

# Spring distribution of beetles (Coleoptera: Carabidae) in abandoned agroecosystems and surrounding forests

*Sergei Alekseev*<sup>1</sup>, and *Alexander Ruchin*<sup>2\*</sup>

<sup>1</sup> Parks Directorate of Kaluga Region, 248000, Kaluga, Russia

<sup>2</sup> Joint Directorate of the Mordovia State Nature Reserve and National Park "Smolny", 430005 Saransk, Russia

**Abstract.** In most habitats in temperate zones, Carabidae show clear intra-annual changes in abundance and species composition. In the spring, we studied the beetle fauna in 5 different biotopes differing in the degree of overgrowth of the birch forest over a period of three years. According to three years of research, 10,528 specimens (64 species from 6 subfamilies) were collected. Twelve species of beetles were found in all biotopes. The highest numbers were obtained in the 12-15-year birch forest; the lowest numbers were obtained in abandoned lands. The highest biodiversity was obtained in the ecotone at the border of young birch forest and fallow lands. A high Shannon Biodiversity Index and a low Simpson Index indicate that the communities of beetles in the abandoned lands are equalized. There is a significant dominance of 1–3 species in fallow lands overgrown with birch forests.

## 1 Introduction

Carabid beetles as inhabitants of the soil surface are found in a wide variety of landscapes, including sites of varying degrees of anthropogenic transformation [1]. They play an essential role in forest ecosystems, agroecosystems, and other ecosystems as entomophages regulating the number of terrestrial invertebrates [2–4]. On the other hand, some plant-eating beetle species can harm crops [5, 6]. In ecosystem studies, Carabidae have long been used as bioindicators of landscape conditions [7–10]. The intensification of agricultural land use in recent decades has resulted in the simplification of agricultural landscapes worldwide and the substantial loss of habitats important for species diversity. The reduction of breeding, migration, offspring development, and feeding habitats in agroecosystems resulting from landscape transformation has led to a decrease in the species diversity of Carabidae [11–14].

Various aspects of the seasonal dynamics of Carabidae communities attract the attention of researchers. Since they are a convenient object for ecological monitoring, the dynamics of Carabidae communities can serve as an indicator of the state of ecosystem functioning, degradation or restoration. The early-season (spring) species composition, comparative

---

\* Corresponding author: [ruchin.alexander@gmail.com](mailto:ruchin.alexander@gmail.com)

abundance, and activity of beetles in the Republic of Mordovia have not been previously discussed and analyzed in publications. In the present study, we investigated the spatial distribution of Carabidae in early spring in overgrown fields, around field borders and birch forests of different ages.

## 2 Materials and methods

The Republic of Mordovia is located in the center of European Russia between the rivers Moksha and Sura (tributaries of the Volga). The eastern part of Mordovia occupies the northwest of the Volga Uplands. The western part of the region is located in the eastern part of the Oka-Don Lowlands. In this regard, there is a diversity of habitats in the study area. Forest-steppe landscapes predominate in the east and southeast. Broadleaved forests cover the central and eastern parts. There are many agricultural landscapes in the central and eastern part of the region. Some of these landscapes are no longer used in agriculture due to poor soil quality, and they are gradually overgrown with forest tree species (mainly pine and birch) [15].

The material for this study was collected in the Republic of Mordovia (Lyambir District) for three years in May. Five biotopes, differing in the degree of development and projective coverage of the tree layer, were investigated:

- Plot 1. Abandoned lands – abandoned agroecosystem, which is overgrown with ruderal herbaceous vegetation. The basis of perennial grasses is various species of cereals and *Echium vulgare*. The grass height is about 20 cm. Projective coverage of herbaceous plants – 70%. There are no trees and shrubs.
- Plot 2. Ecotone – is a border biotope (sharp border between plot 1 and plot 3).
- Plot 3. This plot is a 4-6-year birch forest. The birch forest grows on the site of abandoned agroecosystems. The first layer of the forest consists entirely of birch. The height of the trees is up to 2 m. The crowns of the trees are closing in. There are no shrubs and herbaceous plants. The soil is bare, in some places covered with dry leaves.
- Plot 4. This plot is a 12-15-year birch forest. The first layer of the forest consists entirely of birch. The birch forest grows on the site of abandoned agroecosystems. The height of the trees is 4-5 m. The tree stand is very dense; the crowns are closed. Shrubs and herbaceous plants are practically absent. The soil is covered with a layer of last year leaves.
- Plot 5. This plot is a 27-32-year birch forest. The first layer of the forest consists entirely of birch. The birch forest is of secondary origin. The height of the trees is 15-18 m. The crowns are clear, the tree stand is sparse. The shrub layer of rowan, buckthorn and bird cherry is well-defined. The herbaceous layer consists of perennial plants of various species. This plot is a typical birch forest that grows in the centre of European Russia.

