Highly Productive Boreal Ecosystem Chernevaya Taiga - Unique Rainforest in Siberia

Evgeny Abakumov¹, Sergey Loiko², Nikolay Lashchinsky³, Georgy Istigechev², Anastasia Kulemzina⁴, Alexey Smirnov⁵, Mikhail Rayko⁶, Alla Lapidus*

¹ Department of Applied Ecology, Saint Petersburg State University, University Embankment, 7/9, 199034 St. Petersburg, Russia;
² BIO-GEO-CLIM Laboratory, Tomsk State University, Lenina St. 36, 634050 Tomsk, Russia;
³ Central Siberian Botanical Garden, Zolotodolinskaya St., 101, 630090 Novosibirsk, Russia;
⁴ Institute of Molecular and Cellular Biology SB RAS, Acad. Lavrentiev Ave. 8/2, 630090 Novosibirsk, Russia;
⁵ Department of Invertebrate Zoology, Saint Petersburg State University, University Embankment, 7/9, 199034 St. Petersburg, Russia;
⁶ Center for Algorithmic Biotechnology, Saint Petersburg State University, 6 Linia V.O., 11/21d, 199004 St. Petersburg, Russia;
* Correspondence: a.lapidus@spbu.ru (A.L.)

Abstract: Boreal forests are one of the largest stores of carbon on Earth, and two-thirds of them are located in Siberia. Despite the fact that these forests have a significant influence on the global climate, they continue to remain understudied. Chernevaya taiga is a unique example of a highly productive Siberian boreal ecosystem. This type of forest is characterized by a series of unique ecological traits, the most notable of which are the gigantism of the perennial herbaceous plants and bushes, complete lack of moss cover on soil surface, and the type of soil it grows on, notable for its particularly high rate of decomposition of vegetative remains and low humic acid content. Abundant rainfall actively washes out nutrients from the top layers of the soil, but its fertility level remains very high. In fact, based on the existing data, it is twice as high as that of fertilized agricultural lands. In some ways the conditions within this type of forest closely resemble those observed in tropical rainforests. Microbiota associated with soil and plants represent an integral part of an interconnected system and contribute significantly to productive processes in soils. Its impacts on the environment require further study, since it could lead to discoveries that will help improve soil fertility without harming the natural environment. This manuscript demonstrates for the first time the need of application of systematic analysis of multiple factors for assessing unique properties of Chernevaya taiga in Siberia - potential dormant breadbasket of the Asia-Pacific region and worldwide.

Keywords: taiga; ecosystems; plant’s gigantism; soil processes; spatial analysis; microbiota

1. Introduction

Intact natural ecosystems are islands of wildlife, all components of which interact with each other to form a specific network. The life of such systems is determined by both biotic and abiotic factors. The environment, the climate and type of soils determine what species of animals, plants and microorganisms can live in various terrestrial ecosystems.

One of the most unique ecosystems of the southern Siberian mountains is the Chernevaya taiga (Figure 1) which can be described as a boreal formation, limited in its spread by hyper humid sectors of the Altai-Sayan mountainous region at elevations ranging from 400 to 900 m above the sea level where the soil never freezes due to a lot of snow in winter time.
Figure 1. The area of Chernevaya taiga south of Western Siberia and field research sites.

Chernevaya taiga is listed in the Global 200 project, whose goal is “to identify a set of the Earth’s terrestrial, freshwater, and marine ecoregions that harbor exceptional biodiversity and are representative of its ecosystems” [1]. It is characterized by a series of unique ecological traits, the most notable of which is the gigantism of the perennial herbaceous plants and bushes with the former reaching up to 4.5 m in height and the latter growing as tall as 18 m in height and as thick as 30 cm in diameter. The herbaceous cover of Chernevaya taiga has an average height of 1.5 m in the summer and, in some areas, can, for example, completely obscure a person on horseback.

This is a unique example of an extremely intense biogeochemical turnover on the border of biotic and abiotic interactions. The high intensity of biological processes is attributed to the local hydrothermal and climatic conditions, as well as the functional structure of the communities of living organisms.

It is well known that microbial communities play a major role in virtually every biogeochemical process of the earth, ensuring the carbon and nutrient cycle, which directly affects the functioning and productivity of the ecosystem. Plants are associated with numerous microorganisms that work together as microbiota. Many microbiota participants influence the physiological state and productivity of plants, as well as the level of implementation of the ecological functions of the soil. Many studies have shown that the roots and leaves of plants contain complex and diverse communities of fungi and bacteria that inhabit both the internal tissues and surfaces [5-7]. To date, the composition of the plant microbiome associated with the roots of many plant species, especially the main crops, has been studied using high-throughput sequencing technologies (for example, [5-7]). However, the processes that determine the diversity of the microbiota, as well as their ecological role in natural systems, remain poorly studied.

The growth and development of the plants is supported by the unique soil microbiota, which maintains the homeostasis of the soil ecosystem, performing key functions and actively participating in the carbon cycle. Based on numerous studies the organic portion of soil matter is predominantly microbial in origin, consisting of individual chemicals joined to humic assemblies by non-covalent bonds [8-14].
The world is currently facing a number of significant problems such as global warming, famines, energy shortages, loss of biodiversity and sustainability of ecosystems.

All of these issues bring to the forefront the need for active preservation and protection of soil, since the degradation of this resource would have drastic negative effects on the food supply and ecological security of the nation. Overuse of soil in agriculture leads to an array of negative influence on important soil properties such as degradation of organic matter, increased greenhouse gas emissions, soil depletion and many more. Biogeochemical cycles performed by soil microorganisms undergo significant changes when exposed to agricultural practices.

In comparison, the soils of the Chernevaya taiga represent a unique example of soils characterized by not only an extremely high level of fertility, stemming from the internal biotic and abiotic resources found in the soil instead of being a result of use of agrotechnical methods, but also by the fact that its microbiome has not been affected by the long-term agricultural practices and has been preserved in its natural state.

The uniqueness of the Chernevaya taiga gives grounds to hope that among the biologically active natural compounds synthesized by its microbiota, some will be unique and not produced in other regions of the Earth. The microbiota description of tall Chernevaya taiga plants may contribute to the isolation of the microorganisms that improve plant growth, which seems to be extremely important for the development of effective agricultural practices. Further study of soil ecosystems using metagenomic approaches will have the potential to drastically alter our understanding of diversity and role of microbiomes in soil health.

