

RESEARCH ARTICLE

Pacific ocean mega ecotone of Northern Eruasia as the belt of the origin of the modern continental biosphere

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Received: October 14, 2022; **Accepted:** February 15, 2023; **Published:** March 6, 2023.

Citation: Kolomyts EG. Pacific ocean mega ecotone of Northern Eruasia as the belt of the origin of the modern continental biosphere. *Resour Environ Inf Eng*, 2023, **5**(1): 213-236. https://doi.org/10.25082/REIE.2022.01.005

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Abstract: The Pacific Ocean margin of Eurasia includes the age row (at the geologic time scale) of geoecotone objects which can be imagined by certain nodal stages of the evolutionary trajectory of exogenous landscape genesis in the continental biosphere. The reported strategy of scientific research is aimed at the establishment of zonal-regional and local regularities of landscape organization of insular and marginal-continental land in different morphotectonic and macroclimatic sectors of the Pacific Ocean mega-ecotone of Northern Eurasia, which is considered as a natural laboratory for studying the modern stage of development of the geographical envelope. The empirical statistical models of the island-arc stage of continental biosphere development in the North-West Pacific have been created by the example of experimental test ground of the active Mendeleev volcano on the Kunashir Island (the South Kuril Ridge). It was shown that on this initial stage local geomorphological and hydro-edaphic conditions created the centers of origin of diverse phytocoenological structures. An exceptionally high percentage of green mass in the structure of production results in the acceleration of the biological cycle as a factor of stability of forest community under unfavorable conditions of "cold" oceanicity. Geothermal energy induces rearrangement of the plant cover towards the increase in its floraand phytocoenotic diversity to the detriment of biomass formation rate. The "climatically unjustified" but sufficiently stable sub-boreal forest ecosystems were formed, as well as the early stages of buffer forest communities. The multidimensional empirical-statistical modeling of landscape connections in the marginal-continental sector of the Pacific Ocean mega ecotone has been performed based on an experimental site in the Lower By-Amur Region. The ecology of the boreal-forest landscape of the continental margin characterizes the mature stage of evolution of the continental biosphere. The regularities and causal mechanisms of the formation of buffer forest communities typical of ecotone systems have been represented more integrally. Forests of this phenomenal buffer flora are distinguished by extremely high parameters of structural and functional development and have reached the state approaching the evolutionary climax. The previously advanced concepts of the Pacific ecotone of Northern Eurasia as a focus of evolutionary processes in the continental biosphere have been confirmed.

Keywords: ecotone biogeosystems, insular volcanic and continental marginal landscapes, morphostructures and macroclimate, soil temperature, forest ecosystems, buffer forest communities, evolutionary landscape science, primary landscape genesis

1 Oro-climatic interactions along the Mega ecotone and their ecological consequences

The Pacific Ocean oro-climatic mega-ecotone of Northern Eurasia covers the eastern, tectonically active margin of the continent and the insular land within the temperate and sub-Arctic geographic belts. This transition zone is characterized by the sub-meridional extension of morphostructural belts of different ages and the marked latitudinal and longitudinal-sectoral differentiation of the climate. It is part of the global belt of convergence of matter-energy fluxes on the Earth's surface: the so-called mobile belt of the planet [1,2]. The interaction between and transmutation of the two main types of the geographical environment (oceanic and continental) in this "continental-oceanic suture zone" is extremely dynamic [2–4]; therefore, the insular, peninsular and littoral-continental territories (as well as the coupled shelf areas) are a natural laboratory for studying the modern geological stage of biosphere development, since this stage is most marked exactly in the Pacific mobile belt. The known biogeographical and landscape studies in oceanic mobile belts [5–7] give grounds for this scientific research. The ecotones of lower taxonomic levels (macro- and meso-ecotones), which are clearly distinguished within the Asian-Pacific Ocean mega-ecotone, have been formed by latitudinal and longitudinal-sectoral contrasting differentiation between radiation-thermal and circulatory fields in the atmosphere, as well as by sub-meridional ordering of morphostructural belts (differing in age and modern tectonic activity) and the zones of exogenous relief formation, with the respective paragenesis of soils and vegetation.

Following the main provisions of geotectonic [1,2] and global climatology [8], all continentaloceanic ecotones are of two types: Atlantic and Pacific. The Pacific transition zone of Eurasia, in contrast to the Atlantic one, is characterized by the following features.

(1) The mega-ecotone is confined to destructive plate boundaries (the regions of subduction in the Zavaritsky-Benioff zones), i.e., to the zones of convergence of the ascending global lithodynamic flux and lithospheric contraction. It determines: (a) the long-term tectonic instability of the given continental margin, with the intense influence of the modern volcanism on the biotic medium (Figure 1); (b) the high geomorphological contrast (paragenesis of islandarc ranges of mountains and deep oceanic trenches); and, finally, (c) the distinct meridional age-related sectoral of land [2]. What is meant here is the belt of not only the ancient and modern formation of continental crust but also the age-related growing (increase) of the continent per se – a reciprocal process that continues throughout the entire Phanerozoic. Spatial diversification and contrast of landscape-forming conditions are created here primarily by morphotectonics.



Figure 1 South Kuril ridge. Pacific coast of Kunashir island with a view of the Mendeleev volcano in the foreground (winter aero-photography). The background is the city of Yuzhno-Kurilsk.

(2) This transition zone is an arena of acute rhythmic hydrothermal monsoon-type interaction between the continent and the ocean. Drastic seasonal changes in the land-sea interactions result in the high diversity of landscape-forming environments on relatively small territories and the frequent overlapping of ecological niches for soil-biotic components. The abiotic environment "proposes" quite some possible regimes and structures for the biota; hence, there is the enhanced competitiveness of species and entire communities, the rich blend of flora and fauna, certain abundance, and spatial diversity of life forms. The western boundary of the Pacific Ocean monsoon region passes along the upper reaches of the Amur River and the Great Hingan Range [2]. Within this area, there are three alternating ecological-phytocoenological spaces (from east to west): Neo-pacific \rightarrow Sub-pacific \rightarrow Paleo-pacific, differing in age and degree of the Pacific Ocean influence on vegetation cover [9]. Three western concentric borders take shape here for different extents of expansion of taiga-forest formations with the predominance of Ajan spruce. The core of its areal is in the lower Amur River basin and on Sakhalin [10].

(3) There is an interesting experience of paleogeographical and biogeographical studies of Beringia, which covers the closest parts (joining more than once in the past) of Northeast Asia and Northwest America [1, 12, 13]. This experience showed that the continental-marginal and insular territories of extra-tropical mega-ecotone of the "Ring of Fire" of the Pacific Ocean were the "generators" and "keepers" of continental and oceanic elements of the biota against the background of pulsating abiotic environment. Periodic alternation of natural situations initiated the new form-building processes, accelerated the directed (adaptive) and random transformations of plant and animal gene pools, and opened up the possibilities for hybridogenesis. The modern orographic and climatic contrasts along the oceanity–continentality gradient, which is well-marked on the mega-ecotone, support the work of this "flora-genetic node" and ensure the sustainable existence of mixed (buffer) natural ecosystems, with the conservation of numerous relic species of phytobiota and the plant communities comprising them.

(4) Thus, the Pacific mega-ecotone of Northern Eurasia shows up as one of the sources of

continental biosphere forming beginning in the middle of Mesozoic. Next processes created necessary conditions for that: (a) the frequently repeated joining and isolation of insular and marginal-continental land, which caused periodic isolation of biocoenotic complexes and interchange between them; it accelerated the evolutionary development of plant and animal populations and contributed to the diversity of their modern adaptations; and (b) intensive orogenesis and volcanism, which created the primary altitudinal differentiation of biota on the mountainous islands of the Pacific Ocean. Ecological niches remained permanently vacant, with the migration of modifications of biotic communities from the neighboring altitudinal zones. The primary altitudinal-zonal groupings of organisms and ecosystems were a basis of the formation of the zonal types of geographic environment on the plains of all continents. These are some of the basic points of the concept of evolutionary biogeography put forward by [14].

(5) The mega-ecotone per se, being mainly a mountainous territory, is a three-dimensional structure. It was created by three types of ecotonization processes in the biosphere: latitudinal-zonal (macro-climatic), longitudinal-sectoral (macro-orographic), and altitudinal-zonal (meso-oroclimatic), which is reflected in the formation structure of vegetation cover. The marked regional and local contrasts of natural-territorial structures appear at the geo-ecotone under the conditions of dominant climate-forming influence of the continent, which is expressed in the very concept of "monsoon-continental climate". It results in the high mosaicity of natural complexes, as well as frequent zonal and altitudinal-zonal inversions favoring the formation of biotic communities of the ecotone. The Amur River basin is a sphere of contact between the six phratries of plant formations: Beringian, Angaridian, Ural-Siberian, Manchurian, Mongolian-Chinese, and mountain-tundra (the buffer formations are widespread here) [9]. All sub-taiga dark coniferous forest zone in middle mountains is considered transitional from south taiga to sub-nemoral and nemoral forests [15, 16] by their hydrothermal conditions.

(6) The formation of the Pacific Ocean geoecotone is closely related to the history of the geographic environment in the Meso-Cenozoic era, when not only the fundamental orogenic processes occurred on the eastern margin of the Asian continent but also the essential modern features of monsoon-continental climate were obtained. The near-Pacific continental margin in the Cenozoic era underwent serious neo-tectonic transformations associated with crust warping, increasing crustal thickness, rearrangement of Paleozoic and Mesozoic structures, and creation of newly formed orogenic depression morphostructures. The recent appearance of Amur basin has been formed already in beginning of Neogene [17]. Development of the zones of enhanced magma permeability and jointing resulted in basaltic volcanism, formation of taphrogenic and riftogenic hollows: Zeysko-Bureinskaya, Sredneamurskaya, Amuro-Tugurskaya, Anadyrsko-Penzhinskaya, and the Tatar Strait. The shift of crust granitization from intracontinental regions to continental margin resulted in the formation of elongate orogenic-arch uplifts of asymmetric structure. In the Late Cenozoic era, it favored the development of asymmetric landscapes on the macro scopes of large highlands (Sikhote-Alin, West Priokhotye, Koryakskoye highland) [39]. Latitudinal zonality was complicated by longitudinal sectoral formed due to meridionally elongated orographic barriers.