We used the traditional method of collecting ground Coleoptera – pitfall traps. One line of pitfall traps was installed in each biotope. The traps were 0.5-litre cups containing 200 ml of 4% formalin solution. We set up 10 cups in each biotope. The distance between the traps was 1.1–1.3 m. The material collected was identified by S.K. Alekseev. The identification was done according to Müller-Motzfeld [16] and Isaev [17]. We followed the proposed nomenclature in Lobl and Lobl publication [18]. In the species list, the subfamilies are arranged in systematic order and the species in the subfamilies are arranged alphabetically.

In order to establish the dominance structure, the classes of beetle abundance were determined according to the following scale: eudominant species were those with catchability above 20%, dominant species – from 5 to 20%, subdominant species – from 3 to 5%, rare species (recedents) – from 1 to 3% and occasional species (subrecedents) – less

than 1%. The similarity of beetle groupings was assessed using the Jaccard index. The Shannon index was used to assess diversity, the Simpson index was used to assess evenness.

3 Results

Based on three years of research, 1,528 specimens were collected. The biodiversity of Carabidae in the surveyed area is 64 species from 6 subfamilies. Significant differences were found in the species diversity and abundance of Carabidae in individual plots (Table 1).

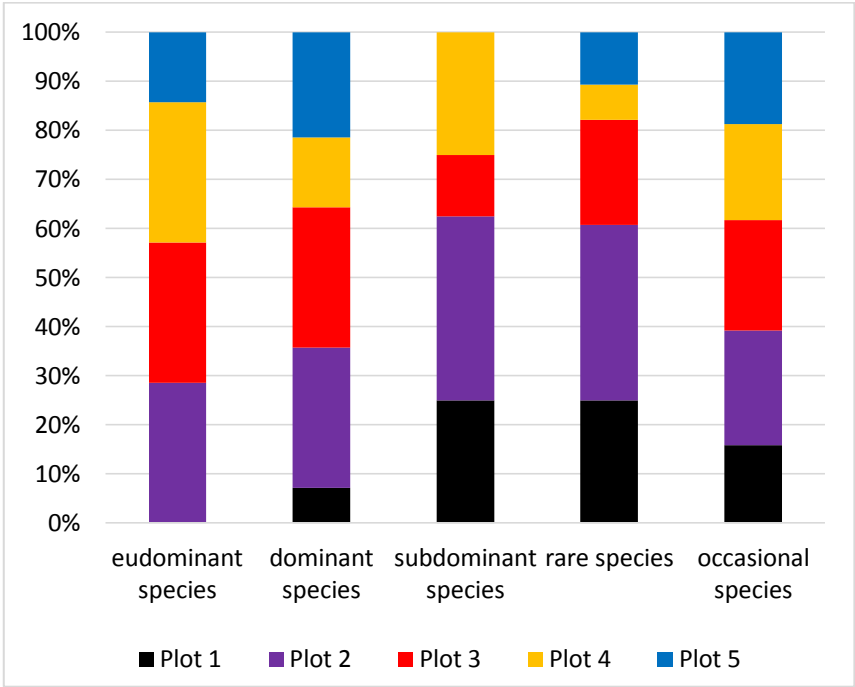
**Table 1.** Biodiversity, distribution in biotopes and catchability (ind./100 trap-days) of ground beetles (total data for three years).

