SPATIAL AND VERTICAL DISTRIBUTION OF LONGICORN BEETLES (COLEOPTERA, CERAMBYCIDAE) IN THE FORESTS OF THE SOUTHERN PART OF THE PRIMORSKY TERRITORY

A. V. Kuprin

Federal Scientific Center of the East Asia Terrestrial Biodiversity, Russian Academy of Sciences,
159 100th anniversary of Vladivostok avenue, Vladivostok, 690022, Russia
E-mail: kyprins@mail.ru

D. A. Yi

Center for the Study of Insect Ecology, Yeongwol Insect Museum, Donggang-ro 716, Yeongwol-gun, Gangwon-do, Republic of Korea
E-mail: zbigstone@hanmail.net

СТАЦИАЛЬНОЕ И ВЕРТИКАЛЬНОЕ РАСПРЕДЕЛЕНИЕ ЖУКОВ-УСАЧЕЙ (COLEOPTERA, CERAMBYCIDAE) В ЛЕСАХ ЮЖНОЙ ЧАСТИ ПРИМОРСКОГО КРАЯ

А. В. Куприн

ФНЦ Биоразнообразия ДВО РАН, Россия, 690022, Владивосток, проспект 100-летия Владивостоку, 159
E-mail: kyprins@mail.ru

Дэ-Ам И

Центр по изучению экологии насекомых, Республика Корея, Канван-до, Йонгволь, ул. Донганд, 716
E-mail: zbigstone@hanmail.net

Abstract. The study of spatial distribution of coleopterous insects in the forest ecosystems of various displacement degrees plays a pivotal role for communities ecology. The present article examines the spatial stratification of the longicorn beetles (Coleoptera, Cerambycidae) in the valley-growing elm and ash forests with Korean pine and in the mountain rhododendron oak-forest. Material is collected by standard entomologic methods using soil and window traps at 6 model sites (five sites are presented by valley-growing forests with dominating of elms, ash tree or Korean pine, and the sixth is by mountain rhododendron oak-forest) with various displacement degree. The information on species composition, habitat conditions and vertical distribution of the longicorn beetles in the forests of the South of the Primorsky Territory has been obtained. It has been established that the biggest number of species is concentrated in the primary forest, community structure of longicorn beetles in these forests has high similarity, which is conditioned by similar space structure of plant association and equal composition of main wood generating species, being both food items and at the same time micro sites for development of larvae of longicorn beetles. Distribution of longicorn beetles has been found by the bio-geological horizons in the old-growth elm forests, the biggest number of species and maximum total abundance are marked on the middle and upper layers of forest canopies. The longicorn beetles, which larvae are sapro-xylo-mycetophages, are indicated to belong to the lower layer, and xylophages longicorn dominate at the upper layer of forest canopy.

Keywords: Coleoptera, Cerambycidae, diversity, abundance, spatial and vertical distribution, forest canopy, Russian Far East.

For citation: Kuprin A.V., Yi D.A. Spatial and vertical distribution of longicorn beetles (Coleoptera, Cerambycidae) in the forests of the southern part of the Primorsky Territory. Russian Journal of Ecosystem Ecology. 2019;4(1). Available from: <https://doi.org/10.21685/2500-0578-2019-1-3>

Аннотация. Актуальность и цели. Изучение пространственного распределения жесткокрылых насекомых в лесных экосистемах разной степени нарушенности имеет фундаментальное значение для экологии сообществ. Работа посвящена изучению пространственной стратификации жуков-усачей (Coleoptera, Cerambycidae) в долинных ильмово-ясеневых лесах с кедром корейским и горным дубняке рододендроновом. Материалы и методы. Сбор материалов осуществлялся стандартными энтомологическими методами с применением почвенных и оконных ловушек на шести модельных участках (пять участков представлены долинными лесами с доминированием ильмов, ясеня или сосны кедровой корейской, а шестой – горным дуб-

няком рододендроновым) с разной степенью нарушенности. **Результаты.** Получены сведения по видовому составу, стациальному и вертикальному распределению жуков-усачей в лесах юга Приморского края. **Выводы.** Установлено, что наибольшее число видов сосредоточено в коренных типах леса, структура сообществ усачей в этих лесах обладает высоким сходством, что обусловлено похожей пространственной структурой фитоценозов и одинаковым составом главных лесообразующих пород, являющихся кормовыми объектами и одновременно микросайтами для развития личинок усачей. Выявлено распределение жуков-усачей по биогеогоризонтам в долинных ильмовниках, наибольшее число видов и максимальное общее обилие отмечены на среднем и верхнем ярусах. Отмечена приуроченность к нижнему ярусу у усачей, личинки которых сапроксило-мицетофаги, а на верхнем доминируют усачи-ксилофаги.

Ключевые слова: жесткокрылые, усачи, разнообразие, обилие, стациальное и вертикальное распределение, верхний ярус леса, Дальний Восток России.

Introduction

The longicorn beetles (Coleoptera, Cerambycidae) are included into one of the most important groups of the xylobiont coleopterous. They play a prominent role in the destruction processes of the spire rot, some of them are secondary insects, and cause vast economic damage to the forest ranges. Currently 240 species of 125 genus of Cerambycidae [1] family have been found in the Primorsky Territory. Good state of exploration of the longicorn beetles' fauna enables their using as models for examining of special distribution of the coleopterous in the forest canopies [2]. Forest canopies comprise hotspots of the biological diversity, which degradation results in the simplification of the biogeochemical cycles and reduction of carbon stocks. Climate fluctuation and human economic activities affect forest canopies through the production change and reflect in the exchange fluxes of the substance and energy. Arthropods forest canopies are among the first to respond to the given changes [3], consequently, finding of the regularities of their special distribution in the ecological systems of various displacement degree presents profound interest.

In recent decades intensive examination of ecology and faunal diversity in forest canopies started all over the world – in Europe (Germany, Switzerland) [4, 5], Asia (Japan, China) [6, 7], Malaysia [8], North and South America (USA, Panama, Venezuela) [9–12], French Guiana [13], and Australia [14]. In 2001–2007 within the framework of the International Biodiversity Observation Year (IBOY), the diversity of insects in the coniferous and broadleaf type of forest at the south of the Primorsky Territory have been studied, which allowed comparing the species composition of the insects communities in the forest ecosystems of the countries in the Pacific Basin: Russia, Japan, Southeast Asia and Australia [14–16]. Later the information of the vertical stratification of the beetles in the primary forests of the Ussurisky Nature Reserve [17] was obtained. The given article shall

be understood as a continuation of this research. It is related to examining the spatial stratification of the longicorn beetles in the valley-growing elm and ash forests with the Korean pine and rhododendron mountain oak-forest.

These forests are widespread in the southern part of the Russian Far East (Primorsky Territory, Amur region, Sakhalin and Southern Kuril Islands), China, Korea and Japan and are characterized by unique combinations of flora and cenogenetic complexes. Due to the epibiotic origin, biogeocenosis of elm and ash forests is specified by poor biopersistence to the human intervention and impossibility of rapid recovery. As a result of high commercial value of the wood of main species the elm and ash forests are disturbed by selection cuttings in most locations of the south of Far East. Old-growth elm and ash forests are preserved generally within the territory of the reserves and can serve as natural samples [18].