The bioclimatic systems of the major meridional sectors of the mega-ecotone are of different ages. The modern zonal and altitudinal-zonal structure on the continental margin, with the mixed flora of representatives of sub-Arctic, boreal, and sub-tropic species, was formed in the early Paleogene: 60–65 million years ago [19]. In the southern part of the Kuril Arc, the bioclimatic zonality similar to the modern one was established only in the late Pleiocene, i.e., no more than 2 million years ago [20].

Latitudinal zonation of landscapes along the Pacific Ocean mega-ecotone, which is typical of internal regions of Eurasia, is shaded by their longitudinal sectorality, many of the physical-geographical boundaries coincide with the geological borders, and the monsoon-continental climate maintains historically blended northern and southern species within each zonal type of plant formations, favoring the development of their sufficiently broad ecological plasticity. Owing to this fact, for example, the spruce-fir forests of the Middle and South Sikhote-Alin, the stone-birch communities of Kamchatka, and the high Chosenia floodplain forests along the banks of the Kolyma, Anadyr, and Penzhina rivers, being the transformed relics of tertiary vegetation of the vast areas of Eurasia [21], are the stable elements of modern Far East landscapes.

Ecological plasticity is a characteristic feature of the main forest-forming species of boreal and sub-nemoral forests. In the dark coniferous taiga, Ajan spruce is rather cold-resistant but highly "oceanic", because it is adapted to high relative humidity (more than 55–60%) in spring and summer. Cedar/broad-leaved forests represented primarily by Korean cedar pine and Mongolian oak have a highly varied phytocoenotic structure depending on the type of location, as well as litho- and hydro-edaphic conditions, which made it possible to distinguish an entire series of "geomorphological types" of this ancient, historically established sub-nemoral formation in the south of the Far East [22]. Most xerophytic cedar-oak communities have no

competitors on rocky sun-heated mountain slopes; at the same time, Mongolian oak tolerates frosts down to -600 without serious consequences. Finally, it is known that the peculiar biological feature of cedar prostrate shrubs is to "lodge" and be submerged in the snow after the first frosts (see Figure 1), which protects it from low temperatures and winter winds [15].

2 Bioclimatic structure of the mega ecotone

The immediate vicinity of the winter Asian baric maximum, with the cold pole of the Northern hemisphere, and prevalence of cold sea currents near the northeast coast of Eurasia (Kurile-Kamchatsky, Primorsky) is the cause of two large-scale physical-geographical phenomena that determine the regional bioclimatic structure of the mega-ecotone. First, due to low thermal energy resources, there is a general substantial shift of natural zones to the south with their simultaneous meridional extension [23]. North-taiga stone-birch and larch forests and thin forests, often waterlogged, with very low productivity, are widespread over the northern and middle Kuril Islands, as well as on the most of northern continental territories up to the lower Priamurye (Figure 2, formation group (GF) 2 of zonal type I). The middle-taiga forests of the plains (GF 4–6) on the Kunashir and Sakhalin Islands and along the Japanese Sea coast of the continent descend to the 52nd–50th parallel. For comparison, let us note that mixed forests and forest-steppe are predominant at the same latitudes on the Russian Plain. The forest types of flat landscapes are predominant over the entire southern part of the Far East: namely, at the latitudes corresponding to the steppe and desert zones in the interior of the continent, e.g., in West Siberia.



Figure 2 The fragment of the ecological-phytocoenotic map for southern part of the Pacific Ocean mega-ecotone of Northern Eurasia [16], with author's additions. Symbols: I–III, the zonal types of plant formations; 1–7, the groups of plant formations.

(1)) Middle taiga forests. Mountain-taiga forests of limited development: (a) middlemountain larch ledum and rhododendron derivative forests; (b) larch ledum/green-moss forests, fir/spruce forests, sphagnum mari and grass bogs.

(2) South taiga and sub-taiga forests: (c) middle-mountain fir/spruce green-moss forests and their restorative series; (d) south-taiga larch forests, grass/dwarf-bush and larch-mari; (e) sub-taiga nemoral-grass larch forests, cedar/broad-leaved forests, maris and meadow bogs.

(3) Sub-nemoral forests, plain and mountain: (f) birch and aspen grass forests with the fragments of primary ones, with reedgrass meadows, yerniks, bogs; 7, broad-leaved and coniferous/broad-leaved tall grass forests and their restorative series.

Additional legends: a the boundaries of formation groups; (b) the boundaries of zonal types of formations.

The predominance of light coniferous and bog/light-forest landscapes, which are gradually replaced by moss/small-shrub tundras in the north and turn into the landscapes with poly-dominant dark-coniferous/broad-leaved forests with a substantial admixture of subtropical flora in the south, is a characteristic feature of the monsoon-continental spectrum, or type, of

latitudinal zonality, which can be retraced both on the plains and along with the mountain ranges. Altitudinal zonation in the South Sikhote-Alin, at the southern extremity of the mountains of Western Sakhalin and on the Kunashir Island repeats this regularity in miniature and, with advance to the north, the spectrum of altitudinal zonation is sequentially "truncated" from below due to the general decrease of upper boundaries of the belts. At the same time, the pinching-out of altitudinal zones on islands proceeds much more rapidly than on the margin of the continent. For example, cedar elfin wood tangle (cedar prostrate shrubs) in the extreme south descend from the height of the sub-goletz zone (1200–1500 m of true altitude) to the sea level near the latitude 470 in the strip of the Kuril island arc and in the region of 58–590 N on the coast of the Sea of Okhotsk.

Second, the cold and humid "respiration" of the ocean and its marginal seas in summer and dramatic cooling of the continent in winter are related to the frequent phenomenon of latitudinal and altitudinal-zonal inversion of landscapes when, for example, sub-Arctic plant groups develop on the coasts and in the intermountain troughs of the taiga zone [23]. On Chukotka, large river valleys in the tundra zone have, on the contrary, a warming effect on soils and vegetation and, therefore, are occupied by flood plain forests and shrubs, which sharply contrast the surrounding moss/small-shrub tundras.

As a rule, the landscapes of more southern appearance maximally advance northwards along the slopes facing the continent. The opposite mountain slopes face cold coastal currents; therefore, orographic barriers create the most favorable conditions for the biota just on the "continental" but not "oceanic" slopes of mountain ridges and close to their feet. Here, the spectrum of altitudinal belts is more diverse, the upper forest line is higher, soil formation processes are more intensive when the cryogenic factors weaken, and the species compositions of flora and fauna are substantially richer.

Thus, the geographic concepts of oceanicity and continentality are rather complicated and ambiguous when applied to the estimation of the level of structural development and functioning of landscapes. The extreme manifestation of oceanicity with predominant windy and cloudy weathers, cold fogs, and drizzling rains is physiologically unfavorable for tree vegetation growth. Hence, e.g., in the narrow coastland near the foot of the eastern slope of the Middle Sikhote-Alin, there is a clearly marked lower natural forest line (shrub/herbaceous oak forests, see below), similar to the forest-tundra boundary at its upper limit in the mountains and to the northern boundary on the plains [24]. At their lower line, arboreal plant communities are replaced by shrub and then herbaceous communities (Figure 2, GF shifts $4 \rightarrow 7$). Shrub-grass formations are known to be widespread on oceanic islands, including the Kuril and Komandorskiye Islands (Figure 3). The extreme oceanicity essentially simplifies the vertical component structure of landscapes and reduces their bio productivity. The traces of oceanicity on the Middle Amur plains are observed up to the western boundaries of distribution of sphagnum larch forest mari [21].



Figure 3 South Kurile Islands, the Shikotan Island. Sparse stunted trees with flag- and umbrella-shaped crowns and crooked trunks against the background of the dominant herbaceous vegetation.

The suboceanic climate is much more favorable in this respect. It combines moderately cold winters with high snowiness and weakened winds, on the one hand (which preserves the vegetative organs of plants from frost-killing and drying up), and summer cloudy weathers with sufficient sums of biologically active temperatures (up to 1800–20000) and a moderate range of humidity factors (0.7–1.5), on the other hand. These climatic conditions maintain stable photosynthesis throughout the entire vegetation period. The processes of organic matter decomposition, humification, soil weathering, and fersiallitization of the soil profile are also more intensive [25]. Thus, the sub-oceanic climate corresponds to a certain *zone of the optimum of exogenous continental-oceanic interaction*. This zone is well observed along the "continental"

slopes of the largest mountain ranges of the continental margin: Sikhote-Alin and its extension along the left bank of the Amur River (Figure 4), the Dzhugdzhur Range, the Kolyma Upland ranges adjacent to the Sea-of-Okhotsk coast and, finally, the Vostochny (Eastern) Range in Kamchatka. The significance of the barrier effect generally decreases northwards, which corresponds to "fuzzification" of the monsoon climate features at high latitudes.