This article is the first attempt to familiarize the scientific community with the unusual properties of Chernevaya taiga, a totally unique part of Siberia and portion of the boreal belt of our planet.

2. Materials and Methods

2.1 Field study

The field study was conducted during the summer season of 2019 on the territory of Novosibirskaya, Tomskaya and Kemerovskaya oblast. Typical undisturbed ecosystems of Chernevaya taiga were selected as benchmark plots for detailed description and taxonomic diagnostics of soil profiles, typical for this type of taiga. Soil horizons types and soil diagnostics were performed according to rules of World Reference Base of Soil Resources [15]. Totally 15 soil pits were analyzed in terms of soil morphology and 6 of them were selected for further more detailed analyses of soil mezomorphology and key properties. These soil profiles abbreviations are N1, N2, N3 (Novosibirsk region) and T1, T2, T3 (Tomsk region). N1 and T1 sections are represented by soils of Chernevaya taiga (Retisols of various parent loams and clays materials), while N2-N3 and T2-T3 soils are represented by soils of oligotrophic environments (primary soils, formed on sands of aeolian genesis).

2.2 Laboratory methods

Soil samples were air dried and used for mezomorphological analysis. Part of soil samples after air drying were grounded and passed through 2 mm sieve. Carbon and Nitrogen percentages were determined with use of C-H-N-analyzer, pH values were measured in soil-water suspensions (1:2.5 ratio) and soil texture (particle size distribution) was determined with use of classical sedimentation method after pyrophosphate peptisation of microaggregates. All these data were used for clarification of soil taxonomy and diagnostics.

2.3 DNA extraction and sequencing

DNA from the 68 soil samples was extracted according to current EMP DNA Extraction Protocol [16] followed by EMP 16S Illumina amplification protocol [16]. Libraries were sequenced on the Illumina MiSeq instrument in the paired-end mode, with median read count 136,501 per sample.
3. Results

3.1 Vegetation in the ecosystems of Chernevaya taiga

Chernevaya taiga was first mentioned in the travel notes of P. S. Pallas in 1786 [20], and later described by P. N. Krylov [21]. Since then many scientists have shared descriptions of these forests from the different parts of the Altai-Sayan mountain system [22-28] and from the Round-Baikal mountains [29]. All of the authors note the unusual structural features and floristic composition of these forests.

Kuminova [23] and Gudoshnikov [27] provide the following definitions of the main characteristic features:

- The tree canopy is predominantly composed of two main species - Siberian fir (Abies sibirica) and common aspen (Populus tremula).
- The shrub layer is very sparse and composed of only a few specimens of tall shrubs/small trees: Siberian mountain ash (Sorbus sibirica) and birds cherry (Padus avium). The individual representatives of these species in Chernevaya taiga can grow to be up to 18 m tall and 30 cm in diameter at breast height (DBH).
- Under the tree canopy herbaceous perennials provide a lush coverage. The average height of the herbaceous layer is about 150 – 200 cm with tallest specimens reaching up to 4.5 m in height in one growing season. The herbaceous layer could be producing up to 4 tons of absolutely dry aboveground biomass per hectare.
- Tertiary relic plant species contribute to the overall floristic composition of the area.
- The surface of the soil is completely devoid or scarcely covered in moss.
- Presence of numerous spring geophytes appearing immediately after snowmelt.

All of the above-mentioned characteristics of the Chernevaya taiga are connected to the local climatic conditions and the historical development of the landscape.

The geographical spread of the Chernevaya taiga in Siberia is not continuous and is represented by a number of fragmented areas located in West Altai, North-East Altai, Salair range, Kuznetsky Alatau, West Sayan and Chamar-Daban at distances of up to a several hundred kilometers from each other. In all of these areas the habitats of Chernevaya taiga are characterized by being the most humid and warm. On average the annual temperature of the air varies between +1°C and -1°C (30-34F). The growing season lasts for about 90 days. The annual precipitation rate ranges from 800 to 1200 mm (32-47 in.) with the largest amount of precipitation falling in the summer and a very thick snow coverage of up to 2 or 3 m remaining in place for six months at a time in the winter. The lowest temperatures in January can reach - 50°C (-60F), but usually do not last for more than two weeks. The average air temperature in January is about -20°C (-4F). The soil, however, remains unfrozen throughout the whole winter, protected by the thick cover of snow. The temperature at the surface of the soil stays about one degree above 0°C during the entirety of winter [30].

These areas have never been glaciated or flooded since the end of the Tertiary times allowing the biota to evolve gradually in accordance with the climatic changes, but without undergoing any catastrophic extinction events. For many years the most intriguing feature of Chernevaya taiga was the presence of Pliocene nemoral relics – remnants of the Tertiary thermophilous vegetation, which in small areas managed to survive through the cold phases of Pleistocene [31,32]. A number of other structural and functional characteristics are also unusual, but are less well known.

For example, the structure and composition of the forest’s canopy has no other analogies in Siberian vegetation. It consists of a stable combination of Populus tremula and Abies sibirica. Only in Chernevaya taiga can these species be observed coexisting together over the span of many generations. In other forest types aspen is a species present during the earlier successive stages of forest growth, while fir is a typical climax species. Aspen is a species of tree that demands a lot of
light. Fir on the other hand is extremely shade-tolerant. Which brings about the question of how these two species can coexist with each other and be codominant for so many generations?

The structure of an old-growth Chernevaya taiga forest is patchy and includes big openings with tall-herbaceous cover and relatively small groups of trees where each group is predominantly composed of one tree species - fir or aspen (Figure 2). The size of the groups varies from 25 to up to 600 square meters. The openings are usually bigger.

Figure 2. Patchy structure of the Chernevaya taiga tree canopy (September 2019, Salair range).

The age spectra for both species on a whole stand are normal with two maximums on juvenile and middle-aged mature trees [33, 34]. It means that both of them are stable in this community. But the age spectra for the patches are very different. Fir-dominated patches usually contain trees in different stages of development but maximum may be on premature, middle-aged mature, or old-mature stages. In aspen dominated patches almost all the trees are usually at the same stage of development.