The objective of the article is to reveal the species diversity and characteristics of spatial distribution of the longicorn beetles in the valley-growing elm and ash forests of the Ussurisky Nature Reserve and adjoining territory, as well as the impact of anthropogenic factor.

Materials and methods

Study areas

Main studies were conducted in 2016 in the Ussurisky Nature Reserve (now branch of FSC of Biodiversity FEB RAS) and at the adjacent to the western frontier of the territory scientific and experimental forest farm. The Reserve is located to the south of the Primorsky Territory in the area of the mixed coniferous-broad leaved forests, and it covers 40 432 ha [19].

We selected 5 model sites for examining habitat conditions. Four sites were presented by valley-growing forests with dominating elms, ash tree or Korean pine (*Pinus koraiensis*), the fifth – by mountain rhododendron oak forest. Elm and ash forests are associated to bottomlands and terraces

above flood-plains of the mountain rivers with rich and steadily hydrated brown soils on the alluvial deposits with ground elevations up to 250 m above sea level. They are characterized by highly-productive multistoreyed forests of the I-st bonitet and highly developed multispecies bottom levels. Rhododendron oak forests vegetate on stiff slopes with exposure to the south with low-powered rock pavements, not capable to retain moisture. In the

conditions of high soil dryness, low production (IV–V bonitet) forest crops of the Mongolian oak (*Quercus mongolica*) are formed with ill-developed dumetous and field layers [18].

I. Valley-growing ash and elm forest after cleaning cuttings. The site is located in the Komarovsky forest district, near the western frontier of the Reserve, on the left bank of kl. Salnikov (Fig. 1).

Fig. 1. Valley-growing ash and elm forest after cleaning cuttings

The forest stand is presented mainly by the Manchurian ash-tree (*Fraxinus mandshurica*) and Japan elm (*Ulmus japonica*) with admixed Manchurian maple (*Acer mandshuricum*) and mycrophyllous maple (*A. mono*), Manchurian walnut (*Juglans mandshurica*), Korean pine (*Pinus koraiensis*), pilose alder (*Alnus hirsuta*) and Amur cork tree (*Phellodendron amurense*). The common canopy density of trees is 0.3. The undergrowth consists of Manchurian hazel (*Corylus mandshurica*), mock orange (*Philadelphus tenuifolius*), spiny eleuterococcus (*Eleutherococcus senticosus*) and Amur honeysuckle (*Lonicera maackii*). Ferns, sedges, Dutch rush (*Equisetum hyemale*) and herbs are common in the herbaceous layer. Soil is alluvial peaty-gley.

II. Fringe of the of elm and ash forest. The site is located in the district of former settlement Komarovo-Zapovednoye (Fig. 2), on the middle bottomland of Komarovka River. Japan elm, Manchurian maple, painted maple, and pilose alder play main role in the forest stand. The associated species are represented by Korean pine and European bird cherry tree (*Padus avium*). The forest understory is formed by Ural false spiraea (*Sorbaria sorbifolia*), willow-leaf spiraea (*Spiraea salicifolia*), and Amur honeysuckle (*Lonicera maackii*). Tall grasses are composed by Amur aster (*Aster maackii*), meadowsweet palmated (*Filipendula palmata*), *Vale-riana fauriei*. Soil is brown mountain-forest, gley, podzolized, with thick humus horizon. The model site is selected on the fringe of the forest.

Fig. 2. Fringe of the elm and ash forest

III. Rhododendron oak forest. The site is located in the Suvorov forest division on the southwestern slope of a watershed between Shipiza and Koryavaya R. (Fig. 3). The slope ratio is 25–30°. The forest stand consists of Mongolian oak, Manchurian maple with wavers of Korean maple. The total closure of tree canopies is 0.8. Certain bushes of belemnoid rhododendron (*Rhododendron mu-*

cronulatum) and bicoloured bush-clover (*Lespedeza bicolor*) are marked in the understory. The herbaceous layer is weakly developed. Soil is brown earth, typical nonsaturated, extremely fine with averagely developed profile on the eluvium of the crystallized light slates; weakly skeletal in the upper and strongly skeletal in the lower parts of the profile.

Fig. 3. Rhododendron oak forest

IV. Primary elm and ash forest. The site is located in the Komarovo forest division on the right bank of the Komarovka River (Fig. 4). Japan and lobed elms (*U. laciniata*), Manchurian ash-tree, common Amur cork tree, Amur linden (*Tilia*

amurensis) and Korean pine dominate in the forest stand. The shrub layer is formed by Manchurian hazel, Amur honeysuckle and Maximovich (*L. maximowiczii*), Manchurian currant (*Ribes mandshuricum*), and Ural false spiraea.

Fig. 4. Primary elm and ash forest

The basis of herbaceous layer is formed by female fern (*Athyrium filixfemina*) and Chinese (*A. sinense*), thick rhizomatous fern (*Dryopteris crassirhizoma*); white-flowered bittercress (*Cardamin eleucantha*), palmate meadowsweet and Dutch rush. Soil is brown mountain-forest, gley, podzolized, with thick humus horizon.

V. Primary cedar forest with elm and ash-tree. The site is located in the Komarovo forest division in the low bottomland of Mironov kl. (Fig.

5). The common closure of the canopy is 0.8. 2-3-fold covering of canopies is typical for trees. Two stories are designated in the polydominant forest stand. The first stand consists of Korean pine, Yeddo spruce, Japan elm, Amur linden. The average height of trees is approximately 26 m. Mean diameter of stocks is 25–28 cm. The second stand is formed by Yeddo spruce (*Picea ajanensis*), Manchurian maple, Manchurian ash-tree, lobed elm, heart-shaped hornbeam (*Carpinus cordata*).

Fig. 5. Primary cedar forest with elm and ash-tree

The understory of the medium density is represented by maple of false-Ziboldoviy (*A. pseudo-sieboldianum*), Manchurian hazel, Ural false spiraea and other bushes. The field layer is presented by mixed herbs and ferns. Soil is brown soil gley undersaturated fine with averagely developed profile; poorly skeletal in the upper part of the profile and greatly skeletal in the lower part.

Works on vertically-storied distribution of beetles were carried out at one site in the valley of the Komarovka River (Fig. 6). The subject of research is primary Siberian elm with complex structure and various species composition. There is multi species stand; common canopy density is 0.8. It consists of Japan elm, Amur linden, Manchurian ash-tree, Manchurian walnut, Manchurian maple, and Korean pine.

Thin understory – canopy density is less than 0.3. The height of the bushes is from 1.2–2.0 (spiny eleuterococus and sessil-flowered (*E. sessiliflorum*), sacred spindle tree (*Euonymus sacrosanta*), honeysuckle (*L. praeflorens* and Maaka) up to 4–5 m, marbate maple (*A. barbinerve*)). The lianas are presented by kolomikta-vine (*Actinidia kolomikta*) and Amur grape (*Vitis amurensis*). Herbaceous layer is thick (plant cover is 95–100 %), grass height is up to 0.9 m. Main background is created by ostrich fern (*Matteuccia struthiopteris*), in which brushing there are various types of tall grasses. Soil is brown soil gley, poorly-saturated, poorly skeletal with deeply developed profile on the alluvial deposits.