There is also an analogous *marked zone of the optimum on the continent-facing slopes of volcanic mountains of insular land* located in the properly oceanic longitudinal sector of the geo-ecotone. Here, the warm and cold sea currents have a greater effect than the orographic factor [23, 26]. One of the branches of the warm Kuroshio Current reaches the west coasts of the Southern Kuril Islands, while their east coasts are washed by the cold Kuril-Kamchatka current. In line with the above, four landscape zones (meadow, stone birch forest, alder/alder-cedar prostrate shrubs, and mountain-tundra) are observed on the western (the Sea of Okhotsk) slope of volcanoes of the Simushir Island (the Kuril Ridge), while only two zones (alder-cedar prostrate shrubs and fragmentary mountain-tundra among the primary volcanic deserts) are observed on the eastern (the Pacific Ocean) slope. The upper belt on the eastern slope is 200 m lower compared to the western one, where the life forms of plants are better developed. The sub-oceanic climate features are associated with a broad distribution of the landscapes of forests of prostrate cedar elfin wood in the mountains of the northern Priokhotye, Kamchatka, and Koryakskoye Upland and dark-coniferous/broad-leaved forests with the elements of sub-tropic flora (Amur cork tree, magnolia, Aralia) on South Sakhalin and the Southern Kuril Islands.



Figure 4 Low Priamurye, Komsomolsk nature reserve, cedar-broadleaf forb forest with multispecies composition and presence of relict flora.

3 Forest-forming processes at the mega ecotone

When describing in detail these processes in the south of the Far East, B.P. Kolesnikov characterized the forests of this vast ecoregion "... as the forests of mountain-valley landscape and monsoon climate, ... most spatially variable and extremely dynamic, i.e., with exclusively multiform and changeable habitus" [22].

Just *multiformity* and *dynamicity* are the characteristic features of forest formations of the boreal and nemoral Eurasian sub-Pacific region from their intracontinental plain and mountain analogs on the Russian Plain and in West Siberia, on the Ural and Altai, in the Sayans and Transbaikalia, in the Carpathians and Alps. These analogs are characterized by a relatively lesser number of ecologically homogenous phytocoenotic components and rather structurally uniform types of forest.

In contrast to Western and Eastern Europe, as well as West Siberia, there has been no solid inland ice sheet in the south of the Far East since the early Quaternary Period; therefore, the development of plant cover was not interrupted here. According to the spore-pollen data from coal-bearing sediments, mixed coniferous-broadleaf forests grew in the Middle-Bikinsk depression [18] as early as in the Miocene (about 25 million years ago), with the involvement of both subtropical species and representatives of moderately thermophilic (sub-boreal) and even moderately psychrophilic (boreal) forms. Thus, there had been an intermixture of very contrasting floras in Primorye and Priamurye (the Amur River basin) long before the Quaternary glaciations, undoubtedly as a result of the influence of the already existing monsoon climate.

The plant cover of the Primorye-Priamurye sub-Pacific region continuously developed as it stayed under these conditions for a long period. The transition of the flora and vegetation from the Tertiary to Quaternary period was relatively smooth [27, 28], with the migration of separate elements of the Tertiary flora from north to south and back north and with the penetration of cold

climate species [21]. The continental margin of Northern Eurasia came to be at the crossroads of migration pathways [29]. Most of the present species constituting the broadleaf–Korean cedar communities had ancestor taxa in the Tertiary palaeofloras of the Late Miocene and Pliocene. During the Pleistocene Ice Age, the rich mesophytic flora in this area lost most of its meso-thermic species. The vegetation of the maximum stage during the last glacial period consisted of drought-tolerant meadows and larch woodlands on the plains and dark-conifer taiga in the lower mountain belts. During the following warming, broadleaf temperate species invaded this territory from warmer and wetter regions in the south.

Such specific and long-term forest-formation processes resulted in the gradual conversion of tertiary thermophilic sub-oceanic formations into more moderate formations adapted to drastic seasonal hydrothermal contrasts. Even representatives of the modern cryogenic-taiga flora, "... larch forests in the process of evolution combined the tertiary species with different genetic relationships and centers of origin and their descendants" [30]. According to the figurative expression of A.N. Krishtofovič, the abundance of flora in the south of the Far East "... is only the result of its reaching the saturation point of climatic possibilities" (cited according to [27].

At the same time, climatic fluctuations manifested themselves mainly in the temperature changes against the permanently high moisture content, which favored the transgression of representatives of the humid Okhtskaya flora, first of all, Ajan spruce, into relic cedar/broad-leaved forests. Such was, e.g., the phase of cedar-spruce-broadleaf forests at the turn of the Atlantic and sub-boreal periods of Holocene (4.7–4.1 thousand years ago), when there was cooling with the yet high moisture content [31]. This forest-forming process as a result of Pacific Ocean influence still goes on in the Priamurye Subpacific Region at present. The transgression of representatives of the Angaridian continental flora (in particular, Dahurian and Kayander larch) proved to be a more localized phenomenon associated with the climatic inversions under the conditions of mountain-valley relief. Nevertheless, the areal of larch extended during the century-long changes, with its penetration into mixed forests [21].

The result of the forest-forming processes described above was the well-known floristic abundance and coenotic diversity of cedar-broadleaf and spruce-broadleaf forests in the South of the Far East. Primarily mixed cedar-broadleaf and, to a lesser extent, coniferous forests are characterized here by the multispecies composition and ecological-biological heterogeneity of phytocoenotic components at all layers, which leads to the complexity and entanglement of interspecies relationships and the diversity of forest-forming processes. This diversity is composed by age-related, secular, and restorative changes of forest communities. The results of these relationships are the vertical closeness (solidity) of vegetation layers, the grouping arrangement of individuals, the presence of differently aged stands in a forest community, the periodicity of tree growth in general and of any generation, and, finally, the aggravated interspecific competition between individuals and, as a consequence, the general decrease in the site quality (bonitet) and productivity of forests, which does not correspond to the potentialities of habitat environment.

The dominants of broadleaf-conifer forest ecosystems differ in growth forms and life strategies. Up to 12 tree species growing together can be found in the upper sublayer of one forest stand [32]. The main species forming the dominant layer are *Abies holophylla*, *Betula costata*, *Fraxinus mandshurica*, *F. rhynchophylla*, *Juglans mandshurica*, *Kalopanax septemlobus*, *Phellodendron amurense*, *Pinus koraiensis*, *Quercus mongolica*, *Tilia amurensis*, *T. mandshurica* and *Ulmus japonica*. Their usual height is 25-35 m, but on rich sites *Abies holophylla* and *Pinus koraiensis* may reach a height of 45 m, exceeding the height of other tree species and forming a sparse layer above the canopy. The century phytocoenotic replacements eventually resulting in the substitution of one forest formation for another consist of a number of stages and, therefore, can be presented as a certain *genetic series of forest groupings* [22]. Uneven age structure is a characteristic feature of old-growth broadleaved–Korean pine forest [32]. Trees in such stands grow in cohorts reflecting the gap character of stand dynamics.

On the other hand, due to multispecies composition, age replacements of forest stands occur in different habitats according to a single spiral scheme, with no less than 2- to 2.5-century cyclicity [22]. The spirality (unclosedness) of these cycles manifests itself in the long-restorative and even stably irreversible successions and evokes a general tendency to displacement of cedar from stand structure by deciduous trees in Primorye and by coniferous trees (mainly Ajan spruce) in the Middle and Lower Priamurye (Figure 5). The emerging long-restorative and even stable naturally irreversible forest communities consist of representatives of other forest floras. For the Priamurye, it means the displacement of Manchurian flora by either Okhotskaya or Angaridian flora. During the cyclic dynamics of forest stands the shade-tolerant nemoral species, as well as shade-intolerant ones, can complete their life cycles. Because normally in old-growth forests the cycles do not coincide, diversity within a forest community with stable edaphe-climatic conditions is maintained [64].

The multispecies composition and structural diversity result from the superposition (mutual overlapping) of age, secular, and restorative (demutational) replacements of forest communities. At the same time, age replacements cause gradual quantitative transformations of habitat conditions from generation to generation: first of all, the accumulation of organic matter and the changes in hydrothermal parameters of edaphe-topes and soil trophicity. Such environment-forming activity of phytobiotic components [33] creates prerequisites for irreversible century-long replacements of the main forest-forming species. This process has become especially widespread at the Far-East boreal ecotone, with its floristic richness of mixed forests and with their complex different-aged and multilayered structure; the striking example is the above-mentioned replacement of cedar by Korean Ajan spruce, with the development of cedar-spruce and spruce/broad-leaved communities.

In other cases, especially after fires, the age and century-long replacements of cedar/broadleaved forests are accompanied by displacement of cedar with small-leaved species (yellow and Amur birch and aspen), with broad-leaved species (oak, ash, lime) pushed to the sidelines and mesophilic Manchurian plant species replaced by psychro-mesophilic taiga species.

4 On development of the theory of evolutionary landscape study

The Pacific Ocean mega-ecotone of Eurasia, being an element of the global belt of convergence of matter and energy flows on the Earth's surface, is one of the *sources of formation of the continental biosphere*. It concentrates the conditions for the development of focal biocoenotic processes [27] and spontaneous hybridization, for the appearance of stable new formations in the natural-territorial structures [18]. According to [14] such conditions in the geological history were as follows: (1) the frequently repeated joining and isolation of insular and marginalcontinental land, which caused periodic isolation of biocoenotic complexes and interchange between them; it accelerated the evolutionary development of plant and animal populations and contributed to the diversity of their modern adaptations; and (2) intensive orogenesis and volcanism, which created the primary altitudinal differentiation of biota on the mountainous islands of the Pacific Ocean. Ecological niches remained permanently vacant, with the migration of modifications of biotic communities from the neighboring altitudinal zones. The primary altitudinal-zonal groupings of organisms and ecosystems were a basis of the formation of the zonal types of geographic environment on the plains of all continents.

The study of modern landscape connections in morpho-structures and morpho-sculptures of different ages is the way to understanding the phylogenetic regularities of the long-term geological trajectory of terrestrial landscape formation. This trajectory begins with the stages of geosynclinal insular arcs (the brilliant example is the Kuril-Kamchatka insular arc), with volcanic relief and the formation of the primary sub-aeral landscapes on volcanic rocks. They are followed by the stages of development of epigeo-synclinal orogens [3]. These are the mountain ranges of Sakhalin and the Sikhote-Alin with its extension along the Amur River left bank, which is characterized by young erosion-denudation and accumulative marginal-continental morpho- and biogeo-systems.