Siberian fir in this ecosystem can reproduce only via seeds, an abundance of which is produced on an almost annual basis. The seedlings are very shade-tolerant and can successfully survive under the canopy of tall herbs and that of the forest itself. The density of fir seedlings is about 8 to 10 thousand per hectare and they are randomly spread throughout the whole ecosystem. In winter months the seedlings remain completely hidden under the snow cover and the juicy remnants of tall herbs. Since the soil does not freeze during the whole winter, the remains of the decaying plants provide an excellent substrate for a variety of microorganisms including pathogenic ones. In cold environments fir seedlings are usually not able to resist pathogenic fungi. As a result, most of the seedlings end up dying during the first winter. The only place where they are able to survive is at the edge of the crown of an already mature fir tree. These areas are characterized by lower root competition, and since the herbaceous layer is not as well-developed as it is in the gaps, the layer of dead plants above the fir seedlings in the winter ends up being much less dense. Fir seedlings can also survive under the canopy of mature fir trees, but when they grow there, they end up having a very low-level of vitality and never reach the maturation stage. This means that Siberian fir can colonize gaps only from the edges of mature tree groups. When a new generation appears at the edge of mature tree crowns, it requires at least 40 more years to reach maturation. Only after that a new “step” towards the gap would be possible. It is a quite slow process and since Siberian firs in these habitats live for about 120-150 years, a continuous forest canopy for the whole area ends up being not possible. After the third “step” the initial set of mature trees dies out creating a new gap [35].
Aspen trees also produce an enormous amount of seeds every year, but this does not result in seedlings. The only way aspen trees are able to reproduce is via root sprouting. Aspen trees have wide and shallow root systems, which span much wider than their crown projection. It seems that all the trees in the ecosystem are united into one huge clone with a joint root system capable of living forever and without dying for any internal reasons. Aspen trees usually die because of windbreak and never or rarely because of windfall. Aspen root sprouts arise sporadically throughout the whole growing season. In one season a hectare of aspen forest could produce up to two million sprouts. They arise everywhere except in the spaces protected by the canopy of mature aspen trees. The variation between sprout vitality can be significant. The linear growth rate varies from 10 to 110 cm per year. Only the sprouts with the highest growth rate can survive under the dense canopy of tall herbs. The rest of the sprouts die in a span of a few weeks. If sprouts arise under the canopy of a fir tree, they end up dying to the lack of sunlight. The resulting density of surviving sprouts does not exceed 5 thousand per hectare. Because of the low density in early growth stages, aspen trees end up being very resistant to pathogenic fungi and can reach the tallest heights for this species—up to 28 m in height and 120 cm at DBH. They can survive to be up to 120-140 years old, which is comparable to Siberian fir.

Based on the above description one of the key contributors to stability of the ecosystem of this type of forest is the well-developed dense herbaceous layer, consisting of tall-herbaceous perennials (Figure 3). In the summer it can regulate the density of the aspen sprouts and in the winter in combination with a thick snow cover can eliminate fir seedlings. In this way it can maintain the density and the distribution of trees, as well as the ratio between the two species of trees. The area under the “canopy” of these huge herbs is always dark and constantly moist. Almost all foliage and inflorescence are concentrated in the upper part of this layer—about 100-120 cm above the soil surface. Underneath, on the bare surface of the soil only straight strong stems and a few small plants can be found. All of these features support a patchy forest structure—the main attribute of an old-growth Chernevaya taiga forest. The mosaic of big open areas and groupings of trees results in the creation of numerous ecological niches, which support a high level of biodiversity.

The structure of the individual groupings of trees changes constantly over time, but on the larger scale the age and species composition of the tree layer remains the same from generation to generation. This means that the temporal dynamic of an old-growth Chernevaya taiga forest is realized as the spatial dynamic of big openings and different tree groups.

Natural disturbances play only a minor role in formation of the structure and dynamics of the Chernevaya taiga forest. This type of forest is very resistant to wildfires because it is constantly wet and is almost completely devoid of forest litter, which completely decays over the winter months.
Fires occur only at the edge of the Chernevaya taiga ecological area in the contact zones with other forest types.

Since the foothills of the Altai-Sayan mountain system are the most suitable place for human beings, starting from the 18th century many areas have been logged or heavily disturbed by humans. Only a few spots of about 10-15 thousand hectares each with real old-growth undisturbed Chernevaya taiga forest remain.

Another specific feature of the Chernevaya taiga ecosystem is the tall-herbaceous layer with high productivity. Unlike typical boreal coniferous forests, the herbaceous layer of Chernevaya taiga is completely devoid of “evergreen” ericoid plants. Compared to birch and pine forests of the forest-steppe zone, the role of grasses in the herbaceous layer is minimal. Only a few forest grasses like Milium effusum, Festuca gigantea, and Brachypodium sylvaticum are present in small amounts. The main part of the forbs is comprised of tall-herbaceous perennials of Asian or Siberian distribution (Euphorbia lutescens, Saussurea latifolia, Heracleum dissectum, Alfredia cernua etc.). Among the legumes only Lathyrus gmelinii and a few Vicia species are present. Based on their habitats, all these species belong to forest or subalpine hyphromesophite species. With respect to soil fertility most of the forbs are eutrophic and nitrophilic (Aconitum septentrionale, Urtica dioica, Delphinium elatum etc.). The level of species diversity is about 45-50 species of vascular plants per 400 m².

3.2 Climatic and hydrothermal conditions of the Chernevaya taiga environment

The unique nature of Chernevaya taiga can primarily be attributed to such characteristics of the soil as the geogenic and bioclimatogenic conditions of pedogenesis. The relief of the mountain-ridge interrupts the typical zonal distribution of the soil, which, combined with a variety of cover loams covering the surfaces of the slopes, results in the high water retention capacity of the soils. Specific climatic conditions such as the great amount of precipitation received in this area result in the formation of an eluvial soil regime. As opposed to the soils of the adjacent ecosystems of Western Siberia known to freeze in the winter, the high thickness of the winter snow cover (Figure 4) of Chernevaya taiga isolates the soils thermally leading to a nonfrozen thermal regime. During a large segment of the year the soils also remain both not frozen and free of snow. The soils of Chernevaya taiga are thus Retisols in terms of taxonomy and morphology, but are close to Cambisols in terms of their thermal regime and biological turnover.

Figure 4. Snow cover at the end of March in Chernevaya taiga (Salair range).

Because the soil remains non-frozen throughout the entirety of the winter, there are numerous spring geophytes similar to those found in the European broadleaf forests. In Chernevaya taiga,
however, this group consists of local endemics and subendemics (*Anemonoides altaica, Erythronium sibiricum, Corydalis bracteata, Dentaria sibirica* etc.).