Fig. 6. Old-growth elm forest

Data sampling

Field works were carried out from April to October 2016. Collecting of longicorn imago is effected from the surface of stocks of feeding trees,

using window traps, which were installed on the stocks of wood raw materials [20], as well as from flowering herbaceous plants, on which beetles have supplemental nutrition. Types were identified with Key to the insects of Russian Far East (1986)

[1], the material in the entomology laboratory collection formerly IBSS FEB RAS (currently FSC of East Asia Terrestrial Biodiversity of FEB RAS), Vladivostok, was additionally examined.

The line consisting of 15 pitfall traps ($n = 15$) has been equipped for examining vertical-storeyed distribution of insects on site in the old-growth elm forest. Window traps, by one at each level were hung up over them at height of 1 m (medium level) and 22 m (upper level). Exposing were carried out from April 15 to October 15, extracting of the material from window traps were carried out once in a decade.

Data analysis

Statistical data processing and charts construction were conducted using programs PAST – PAleontological STatistics, version 1.57 [21] and Microsoft Excel. As similarity the ratio of Tchekanovskiy-Serensen [22] was used. Statistical assurance of clustering is assessed using bootstrap

analysis in 1000 replications. Systematics and nomenclature of longicorn beetles (Cerambycoidea) follow M. L. Danilevskiy (2018) [23].

Results and discussion

Spatial distribution. As a result of the executed studies it was found that the complex of the longicorn beetles of valley-growing forests of the Ussurisky Nature Reserve consists of 71 species from 6 subfamilies (Table 1), which amounts 40 % from all fauna of Cerambycidae of the reservation [24]. The basis of the species diversity is formed by representatives of three subfamilies: Lepturinae (29 species, 16,5 % of fauna from reservation), Cerambycidae (19 species, 11 %), and Lamiinae (17 species or 10 %).

Within the examined habitats the cenotic range of species of the longicorn varies from 19 to 65, and the number of collected samples is from 52 to 198 (Table 1).

Table 1

Spatial distribution and abundance of the longicorn beetles on model sites in the Ussurisky Nature Reserve (within the whole period of research)

Species	I	II	III	IV	V	Abundance
1	2	3	4	5	6	7
Subfamily Prioninae Latreille, 1802						
1. <i>Callipogon (Eoxenus) relictus</i> (Semenov, 1899)	0	0	0	1	0	1
2. <i>Prionus insularis insularis</i> (Motschulsky, 1858)	0	1	1	1	0	3
Subfamily Lepturinae Latreille, 1802						
3. <i>Rhagium inquisitor rugipenne</i> (Reitter, 1898)	0	1	0	0	1	2
4. <i>Stenocorus amurensis</i> (Kraatz, 1879)	1	1	1	1	0	4
5. <i>Pachyta bicuneata</i> (Motschulsky, 1860)	0	1	0	0	2	3
6. <i>Pachyta lamed lamed</i> (Linnaeus, 1758)	0	1	0	0	4	5
7. <i>Brachyta amurensis</i> (Kraatz, 1879)	2	6	1	7	9	25
8. <i>Paragaurotus ussuriensis</i> (Blessig, 1873)	0	2	0	3	6	11
9. <i>Euracmaeops angusticollis</i> (Gebler, 1833)	0	0	0	1	1	2
10. <i>Dinoptera minuta minuta</i> (Gebler, 1832)	0	0	0	2	1	3
11. <i>Cortodera ussuriensis</i> (Tsherepanov, 1978)	1	1	0	1	1	4
12. <i>Pidonia (Mumon) debilis</i> (Kraatz, 1879)	0	1	0	3	1	5
13. <i>Pidonia (Pseudopidonia) amurensis</i> (Pic, 1900)	1	1	0	1	1	4
14. <i>Sachalinobia koltzei</i> (Heyden, 1887)	0	0	0	1	1	2
15. <i>Nivellia extensa</i> (Gebler, 1841)	5	1	3	5	4	18
16. <i>Nivellia sanguinosa</i> (Gyllenhal, 1827)	9	2	6	7	6	30
17. <i>Strangalomorpha tenuis tenuis</i> (Solsky, 1873)	1	0	0	1	1	3
18. <i>Pseudalosterna elegantula</i> (Kraatz, 1879)	0	0	0	1	0	1
19. <i>Anoplodera (Anoploderomorpha) cyanea</i> (Gebler, 1832)	1	1	3	5	8	18
20. <i>Stictoleptura (Aredolpona) dichroa</i> (Blanchard, 1871)	1	1	1	2	3	8
21. <i>Stictoleptura (Variileptura) variicornis</i> (Dalman, 1817)	1	1	1	4	3	10
22. <i>Anastrangalia renardi</i> (Gebler, 1848)	0	0	0	6	7	13
23. <i>Pedostrangalia (Neosphenalia) femoralis</i> (Motschulsky, 1860)	0	0	0	1	0	1
24. <i>Judolia dentatofasciata</i> (Mannerheim, 1852)	0	0	0	2	3	5
25. <i>Pachytodes longipes</i> (Gebler, 1832)	4	2	5	7	9	27
26. <i>Oedecnema gebleri</i> (Ganglbauer, 1889)	12	7	8	10	14	51
27. <i>Leptura (Macroleptura) thoracica</i> (Creutzer, 1799)	1	0	0	5	8	14
28. <i>Leptura annularis annularis</i> (Fabricius, 1801)	3	2	5	6	9	25
29. <i>Leptura duodecimguttata</i> (Fabricius, 1801)	6	3	2	7	5	23
30. <i>Leptura aethiops</i> (Poda, 1761)	1	3	2	5	4	15
31. <i>Strangalia attenuata</i> (Linnaeus, 1758)	4	5	8	11	17	45