This is the first stage of the formation of continental landscapes of the *evolutionary series*, *or progressive development*. At this stage, one should expect a general increase in the level of biogeo-system organization: the complication and ordering of their structure, the increase in spatial differentiation of landscape connections, the enhancement of the system-organizing role of soil-biotic components [34]. As a result, the efficiency of exploitation of environmental sources by biogeocoenoses increases, predetermining the biosphere evolution [35]. Henceforth, there is a much longer change of the stages of origination and reformation of residual/denudation "senile" landforms, when the territory passes into the state of intra-continental ancient platforms (Siberian, East-European).

In parallel with the above, the reverse processes of landscape-geomorphological disintegration on the continental margin can also be traced. They are manifested in the replacement of roof plastic deformations by faults and differentiated block movements, in the fragmentation of separate marginal parts of the continent and their foundering below sea level [3], with the formation of *continental islands of the regression series* (the islands of Peter the Great Bay, Shantarskiye and Yamskiye). An analogous effect of "attenuating" landscape evolution is observed when land stays too long at the island-arc stage and sedimentary rocks are formed (the islands of the Lesser Kuril Ridge [20]. The trajectory of regressive natural complexes is characterized by depleted composition, simplification of landscape-ecological connections, and the enhanced role of abiotic factors. In this case, we can obtain the natural analog of anthropogenic changes in continental geosystems: the processes of disintegration of landscape connections have different characteristic times but are analogous.

The presented concept of the Pacific Ocean mega-ecotone of Northern Eurasia as a focus of evolutionary processes in the continental biosphere was published by the author in his book [34]. Similar ideas had been put forward somewhat earlier concerning flora-genesis of the northern wing of the mega-ecotone, Beringia, which had been denoted as "... a peculiar flora-genetic laboratory of the northern areas of the Earth" [12].

The modern landscapes of the Pacific Ocean mega-ecotone of Eurasia have been formed in a very broad age spectrum of morpho-tectonic structures [3] with two notable geologicalgeomorphological borders separating the sectors of Cainozoic, Mesozoic, and still earlier folding [10]. In the direction from oceanic islands to the marginal and then interior regions of the continent, the landscape connections of land are formed on a more and more ancient lithogenic base, under the conditions of weakening of the neo-tectonic movements and successive burial of the main source of mineral nutrition for phytobiota (crystalline bedrocks) under the increasing sheath of loose sediments, which are much more depleted in this respect, that have passed through numerous cycles of siallitization (clay formation), denudation ablation and accumulation.

On the other hand, the role of radiation climate-forming factors enhances and the influence of circulation (advective) factors decreases in the westward direction. Therefore, continentality of the climate generally increases. As a consequence of interference between both groups of factors in the direction from the margins to the interior of the continent, the total intensity of biogeochemical cycles of matter in the soil-plant system weakens (under certain zonal conditions), the processes of weathering and soil formation slow down and, finally, the biological productivity of landscapes decreases. All the above occurs against the background of weakening of the direct landscape-forming role of morpho-tectonic factors and increasing significance of exogenous geomorphological processes. Landscape appearances show fewer and fewer traces of endogenous forces (tectonic benches, volcanic cones, lava beds, etc.), while residual-denudation and accumulative landforms become more and more prevalent.

All intra-continental territories of Eurasia passed, in one way or other, through the abovedescribed sequence of changes of landscape situations in their geological past. In the past, the continental-oceanic seam zones were the Alpine-Caucasus-Himalayan mountain belt, as well as even more ancient folded Hercynides of the Urals and Kazakhstan [2]. The latest orogenicgeosynclinal region of the Pacific Ocean mega-ecotone is characterized by the initial stages of development of the next continental part of the geographical envelope of the Earth during the age-related buildup of the area of the given continent. In essence, the matter in question here is the *primary landscape genesis on land*: a rather poorly studied branch of complex physical geography. In the meantime, the primary landscape genesis is directly related to the fundamental problems of continental biosphere formation and development, understanding the initial mechanisms of surface physical-geographical process, according to [35], which was created in the past and continuously forms in the present landscape appearances of continents.

The comparative analysis of modern landscapes of the Far East (island-arc volcanic, continentalinsular, and marginal-continental) will probably reveal the regularities of formation and development of landscape connections on land, as well as their degradation and disappearance. Undoubtedly [9], meant precisely the evolutionary direction of sub-latitudinal variation of landscape connections on the Pacific Ocean geo-ecotone, distinguishing three sectorial geospace: neo-Pacific, sub-Pacific, and paleo-Pacific. It can be illustrated by the following example. In the sub-taiga coastal strip of the Middle Sikhote-Alin (Figure 2, GF 12), in the direction from the Japanese Seashore to low mountains, one can trace a certain topological series of associations, with the incumbation series of indigenous life forms of Mongolian oak [24]: herb-cereal meadow \rightarrow bush-clover/hazel cereal/herb association \rightarrow herb/hazel low (up to 1 m) bushy oak forest \rightarrow herb/bushy crooked oak forest (3–6 m in height) with wind-shaped crowns \rightarrow straightstemmed oak forest (up to 15-17 m in height). Considering the first and second associations to be oceanic (neo-Pacific representatives) and the third and forth associations to be sub-oceanic and continental (sub-Pacific and paleo-Pacific representatives), respectively, we obtain the local model of evolution of the given zonal type of vegetation cover on the mega-ecotone in the direction from the youngest to more ancient formations.

Thus, the Pacific Ocean mega-ecotone of Eurasia is a highly favorable object for addressing the problems of *evolutionary landscape science*. This novel field of complex physical geography must be aimed at the study of "supporting mechanisms" of the formation, development, and degradation of landscape connections on land, the search of motive forces determining the tempos of the evolutionary process (both ascending and descending), the revealing of taxonomic and age-related correlations between the structure and function of geo(eco)systems, their ontogeny, and phylogenetic shifts. We believe that the solution of these problems will contribute to the development of scientific and methodological bases of controlling natural processes and creating new ecological equilibriums in nature.

Our initial working propositions of the future concept of evolutionary landscape science provide for the study of the structure and function of insular geosystems in their spatial-genetic diversity and as components of the continent-to-ocean transition zone. At the same time, the study of spatiotemporal organization of insular landscapes (both evolutionary development and regression series), together with the assessment of potential natural resources of islands and recommendations on the maintenance of their ecological balance, must be aimed at the eventual creation of complex and sectoral physical-geographical models simulating the structural and functional changes in continental landscapes at the initial stages of their formation.

In particular, the coastal–continental islands of the regressive series, with their general descending trajectory of the system of landscape connections, may serve as a natural model of anticipated events for many intra-continental regions of the Far East in the foreseeable future, with the estimated intensification of development of their natural resources and expansion of technogenic zones. These islands, being at different stages of anthropogenic transformation and territorially closed, are a favorite object for addressing the scientific and methodological problems of resistance of natural landscapes to external impacts.

The study of insular and marginal-continental geo(eco)systems of the progressive series (the Kuril Islands, Kamchatka, etc.) will be aimed at understanding the regularities of formation and development of landscape connections on land during its gradual transition from insular to the continental regime. Here, nature can demonstrate the ways and stages of the formation of landscape systems of different levels of development, which will be directly related to the problem of artificial creation of new ecological balances in nature. As is known [6, 23], the process of species formation and phytocoenotic successions is more rapid on oceanic islands compared to the continents.

In the landscape-ecological analysis of the Pacific Ocean mega-ecotone, it would be advisable to compare the data on the intra-continental East-Eurasian system of transition zones: e.g., on the bioclimatic boreal ecotone of the Volga river basin [36], which is tectonically stable and is characterized by "senile" farewell-rock erosion-accumulative landforms. Both mega-ecotones are components of the global Eurasian "ocean–continent" ecotone system [37, 38], with the spatial ordering of geo-textures of different ages [4] and modern macroclimatic fields, as well as with the respective change of zonal/regional and local vegetation and soil spectra. Such transition from young insular geosystems of the evolutionary series to marginal-continental natural complexes of epigeo-synclinal orogens and then to intra-continental landscapes, already having a rather long history of sub-aerial development, represents the basic geological stages of formation of the natural-territorial structure of the continents [9, 34].

The most important indicator of the geo(eco)system state is known to be its primary bio productivity. The coastal and insular landscapes of the Pacific Ocean mega-ecotone differ from their intra-continental analogs in the higher phytomass reserves and productivity. For example, these indices for boreal forests are 500–800 tons/ha and 10–18 tons/ha•yr in the former case and more than 300–350 tons/ha and 5–9 tons/ha•yr in the latter case [36, 39]. At the same time, the portion of green photosynthesizing mass on islands is much higher compared to the mass of the above-ground skeletal part of plants and the root mass. They are also characterized by much greater (compared to the continent) involvement of the lower, especially near-ground, biogeo-horizons in organic matter production.

The very structure of phytobiota also undergoes the respective changes. The phenomenon of insular ecosystems is known [40,41] to be high- and tall-grass communities with the elements of gigantism. These are, for example, the high-grass dropwort coenoses on the Kamchatka and the Kuril bamboo underbrush on Sakhalin and the Southern Kurils. Herbaceous formations, as opposed to forest ones, are characterized by much higher solar energy utilization and water use efficiency. They also accumulate much greater amounts of nitrogen and ash substances per unit of products [42]. All the above make insular landscapes with herbaceous phytocoenoses more economically and contribute to their broad distribution at the initial stages of landscape genesis.

