecosystems to climate change.

We still lack direct field measurements and open experimental data on invertebrate soil saprophages in forests. It is necessary to develop standard protocols for the study of soil biodiversity in structurally diverse ecosystems such as forest ecosystems, taking into account the maximum set of mosaic elements that make up the forest cover, including deadwood,

which, as a rule, is not taken into account when conducting field research. We also lack quantitative estimates of the contribution of different elements of the spatial mosaic to the diversity, density, and total saprophage biomass. The issues of the functional affiliation and even the taxonomic status of invertebrates remain relevant. They need to be addressed because many forms differ in the horizons of trophic and locomotor activity in the soil. Most of the forest fungal species remain unknown. Therefore, these studies need to be intensified. In recent decades, the biodiversity of soil fungi has been actively determined using molecular biological methods, primarily metabarcoding and metagenomics. To study trophic relations in soil, it is important to use both molecular genetic methods and methods of stable isotopes.

- **Comparatively assess the influence of species identity and the combined influence of the diversity of biota of different trophic levels and groups on the completeness of the implementation of climatic regulation functions at different spatial levels in different time scales**

To solve this problem at the level of the biogeocenosis type, it is advisable to conduct studies in monodominant and polydominant forests. These forests represent different succession stages, but they function in similar climatic conditions and are formed at similar positions of the landscape and on parent rocks of similar mechanical and chemical composition. The completeness of the implementation of functions can be assessed by comparing with forests at the most advanced succession stages, that is, old-growth intact forests.

Assessment of the contribution of individual forest types to the functioning of geochemically coupled landscapes and whole catchments using remote sensing methods will make it possible to assess the impact of

biodiversity on the climate-regulating functions of forests at different spatial levels. Mapping the climate-regulating functions of forests is a critical scientific task of great value both for investigating the links between biodiversity and these functions, and for designing decision support systems. Development and application of simulation mathematical modelling methods and designing model platforms will make it possible to assess the relationships between functions and to predict the dynamics of climate-regulating functions.

- **Assess the impact of the structural diversity of forests on climate regulation functions**

Highly mosaic and structurally complex forests are characterised by a higher level of resilience to stresses, including climate change. However, climate-regulating functions of forests, as a rule, are assessed without taking into account their structural diversity. Therefore, the task of assessing the links between the structural diversity of forests and the completeness of their performance of climate-regulating functions is necessary.

- **Develop mathematical model platforms to assess and to predict the relationships between ecosystem functions and services**

To simulate the ecosystem functions and services, a large number of computer models have been developed. They differ in structure, the degree of detail, spatial and temporal discreteness, etc. Professional attitudes to the structure and patterns of the functioning of forest ecosystems and improvement of computer and programming technologies and mathematical apparatuses have created the prerequisites for the widespread use of ensembles of ecological models for a comprehensive assessment of a wide range of ecosystem services and the relationships between them. Accordingly, it is necessary to develop methodological approaches as well as

software and hardware solutions to design a platform for integrating a system of models (Grabarnik et al., 2020).

- **Develop concepts and approaches to forest management, taking into account the conservation and restoration of biodiversity and ecosystem functions of forests**

Developing approaches to forest management at different spatial levels remains a crucial scientific problem taking into account the conservation and restoration of biodiversity and the provision of all ecosystem services. From our point of view, binary approaches (segregation or integration) are conditional. The most promising are the approaches that take into account the combination of segregation and integration approaches, conservation, and creation of self-regulating forest ecosystems by restoring biodiversity.

To conserve forest genetic resources in Russia, it is necessary to implement the programme on forest genetic resources.

Long-lasting transformation of forests by humans contribute to the dominance of some species and the elimination of others. Human activities associated with land-use change and the destruction of predators can be a direct or indirect cause of an imbalance between populations of different species, a phenomenon that leads to overgrazing of herbivores in forests, outbreaks of mass reproduction of insects, or mass drying of woody plants as a result of fungal diseases (i.e., when creating monodominant forest plantations). We need to develop mechanisms for regulating the size of populations of different species to create managed forests that can adapt to climate change, that is, capable of self-regulation.

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