The main reason behind the ability of the ecosystems of the Chernevaya taiga region to adapt to humid climate conditions is the special organization of the soil profile and the fact that topsoil humus horizons have increased filtration capacity and low density (0.5-0.8 g/cm$^3$). The rainfall and melted waters are therefore quickly absorbed into the soil. These factors also decrease the rate of soil erosion and prevent the leaching of forest litter and humus horizons by slope waters. At the same time, the perched groundwater (soil water) helps provide phytocoenosis with water even during the summer. In the zone where the topsoil accumulates water (horizon EL at a depth of 40-50 cm) the redox potential declines to 240-300 mV, at the same time in the upper 0-20 cm its values can reach 540 mV. Due to the low density and high porosity of the upper 20 cm of soil, the roots have practically never had to face a deficit in oxygen [36]. It is also worth highlighting that at a depth of about 50 cm the topsoil remains well hydrated. Soil water overall plays a key role in the functionality of the ecosystems of the Chernevaya taiga, regardless of where it is located.

Albic Retisols of the central parts of the Chernevaya taiga area (Salair Ridge, Mountain Shoria) never freeze in winter. The depth of freezing of Albic Retisols in the marginal parts of the Chernevaya taiga rarely reaches 40-60 cm even in the coldest winters. Soil freezes very slowly and the process tends to start much later, after the snow cover has had a chance to stabilize. The snow thawing process on the other hand is very quick as it is influenced by the surface water [37]. Recent measurements of soil temperatures in the northern part of the Chernevaya taiga area showed that the Albic Retisols have a freezing depth of about 60 cm and that the temperature of the soil never descends lower than -1°C. At the same time, in the Luvic Stagnic Phaeozems characterised by high levels of humidity freezing depth reaches only 30 cm (temperature in the range from 0 to -0.2°C), exhibiting temperatures of above 0°C in the deeper layers of the soil (Figure 5). These thermal characteristics result in active movement of capillary moisture and surface water saturation during the winter months. The melting of the snow increases the moisture content of the soil even further.

![Figure 5. Albic Retisols temperature dynamics.](image)

The temperature in the Luvic Stagnic Phaeozems during the period from July 2019 to April 2020. The measurements were carried out in the Chernevaya taiga near Tomsk. Air temperature was measured at a height of 1.5 m, directly above the measuring logger.

Measurements of the depth of the snow cover in the fir-aspen forest demonstrated that the average depth ranges from 68 cm in the areas devoid of trees to 85 cm under crowns. In a few rare cases, such as under the crowns of large fir trees, the thickness of the snow cover may be reduced to as little as 55 cm. During especially snowy winters (like the winter of 2012-2013) the open glades could be covered in as much as 1.5 - 2.0 meters of snow. The combination of frequently present surface water, the presence of a hydrological barrier and the dense argillic horizon often leads to windthrows [38].

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The formation of Chernevaya taiga ecosystems is defined by climatic conditions and
topographical position. Thus, the low mountain ridges act as barriers for the western air masses and
concentrate humidity on western slopes. Resulting high amount of precipitation, humid climate, high
thickness of the snow cover and specificity of the hydrological regime of the soil in these regions
create a set of unique thermic conditions within the profile of the soil, resulting in either a low frost
depth or no frost at all throughout all of the winter months.

3.3 The parent material characterization

The composition of the soil profile and key properties of the soil greatly depend on the initial
parameters and quality of parent material. Parent material of the soils and ecosystems of Chernevaya
taiga is represented by four groups of parent materials [39-42].

A. classic version of cover carbonate clays and loams (Salair, northern tip of Kuznetskii Alatau);
B. cover carbonate-free clays of Kuznetskii Alatau and Mountain Shoria, Northern Altai;
C. eluvium-deluvium covered with thick loams (not more than half a meter. Kuznetsk Alatau);
D. eluvo-deluviums with thick fine earth layer depth, but under conditions of parent material
enrichment with easy decomposable deposits, enriched by iron, form Cambisols. Cambic Phaeozems
form on the eluvium-deluvium of limestone or carbonaceous schists.

3.4 Soil Morphology and Soil Taxonomy

The soils of Chernevaya taiga are quite diverse in terms of their morphology and classification.
They are presented by Planosols (eluvozems) and Umbric Planosols (humus-eluvozems), Retisols
and Umbric Retisols, Cambisols and Cambisols Mollic, Phaeozems and Umbrisols [36, 41, 42]. The
most typical types of soil in Chernevaya taiga are Albic Retisols with thick eluvial horizons. These
soils usually have a low boundary of eluvial and transitional horizons at a depth of 60-80 cm, so that
they do not fit the necessary depth requirement for being qualified as Hyperalbic. These soils also
vary considerably in their morphology and properties, but their common profile organization has the
following key features. Albic Retisols of Chernevaya taiga are formed primarily on calcareous loess-
like fine-textured materials: clay loams and clays. The soils have a perfectly well differentiated profile
with abrupt textural contrasts. High biological activity assures a high rate of plant matter
decomposition (within one-two years), which results in a complete absence of litter on the soil surface
[36]. The general horizontal organization of the profile of Retisols is (A)-AE(g)-E(g)-Bt-BtC-C. The
most typical feature of these Retisols is a very deep eluvial horizon with evident redoximorphic
features related to seasonal water stagnation. This feature is quite important in terms of water regime
and weathering processes.
The description of typical soil profile of Albic Retisol from Chernevaya taiga (Figure 6) is given below:

**A** 0-15/22 cm gray with a slight brownish tint and whitish spots (about 5 cm) in the lower part, silt loam, weak, fine subangular structure. Abundant roots of trees and herbs. Clear, wavy boundary.

**E** 15/22-50/56 cm bleached, light-gray with small brownish mottles, silt loam, weak medium-fine subangular blocky structure. Bleached grains along ped surfaces. There are roots. Gradual transition in color.

**BtE1** 50/56-62 cm uneven colour: an alternation of dark brown, reddish-brown, bleached whitish, gray-whitish mottles at the bleached whitish background; silty clay loam. Weak to moderate angular (nutty) and subangular blocky structure, compacted. There are some small (first millimeters) blackish Fe-Mn nodules, their number increases with depth; roots. The transition between horizons is gradual.

**BtE2** 62-80 cm the same material as in BtE1 hor., but reddish-brown zones prevail. The transition between horizons is clear.