5 Ecology of island-arc volcanic landscapes

The empirical statistical models of the island-arc stage of continental biosphere development in the North-West Pacific have been created by the example of experimental testing area near the active Mendeleev Volcano on the Kunashir Island (the South Kuril Ridge). It was shown that on this stage local geomorphological conditions created the centers of origin of diverse phytocoenological and soil structures of the higher (zonal-regional) level at the initial stages of continental biosphere development.

We consider the plant cover and landscapes of volcanic islands, in contradistinction to the authors who have put forward the basic postulates of insular biogeography and insular landscape science (E. Hulten; M. Tatewaki; A.G. Voronov; G.M. Ignatyev; K.N. Dyakonov; Yu.G. Puzachenko; A.N. Ivanov; etc), not in contrast to the analogous formations on continents but in their dynamic unity – as *particular elements of a single evolutionary physical-geographical process* (according to A.A. Grigoryev [35]) forming the new territories of continental biosphere in the mobile belt of the planet. The main spectrum of altitudinal zonality originated at a rather early stage of development of subaerial landscapes, when the tectonic-volcanic massifs emerging from the oceanic abyss had yet stayed within the confines of low-mountain relief.



Figure 5 Iturup Island (Kuril Ridge). Phreatic eruption of Ivan Grozny volcano (gas ejection without lava release) in August 2012. The foreground is a dark coniferous forest with deformed tree crowns.

The processes of the primary sub-aerial biogenesis occurring at the Pacific Ring of Fire (the mobile belt of the Earth) are the successive stages of modern increment of the continental biosphere (Figure 5). Hence, the "Mendeleev Volcano" experimental test site on the Kunashir Island is undoubtedly representative for perceiving the initial stages of establishment and development of terrestrial geo(eco)systems in the surrounding oceanic environment. The Mendeleev Volcano belongs to an extrusive "bushed" type of isolated stratovolcanoes, with an absolute height of 850 m and the age of the oldest caldera is about 40,000 years. This region characterizes one of the initial stages of sub-aerial landscape genesis. At this stage, *active volcanism* with its intensive eruptive processes is completed and changes into *passive volcanism*. The determining endogenous factor is the energy-consuming deep *fluid systems*, with their conduits (fumaroles) forming solfatare fields. However, even for the *fluid stage*, our model describes a rather stable biogeocoenological structure of this territory aged 39–40 000 years. It is just the period when landscape genesis is carried out not only by the morphotectonics and hydro-climatic regime but also by the intensive "work" of soil-biotic components.

The latest (pyroclastic) eruption of the Mendeleev Volcano occurred in 1880 [43], and its steam and gas activity was observed in 1901, 1946 and 1977. The current state of the volcano figuratively called "the Sleeping Beauty" by people, with reference to volcanic landscape itself, will be denoted as a *passively active state* and its fumarole activity will be denoted as a manifestation of *passive magmatic energy*. The intensive gas-hydrothermal activity of the volcano (Figure 6) began to develop exactly at the final Late Quaternary (andesitic) stage of its history and, thus, characterizes its passive active state.



Figure 6 The solfatare field on the northeastern slope of the Mendeleev Volcano. The belt of stone-birch/spruce forests changing higher into the belt of cedar elfin wood is in the background.

The processes of formation of volcanogenic-accumulative morphosculpture created a lithogenic

basis of the island-arc stage of establishment and development of the next part of the continental biosphere. All of the newly-formed terrestrial natural complexes in the oceanic mobile belts pass through this stage; therefore, the Mendeleev volcanic landscape is a typical model of one stage of the primary sub-aerial landscape genesis.

The most pronounced features of this stage are as follows: (a) the direct influence of morphotectonic factor on landscape structure; (b) the high degree of conformity between the age of relief and the age of soil-forming bedrocks; (c) the distinct geological-geomorphological and bioclimatic sectorality of island territory (the Okhotsk Sea and Pacific Ocean sectors are distinguished over the entire Kuril Ridge); and (d) the youth and dynamicity of the soil-lithogenic unit of geo(eco)systems due to the thick layers of pyroclastic deposits, where soil formation is accelerated.

The South Kuril Islands, especially Kunashir, are an example of extremely high diversity and contrasts between the *non-relict types of vegetation* of the temperate belt in Northwestern Pacific [44, 45], from mountain tundras to coniferous-broadleaf and broad-leaf forests with abundant evergreen sub-tropical and relict species. Among the latter, there are the species both present and absent on the continent: holly (*Ilex crenata* Thunb), skimmia (*Skimmia repens* Nakai), yew (*Taxus cuspidata* S), magnolia (*Magnolia abovata* Thunb), onoclea (*Onoclea sensibilitis* L.), etc. However, the number of endemics is insignificant because of heavy volcanic activity on the Kuril Islands. The morphological similarity of endemics to species of the neighboring territories (the Sakhalin and Hokkaido Islands and the Kamchatka Peninsula) is a result of recent isolation of the islands [40]. Not only broad-leaved but also coniferous forests of the South Kuril Islands are saturated with relict species [46]. Thus, the floristic richness and phytocoenotic diversity of forest ecosystems, as well as adequate soil development, so typical of the marginal-continental sector of the Pacific Ocean mega ecotone, emerged already at the initial indular-arc stage of sub-aerial biogeogenesis, and the loci of formation of buffer communities were the phytocoenoses of not only dark-coniferous but also sub-alpine belt.

In the experimental test site on the Mendeleev Volcano, we have distinguished six groups of forest types (the symbols and taxonomic norms of true altitudes are given in parentheses): (1) mixed dark-coniferous/broad-leaved forests (\$ 0 - CB; 184 m; Figure 5.2); (2) dark-coniferous (spruce/fir) forests (\$ - DC; 379 m; Figure 5.3); (3) buffer stone birch/spruce forests (\$ - SbS; 575 m); (4) stone birch elfin woodland with cedar elfin wood ($\varPsi a - SbCe$; 685 m; (5) cedar elfin wood ($\varPsi - CeW$; 718 m; Figure 5.4); (6) buffer cedar-elfin-wood/birch/spruce communities ($\$ \psi - CeSbS$; 575 m). These types belong to the respective floristic phratries: (1) – Manchurian-Okhotsk (MO); (2) and (3) – Okhotsk (Okh); (4) –Beringian-Kamchatka (BK); (5) – Beringian (Ber); and (6) – Beringian-Kamchatka-Okhotsk (BKO). (Figure 7, 8 and 9)



Figure 7 The mixed dark-coniferous/broadleaf forest in the piedmont zone of the Mendeleev volcano landscape.



Figure 8 The mountain spruce-fir forest in the lower layer of the Mendeleev volcano. There is a well marked alteration of generations of the stand.



Figure 9 The sub-goltsy zone with cedar elfin wood and goltsy in the upper zonal layer of the Mendeleev volcano.

The buffer Manchurian-Okhotsk phratrie is represented by coniferous/broad-leaved forests being fragments of the lowest bioclimatic belt of the Mendeleev Volcano and its surroundings. Before the beginning of Late Holocene (2–3 thousand years ago), this ecoregion (as well as the entire southwest of the Kunashir Island) had been occupied by purely nemoral forests [47] of the Manchurian flora with subtropical relicts. The transgression of fir-spruce forests and the emergence of buffer Manchurian-Okhotsk communities was related to the cold snap in the first half of Late Holocene.

Distribution of groups of forest 1 types (*GFT*) for Mendeleev volcano landscape is presented on Figure 10. This map was created by L.S. Sharaya with the help of the education of logistical multiple regression:

 $\begin{aligned} \ln(GFT) &= 0.002617 \cdot Z_{+14.13} - 0.8907 \cdot \cos(A_{45}) / GA_{-2.79} + \\ &+ 0.01125 \cdot [\text{GrW}(10 - 20)]_{+2.44} - 0.03613 \cdot t(40)_{-1.59} + 0.1289. \\ &R^2 &= 0.919; \ Degr &= 5.0\%); \ P < 10^{-6} \end{aligned}$

Here $\ln(GFT) - \log$ arithmic series of groups of forest types, which are distributed by altitude; Z – absolute elevation; $\cos(A_{45})/GA$ – north-west component of exposition for gentle sloping; GrW(10–20) – moisture vertical gradient in soil layer 10–20 cm; *t* (40) – temperature of soil on depth 40 cm. The subscripts of each predictor are *t*-statistics; their module determines the significance of contribution of predictors to the spatial variability of temperature. R^2 is the coefficient of determination and *P* is the statistic characterizing the probability of error in the establishment of statistical dependence.



Figure 10 Map of groups of forest types on the Mendeleev volcanic landscape (see Figure 1). The map has been calculated and created by L.S. Sharaya (explanation in the text).

The materials of large-scale landscape-ecological survey at the Mendeleev test site were used to construct a general information model describing the ordered system of chain reactions between the state characteristics of natural geo(eco)systems of insular-arc Neo-Pacific (Figure 11). The model presents: the primary (morpho-structural) factors of abiotic environment and their localized geomorphological manifestations, lithoedaphic and hydrothermal conditions, and the floristic and phytocoenotic unities of forest cover. The methods of information model calculation and construction are described in [48].

First of all, the model clearly demonstrates that the considered inter-componental relations are organized into a highly determined system, with its core being the completely dominant

factor of true altitude. It forms low-mountain micro-landscapes of the volcanic cone (the first retransmitter with normalized contingency coefficient C(A;B) = 0.466) by its altitudinal strata (see above) and has a direct effect on floro- and phytocoenotic structures of forest cover, outlining the lithoedaphic and hydrothermal boundary conditions of their differentiation. The C(A;B) coefficient of floristic phratries and groups of forest types with true altitude and micro-landscapes has rather high values (0.322 and 0.325, respectively), which forms the two main channels of inter-componental relations.