Species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Total
<b>Carabinae</b>						
<i>Carabus cancellatus</i> Illiger, 1798	0.65	1.45	1.13	0.32	2.90	40
<i>Carabus convexus</i> Fabricius, 1775	1.29	0.48	0.65	0.97		21
<i>Carabus hortensis</i> Linnaeus, 1758			0.32	0.32		4
<i>Carabus granulatus</i> Linnaeus, 1758	1.13	5.81	16.13	14.03	10.48	295
<i>Carabus schoenherri</i> Fischer von Waldheim, 1820					0.65	4
<b>Cicindelinae</b>						
<i>Cicindela campestris</i> Linnaeus, 1758		0.48				3
<b>Broscinae</b>						
<i>Broscus cephalotes</i> (Linnaeus, 1758)		0.16				1
<b>Harpalinae</b>						
<i>Acupalpus meridianus</i> (Linnaeus, 1761)		0.16				1
<i>Agonum gracilipes</i> (Duftschmid, 1812)			0.32	0.32	0.16	5
<i>Agonum sexpunctatum</i> (Linnaeus, 1758)		0.16				1
<i>Amara aenea</i> (De Geer, 1774)	2.74	5.00	1.45	3.75	0.16	70
<i>Amara apricaria</i> (Paykull, 1790)			0.16			1
<i>Amara aulica</i> (Panzer, 1796)		0.16	0.16			2
<i>Amara communis</i> (Panzer, 1797)	1.29	1.77	0.48	0.81	0.48	30
<i>Amara eurynota</i> (Panzer, 1796)	0.16	0.16	0.32			4
<i>Amara familiaris</i> (Duftschmid, 1812)	0.16	1.13	0.32	0.16	0.16	12
<i>Amara ingenua</i> (Duftschmid, 1812)					0.32	2
<i>Amara ovata</i> (Fabricius, 1792)	0.48					3
<i>Amara nitida</i> Sturm, 1825	0.48	3.71	1.29	0.16	0.65	39
<i>Amara plebeja</i> (Gyllenhal, 1810)		0.16				1
<i>Amara tibialis</i> (Paykull, 1798)		0.16				1
<i>Anchomenus dorsalis</i> (Pontoppidan, 1763)	6.13	7.90	37.26	8.39	1.45	379
<i>Anisodactylus binotatus</i> (Fabricius, 1787)	0.65	0.65			0.16	9
<i>Anisodactylus nemorivagus</i> (Duftschmid, 1812)	0.16					1
<i>Badister lacertosus</i> Sturm, 1815				0.48	0.48	6
<i>Calathus fuscipes</i> (Goeze, 1777)			0.16			1
<i>Calathus melanocephalus</i> (Linnaeus, 1758)			0.16	0.32		3
<i>Callistus lunatus</i> (Fabricius, 1775)	0.48	1.77	0.65			18
<i>Harpalus affinis</i> (Schränk, 1781)	2.58	1.77	1.29	0.16	0.65	40
<i>Harpalus distinguendus</i> (Duftschmid, 1812)	0.32	0.65		0.16		7
<i>Harpalus griseus</i> (Panzer, 1796)		0.16	0.32			3
<i>Harpalus latus</i> (Linnaeus, 1758)		0.32				2
<i>Harpalus progrediens</i> Schaubberger, 1922	1.45	0.65	1.29	0.16		22
<i>Harpalus rubripes</i> (Duftschmid, 1812)	4.52	7.26	5.48	1.13	0.48	117
<i>Harpalus rufipes</i> (De Geer, 1774)		1.13	0.81	0.16	0.81	18
<i>Harpalus signaticornis</i> (Duftschmid, 1812)	0.16	0.48			0.16	5
<i>Harpalus tardus</i> (Panzer, 1796)	0.48	0.16				4
<i>Harpalus xanthopus winkleri</i> Schaubberger, 1923		0.48				3
<i>Lebia cruxminor</i> (Linnaeus, 1758)	1.45	0.65				13