End of Table 1

1	2	3	4	5	6	7
Subfamily Necydalinae Latreille, 1825						
32. <i>Necydalis major</i> (Linnaeus, 1758)	0	0	0	0	1	1
33. <i>Necydalis (Necydalisca) pennata</i> (Lewis, 1879)	0	0	0	1	0	1
Subfamily Spondylidinae Serville, 1832						
34. <i>Megasemum quadricostulatum</i> (Kraatz, 1879)	0	0	0	1	1	2
35. <i>Tetropium castaneum</i> (Linnaeus, 1758)	0	0	0	2	1	3
Subfamily Cerambycinae Latreille, 1802						
36. <i>Neocerambyx raddei</i> (Blessig, 1872)	0	0	1	0	0	1
37. <i>Rosalia coelestis</i> (Semenov, 1911)	1	1	0	1	1	4
38. <i>Purpuricenus sideriger</i> (Fairmer, 1888)	5	8	0	9	6	28
39. <i>Amarysius sanguinipennis</i> (Blessig, 1872)	1	0	0	1	1	3
40. <i>Chloridolum sieversi</i> (Ganglbauer, 1887)	0	0	0	3	2	5
41. <i>Aromia orientalis</i> (Plavilstshikov, 1932)	1	1	0	1	1	4
42. <i>Molorchus starki</i> (Shabliovskiy, 1936)	0	0	0	1	1	2
43. <i>Molorchus (Caenoptera) minor</i> (Linnaeus, 1767)	0	0	0	1	1	2
44. <i>Rhopalopus (Prorrhopalopus) signaticollis</i> (Solsky, 1872)	1	1	0	1	0	3
45. <i>Oupyrrhidium cinnabarinum</i> (Blessig, 1872)	2	4	1	5	3	15
46. <i>Callidium violaceum</i> (Linnaeus, 1758)	0	0	0	2	2	4
47. <i>Phymatodes (Poecilium) maacki</i> (Kraatz, 1879)	0	0	0	1	0	1
48. <i>Teratoclytus plavilstshikovi</i> (Zaitzev, 1937)	0	0	0	1	0	1
49. <i>Rhabdoclytus acutivittis</i> (Kraatz, 1879)	1	3	0	1	2	7
50. <i>Rhaphuma diminuta diminuta</i> (Bates, 1873)	0	0	0	1	0	1
51. <i>Rhaphuma gracilipes</i> (Faldermann, 1835)	0	0	0	1	0	1
52. <i>Xylotrechus cuneipennis</i> (Kraatz, 1879)	0	0	0	1	1	2
53. <i>Clytus nigrifrons</i> (Kraatz, 1879)	0	0	0	1	1	2
54. <i>Cyrtoclytus capra</i> (Germar, 1824)	0	0	0	1	1	2
Subfamily Lamiinae Latreille, 1825						
55. <i>Moechotypa diphyis</i> (Pascoe, 1871)	0	0	0	1	3	4
56. <i>Mesosa myops</i> (Dalman, 1817)	0	0	0	2	2	4
57. <i>Monochamus guttulatus</i> (Gressitt, 1951)	0	0	0	0	1	1
58. <i>Monochamus urussovii</i> (Fischer von Waldheim, 1805)	0	0	0	5	8	13
59. <i>Lamiomimus gotschei</i> (Kolbe, 1886)	0	0	0	2	1	3
60. <i>Lamia textor</i> (Linnaeus, 1758)	0	0	0	1	0	1
61. <i>Olenecamptus octopustulatus</i> (Motschulsky, 1860)	0	1	0	1	0	2
62. <i>Pterolophia maacki</i> (Blessig, 1873)	0	0	0	1	0	1
63. <i>Exocentrus marginatus</i> (Tsherepanov, 1973)	0	0	0	1	1	2
64. <i>Eutetrappa metallescens</i> (Motschulsky, 1860)	3	4	0	8	10	25
65. <i>Eutetrappa sedecimpunctata sedecimpunctata</i> (Motschulsky, 1860)	0	1	0	5	4	10
66. <i>Saperda (Lopezcolonia) perforata</i> (Pallas, 1773)	1	0	0	2	5	8
67. <i>Saperda (Lopezcolonia) interrupta</i> (Gebler, 1825)	2	1	0	3	2	8
68. <i>Menesia sulphurata</i> (Gebler, 1825)	0	0	0	1	0	1
69. <i>Thyestilla gebleri</i> (Faldermann, 1835)	3	2	1	3	4	13
70. <i>Agapanthia (Amurobia) amurensis</i> (Kraatz, 1879)	2	1	1	1	1	6
71. <i>Agapanthia (Epoptes) daurica</i> (Ganglbauer, 1884)	2	2	1	1	1	7
Total number of samples	79	74	52	182	198	585
Total number of species	31	34	19	65	56	71

Note. The list of species is given in the classified order. The number of samples of longicorn beetles collected using window traps is shown by Arabic figures. The model sites: I – Valley-growing ash and elm forest after cleaning cutting, II – Fringe of the of elm and ash forest, III – Rhododendron oak forest, IV – Primary elm and ash forest, V – Primary cedar forest with elm and ash-tree are expressed in Roman numerals.

As could be expected, the highest abundance of species refers to primary types of forest: elm and ash forest (IV) (65 species or 36.9 % from fauna of the reservation) and cedar forest with elm and ash-tree (V) (consequently 56 species and 31.8 %).

In the primary forests the dominant group is represented by the following species of longicorn beetles: *Brachyta amurensis* Kraatz, 1879, *Nivellia sanguinosa* (Gyllenhal, 1827), *Nivellia extensa* (Gebler, 1841), *Anoplodera (Anoploderomorpha)*

cyanea (Gebler, 1832), *Pachytodes longipes* (Gebler, 1832), *Oedecnema gebleri* (Ganglbauer, 1889), *Leptura (Macroleptura) thoracica* (Creutzer, 1799), *Strangalia attenuata* (Linnaeus, 1758), *Leptura duodecimoguttata* (Fabricius, 1801).

Relict longicorn beetle (*Callipogon (Eoxenus) relictus*) (Semenov, 1899) (Fig. 7) included into the Russian Red Book was found only in the pri-

mary elm and ash forest. This species is typical for declining mixed coniferous-broad leaved forests of the Russian Far East, North-East China and Korean Peninsula, and it is annually registered in the reservation in the valley-growing elm forests. The development of its larvae is effected in the lumber of the broad-leaved species [25–28].

Fig. 7. Female of the relict longicorn beetle (*Callipogon relictus*) using supplemental nutrition (a) and females during egg laying (b) in the primary elm and ash forest

The primary forests are similar not only by the number of beetles, but also by dominant composition. Therewith in the cedar forest with elm and ash forest the number of species developing in the wood of coniferous trees is just over than in the wood of broad-leaved species of the elm forest. Such species include representatives of subfamily Lamiinae: *Eutetrappa metallescens* (Motschulsky, 1860), *Moechotypa diphysis* (Pascoe, 1871), *Mesosa myops* (Dalman, 1817), *Monochamus guttulatus* (Gressitt, 1951), *Monochamus urussovii* (Fischer von Waldheim, 1805).

Assemblies of longicorn beetles of the valley-growing ash and elm forest after cleaning cutting (I) and edge of the elm and ash forest (II) by number of species and collected samples are approximately equal to 31 (17.6 % from fauna of the reserve) and 34 (19.3 %) of species consequently. The dominating complex is represented by the species of Lepturinae: *Brachyta amurensis* (Kraatz, 1879), *Nivellia extensa* (Gebler, 1841), *Nivellia sanguinosa* (Gyllenhal, 1827), *Pachytodes longipes* (Gebler, 1832), *Oedecnema gebleri* (Ganglbauer, 1889), *Strangalia attenuata* (Linnaeus, 1758). The subdominants are *Paragaurotes ussuriensis* (Blessig, 1873), *Leptura aethiops* (Poda, 1761), *Agapanthia (Amurobia) amurensis* (Kraatz, 1879), *Agapanthia (Epopetes) daurica* (Ganglbauer, 1884). The domination of Lepturinae in these types of the forest is conditioned by higher level of insolation as compared to climax forests and availabil-

ity of various plants, at which additional nutrition of longicorn imago takes place during blooming period. These assemblages are distinct – singular samples of red book longicorn beetle *Rosalia coelestis* (Semenov, 1911) were trapped in them. This species is common in well-lit sites in the large-leaved and in the mixed coniferous broad-leaved forests of the Ussurisky Nature Reserve and often registers in its surroundings. Larvae of *Rosalia coelestis* are developed in the dried out stocks of the manchus maple (*Acer tegmentosum*) and false-Ziboldov [24].