Figure 11 General information-statistical model of geo-component interrelations for low mountain ecoregion of Mendeleev landscape. Geo-component blocks: 1 – initial abiotic factors; 2 – second abiotic factors – retransmit-ters; 3 – hydro- and thermo-edaphic conditions; 5 – structure characteristics of forest communities. Normalized coefficient of interrelation C(A;B) between the geo-component attributes: 6 - 0.071 - 0.100; 7 - 0.101 - 0.130; 8 - 0.131 - 0.160; 9 - 0.161 - 0.190; 10 - 0.191 - 0.220; 11 - 0.221 - 0.250; 12 - 0.251 - 0.300; 13 - 0.301 - 0.440; 14 - 0.441 - 0.720.

Representing the vertical differentiation of regional climatic background, altitudinal zonation discloses the principal phenomenal feature of the bioclimatic system at the stage of primary insular-arc biogeocoenogenesis. What is meant here is the direct subordination *of phytobiota to vertical hydrothermal gradients* and the formation of plant communities under climatic conditions similar to the "climate of free atmosphere" [49], with the predominant influence of moist and unstable oceanic air masses [8] and with a relatively low refraction of climatic background by local geomorphological and edaphic factors.

The South-Kunashir low-mountain region has four distinct altitudinal bioclimatic belts (Figure 12, *a* and *b*): (1) coniferous/broad-leaved (of the Manchurian-Okhotsk phratrie); (2) dark-coniferous fir/spruce (Okhotsk); (3) spruce/stone-birch and complex spruce/cedar-elfin-wood/stone-birch (of the Okhotsk-Kamchatka and Okhotsk-Kamchatka-Beringian phratries, respectively); and (4) birch/cedar-elfin-wood (Kamchatka-Beringian).

The force of solar-circulation exposure (the second channel of relations) on the floro- and phytocoenotic structure of plant cover of the volcanogenic-insular ecosystem is more than three times weaker (C(A;B) = 0.109) compared to the factor of true altitude. Nevertheless, there is no denying that the solar-exposure factor has some influence (see Figure 12 *c* and *d*). Coniferous-broadleaf forests are widespread mainly on sub-horizontal surfaces of piedmont plains and marine terraces and occur much less frequently in the lower low-mountain stratum on the NE–E–SE slopes (here, they gravitate rather toward the Pacific sector; however, this question



Figure 12 The binary ordination of forest type groups and floristic phratries by the true altitude and exposure factors. 1 – the ecological dominant; 2 – the "fuzzy" part of ecological niche; 3 – the trajectory connecting ecological dominants; 4 – the space of ecological niche; 5 – the enclave; 6 – the altitu-dinal interval of fractionation of ecological dominants; 7 – the area of sporadic distribution of phe-nomenon within the given gradations of factor. Altitude bioclimatic zones: I – coniferous-deciduous forests; II – dark coniferous forests; III – stone-birch elfin woodland; IV – cedar elfin wood.

is still open because of the lack of test sites). The fir/spruce forests of the Sea-of-Okhotsk flora are confined mainly (by 60%) to the northern and western quarters of the horizon, i.e., the Sea-of-Okhotsk sector, which is warmer and less humid; however, the graphs of relationships show more than 20% occurrence of enclaves belonging to the more humid sector (Pacific Ocean).

The third channel, almost as powerful as the first one (C(A;B) = 321-0.350), goes through the altitudinal-exposure zonation. It is the second retransmitter taking into account the corrections for solar-circulation exposure in vertical zonality. It belongs to the category of dislocation zonality, according to [49], which plays the key role in the bioclimatic system of the Pacific Ocean mega ecotone [34].

During the formation of young island-arc volcanic landscapes, the topological structuralfunctional contrasts encompass the taxonomic norms of soil-biotic characteristics of quite a number of zonal-regional units, which are as though *focused on various forms of lowland microrelief*. Thus, at the initial stages of sub-aerial landscape genesis, the *local geomorphological conditions create the centers of origin of different phytocoenological and soil structures of a higher (zonal-regional) level*. The first cause is the pronounced thermo- and hydroedaphic contrasts formed on local catenas. Such contrasts quite definitely simulate the altitudinal-zonal and expositional differentiation of hydrothermal conditions of forest growth and soil formation.

6 Forest-forming bioclimatic processes on the Far-East branch of the Eurasian boreal ecotone

The Far-East branch of the boreal bioclimatic ecotone of Eurasia [34, 50] embraces the marginal-continental mountain and valley systems of the Lower Priamurye being under specific monsoon-continental climatic conditions [51]. The territory of the Lower Priamurye is part of the Mesozoic morpho-texture and "The Systems of Mountains and Intermontane Valleys of the Middle and Lower Amur River" physical-geographical country [52]. V.B. Sochava [10] includes this territory into the larger Amur-and-Sakhalin physical-geographical domain. It is characterized by two longitudinal-sectoral rows of latitudinal zonality: the eastern one, most completely reflecting the influence of the Pacific monsoon, and the western one with more marked continental features. The mostly mountain relief of this territory predetermined rather high levels of habitat diversity, habitat isolation, and often relative antiquity, the accelerated evolutionary rate in bionts [14,27], and their proper species saturation. In 1931, the well-known biogeographer D.N. Kashkarov wrote that "mountains are a smith's shop where novel species are molded by the environment and developed" [38].

The structural "core" of this part of the Eurasian boreal ecotone is represented by the subtaiga zone [53]. The model territory of the Komsomolsky State Nature Reserve characterizes only the low-mountain/plain part of the Priamurye boreal ecotone (with absolute heights below 1000 m). The Nature Reserve is situated at the zonal boundary between boreal and sub-boreal landscapes of the South of the Far East. In this territory, there is one of the large stands of dark-coniferous and coniferous-broadleaf forests preserved in the Lower Priamurye (Figure 13). The widespread type of soils under forest communities is brownified soils: brown-taiga (including illuvial-humus) soils in the southern taiga and sub-taiga forests and brown (including brown mountain-forest) soils in sub-nemoral forests.



Figure 13 Lower Priamurye. Territory of Komsomolsky State Nature Reserve. The valley of Gorin river, left tributary of Amur river, and surrounding low mountain.

When thoroughly describing the bioclimatic processes in the south of the Far East, B.P. Kolesnikov characterized the forests of this vast ecoregion "... as the forests of mountain valley landscape and monsoon climate, ... highly variable in space and extremely dynamic, i.e., as exclusively multiform, with a versatile appearance" [22]. It is exactly *multiformity* and *dynamic-ity* that make the forest formations of boreal and nemoral Eurasian sub-Pacific different from their intracontinental plain and mountain analogs on the Russian Plain and in West Siberia, in the Ural and Altai Mountains, in the Sayan Mountains and Transbaikalia, in the Carpathian Mountains and in the Alps. These analogs are characterized by a relatively poor and ecologically homogenous set of phytocoenotic components and rather structurally uniform forest types.

In contrast to Western and Eastern Europe, as well as West Siberia, there was no continuous glacial cover throughout the entire Quaternary Period in the South of the Far East, and it had absolutely no effect on the Priamurye plains [17]; therefore, the plant cover here had no developmental hiatus. Beginning from Paleogene/Neogene, the Amur river valley played the role of a vast refugium of the forest, steppe, and floodplain meadow plants of highly different ecology; it also proved to be the arena of their migration pathways [54]. According to the spore-pollen data of coal sediments in the Middle Bikinskaya depression [18], the mixed coniferous/broad-leaved forests grew as early as in the Miocene period (about 25 million years ago), with the involvement of both sub-tropical species and representatives of moderately thermophilic (sub-boreal) and even moderately psychrophilic (boreal) forms.

Thus, the highly contrasting floras in Primorye and Priamurye were mixed long before the Quaternary glaciations, undoubtedly as a result of the influence of the already existing monsoon climate. Previously it was believed [55,56] that the climate in Primorye and Priamurye always remained humid, which must have facilitated the preservation of the floristic richness of forests. However, the later studies [31] showed substantial variations not only in temperature but also in annual precipitation of this region in the Pleistocene and Holocene, which could play a progressive role in forest formation. The varying moisture conditions extremely stimulate morphogenesis [28], which should contribute to the increase in phytocoenological diversity of forests.

The plant cover of Priamurye and Primorye continuously developed while staying under the conditions of monsoon climate for a long time. At a scale of the entire south of the Far East, the transition of flora and vegetation from the Tertiary to Quaternary Period was relatively smooth though wave-like [27, 28], with the migration of single elements of the Tertiary flora from north to south and back and with the intrusion of cold climate species [21]. It resulted in the "assemblage" of flora typical of the Manchurian floristic region [52].

The four basic phratries were distinguished: Manchurian mesophilic (Mm), Manchurian xerophilic (Mx), Okhotian (Okh), and Angaridian (An). The extensive migration and regional

differentiation of the tertiary pra-Manchurian/North Japanese formation [28, 32] resulting in isolation of the above basic floras was accompanied by their *integration* – certain mixing in favorable habitats, with the formation of stable buffer (transient) phratries. We have distinguished two buffer phratries on the territory of Priamurye sub-Pacific: Manchurian–Okhotian (MO) and Manchurian-Angaridian (MA). The buffer Ohkotian-Angaridian phratrie has not been distinguished as it has no independent forest-typological significance.

The formation of a relief-substrate basis under conditions of frequent and dramatic climate changes in the Quaternary Period resulted in the enhanced plasticity of landscapes, while the common trend of continentalization determined still more and more increasing landscape-forming role of climatic processes [53]. There was "... a successive formation of plant cover as surf waves from north and northeast, with sedimentation ... of the products of floristic input" [27]. Therefore, although the Manchurian coniferous-broadleaf forests are rather young, they have been found to be depositories of many ancient elements of the flora (*Alnus japonica, Ulmus laciniata, Quercus mongolica*, etc.), the generic groups of which ascend to the Cretaceous period [29].