Species	Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Total
<i>Limodromus assimilis</i> (Paykull, 1790)				0.32	2.10	15
<i>Microlestes minutulus</i> (Goeze, 1777)		0.16				1
<i>Ophonus cordatus</i> (Duftschmid, 1812)					0.16	1
<i>Ophonus puncticeps</i> Stephens, 1828	0.16	0.32			0.16	4
<i>Panagaeus bipustulatus</i> (Fabricius, 1775)			0.16			1
<i>Poecilus cupreus</i> (Linnaeus, 1758)	0.81	77.58	17.90	37.90	6.61	873
<i>Poecilus lepidus</i> (Leske, 1785)	0.81	1.77	0.81	0.65	0.16	26
<i>Poecilus punctulatus</i> (Schaller, 1783)		0.65				4
<i>Poecilus versicolor</i> (Sturm, 1824)	4.84	85.81	321.13	775.00	121.29	8110
<i>Pterostichus diligens</i> (Sturm, 1824)		0.16				1
<i>Pterostichus melanarius</i> (Illiger, 1798)			0.65	3.55	7.90	75
<i>Pterostichus niger</i> (Schaller, 1783)		1.29	2.26	0.32	0.32	26
<i>Pterostichus nigrata</i> (Paykull, 1790)		0.16				1
<i>Pterostichus strenuus</i> (Panzer, 1796)		0.65	0.32	0.32	0.16	9
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)			0.65	2.90	0.65	26
<i>Pterostichus vernalis</i> (Panzer, 1796)		0.16	0.32			3
<i>Syntomus truncatellus</i> (Linnaeus, 1761)				0.16		1
<b>Nebrinae</b>						
<i>Leistus ferrugineus</i> (Linnaeus, 1758)			0.32			2
<i>Notiophilus palustris</i> (Duftschmid, 1812)			0.16	0.48		4
<b>Trechinae</b>						
<i>Asaphidion flavipes</i> (Linnaeus, 1761)	0.97	2.42	5.16	0.48		56
<i>Asaphidion pallipes</i> (Duftschmid, 1812)			0.16			1
<i>Bembidion lampros</i> (Herbst, 1784)	1.61	4.19	3.06		0.48	58
<i>Bembidion properans</i> (Stephens, 1828)	0.48	4.03	0.16	0.32		31
<i>Bembidion quadrimaculatum</i> (Linnaeus, 1761)		1.13	0.16			8
<b>Number of species</b>	<b>27</b>	<b>44</b>	<b>37</b>	<b>29</b>	<b>27</b>	<b>64</b>
<b>Shannon Index</b>	<b>2.82</b>	<b>1.94</b>	<b>1.09</b>	<b>0.47</b>	<b>1.11</b>	<b>1.11</b>
<b>Simpson Index</b>	<b>0.18</b>	<b>0.27</b>	<b>0.59</b>	<b>0.83</b>	<b>0.58</b>	<b>0.60</b>
<b>Total of trap-days</b>	<b>620</b>	<b>620</b>	<b>620</b>	<b>620</b>	<b>620</b>	<b>3100</b>
<b>Total of individuals</b>	<b>226</b>	<b>1398</b>	<b>2626</b>	<b>5285</b>	<b>993</b>	<b>10528</b>

Twelve species were found in all habitats (*Carabus cancellatus*, *Carabus granulatus*, *Amara aenea*, *Amara communis*, *Amara familiaris*, *Amara nitida*, *Anchomenus dorsalis*, *Harpalus affinis*, *Harpalus rubripes*, *Poecilus cupreus*, *Poecilus lepidus*, *Poecilus versicolor*). The minimum number of individuals was characteristic of plot 1 (abandoned lands). However, in this biotope the calculated Shannon index showed the maximum value, while the Simpson Index was the minimum. In the remaining habitats, the total abundance of Carabidae was higher than in plot 1. Plot 4 was particularly abundant, capturing 50.2% of the sum of all individuals from all plots. However, the species diversity of beetles on plot 4 was almost the same as on plot 1. The increase in the number of individuals captured was due to multiples of one species – *Poecilus versicolor*. The Shannon Index was therefore calculated to be very low and the Simpson index very high, which shows the dominance of the species in captures.

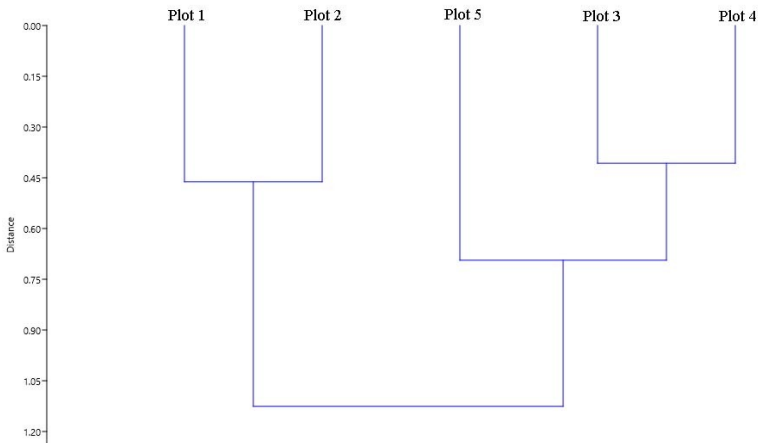
In plot 1, *Poecilus versicolor* did not outnumber *Anchomenus dorsalis* and was comparable in abundance to *Harpalus rubripes*. Thus, plot 1 was dominated by 3 species. Two species, *Poecilus versicolor* and *Poecilus cupreus*, dominated plot 2. The structure of species dominance differed from plots to plots. Thus no eudominant species were identified in plot 1 (Figure 1). Dominants were represented by 1 species (3.7% of species composition of ground beetles) and subdominants by 2 species (7.4% of species composition of ground beetles).