The poorest fauna is marked in the rhododendron oak forest (III), 19 species (10.8 % from fauna of the reservation) were found here. The dominating species in the samples are *Nivellia sanguinosa* (Gyllenhal, 1827), *Oedecnema gebleri* (Ganglbauer, 1889), *Strangalia attenuata* (Linnaeus, 1758), subdominants – *Nivellia extensa* (Gebler, 1841), *Anoplodera (Anoplocleromorpha) cyanea* (Gebler, 1832), *Leptura duodecimoguttata* (Fabricius, 1801), *Leptura aethiops* (Poda, 1761). The rest species are presented by singular findings.

Using of clustering analysis for comparing of lists of species of the longicorn beetles of the model sites showed that two clusters are allocated under the similarity ratio of 0.42 (bootstrap-value is 100 %) (Fig. 8). The first cluster combines rhododendron oak forest (III), valley-growing ash and elm forest after cleaning cuttings (I) and the fringe of elm and ash forest (II) (similarity ratio is 0.68,

bootstrap-value is 91 %), and the second cluster – primary elm and ash forest (IV) and primary cedar forest with elm and ash-tree (V) (similarity ratio is 0.72, bootstrap-value is 99 %). Combining into single cluster of site (IV) and (V) at high similarity level is explained by similar environmental and microclimatic conditions, availability of polydominant phytocenosis with complex structure and various species composition of lower decks. It enables

longicorn beetles to have a vast range of possibilities for implementing trophic and topographical couplings within the habitat. It should be noted that the similarity of disturbed phytocenosis is as high to each other as similarity of primary and varies drastically from the oak forest. In this case we undoubtedly deal with similarity of soil conditions, equal by moistening degree.

Fig. 8. Dendrogram of similarity of species composition of the longicorn beetles of explored habitats (Ratio of Tchekanovskiy-Sørensen, bootstrap is 1000). Designation of sites see Table 1

Vertical distribution of longicorn beetles

131 samples of beetles relating to 40 species (23 % from fauna of the Ussurisky Nature Reserve) were collected in the old-growth elm forest.

Species composition, imago distribution by the storeys and total abundance of cerambycids are presented in Table 2.

Table 2

Species composition and abundance of the longicorn beetles (Cerambycidae) at the various storeys in the old-growth elm forest for the whole period of research

Species	0 m	1 m	22 m	Abundance	Total, %
1	2	3	4	5	6
1. <i>Prionus insularis insularis</i> (Motschulsky, 1858)	2			2	1,53
2. <i>Pachyta bicuneata</i> (Motschulsky, 1860)		5	1	6	4,58
3. <i>Pachyta lamed lamed</i> (Linnaeus, 1758)		4	1	5	3,82
4. <i>Brachyta amurensis</i> (Kraatz, 1879)		1		1	0,76
5. <i>Stictoleptura (Aredolpona) dichroa</i> (Blanchard, 1871)		2		2	1,53
6. <i>Judolia dentatofasciata</i> (Mannerheim, 1852)		3		3	2,29
7. <i>Oedecnema gebleri</i> (Ganglbauer, 1889)		5		5	3,82
8. <i>Leptura (Macroleptura) thoracica</i> (Creutzer, 1799)		1	1	2	1,53
9. <i>Leptura annularis annularis</i> (Fabricius, 1801)		1	1	2	1,53
10. <i>Leptura duodecimguttata</i> (Fabricius, 1801)		2	1	3	2,29
11. <i>Leptura aethiops</i> (Poda, 1761)		1		1	0,76
12. <i>Necydalis major</i> (Linnaeus, 1758)		1		1	0,76

End of Table 2

1	2	3	4	5	6
13. <i>Necydalis (Necydalisca) pennata</i> (Lewis, 1879)		1	1	2	1,53
14. <i>Megasemum quadricostulatum</i> (Kraatz, 1879)	1			1	0,76
15. <i>Tetropium castaneum</i> (Linnaeus, 1758)		1	1	2	1,53
16. <i>Neocerambyx raddei</i> (Blessig, 1872)		2	2	4	3,05
17. <i>Purpuricenus sideriger</i> (Fairmer, 1888)	1	1		2	1,53
18. <i>Amarysius sanguinipennis</i> (Blessig, 1872)		1	1	2	1,53
19. <i>Chloridolum sieversi</i> (Ganglbauer, 1887)			1	1	0,76
20. <i>Oupyrrhidium cinnabarinum</i> (Blessig, 1872)		5	1	6	4,58
21. <i>Rhabdoclytus acutivittis</i> (Kraatz, 1879)		6		6	4,58
22. <i>Clytus nigrutilus</i> (Kraatz, 1879)			2	2	1,53
23. <i>Cyrtoclytus capra</i> (Germar, 1824)		2		2	1,53
24. <i>Moechotypa diphysis</i> (Pascoe, 1871)		1	2	3	2,29
25. <i>Mesosa myops</i> (Dalman, 1817)	1	2		3	2,29
26. <i>Monochamus guttulatus</i> (Gressitt, 1951)			1	1	0,76
27. <i>Monochamus urussovii</i> (Fischer von Waldheim, 1805)			4	4	3,05
28. <i>Lamiomimus gottschei</i> (Kolbe, 1886)			1	1	0,76
29. <i>Lamia textor</i> (Linnaeus, 1758)			1	1	0,76
30. <i>Olenecamptus octopustulatus</i> (Motschulsky, 1860)		1		1	0,76
31. <i>Pterolophia maacki</i> (Blessig, 1873)	1	2		3	2,29
32. <i>Exocentrus marginatus</i> (Tsherepanov, 1973)		2	3	5	3,82
33. <i>Eutetrappa metallescens</i> (Motschulsky, 1860)		4	11	15	11,45
34. <i>Eutetrappa sedecimpunctata sedecimpunctata</i> (Motschulsky, 1860)		3		3	2,29
35. <i>Saperda (Lopezcolonia) perforata</i> (Pallas, 1773)		4		4	3,05
36. <i>Saperda (Lopezcolonia) interrupta</i> (Gebler, 1825)		4	1	5	3,82
37. <i>Menesia sulphurata</i> (Gebler, 1825)		2	1	3	2,29
38. <i>Thyestilla gebleri</i> (Faldermann, 1835)	5	1		6	4,58
39. <i>Agapanthia (Amurobia) amurensis</i> (Kraatz, 1879)		3	1	4	3,05
40. <i>Agapanthia (Epoptes) daurica</i> (Ganglbauer, 1884)		5	1	6	4,58
Total number of samples	11	79	41	131	100
Total number of species	6	32	23	40	40

The biggest number of species and general abundance are marked on the middle (32 species, 79 samples) and upper (23 species, 41 samples) forest canopies levels. 6 species of longicorn beetles (11 samples) are found on the lower (soil surface) level. Our information is consistent with the obtained data for the forest of central Japan [29], however, it does not confirm the conclusion that in the upper storeys of forest canopies the number of insects is higher comparing with the lower storeys [30–34].