As is known [54,55], plant migration in geological history was especially efficient during changes in the land to ocean ratio, with the appearance and disappearance of bridges as a result of tectonic and glacioeustatic processes. The continental margin of Northern Eurasia proved to be the intersection of migration pathways [12]. Such specific and long-term forest-forming processes resulted in a gradual metamorphosis of tertiary thermophilic suboceanic formations into more temperate formations adapted to the marked seasonal hydrothermal contrasts. Even representatives of the contemporary permafrost-taiga flora, "…larch forests during their evolution combined tertiary species and their descendants different in genetic relations and centers of origin" [30]. According to the figurative expression of A.N. Krištofovič, the richness of flora in the South of the Far East "… is merely a result of its saturation to the climatic limit" [21].

The most important factor of these forest-forming processes was the latest tectonic uplifts in the area of the Sikhote-Alin, Badzhalsky, and Bureinsky Ridges, with the emergence of altitudinal bioclimatic zonality and numerous trenches – the foci of formation of continental air masses [56].

In the Quaternary Period, the dominant process was steady subsidence of trenches in the Far East seas, with the involvement of continental margins [3]. Against this background, the higher-frequency glacioeustatic fluctuations of sea level in the Late Pleistocene–Holocene created the transitions (extremely constrained by mountains) from the subtropical belt via taiga to the sub-alpine altitudinal zone [57].

The known meta-chronicity of over-century temperature and precipitation fluctuations in the Pleistocene [58] seemed to be one of the causes of the transgression of the members of cold humid Okhotian flora (first of all, the Ajan spruce), which composed the coniferous taiga zone as early as in the Miocene, into cedar-broadleaf forests [27]. One of the latest transgressions could be such transgression, e.g., in the phase of cedar/spruce/broad-leaved forests at the interface of the Atlantic and sub-boreal periods of the Holocene (4.7–4.1 thousand years ago), during a cold snap at a still high moisture content [31]. This forest-forming process, as a result of Pacific Ocean influence, continues in the Priamurye sub-Pacific at present. Transgression of the members of Angaridian continental flora (in particular, the Dahurian and Cajander larch) proved to be a more localized event associated with climatic inversions under conditions of mountain and valley relief. Nevertheless, the larch area extended during century-long successions, with its intrusion into mixed forests [30].

The result of the described forest-forming processes was the known floristic richness and coenotic diversity of forests in the south of the Far East. First of all, the mixed cedar/broad-leaved and, to a lesser extent, coniferous forests here are characterized by the "assemblage of flora" [59], i.e., the multispecies composition and ecological-biological diversity of phytocoenotic components at all layers. It is associated with the complexity of interspecies relationships and the diversity of forest-forming processes including the age-related, century-long and restorative successions of forest communities. These relationships result in the vertical density (monolithic character) of plant layers, the arrangement of individuals into groups, the presence of many generations in a forest community, the periodical pattern of tree growth in general and any generation in particular, the fierce competition between the species and, as a consequence, the general decrease in the quality class and productivity of forests, which does not correspond to the potentialities of habitats [22].

On the other hand, due to multispecies composition, the age-specific successions of forest stands occur in different habitats by the common helical scheme, with no less than 2–2.5-century cycles [22]. The helical (unclosed) pattern of these cycles is manifested in long-term restorative and even stably-irreversible successions and causes a general tendency to replace cedar in the

stand structure by deciduous species in Primorye and coniferous species (mainly the Ajan spruce) in the Middle and Lower Priamurye. The emerging long-term restorative and even stable naturally irreversible forest communities consist of the members of other forest floras. For the Priamurye, it is the replacement of Manchurian flora by either Okhotian or Angaridian flora. The nonuniform age structure is a characteristic feature of virgin broadleaf-cedar forests [32].

The dramatic spatial variability of forests is determined by the change of habitat conditions, i.e., meso- and micro-scale geomorphological factors and territorial contrasts of oro-climatic interactions, while their multispecies composition and structural diversity result from superposition (interpenetration) of age, century-long and restorative (demutational) successions of forest communities. At the same time, age successions cause gradual qualitative transformations of habitat conditions from generation to generation, primarily the accumulation of organic matter, the changes in the hydrothermal parameters of edaphe-topes, and soil trophicity. Such environment-forming activities of some components of the phytobiota [33] create preconditions for irreversible century-long alternations of basic forest-forming species. Each of these alternations signifies the natural completion of a given climax, with mineral resource depletion in the edaphetope and subsequent succession of the phytocoenosis aimed at restoration of soil resources favorable for the functioning of a new climax [60].

On the Far East boreal ecotone, with its floristic richness of mixed forests and with their complex multilayer structure of different ages, this process has become especially widespread, a vivid example of which is the above-mentioned replacement of Korean cedar by the Ajan spruce, with the development of cedar-spruce and spruce/broad-leaved communities. The multiyear dynamics of cedar/broad-leaved forests, according to the scheme of Ivashkevich–Kolesnikov, is described in detail in the work [32].

In other cases, especially after fires, the process of age-related and century-long alterations of cedar/broad-leaved forests is accompanied by the replacement of cedar by small-leaved species (yellow and Amur birch and aspen), with broad-leaved species (oak, ash, linden) moved towards the middle ground and with mesophilic Manchurian plant species replaced by psychromesophilic taiga species [22]. Such pyrogenic alterations of forest cover can be classified as *explerents* [61]. They are typical of many areas of the Komsomolsk State Nature Reserve, especially in its northeastern, flattest region.

Thus, the century-long phytocoenotic successions, eventually resulting in the substitution of a forest formation for another one, are composed of some stages and, therefore, can be presented as a certain *genetic series of forest groups* [22]. Consequently, the forest type groups distinguished for the ecoregion of the Komsomolsk State Nature Reserve reflect not only the zonal-geographical, altitudinal-zonal and local spatial differentiation of plant cover in this territory but also certain stages of endo-ecogenetic successions [62] in the framework of particular oro-climatic conditions. This is the undoubted complexity of factorial-dynamic ordination of Priamurye sub-Pacific forests, since it is necessary to differentiate between the phytocoenological structures determined by external (climatic, geomorphological, and litho-edaphic) factors, on the one hand, and by the processes of autochthonous development of forest communities, on the other hand; the latter can significantly "blur" the role of some external factor or another, reducing the results of gradient factor analysis of forest type groups and forest biogeocoenoses in general.

The basic regularities of mono-systemic organization of the geographical environment in the Priamurye sub-Pacific at the sub-regional (topological) level are presented in the general information model (Figure 14). In general, the mono-systemic organization of local natural complexes of the low-mountain Lower Amur sub-Pacific is formed by moderate information couplings, from the four initial abiotic factors to phytocoenological characteristics. Normalized coefficient of interrelation C(A;B) = 0.160-0.220 (clarification see in [48]). The predominant relatively low contingency coefficients (≤ 0.130) not only create certain information "noise" in the channeled system of the dominating chain reactions but also make this system more diversified. This testing ground of the Lower Amur sub-Pacific is different from the test grounds of the intracontinental ecoregions of the Russian Plain, where, firstly, the very scheme of landscape connections is thinned out by disappearance of weak links, and secondly, the mutual conjugation of intermediate chain reactions — types of locations and habitats, hydroedaphotopes sharply increases and biogeocenoses ($C(A;B) \geq 0.300-0.450$).

It implies, first, the yet insufficiently developed hierarchic structure of mono-systemic landscape organization in Lower Amur sub-Pacific and, second, the possibility of creating similar (and even analogous) phytocoenological formations at different combinations of geological-geomorphological and hydro-edaphic factors. It leads to the essential diffuse "fuzziness" and fractionation of ecological niches of phytobiota, often to the appearance of several ecological dominants in a niche, to the formation of numerous enclaves distant from the main niche under the influence of local factors and, finally, to the emergence of mixed (buffer) flora-genetic and



Figure 14 General information-statistical model of geo-component interrelations for regional ecosystem on the Pri-amurye sub-Pacific (Komsomolsky Nature Reserve). Normalized coefficient of interrelation C(A;B) between the geo-component attributes: 1 - 0.101 - 0.130; 2 - 0.131 - 0.160; 3 - 0.161 - 0.190; 4 - 0.191 - 0.220; 5 - 0.221 - 0.250; 6 - 0.251 - 0.300; 7 - 0.301 - 0.440.

forest-typological formations.

According to the known concept of plant cover evolution [27, 29], the above characters demonstrate that the given *mono-system landscape structure of the boreal sub-Pacific type* could be created only due to the *migration biogeocoenotic processes implementing this evolution*, which have occurred in the recent past and continue at present. The necessary condition of manifestation of evolutionary processes has been, and still is, the marked seasonal hydrothermal contrasts associated with the monsoon circulation of air masses. They have created and continue to recreate the known florogenetic richness and phytocoenotic diversity of forest cover of the plain and mountain landscapes of Priamurye Sub-Pacific. The complicated structure of intercomponent relationships, with the presence of numerous doubling connections and fractionation or, on the contrary, generalization of information signals at certain stages of their transduction, must ensure rather high stability of phytocoenological and landscape structures during multiyear and supercentury climatic fluctuations.

Judging by the known paleogeographic materials [31, 63, 64], their stability in Primorye and the Amur region during the Pliocene-Quaternary period was supported by relatively weak climatic fluctuations. The latter manifested themselves mainly in temperature variations (January, July and annual temperatures, by not more than $8-13^{\circ}$), in the absence of drought warm epochs. In the warm climatic epochs, the climate was sufficiently humid, which was an important factor in preserving the mixed Manchurian-Okhotian floras. In the cold and more arid epochs, on the contrary, the Manchurian flora was mixed with the Angaridian flora. The low mountain regions and adjacent valleys of the Middle Priamurye (in the area of Komsomolsky nature reserve) were covered with cedar/broad-leaved forests in the Riss-Würm Interglacial epoch (130-75 thousand years ago) and with open larch and birch forests in the climatic minimum of the Late Würm (20-18 thousand years ago), in the absence of periglacial tundras and forest tundras. By analogy with the Quaternary paleogeography of Beringia [12] it may be supposed that the Manchurian and Okhotian floras were mixed in the warm climatic epochs with marine transgressions, while the Manchurian and Angaridian floras were mixed in the cold snap epochs with marine regression. This process was facilitated by the periodic weakening of temperature gradients: latitudinal-zonal in the former case and longitudinal-sectoral in the latter case.