**Bt1** 78/83-95 cm reddish-brown to brown, shiny on ped surfaces; moderate, fine angular blocky structure (polyhedral structure); silty clay loam. There are small Fe-Mn nodules, roots, mostly silty coatings on ped surfaces. Compacted. The transition between horizons is gradual.

**Bt2** 95-127 cm reddish-brown to brown, intra-pedal mass is lighter comparatively to ped surfaces covered by thin clay coatings; moderate, medium angular blocky (nutty) structure; silty clay. The transition between horizons is clear.

**Bt3** 127-160 cm reddish-brown; moderate, medium to coarse angular blocky structure; silty clay. Reddish brown and brown clay coatings along trans horizontal fissures and root channels. The transition between horizons is gradual.

**BtC1** 160-200 cm reddish-brown; moderate, coarse, angular blocky structure; silty clay, sticky and plastic. Dark-gray brownish and dark gray clay coatings are only along root channels. Local impoverishment with iron oxides along ped surfaces. The transition between horizons is gradual.

**BtC2** 200-250 cm uneven color: at the red-brownish background bluish-gray and bluish-gray brownish-gray zones, ocherous dots and stripes along pores. Silty clay, weak, coarse angular blocky structure, sticky, plastic.

The soils investigated were characterised in terms of key analytical features (Table 1) and particle size distribution (Table 2).
Table 1. Basic analytical characteristics of topsoil horizons of the soils at Novosibirsk (N) and Tomsk (T) locations.

<table>
<thead>
<tr>
<th>Type of the value/soil section</th>
<th>N1</th>
<th>N2</th>
<th>N3</th>
<th>T1</th>
<th>T2</th>
<th>T3</th>
</tr>
</thead>
<tbody>
<tr>
<td>TOC, %</td>
<td>4.8</td>
<td>2.1</td>
<td>2.7</td>
<td>9.9</td>
<td>4.0</td>
<td>2.4</td>
</tr>
<tr>
<td>TON %</td>
<td>0.4</td>
<td>0.2</td>
<td>0.2</td>
<td>0.6</td>
<td>0.4</td>
<td>0.2</td>
</tr>
<tr>
<td>pHCl2</td>
<td>5.8</td>
<td>5.9</td>
<td>6.3</td>
<td>6.3</td>
<td>6.2</td>
<td>6.2</td>
</tr>
<tr>
<td>Sand</td>
<td>20</td>
<td>23</td>
<td>51</td>
<td>19</td>
<td>24</td>
<td>23</td>
</tr>
<tr>
<td>Silt</td>
<td>50</td>
<td>42</td>
<td>21</td>
<td>42</td>
<td>44</td>
<td>19</td>
</tr>
<tr>
<td>Clay</td>
<td>30</td>
<td>35</td>
<td>28</td>
<td>39</td>
<td>32</td>
<td>58</td>
</tr>
</tbody>
</table>

Soils of Chernevaya taiga N1 and T1 showed essentially higher content of total organic carbon (TOC) and total organic nitrogen (TON) in topsoil layers, this could be connected with few factors, namely: (1) higher productivity of Chernevaya taiga in comparison with oligotrophic ecosystems, (2) higher stabilization rate of organic matter in black colored soils of chernevaya taiga caused by intensive biological turnover, (3) higher content of fine particles, which are responsible for intensity of organo-mineral interactions in soils.

As for pH values measured in soils-salt suspension with the aim to characterize exchangeable forms of acidity, the acidity of the topsoils is equal if one compares soils of chernevaya taiga and oligotrophic ecosystems.

Parameters of texture class – the content of sand, silt and clay - are not very different for two locations – Tomsk and Novosibirsk. There is an essential difference in sand content in topsoils – higher content of sand in soil oligotrophic environments than in soils of Chernevaya taiga. This indicates that edaphic conditions in two biotopes surveyed are completely different in terms of granulometric composition of the fine earth, mineralogical composition and nutrient regime. But differences are even sharper within vertical soil sections (Table 2).

Table 2. Soil texture of selected profiles.

<table>
<thead>
<tr>
<th>Soil section index</th>
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In the soils section N1 there is monotonous vertical distribution of sand fraction, but there is an intensive increasing of clay fraction in the middle and lower parts of profile which indicates of the appearance of illuviation process – translocation of fine soil particles with gravitational flow of soil water from top soil layers to lower located horizons. This is a quite typical feature of Retisols or Luvisols, and soils of Chernevaya taiga belong to this soil taxonomy order. The soil section N3 showed very high sand fraction content due to different origin of parent material, than in case of N1 profile. There is an opposite distribution of clay fraction – decreasing from top to below layers. So, illuviation is not expressed in soils of oligotrophus environments. The same trend in vertical changes of texture has been revealed for T1 and T3 soils – Chernevaya taiga and oligotrophus environments correspondingly. Thus, data obtained confirms that soils of Chernevaya taiga could be classified as Retisols, while oligotrophic soils are similar to Arenosols or Gray Humus soils. So, there is an evident difference on morphological and taxonomy levels between the soils of Chernevaya taiga and Oligotrophic ecosystems.
3.5 Biotic parameters

The biotic parameters of soil formation and Chernevaya taiga activity is characterized by an extraordinary high biological productivity of all of the components of the ecosystems (Figure 7). This is a unique type of biological cycle within the landscape of the entirety of Siberia. It is unique both in terms of the organic portion of the biomass and in terms of its impact on the geogenic and microclimatic factors. The fractions composition of plant remnants [37] is presented by: phytomass - up to 40 000 g m$^{-2}$, zoomass (herpetory and pedobionts) - 40-80 g m$^{-2}$, biomass of soil-bearing microorganisms - 800-900 g m$^{-2}$.

Figure 7. Image of the ecosystem.

If the total annual quantity of the plant remnants input into soil in the forests of Chernevaya taiga amounts to 550-630 g m$^{-2}$ y$^{-1}$ of air dry biomass, 280-400 g m$^{-2}$ y$^{-1}$ of them are presented by organic materials, originated from the tall-herbaceous layer. The nitrogen content and percentage of ash elements in herbaceous remnants are much higher than those found in the woody remnant (ash content of herb remnants - 11.3%, woody remnants - 3.4%; nitrogen content of 2.4% and 1.6%, accordingly) [38]. The wood part of the ecosystem, with its increased rate of phytomass formation, returns a disproportionately small amount of ash elements and nitrogen to the cycle every year, almost 3-4 times less than what is returned to the surface of the soil due to the decay of herbaceous plants.