Confinedness to the certain storeys was indicated in *Prionus insularisinsularis* (Motschulsky, 1858) and *Megasemum quadricostulatum* (Kraatz, 1879), which larvae are xylo-mycetobionts and are developed in the decaying wood on the basis of tree and roots of hard wood, consequently these types are marked only on the surface of the soil.

Clear confinedness of certain species of longicorn beetles to the middle storey of forest canopies was not detected. High total abundance of longicorn imago (60,3 %) and species diversity in this storey probably related to the availability in this part of phytocenose of high species abundance of plants, primarily shrubs, used for additional nutri-

tion of Cerambycids imago within blooming period. Similar regularity was found earlier for tropical forests of Australia. According to the information of P. Grimbacher and N. Stork (2007) [35], vertical distribution of insects including insects is determined by the number and composition of plant elements (branches with leaves, stocks, liana, fossil parts and epiphytes) on the given specific altitude level. High diversity of species and abundance of antophags of the other families of beetles in the given storey was also found by us in the similar habitats of the reservation [17].

Marked confinedness to the upper storey of forest canopies is marked in *Monochamus guttulatus*, *Monochamus urussovii*, *Lamia textor*, *Lamiomimus gottschei* and in *Chloridolum sieversi*. Total abundance of these beetles in this storey was 6 %. The first three species are xylophages. At the stage of imago their species flaw cortex and wood of cuttings of feeding plants. The larvae of these species are developed in the wood of vigorous trees. It is shown that invasion of xylophages on the vigorous tree is effected from the top downward, i.e. from canopy to the root part [36, 37]. Thus, vertical distribution of the beetles in the forest eco-

systems of the South of the Primorsky Territory is defined by their functional traits. Earlier it was revealed that by increasing height the number of phytophagans is increased and the number of zoophages, coprophages and necrophages is decreased [20].

Conclusion

1) 71 species of longicorn beetles from 6 subfamilies which consists in approximately 40 % from all fauna of the reserve were found in the examined forests. The basis of species diversity is composed by the representatives of three subfamilies: Lepturinae (29 species, 16.5 % of fauna from the reserve), Cerambycinae (19 species, 11 %), and Lamiinae (17 species or 10 %). The rest of subfamilies (Prioninae, Necydalinae and Spondylidinae) have only by 2 species in each;

2) The analysis of horizontal distribution of the longicorn beetles showed that the biggest number of species is concentrated in the primary types of the forest: valley-growing elm and ash forest and in the cedar forest with elm and ash tree. The structure of assemblies of the longicorn beetles in these forests have high similarity (72 %), which is conditioned by similar spatial structure of phytocenosis and equal composition of main forest forming species, being food items and simultaneously by microsites for development of larvae of the longicorn beetles. The least species diversity of the longicorn beetles is marked in the rhododendron oak forest, which can be related to its lower productivity and uniform micro habitat conditions;

3) The assemblies of the longicorn beetles in ash and elm forest, passed by cleaning cuttings, and on the edge of elm and ash forest by number of species and collected samples are approximately equal. The core of the complex in these plants is representatives of Lepturinae family. Their domination is conditioned by high level of insolation

and complex composition of flowering plants, at which additional nutrition of longicorn imago takes place during blooming period. The longicorn beetles of this subfamily have low species specificity – almost all types occurred in two or more types of forest;

4) When examining vertical distribution of the longicorn beetles it was found that the biggest number of species and maximum total abundance were marked at the middle and upper levels of forest canopies, and the least – at the lower level. Confinedness to the lower level of the longicorn beetles was found, which larvae are sapro-xylo-mycetophages and develop in the fossil wood of the root part of stock or roots of trees. Longicorn beetles-xylophages, which imago have additional nutrition and which larvae are developed in the wood of vigorous trees, dominate at the upper altitude level;

5) The underwood storey is not only trophic habitat but also reproduction habitat and adverse conditions for many forest anthophilous, hortophilous and dendrophilous species of the longicorn beetles. High common abundance and species diversity of longicorn imago in the underwood storey (0–1 m) is related probably to the availability of big stocks of crop of various composition (fallen stocks, foliate branches, lianas and etc.), and ground mass of flowering grass and shrubs is concentrated in this storey.

Acknowledgements

The authors express much appreciation to the director of the Ussurisky Nature Reserve A. Kotlyar for the opportunity to carry out the study, Dr. Sci. T. Moskalyuk for valuable guidelines and help in the geobotanical descriptions of the model sites, as well as to all the colleagues taking part in collecting and processing of the material: V. Kovalev, Dr. L. Fedina and Dr. M. Maslov.

References

1. Сем. Cerambycidae – Усачи, или дровосеки / Г. Ш. Лафер, А. Б. Егоров, Г. О. Криволуцкая, А. Н. Купянская, А. С. Лелей ; под ред. П. Г. Немкова // Определитель насекомых Дальнего Востока России. – Владивосток : Дальнаука, 1996. – Т. 3 (3). – С. 56–140.
2. Vertical and seasonal distribution of flying beetles in a suburban temperate deciduous forest collected by water pan trap / A. S. Leksono, K. Takada, S. Koji, N. Nakagoshi, T. Anggraeni, K. Nakamura // Insect Science. – 2005. – Vol. 12. – P. 199–206.
3. Forests and their canopies: achievements and horizons in canopy science / A. Nakamura, R. L. Kitching, C. Min, T. J. Creedy, T. M. Fayle, M. Freiberg, C. N. Hewitt, I. Takao, P. K. Lian, K. Ma, Y. Malhi, A. Mitchell, V. Novotny, C. M. P. Ozanne, S. Liang, H. Wang, L. A. Ashton // Trends in Ecology and Evolution. – 2017. – Vol. 32. – P. 438–451.
4. Canopy arthropod research in Europe: basic and applied studies from the high frontier / ed. by A. Floren, J. Schmidl. – Bioform, 2008. – 576 p.
5. Stork, N. E. The spatial distribution of beetles within the canopies of oak trees in Richmond Park, U.K. / N. E. Stork, P. M. Hammond, B. L. Russel, W. L. Hadwen // Ecological Entomology. – 2001. – Vol. 26. – P. 302–311.