In highlands, natural zonality is much more diverse than on plains as is represented in further development of the Dokuchaev's theory of geographical zonality [51]. The superposition of two principles of regional differentiation of mountain territory (morphotectonic and macroclimatic)

predetermines the entire gamut of zonal phenomena: latitudinal, altitudinal, longitudinal- and exposure-circulatory, barrier, and solar exposure. Being combined, they yield the complex forms of so-called *dislocation zonality*. In this context, zonality is closely related to the concept of vector (gradient) and defined as a regular, spatially ordered trend of changes in the properties of natural complexes in general and of their individual components.

Let us follow the manifestation of dislocation zonality in forest vegetation of the lowmountain boreal ecotone of Priamurye. To this end, let us imagine the oroclimatic system in the territory of the Komsomolsky Nature Reserve as a superposition of two major abiotic factors: true altitude (A) and slope exposure (B). The following three altitudinal bands (and, accordingly, three gradations of this factor) can be distinguished in the sample of our testing areas: A_1 (20–110 m abs.), A_2 (110–310 m), and A_3 (310–680 m). The first band includes the plain and piedmont territories with river valleys, as well as the lower parts of mountain slopes; the second band includes the middle, most part of slopes and peaks of bald mountains; and the third band includes near-peak slopes and crests of the highest ridges.

The binary ordination of the above phytocoenological and landscape indicators by the factor of dislocation zonality (Figure 15), with rather high C(A;B), demonstrates that the altitudinal bioclimatic zonality of low mountains under the conditions of monsoon-continental climate is very selectively manifested and significantly disturbed by exposure contrasts. The measure of partial contingency C(A;B) of floristic phratries and forest types with true altitude is 0,126 and 0,102, respectively, while for the solar exposure of slopes it is even higher: 0,174 and 0157, respectively



Figure 15 The binary ordination of floristic phratries and forest type groups by the factor of altitudinal-exposure (dislocation) zonality. Symbols: 1 – the ecological dominant; 2 – the "fuzzy" part of ecological niche; 3 – the trajectory connecting ecological dominants; 4 – the space of ecological niche; 5 – the enclave; 6 – the altitudinal interval of fragmentation of ecological dominants; 7 – the direction of possible transgression of a given phenomenon from its ecological dominant; 8 – the direction of transgression of basal phratries (or forest type groups), with their mutual displacement and formation of buffer phratries (forest type groups); 9 – the direction of a phenomenon with the given gradations of a factor. I, II, and III – the upper, middle and lower altitudinal layers of low mountains, respectively.

The deflection of altitudinal zonality by the complex factor of circulatory-solar exposure is determined, as one may believe, by the duality of regional bioclimatic system of the southern Far East. What is meant here is the commensurate expression of sub-oceanic latitudinal zonality (broad-leaved forests \leftrightarrow mixed forests \leftrightarrow dark-coniferous forests) and eastern marginal-continental longitudinal sectorality. Sectorality manifests itself first of all in the intrusion of plain and mountain larch forests (representatives of the taiga Angaridian flora) into river valleys and the NW–N–NE–E mountain slopes of the middle band of low mountains, respectively. As a result of mixing the latter with the xerophilic Manchurian flora, the complex larch forests with broad-leaved species belonging to the buffer Manchurian-Angaridian phratrie appeared in the same band and on the slopes of the same exposures.

In addition, there is no unambiguous altitudinal-zonal correspondence of Manchurian floristic phratries as the primary phytocoenological representatives of Priamurye sub-Pacific. The broad-leaved and cedar/broad-leaved forests occur almost over the entire altitudinal profile of low mountains (even though sporadically) and, in addition, have two ecological dominants: (1) xerophytic on the plains and in piedmonts and (2) mesophytic on the southern and southwestern

slopes in the upper band of ridges. The predominant area of fir-spruce forests appears in the same band but on the northeastern slopes; it is the type of forest formations represented by the Okhotian flora.

The typical ecological consequence of dislocation geographical zonality in the low mountains of Priamurye sub-Pacific is the mutual penetration of representatives of different floras into some or other forest type selectively by altitudinal belts and slope exposures. The combination of the true altitude and solar-circulation exposition created certain "ecological corridors" for the *migration flows* of phytobiota and the habitats for *selection* of novel plant communities. Thereby, the conditions were created for evolutionary transformation processes in forest cover in the south of the Far East, according to the concept [27, 29]. The correlation between forest type groups with the forming floristic phratries is exclusively high (the measure of C(A;B) = 0.313). It demonstrates that oro-climatic conditions predetermine certain stability of florogenesis creating some or other type of forest. The stability of florogenesis is also confirmed by the fact that the ecological niches of floristic phratries and forest type groups in the space of dislocation zonality (see Figure 15) are very discrete. They are "fuzzed" very little and represented mainly by their dominant areas and numerous enclaves. There was territorial differentiation of forestformation process by the elements of rather complex dislocation zonality, with the formation of the respective phytocoenological structures. It seems to be one of the mechanisms of origination of the known floristic richness and species abundance in the forests of the Primorye-Priamurye sub-Pacific.

7 Conclusion

The problems of the study of geo(eco)system organization of insular and marginal-continental land in different morphotectonic and macroclimatic sectors of the Pacific ocean mega-ecotone of Northern Eurasia are set forth. The ecological and phytocoenotic effects of oro-climatic interactions along the mega-ecotone are described. The issues of the theory of evolutionary landscape study are considered as a novel trend of complex physical geography; its subject must be the processes and events of landscape formation in the tectonically and climatically active ocean-continent interface. A comprehensive evolutionary landscape-evolutionary concept of organization of terrestrial geo(eco-)systems in the Pacific Ocean Mobile Belt – the tectonically and climatically active ocean-continent interface as a focus of evolutionary ecological and geographical processes and phenomena at the modern stage of development of the biosphere has been set forth. The empirical statistical modeling of forest natural complexes has been performed using the materials of large-scale landscape-ecological surveys performed at experimental sites on the Pacific Ocean mega ecotone of Northern Eurasia. The theses put forward on the basis of evolutionary landscape studies have been substantiated.

The evolutionary model of continental biosphere presented in this book is substantially different from the theses about the "law of geoecosystem evolution of the biosphere" proposed in the works [65, 66]. This concept, applying for the development of V.I. Vernadsky's theory of biosphere, involves consideration of the development of the latter as "… a close spatial-temporal contingency of tectonic-geomorphological evolution of the Earth's surface with the formation of landscape complexes and the related biotic … associations" [66]. The two ecological potentials (ecosystemic and biogeochemical) are proposed to be integral indicators of a paragenetic triad: "tectonics – type of continental lithogenesis – biotic associations". This model corresponds to the "tectonic" hypothesis of "evolutionary-biological effects" on the Kuril Islands [59, 67, 68], which also states the existence of a direct and moreover synchronous relationship between tectonic and phytocoenological processes.

Let us say right away that the logical construction of the authors per se is static and dimensionless (and, in this sense, not geographical). It is hardly able to describe evolution as a multilevel process, because it includes geocomponents with highly diverse, merely incomparable characteristic times. Therefore, there is no point in speaking about the one-to-one (isomorphic) spatial-temporal contingency of the members of this triad, and the authors perceive the basic content of evolution in this very contingency. The representations of lithogenesis in morphotectonics and both of them in soil-biotic components are multiple-valued (homomorphic), and these representations should be considered only as the framework conditions for creating the variety of contacts between different natural environments but not as the biosphere evolution mechanisms per se. The evolutionary mechanisms are concentrated primarily in the transformations of the most high-frequency geocomponents, as it has already been mentioned by V.P. Semenov-Tyanshansky [69].

The morphotectonic predetermination of soil-biotic components is too rough and generalized, adequate only for the largest subdivisions of the biosphere, which are ranked as physical-geographical countries and geographical belts, with their characteristic times of tens and

hundreds of millions of years. This determination prevents from disclosing the entire spatialtemporal diversity of the states and dynamics of biota, which occurs within the same morphostructure and conceals the mechanisms and driving forces of evolutionary process per se.

The most important peculiarities of functioning of the "lithogenic geom – pedon – phytobiota" triad are the incomparability of the temporal frequencies of oscillations, or times of relaxation, of its components, according to [70], as well as the absence of any reliable correlations between them with a more than 3–4-fold difference between their relaxation periods [71], including the age of their modern state. *Such are the real fundamental laws of formation of the biosphere*.

Strictly speaking, our empirical model is also based on such a triad. However, as opposed to the mentioned authors who confine to the scales of large zonal-regional units of Northern Eurasia along the meridian transects, the "center of gravity" of our evolutionary analysis is shifted towards the local (topological) level of natural complexes. It is a basically novel model disclosing rather deep mechanisms of evolutionary processes in the biosphere. As is known, the sphere of ecosystems at the topological level is the most complex and active part of natural environment, its functional "core" [72]. The "matter and energy turnovers of biogeocenoses are interrelated and form a giant cycle of biosphere of the Earth" [73]. The structure and function of topogeo(eco)systems are the sources of global biosphere processes and driving forces of the biosphere evolution [74], and here one should search for the "laws of geoecosystem that we have carried out.

Acknowledgements

The work on the book preparation was supported by the Russian Foundation for Basic Research (grant No. 14-05-00032-a).

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