The plant sprouts found in Chernevaya taiga are 1.5-2 times taller than those found in the West Siberian southern taiga. Ca content is higher by 1.4-1.8 time, N- by 2-2.5 times, and annual amount of Ca returned to the soils is 4 times higher than in the soils of southern taiga [43]. The number of actinomycetes and spore-forming forms of bacteria is comparative to what can be found in the soils of the steppe, while the low number of micromycetes is typical for chernevaya taiga soils [42].

The turnover rate of litter mineralization is 1-1.5 years. The litter consists of a number of different components with varying decomposition rates. The slowest to decay are fir needles, birch leaves, and debris composed of tree and bush branches and bark. The debris from the tall herbs has a high rate of decomposition and deteriorates within the span of a year.

It was demonstrated that the phosphorus content of the soils of Chernevaya taiga is around 1000 mg/kg [44], which makes it comparable to the soils of some of the most productive ecosystems in the Earth’s biosphere including tropical and temperate belt rainforests.
3.6 Virgin soils of Western Siberia - the “hidden food basket”

The soils of highly productive forests of boreal and subboreal zones represent a huge reservoir of fertility and could in the near future prove themselves to be a crucial resource for food production as climate changes take place across the world, including in Western Siberia.

Nowadays the most fertile soils of the southern part of Western Siberia are Chernozems (Mollisols) and Forest Gray soils (Albic and Umbric Retisols - Figure 6 and Figure 8). They are intensively used for agricultural purposes, predominantly as arable and pasture soils. As these soils suffer the effects of intensive dehumification and erosion, they are gradually becoming more and more exhausted and will likely lose many of their fertility indexes in the nearest future. This is why it is important to discover and study new soil types capable of supporting natural benchmark ecosystems in hopes that they could become new integral components of agricultural landscapes of tomorrow.

The soils mentioned above are known as Retisols and Leached Mollisols of warm and humid landscapes of the boreal climate belt. They are comparable in terms of fertility with East-European Cambisols. While the Cambisols dominate mainly in coastal and mountainous areas of Europe and Primorye with increased humidity, the Retisols of Chernevaya taiga represent the most fertile soil types of the boreal humid part of Western Siberia. They are typical for the high-level Chernevaya taiga foothills and the mountains of the Southern part of Western Siberia. It is one of the largest preserved refugium of high-level forests in Russia. Its least disturbed areas meet the definition of climax ecosystems according to both their terrestrial ecosystems criteria and the ones of the soil.

![Figure 8. Umbric Retisol, benchmark soil of Chernevaya taiga, Tomsk region](image)

The high fertility of the soils of Chernevaya taiga is made possible through the presence of internal biotic and abiotic resources, rather than via agricultural techniques. They therefore contain a "pre-agricultural" microbiota that has not been affected by the negative effects of long-standing agricultural practices.
It is also worth mentioning that the Retisols of Western Siberia can be called Retisols only from the taxonomic standpoint, but not in the sense of soil fertility and productivity since Retisols are usually not considered very fertile and productive types of soil.

3.7. Fauna of Chernevaya taiga

The notable features of the hydrothermal regime of soils mentioned above allow soil invertebrates to remain active all year round. For this reason, there are more of them in Chernevaya taiga than in any of the other automorphic ecosystems of southern Siberia [45,46]. Among the mesofauna, the dominant group of species are enchytraeids (Enchytraeidae, Oligochaeta), reaching up to 47% density of animals in the forest floor and 62.7% at the topsoil horizon. The next group of species are earthworms (Lumbricidae, Oligochaeta), which are present in lower numbers, but possess a higher biomass. Millipedes (Diplopoda) play an equally important role in the composition of the soils. The amount of predators (Carabidae, Staphylinidae, Chilopoda) and phytophages (Elateridae) [47] is lower than that of Diplopoda. These three groups of animals are the main agents for the decomposition of litter, the accumulation of organic carbon and the recycling of key nutrients. As they move through the soil, they carry microorganisms thus "infecting" the organic material of the forest floor, which in turn exponentially increases the speed of decomposition.

Due to the activity of biota and the high rate of debris decomposition, in spring the surface of the soils in open areas ends up being completely free from forest litter. Under the trees the decomposition rate is slower. It is worth noting that the number of invertebrates increases from 570 ex/m² to 1464 ex/m² within the catenas from Albic Retisol to Luvic Stagnic Phaeozems [45]. Such changes do not take place without having an effect on plant ecosystems as well as the size of the carbon stock in soils.

According to our study, carbon reserves in Albic Retisols Chernevaya taiga are 9.8 ± 2.6 kg m⁻² of carbon organic compounds, while in Luvic Greyzem Stagnic Phaeozems and Luvic Stagnic Phaeozems (Albic) the reserves fluctuate within 5.18 ± 3.0 kg m⁻². Soils are classified as slightly acidic or close to neutral, with pH about 6.5 in topsoil, decreasing pH values to 5.5 units in eluvial bleached part and following increase in illuvial layers till 6.4-6.5 units.

3.8. Soil Microbiota of Chernevaya taiga

Soil, as the largest reservoir of biological diversity on the planet, contains bacteria and fungi that are a source of enzymes and other molecules with meaningful biochemical, industrial, and pharmaceutical applications. For example, 70% of all antibiotics currently in use have been isolated from pedobionts. It follows that a more extensive study of soil organisms will provide humanity with an almost unlimited source of new biologically active molecules, significantly exceeding the amount that could have been obtained via synthetic pathways. In addition, soil microorganisms are a very significant and most reactive part of ecosystems as they play a leading role in the processes of transformation of substances and energy [48].

Despite numerous international soil microbiota related projects including Earth Microbiome Project (EMP) ([https://www.protocols.io/groups/earth-microbiome-project]) [47], the microbiological composition of Albic Retisols of the Chernevaya taiga remains predominantly unstudied. The studies that have been carried out so far using traditional microbiological analysis of the qualitative and quantitative composition of soil microorganisms in the aspen-fir forest and on the forestless areas under the tall herbs of Chernevaya taiga of the Salair ridge [49], showed a high number of microorganisms that destroy nitrogen-free organic compounds, a slightly lower number of ammonifiers and further lower amount of oligonitrophilics and aerobic nitrogen fixers. Moreover, the amount of studied physiological groups of microorganisms from the soil of the forestless gap under the tall herbs is almost 10 times lower than in the soil of aspen-fir forest [50].