**Fig. 1.** Distribution of Carabidae species by dominance classes in different biotopes in early spring.

There were no subdominant species in plot 5. Significant relative numbers of rare species were observed only in the first three plots. It is at the expense of rare species that the biodiversity of ground beetles has increased in plot 2. Let us note that in all habitats occasional species were the backbone of the beetle community.

The plots were divided into two clusters according to the Jaccard index. One includes abandoned lands and ecotone, while the second cluster includes the remaining three plots (Figure 2). In the second case, plot 3 and plot 4 were as similar as possible in terms of species diversity, while being slightly different from plot 5.



**Fig. 2.** The similarity of beetle species composition between all sampling variants based on the Jaccard index.

## 4 Discussion

Due to the decline in agriculture in the 1990s, there were a number of abandoned lands in the central regions of Russia, which began to overgrow with trees. This usually took place on lands with crushed or sandy soils that were not suitable for cultivation. The study of the natural overgrowth of abandoned agricultural lands is of interest to forestry theory and practice. Pioneer species, birch and aspen, dominate the natural regeneration on unused agricultural lands. Such regeneration occurs as a result of the influx of tree seeds into areas that have been cleared of forest. The birch is one of the most active pioneer species. Due to its high seed and seedling reproductive capacity, it intensively invades all suitable land devoid of forest vegetation. When the areas are densely populated, the birch successfully competes with meadow vegetation and forms birch associations of different forest types. The dense self-seeding of birch on agricultural lands after canopy closure depresses the herbaceous vegetation. Resilient living ground cover, usually represented by shade-tolerant species, develops 10-15 years after self-seeding in the field, a sustainable forest ecosystem with all layers after 30-35 years [19–21].

Most studies on the impact of abandoned lands and their subsequent overgrowth on insects have assessed the density and species richness in the communities [22, 23]. It remains unknown whether arthropod predator species colonise fallow lands from the surrounding landscape with larvae living in the soil, or whether individuals emerge locally from fallow soils. Studies have shown that the total number of species from different beetle families varied considerably between arable fields and meadows [24, 25].

In our studies, we obtained data that show a significant difference in the spring fauna of Carabidae in fallow lands and birch forests growing on these sites. The species diversity of Carabidae was significantly higher in the ecotone at the edge of fallow lands and young birch forest. Similar data are found in other studies [26, 27]. The Shannon biodiversity index and the Simpson index show that beetle communities are equilibrated in the abandoned lands. Similar information was obtained in a fallow study in Sweden, where the highest Shannon index values were obtained in fallow lands after crops with thin and low vegetation of small perennial and annual grasses [28].

This was not observed in the other plots, as a significant dominance of one or two species was obtained. There is evidence of a significant role of litter for Carabidae. For example, the addition of litter has affected the community structure of Carabidae, increasing catches of some species and decreasing catches of one species [29]. This probably explains the super-dominance of *Poecilus versicolor* in plot 4, where litter was most expressed compared to the other plots.

In general, between 3 (plot 1) and 9 (plot 2) species of common ground beetles (eudominant, dominant and subdominant species) were identified in all surveyed plots. The increase in the number of common species in plot 2 is due to the appearance of species that actively move between the two biotopes in this area.

In spring, *Poecilus versicolor* proved to be the main dominant species in the plots 2–5 studied. This species clearly preferred forested biotopes and was most abundant in 12-15-year birch forests, where projective cover of herbaceous plants is minimal. This species occurs in meadows, fields and heathland, often in agrosystems. *Poecilus versicolor* is more xerophilic than *Poecilus cupreus*. *Poecilus versicolor* prefers fairly dry, sandy soil with scattered vegetation. It is occasionally found together with clay-sandy soil [30, 31]. It is a predator, but the beetles sometimes damage mushroom pulp, fruit, sprouted seeds and fallen fruit in orchards. *Poecilus versicolor* tolerates very severe anthropogenic transformation of forest ecosystems; often abundant in areas affected by fires, clearcuts, natural disasters [30, 32].