6. Vertical stratification of spider assemblages in two conifer plantations in central Japan / H. Oguri, T. Yoshida, A. Nakamura, M. Soga, N. Hijii // *Journal of Arachnology*. – 2014. – Vol. 42. – P. 34–43.
7. Partitioning beta diversity in a subtropical broad-leaved forest of China / P. Legendre, X. Mi, H. Ren, K. Ma, M. Yu, I. F. Sun, F. He // *Ecology*. – 2009. – Vol. 90. – P. 663–674.
8. Chung, A. Y. C. Vertical stratification of beetles (Coleoptera) using flight intercept traps in a lowland rainforest of Sabah, Malaysia / A. Y. C. Chung // *Sepilok Bulletin*. – 2004. – Vol. 1. – P. 29–41.
9. Schowalter, T. Vertical and seasonal variation in canopy arthropod communities in an old-growth conifer forest in southwestern Washington, USA / T. Schowalter, L. Ganio // *Bulletin of Entomological Research*. – 1998. – Vol. 88. – P. 633–640.
10. Herbivory in epiphytic bromeliads, orchids and ferns in a Mexican montane forest / M. Winkler, K. Hülber, K. Mehlreter, J. Franco, P. Hietz // *Journal of Tropical Ecology*. – 2005. – Vol. 21. – P. 147–154.
11. Preisser, E. Canopy and ground level insect distribution in a temperate forest / E. Preisser, D. C. Smith, M. D. Lowman // *Selbyana*. – 1998. – Vol. 19. – P. 141–146.
12. Basset, Y. Short-term effects of canopy openness on insect herbivores in a rain forest in Guyana / Y. Basset, E. Charles, D. S. Hammond, V. K. Brown // *Journal of Applied Ecology*. – 2001. – Vol. 38. – P. 1045–1058.
13. Janda, M. Canopy assemblages of ants in a New Guinea rain forest / M. Janda, M. Konecna // *Journal of Tropical Ecology*. – 2011. – Vol. 27. – P. 83–91.
14. Stork, N. E. Beetle assemblages from an Australian tropical rain forest show that the canopy and the ground strata contribute equally to biodiversity / N. E. Stork, P. S. Grimbacher // *Proceedings of the Royal Society B: Biological Sciences*. – 2006. – Vol. 273. – P. 1969–1975.
15. Стороженко, С. Ю. Международный год изучения биоразнообразия (ИБОУ): насекомые лесных экосистем Приморского края / С. Ю. Стороженко, В. С. Сидоренко, Г. Ш. Лафер, С. К. Холин // *Чтения памяти А. И. Куренцова*. – 2003. – Вып. 13. – С. 31–52.
16. Barsulo, C. Y. Abundance and diversity of flying beetles (Coleoptera) collected by window traps in Satoyama pine forests in Noto peninsula, Japan, with special reference to the management conditions: a family level analysis / C. Y. Barsulo, K. Nakamura // *Far Eastern Entomologist*. – 2011. – Vol. 222. – P. 1–23.
17. Kuprin, A. V. Stratification and diversity of beetles (Insecta, Coleoptera) in native elm forests of the Ussuri Nature Reserve, Russia / A. V. Kuprin, A. Drumont // *Entomology and Applied Science Letters*. – 2016. – Vol. 3. – P. 1–8.
18. Флора, растительность и микобиота заповедника «Уссурийский»: монография / отв. ред. Л. Н. Васильева. – Владивосток: Дальнаука, 2006. – 300 с.
19. Абрамов, В. К. Уссурийский заповедник им. В. Л. Комарова / В. К. Абрамов, Б. С. Петропавловский, С. С. Харкевич // *Вестник ДВО РАН*. – 1996. – № 1. – С. 70–78.
20. Куприн, А. В. Экология и биология жесткокрылых (Coleoptera) в долинных лесах Уссурийского заповедника: автореф. дис. ... канд. биол. наук / Куприн А. В. – Владивосток, 2012. – 19 с.
21. Hammer, Ø. PAST: Paleontological Statistics Software Package for Education and Data Analysis / Ø. Hammer, D. A. T. Harper, P. D. Ryan // *Palaeontologia Electronica*. – 2001. – Vol. 4. – P. 1–9.
22. Песенко, Ю. А. Принципы и методы количественного анализа в фаунистических исследованиях / Ю. А. Песенко. – Москва: Наука, 1982. – 136 с.
23. Danilevsky, M. L. A check list of the longicorn beetles (Cerambycoidea) of Russia / M. L. Danilevsky. – 2018b. – URL: <http://www.zin.ru/Animalia/Coleoptera/rus/danlistr.htm> (accessed at 18.02.2019).
24. Kuprin, A. V. The longicorn beetles (Insecta, Coleoptera: Cerambycidae) of the Ussuri Nature Reserve and adjacent territories / A. V. Kuprin // *Far Eastern Entomologist*. – 2016. – Vol. 309. – P. 21–28.
25. Kuprin, A. V. Areal of *Callipogon relictus* Semenov, 1899 (Coleoptera, Cerambycidae) in the Russian Far East / A. V. Kuprin, V. G. Bezborodov // *Biology Bulletin*. – 2012. – Vol. 4. – P. 387–391.
26. Survey research on the habitation and biological information of *Callipogon relictus* Semenov (Coleoptera, Cerambycidae, Prioninae) in Gwangneung forest, Korea and Ussurisky nature reserve, Russia / S. G. Lee, C. Kim, A. V. Kuprin, J.-H. Kang, B.-W. Lee, S. H. Oh, J. Lim // *Zookeys*. – 2018. – Vol. 792. – P. 45–68.
27. Yi, D. A. Distribution of the longhorned beetle *Callipogon relictus* (Coleoptera: Cerambycidae) in Northeast Asia / D. A. Yi, A. V. Kuprin, Y. J. Bae // *Zootaxa*. – 2018. – Vol. 4369. – P. 101–108.
28. Lee, S. G. A review of host plants of *Callipogon (Eoxenus) relictus* Semenov (Coleoptera: Cerambycidae: Prioninae), a Korea natural monument, with a new host, *Quercus aliena* Blume / S. G. Lee, C. Kim, I. J. Choi, A. V. Kuprin, J. Lim // *Journal of Asia-Pacific Entomology*. – 2019. – Vol. 22. – P. 353–358.
29. Leksono, A. S. Species composition of Modellidae and Cerambycidae (Coleoptera) in a coppice woodland / A. S. Leksono, S. K. Takada, N. Nakagoshi, K. Nakamura // *Journal of Forest Research*. – 2006. – Vol. 11. – P. 61–64.
30. Sutton, S. L. The vertical distribution of flying insects in the lowland rain forest of Panama, Papua New Guinea and Brunei / S. L. Sutton, C. P. Ash, A. Grundy // *Zoological Journal of the Linnean Society*. – 1983. – Vol. 78. – P. 287–297.
31. Sutton, S. L. The spatial distribution of flying insects in tropical rain forest / S. L. Sutton // *Ecosystems of the World*; ed. by H. Leith, M. J. A. Werger. – Amsterdam: Elsevier, 1989. – P. 427–436.
32. Basset, Y. Abundance and stratification of foliage arthropods in a lowland rain forest of Cameroon / Y. Basset, H. P. Aberlenc, G. Delvare // *Ecological Entomology*. – 1992. – Vol. 17. – P. 310–318.

33. Schowalter, T. D. Vertical and seasonal variation in canopy arthropod communities in an old-growth conifer forest in southwestern WA, USA / T. D. Schowalter, L. M. Ganio // *Bulletin of Entomological Research*. – 1998. – Vol. 88. – P. 633–640.
34. Shaw, D. C. Vertical organization of canopy biota / D. C. Shaw // *Forest Canopies*; ed. by M. D. Lowman, H. B. Rinker. – New York: Elsevier; Academic Press, 2004. – P. 73–101.
35. Grimbacher, P. S. Vertical stratification of feeding guilds and body size in beetle assemblages from an Australian tropical rainforest / P. S. Grimbacher, N. E. Stork // *Australian Ecology*. – 2007. – Vol. 32. – P. 77–85.
36. Мамаев, Б. М. Биология насекомых – разрушителей древесины / Б. М. Мамаев // *Итоги науки и техники. Энтомология*. – Москва: ВИНТИ, 1977. – Т. 3. – 213 с.
37. Исаев, А. С. Взаимодействие дерева и насекомых ксилофагов (на примере лиственницы сибирской) / А. С. Исаев, Г. И. Гирс. – Новосибирск: Наука, 1975. – 347 с.