It was also found that the highest number of microorganisms inhabit the forest litter and the humus-accumulative horizon enriched with organic matter and plant remnants. Moreover, with increasing depth the number of microorganisms decreases stepwise. The first jump occurs at the
border between the sod (accumulative) and eluvial horizons, and the second one at the border between the podzolic and illuvial horizons [51].

The nature of the distribution of microorganisms in the soil profiles of the aspen-fir forest and under the tall herbs is similar: the upper soil horizon is the richest, the number decreases with depth, and then levels off.

Findings demonstrated that actinomycetes dominate among the microorganisms that destroy nitrogen-free organic compounds. Ammonifiers, that are most abundant in the soil of a treeless area, are represented by microorganisms belonging to the genera Bacillus, Sarcina, Pseudomonas, Flavobacterium, Micrococcus, Achromobacter. Among microscopic fungi, representatives of the genera Penicillium and Mucor are most often found. Fungi of the genera Trichoderma and Alternaria were also found in the soil of the aspen-fir forest.

Since the early days of biological research and all the way up to the modern times scientists have managed to collect data about less than 3-5 % of the trillion types of organisms inhabiting our planet. The largest part of this unknown bulk can be attributed to bacteria, archaea, fungi and Protista, which are predominantly pedobionts and hydrobionts. Metagenomics allows to gather information about biodiversity and the interactions occurring within the most complex and so far unstudied ecosystems, contributing to the development of innovative strategies for the protection and preservation of the environment.

Heterotrophic protists play one of the key roles in soil ecosystems. They are believed to be important grazers of bacteria and other microorganisms, and thus stimulate rates of carbon and nitrogen cycling in the soil [52-54].

Amoebae are rather abundant in the soil. Finlay et al. [55] demonstrated that naked and testate amoebae may be the second largest group in the soil, outnumbering only flagellates. Qualitative estimates based on morphological methods (dilution method based on MPN numbers) are scarce, but available data suggests that the abundance of soil amoebae varies from 3,200 to 2,000,000 specimens per gram of dry weight soil [56-58]. Amoebae may represent up to 50% of the total number of protozoa in edaphic environments [59]. Foster and Dormaar demonstrated that soil amoebae produce pseudopods that can penetrate into tiny micropores of soil aggregates in order to engulf bacteria [60]. They suggest that this partially explains why bacteria are generally confined to the interior of soil macroaggregates, where they are beyond reach of amoebae. Besides bacteria, soil amoebae can feed on diatoms, fungi and other protozoa [61-63].

In turn, amoebas are an important food source for soil nematodes [64-66] and other metazoans living in the soil [67]. However, some amoeba in this food chain have switched from being prey to being hunters, developing specific devices for feeding on soil nematodes [68].

Due to their feeding activity, amoebae play an important role as one of the main controllers of bacterial population in the soil. They enhance nutrient cycling in the soil [69] and, together with other protozoa, stimulate carbon and nitrogen cycling [55, 70].

Despite the importance of amoebae for soil health, there is almost no data about amoebae found in the soils of Chernevaya taiga. As a part of our own study of this ecosystem, we are analysing the diversity of soil naked amoebae. Our preliminary data obtained over the course of 2019 demonstrate that the soil of Chernevaya taiga contains a fairly rich variety of naked amoebae. Even in a brief survey, representatives of twelve families of amoeba were discovered at the morphological level, belonging to three amoeba classes (Discosea, Tubulinea and Variosea). The most remarkable finding so far is the amoeba from the genus Thecochaos - a group of large amoeba that was last isolated more than 100 years ago [71]. Findings of this type are likely to be indicative of the high level of microbial wealth within the sampled soils. It is obvious that a more detailed analysis of amoebae diversity and abundance in Chernevaya taiga soils is required.

In our study (summer 2019, Novosibirsk and Tomsk regions), we apply metagenomic approaches to also study the composition and diversity of the microbiota of Chernevaya taiga and its influence on the formation of the unique properties of Albic Retisols and Luvic Stagnic Phaeozems that lead to the gigantism of its flora. First of all we explored the diversity of the microbial communities of the soils of biotopes with varied trophism.
It was confirmed that the richness of the soil microbiota decreases significantly with increasing sampling depth (Figure 9.A). The taxonomic structure of the microbiota of the top layers (0-15 cm) has similar properties in the different geographical locations of the Chernevaya taiga being studied [72].

Weighted UniFrac distance [73] approach and analysis of principal components allowed to demonstrate that bacterial taxa and their abundances in different samples of top soil layers of Chernevaya taiga are closer to each other than to the ones in samples from the control zone (Figure 9.B).

Figure 9. Beta-diversity (weighted UniFrac) of the soil microbiomes, PCoA, visualization in the Emperor package. A - color-coded samples from top soil level and deeper levels, B - Chernevaya taiga and control samples from different locations.

We explored the top layer of the soil in detail. The most prevalent phyla in all these samples are Proteobacteria, Acidobacteria and Verrucomicrobia. It is worth noting that the Proteobacteria phylum belongs to the group of phyla with which most of the cultivated microbes are affiliated, while the phylum Acidobacteria and Verrucomicrobia been widely distributed and abundantly detected in natural ecosystems, mainly consist of rarely cultivated microbes (Genomes OnLine Database - https://gold.jgi.doe.gov). Thus it is not surprising that we discovered a significant number of unclassified operational taxonomic units (OTU) that require further study - they could belong to previously uncharacterized microorganisms.

We also investigated the differences in microbiota composition of the rhizosphere of Crepis sibirica between Chernevaya taiga and control regions, using linear discriminant analysis effect size approach [20] and identified bacterial taxa that are relatively abundant between both groups. In this, Bacteroidetes (in particular Sphingobacteria and Cytophagia) were more abundant in the control group, and Actinobacteria (mostly Thermoleophilia) and Verrucomicrobia (Chthoniobacterales) in the Chernevaya taiga samples (Figure 10).
Figure 10. Result of LEfSe analysis of the C.sibirica rhizosphere in Chernevaya taiga (N1) and control samples (N2).

We expect that more extensive analysis of a bigger number of samples that we plan to collect and investigate in the nearest future will shed light on and support the idea that microbes and Protista play an important role in the specific features of the Chernevaya taiga biotope.