Catchability of *Poecilus cupreus* in abandoned lands is recorded at a very low level than in birch forests. And the greatest catchability is obtained in the ecotone on the border of open biotope and birch forest. It is a eurybiont species that reaches its greatest abundance within the steppe zone in fields and meadows and is often found in agroecosystems [33]. It is considered a predator that sometimes damages crops. There is evidence that *Poecilus cupreus* abundance correlates positively with tree crown thinning [33]. However, in our studies in plot 5, with a sparser tree stand and sparse crown, the numbers of the species were lower than in plots with a more closed crown. In Italy, *Poecilus cupreus* was dominant in all recovered habitats in the agricultural area [31].

*Anchomenus dorsalis* is found in a variety of habitats, but more commonly in open, sunny and dry areas, sometimes covered by tall loose vegetation [34]. On the other hand, there is evidence that the abundance of this species is higher in forested areas with low crown density and maximum grass cover [35]. In our spring surveys, catchability of *Anchomenus dorsalis* was most abundant in plot 3 (4-6-year birch forest), plot 4 and plot 2, i.e. the highest numbers were found in areas with dense crowns and almost no herbaceous cover.

Catchability of *Carabus granulatus* was the greatest in birch forests of different ages. According to other publications, the species is an active predator and is found in a variety of biotopes. But it prefers forest ecosystems with varying degrees of moisture, litter development and crown cover [32, 36, 37]. *Harpalus rubripes* clearly preferred abandoned lands, ecotones and young birch forests, where its catchability was high. It occurs in a variety of biotopes, but has a definite preference for open habitats, including those disturbed by human activity [32, 38, 39].

Catchability of *Pterostichus melanarius* was high in a 27-32-year birch forest. *Pterostichus melanarius* is a generally eurytopic species that inhabits a wide range of biotopes. It occurs in meadows, pastures, orchards and forests [40, 41]. It is resistant to anthropogenic influences [42]. In our surveys, it was not recorded in meadows and young birch forests, occurring only in older forests.

## 5 Conclusion

Differences were found in the spring beetle fauna in five different biotopes, which differ from each other in the degree and timing of birch forest overgrowth. 64 species from 6 subfamilies were identified. Twelve species of beetles were found in all biotopes, which are eurytopic and quite common in the centre of European Russia. The highest total numbers of Carabidae were obtained in 12-15 year birch forest, the lowest numbers were obtained in abandoned lands. However, the highest biodiversity was obtained in the ecotone at the border between young birch forest and fallow lands. A high Shannon Index and a low Simpson Index indicate that the beetle communities are equalized in the abandoned lands. In fallow lands with birch forest overgrowth, there is a significant dominance of 1-3 eurytopic species, which worsens the calculated values of these indexes. Differences in biotope preference over other parts of the range were found for some dominant species. It appears that young regenerating forests can provide suitable habitat for most of the forest eurytopic species of Carabidae.

## Acknowledgements

This research was funded by the Russian Science Foundation, grant number 22-14-00026.