References

1. Lafer G. Sh., Egorov A. B., Krivoluckaya G. O., Kupyanskaya A. N., Lelej A. S. *Opredelitel' nasekomykh Dal'nego Vostoka Rossii* [Identification guide of insects in the Russian Far East]. Vladivostok: Dal'nauka, 1996, vol. 3 (3), pp. 56–140.
2. Leksono A. S., Takada K., Koji S., Nakagoshi N., Anggraeni T., Nakamura K. *Insect Science*. 2005, vol. 12, pp. 199–206.
3. Nakamura A., Kitching R. L., Min C., Creedy T. J., Fayle T. M., Freiberg M., Hewitt C. N., Takao I., Lian P. K., Ma K., Malhi Y., Mitchell A., Novotny V., Ozanne C. M. P., Liang S., Wang H., Ashton L. A. *Trends in Ecology and Evolution*. 2017, vol. 32, pp. 438–451.
4. *Canopy arthropod research in Europe: basic and applied studies from the high frontier*. Ed. by A. Floren, J. Schmidl. Bioform, 2008, 576 p.
5. Stork N. E., Hammond P. M., Russel B. L., Hadwen W. L. *Ecological Entomology*. 2001, vol. 26, pp. 302–311.
6. Oguri H., Yoshida T., Nakamura A., Soga M., Hijii N. *Journal of Arachnology*. 2014, vol. 42, pp. 34–43.
7. Legendre P., Mi X., Ren H., Ma K., Yu M., Sun I. F., He F. *Ecology*. 2009, vol. 90, pp. 663–674.
8. Chung A. Y. C. *Sepilok Bulletin*. 2004, vol. 1, pp. 29–41.
9. Schowalter T., Ganio L. *Bulletin of Entomological Research*. 1998, vol. 88, pp. 633–640.
10. Winkler M., Hülber K., Mehlreter K., Franco J., Hietz P. *Journal of Tropical Ecology*. 2005, vol. 21, pp. 147–154.
11. Preisser E., Smith D. C., Lowman M. D. *Selbyana*. 1998, vol. 19, pp. 141–146.
12. Basset Y., Charles E., Hammond D. S., Brown V. K. *Journal of Applied Ecology*. 2001, vol. 38, pp. 1045–1058.
13. Janda M., Konecna M. *Journal of Tropical Ecology*. 2011, vol. 27, pp. 83–91.
14. Stork N. E., Grimbacher P. S. *Proceedings of the Royal Society B: Biological Sciences*. 2006, vol. 273, pp. 1969–1975.
15. Storozhenko S. Yu., Sidorenko V. S., Lafer G. Sh., Holin S. K. *Chteniya pamyati A. I. Kurencova* [A.I. Kurentsov memorial lectures]. 2003, iss. 13, pp. 31–52.
16. Barsulo C. Y., Nakamura K. *Far Eastern Entomologist*. 2011, vol. 222, pp. 1–23.
17. Kuprin A. V., Drumont A. *Entomology and Applied Science Letters*. 2016, vol. 3, pp. 1–8.
18. *Flora, rastitel'nost' i mikrobiota zapovednika «Ussurijskij»: monografiya* [Flora, vegetation and mycobiota in the Ussurisky Nature Reserve: monograph]. Execut. ed. L. N. Vasil'eva. Vladivostok: Dal'nauka, 2006, 300 p.
19. Abramov V. K., Petropavlovskij B. S., Harkevich S. S. *Vestnik DVO RAN* [Bulletin of the Far East Branch of the Russian Academy of Sciences]. 1996, no. 1, pp. 70–78.
20. Kuprin A. V. *Ekologiya i biologiya zhestkokrylykh (Coleoptera) v dolinnykh lesakh Ussurijskogo zapovednika: avtoref. dis. kand. biol. nauk* [Ecology and biology of beetles (Coleoptera) in the valley forests of the Ussurisky Nature Reserve: abstract of thesis of the Candidate of Biological Sciences]. Vladivostok, 2012, 19 p.
21. Hammer Ø., Harper D. A. T., Ryan P. D. *Palaeontologia Electronica*. 2001, vol. 4, pp. 1–9.
22. Pesenko Yu. A. *Principy i metody kolichestvennogo analiza v faunisticheskikh issledovaniyakh* [Principles and methods of quantitative analysis in faunal studies]. Moscow: Nauka, 1982, 136 p.
23. Danilevsky M. L. *A check list of the longicorn beetles (Cerambycoidea) of Russia*. 2018b. Available at: <http://www.zin.ru/Animalia/Coleoptera/rus/danlistr.htm> (accessed at 18.02.2019).
24. Kuprin A. V. *Far Eastern Entomologist*. 2016, vol. 309, pp. 21–28.
25. Kuprin A. V., Bezborodov V. G. *Biology Bulletin*. 2012, vol. 4, pp. 387–391.
26. Lee S. G., Kim C., Kuprin A. V., Kang J.-H., Lee B.-W., Oh S. H., Lim J. *Zookeys*. 2018, vol. 792, pp. 45–68.
27. Yi D. A., Kuprin A. V., Bae Y. J. *Zootaxa*. 2018, vol. 4369, pp. 101–108.
28. Lee S. G., Kim C., Choi I. J., Kuprin A. V., Lim J. *Journal of Asia-Pacific Entomology*. 2019, vol. 22, pp. 353–358.
29. Leksono A. S., Takada S. K., Nakagoshi N., Nakamura K. *Journal of Forest Research*. 2006, vol. 11, pp. 61–64.
30. Sutton S. L., Ash C. P., Grundy A. *Zoological Journal of the Linnean Society*. 1983, vol. 78, pp. 287–297.
31. Sutton S. L. *Ecosystems of the Worl*. Amsterdam: Elsevier, 1989, pp. 427–436.
32. Basset Y., Aberlenc H. P., Delvare G. *Ecological Entomology*. 1992, vol. 17, pp. 310–318.
33. Schowalter T. D., Ganio L. M. *Bulletin of Entomological Research*. 1998, vol. 88, pp. 633–640.

34. Shaw D. C. *Forest Canopies*. New York: Elsevier; Academic Press, 2004, pp. 73–101.
35. Grimbacher P. S., Stork N. E. *Australian Ecology*. 2007, vol. 32, pp. 77–85.
36. Mamaev B. M. *Itogi nauki i tekhniki. Entomologiya* [Science and technology findings. Entomology]. Moscow: VINITI, 1977, vol. 3, 213 p.
37. Isaev A. S., Girs G. I. *Vzaimodejstvie dereva i nasekomyh ksilofagov (na primere listvennicy sibirskoj)* [Interaction of trees and xylophage insects: case study of Siberian larch]. Novosibirsk: Nauka, 1975, 347 p.