4. Discussion

4.1. Boreal forests

Boreal forests are one of the largest ecosystems on Earth. They occupy approximately 35% of Earth’s forested area and 14% of Earth’s land forming a circular belt traversing the territory of Russia, China, Canada, the United States, Norway, Sweden and a few others. This ecosystem is one of the biggest producers of oxygen on the planet, that removes carbon dioxide from the atmosphere by absorbing and storing it [1]. The boreal zone includes both forests and treeless types of ecosystems. Needleaf, coniferous trees (pine, larch, fir, spruce) are the dominant plants of the boreal biome as they are more adapted to life in the cold climate than broadleaf trees. The admixture of hardwood in boreal forests increases as you move south. Broadleaf deciduous trees and shrubs are members of early successional stages of both primary and secondary succession types. Most common are alder (Alnus), birch (Betula), and aspen (Populus). Well-developed moss or lichen cover on the soil surface is an important structural component of the coniferous boreal forests.

One of the most important features of coniferous boreal forests is the ability to grow and reproduce itself on seasonally frozen soils, withstand a long low-temperature period and insufficient moisture. This is largely facilitated by the availability of high snow cover, creating a special microclimate and helping plants and living organisms withstand severe frosts.

Soils in the boreal forest are typically podzols (from the Russian word for “ash”), gray soils that are thin, acidic, and poor in nutrients. These soils are covered by coniferous tree needles and other organic material that accumulates due to the slow rate of its decomposition and limited soil microorganism metabolic activity that is typical for cold climates. Podzols are formed when precipitation rates exceed evaporation, and nutrients, minerals, and organic matter are leached by acidic water moving down from the upper soil layers. These soils support numerous species of trees, shrubs, and other plants that have adapted to these soil conditions but they are unsuitable for agriculture.
Natural disturbances affect boreal forests and stimulate new growth. Thus, forest fires release valuable nutrients stored in the litter on the forest floor and expose the land to sunlight again. Insects reduce aging trees and make the forest more productive, while diseases eliminate weak trees and give new species a chance to thrive.

4.2. Chernevaya taiga

Being a part of the global boreal ecosystem, Chernevaya taiga of Western Siberia (Novosibirsk, Tomsk, Kemerovo, and Altai regions) possesses properties that distinguish it from the classic boreal forest. Main features of Chernevaya taiga such as joint dominance of aspen and fir in the forest stand; presence of large shrubs (Sorbus sibirica, Padus avium, Salix caprea), which do not, however, form a closed layer of undergrowth; presence of well-developed grass cover formed by tall (gigantic) grass perennials and of a group of species classified in Siberia as moral Pliocene relics; almost complete absence of ground moss cover and very high soil fertility clearly support that.

In some ways the conditions within this type of forest closely resemble those observed in tropical rainforests. In addition, the soils of Chernevaya taiga that were formed as a result of a unique combination of geogenic and bioclimatic conditions makes them comparable to the soils of some of the most productive ecosystems in the Earth’s biosphere including tropical ones.

Gigantism of plants, observed in Chernevaya taiga, of course, is not a unique ecosystem phenomenon. It occurs in tropical forests, in the Caucasus, the Southern Urals, Carpathians, Altai, Tien Shan, Kamchatka, in the south of Sakhalin and the South Kuril Islands, in Japan [74-75], but for boreal forests it is not described anywhere except in the Chernevaya taiga.

It is logical to assume that the striking development of tall herbaceous layer in conditions of nutrient-poor soil of the Chernevaya taiga may be associated with the activity of soil microorganisms associated with soil and plant roots. The thick snow cover that is typical for Chernevaya taiga in winter protects the soil from freezing and provides enough moisture during the winter time, which significantly prolongs the activity of microbiological processes.

A thorough study of absolutely unexplored microbial diversity (including fungi, bacteria and archaea) associated with abnormally tall plant species of Chernevaya taiga, as well as the identification of microorganisms that may be responsible for the high primary productivity of this ecosystem in poor soil conditions in conjunction with the detailed analysis of biotic and abiotic parameters of the Chernevaya taiga, can shade the light to the understanding of the phenomenon of this unique part of Siberian taiga.

5. Conclusions

The unique type of Siberian forests known as Chernevaya taiga is significantly understudied. We still do not know (1) what is causing the abnormal height of the plants growing on the relatively poor soils and within the temperate climate of Chernevaya taiga; (2) what factors determine the effective soil fertility; (3) the specificity of the microbiota of the soils of Chernevaya taiga; (4) how the relationships between the plants and soil microbiota in that area are structured; (5) whether there are any new biologically active compounds in the soil microbiome of the Siberian Chernevaya taiga (Figure 11).
Figure 11. Chernevaya taiga - unique region of Siberia

The use of modern metagenomic methods to evaluate the fertility of the soil, the detailed study of the genetic information of the structure and functional activity of the microbiome of the soil, as well as the efforts to isolate useful genes from soil microorganisms has the potential to usher in a transition to high yield ecologically clean agricultural practices employing the natural potential of the ecosystem in addition to the usage of chemical fertilizers and substances meant to protect the plants from harm. As a result, the change of paradigm in the agricultural industry will contribute to the production of safe, high quality, functional consumable goods.

Further advancements in modern microbiology are at this point no longer possible without the usage of molecular-genetic methods as part of the analysis of biological specimens. The active usage of new high throughput sequencing has led to an avalanche-like increase in the amount of available data related to the structure of microbial communities. Despite this seeming progress, the large volume and complex structure of this data in combination with the scarcity of fully assembled genomes of the individual members of the soil communities require a variety of Bioinformatics methods for their processing and functional annotation.

The analysis of the full metagenomic data in combination with the newest statistical models will allow extracting biologically notable information, allowing to make the translation from descriptive microbial ecology to the reconstruction of the interactions between the individual members of the microbiotic community as well as metabolic transformation pathways employed by the substrates they use.

We envision the need to discover and parametrize the main factors that lie at the foundation of such characteristic differences of the ecological functions of the soil of Chernevaya taiga as anomalously heightened effective fertility and ability to grow forest coverage.

The idea behind this is to establish a link between the distinct properties of Chernevaya taiga with the chemical parameters of the soil, the rate of moisturization, the unique composition of the microbiota or the aggregate of all of these factors.
Author Contributions:


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