## References

1. T.A. Gordienko, D.N. Vavilov, Yu.A. Lukyanova, Proc. Mordov. State Nat. Res., **29**, 38-50 (2021)
2. G. Pozsgai, L. Quinzo-Ortega, N.A. Littlewood, Insect Cons. Divers., **15**, 36-47 (2021)
3. Y.N. Sundukov, K.V. Makarov, Nat. Cons. Res., **6**, 15–51 (2021)
4. F. Khalimov, Biosyst. Divers., **28**, 265–271 (2020)
5. B. Baranová, P. Manko, T. Jászay, Ecol. Eng., **81**, 1-13 (2015)
6. N.S. Piotrowska, S.Z. Czachorowski, M.J. Stolarski, Agriculture., **10**, 12, 648 (2020)
7. A.S. Bondarenko, A.S. Zamotajlov, A.I. Belyi, E.E. Khomitskiy, Nat. Cons. Res., **5**, 66–85 (2020)
8. M.J. Koivula, ZooKeys, **100**, 287–317 (2011)
9. O. Parhomenko, V. Langraf, K. Petrovičová, V. Komlyk, V. Brygadyrenko, Nat. Cons. Res., **7**, 1, 42-69 (2022)
10. T.A. Avtaeva, R.A. Sukhodolskaya, V.V. Brygadyrenko, Bios. Div., **29**, **2**, 140–150 (2021)
11. N.V. Ivanova, M.P. Shashkov, Nat. Cons. Res., **7**, 52–63 (2022)
12. L. Anselmo, B. Rizzoli, Nat. Cons. Res., **7**, **3**, 88–94 (2022)
13. A.B. Ruchin, A.A. Khapugin, Acta Zool. Acad. Sci. Hung., **65**, **4**, 349–370 (2019)
14. A.Ş. Cicort-Lucaciu, Nat. Cons. Res., **5**, **3**, 134–138 (2020)
15. A.B. Ruchin, L.V. Egorov, G.B. Semishin, Biodiversitas, **19**, **4**, 1352–1365 (2018)
16. G. Müller-Motzfeld, Bd. 2, *Adephaga 1: Carabidae (Laufkäfer)*, Die Käfer Mitteleuropas. Spektrum-Verlag, Heidelberg/Berlin (2004)
17. A.Y. Isaev, *Keys to Coleoptera of the Middle Volga Region. Part 1. Adephaga and Myxophaga*, 1–120 (2002)
18. I. Lobl, D. Lobl, *Catalogue of Palaearctic Coleoptera*, Revised and Updated Edition, **1** (2017)
19. A.O. Kharitonova, T.I. Kharitonova, Nat. Cons. Res., **6**, **2**, 29–41 (2021)
20. E.A. Borisova, Russ. J. Ecol., **37**, 152–155 (2006)
21. V.K. Popov, *Birch forests of the Central forest-steppe of Russia*. Voronezh: Publishing House of the Voronezh State University (2003)
22. E. Marshall, T. West, D. Kleijn, Agricult. Ecosyst. Envir., **113**, 36–44 (2006)
23. J. Holland, F. Bianchi, M. Entling, A. Moonen, B. Smith, P. Jeanneret, Pest Manag. Sci., **72**, 1638–1651 (2016)
24. H. Hanson, K. Birkhofer, H. Smith, E. Palmu, K. Hedlund, Basic Appl. Ecol., **18**, 40–49 (2017)
25. K. Birkhofer, V. Fevrier, A. Heinrich, K. Rink, H. Smith, Agricult., Ecosyst. Envir., **255**, 84–94 (2018)
26. J. Heliölä, M. Koivula, J. Niemelä, Conserv. Biol., **15**, **2**, 370-377 (2001)
27. R.J. Fuller, T.H. Oliver, S.R. Leather, Insect Conserv. Div., **1**, **4**, 242-252 (2008)
28. G. Tyler, Biodiv. Conserv., **17**, 155-172 (2008)
29. M. Koivula, P. Punttila, Y., Haila, J. Niemelä, Ecography, **22**, **4**, 424-435 (1999)
30. A.V. Putchkov, ZooKeys, **100**, 503-515 (2011)



31. N. Pilon, E. Cardarelli, G. Bogliani, Biodiv. Data J., **1**, 972 (2013)
32. A.B. Ruchin, S.K. Alekseev, A.A. Khapugin, Nat. Cons. Res., **4**, 11–20 (2019)
33. V. Brygadyrenko, Entomol. Fenn., **27**, **2**, 81–100 (2016)
34. J. Bennewicz, T. Barczak, Biologia, **75**, 1631–1641 (2020)
35. V.V. Brygadyrenko, Folia Oecol, **42**, **2**, 75–88 (2015)
36. W.W.K. Houston, Ecol. Entomol, **6**, **3**, 263–271 (1981)
37. E. Pulliainen, J. Itamies, P., Jussila, P. Tunkkari, Entomol. Fenn., **4**, **1**, 27–30 (1993)
38. A. Schwerk, M.A. Kitka, Period. Biology, **118**, **3**, 163–169 (2016)
39. A. Schwerk, Europ. J. Entom, **111**, **5**, 677–685 (2014)
40. K. Hurka, *Carabidae of the Czech and Slovak Republics*. Print Centrum, a. s., Zlin, Czech Republic (1996)
41. R. Andorko, F. Kadar, Entomol. Fenn., **17**, 221–228 (2006)
42. A.V. Matalin, Zoolog. Zhurnal, **85**, 573–585 (2006)