Evaluation of the ecological niche of some abundant species of the subfamily Platyninae (Coleoptera, Carabidae) against the background of eight ecological factors

Viktor V. Brygadyrenko

Department of Zoology and Ecology, Oles' Honchar Dnipropetrovsk National University, pr. Gagarina, 72, 49010 Dnipropetrovsk, Ukraine; e-mail: brigad@ua.fm

Abstract

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Based on the results of 15 years of research in five regions in the steppe zone of Ukraine we have analysed the relationship between species of the subfamily Platyninae and the eight most significant ecological factors for litter macrofauna in forest ecosystems. In the forests of Ukraine *Calathus ambiguus* (Paykull, 1790) is a typical mesophile, with a slight preference for pine forests. *C. erratus* (C.R. Sahlberg, 1827) is at its most numerous in xeromesophilous moisture conditions with an average abundance of ants. *C. fuscipes* (Goeze, 1777) favours broadleaved forests with 40–80% tree crown density, a sparse herbaceous layer, and clay soil with high salinity. *C. melanocephalus* (Linnaeus, 1758) is at its most numerous in forests with a deep litter layer with average soil salinity. *Dolichus halensis* (Schaller, 1783) is often found in forests with of low crown density and favours areas with high salinity. *Anchomenus dorsalis* (Pontoppidan, 1763) favours plots with scattered trees, thick grass, mesophilous moisture conditions and low abundance of ants. *Limodromus krynickii* (Sperk, 1835) inhabits forests with a thin litter layer, hygrophilous moisture conditions and soils with low salinity. *Oxypselaphus obscurus* (Herbst, 1784) inhabits moist areas of forests with acid, sandy soil. The methods used in this research allow a quantitative multiple level assessment of the ecological niches of different species of litter invertebrate to be made.

Key words

density of the herbaceous layer cover, ecological niche, litter, moisture, soil salinity, tree crown density

Introduction

The requirements of a species of litter invertebrate regarding level of humidity, light, soil salinity and soil texture are among the basic parameters which determine whether it is present or absent in a given ecosystem (Thiele, 1977). The presence of a species at a particular site means that its environmental requirements are met, that a potential ecological niche is filled (Hutchinson, 1957).

The borders between potential ecological niches are harder to research than those between niches which are occupied. The data for laboratory research on the influence of tolerance of species, for example, for a light or temperature regime cannot always be extrapolated for natural habitats (Thiele, 1977). Assessment of potential ecological niches in natural ecosystems of a particular climatic zone can only be made by analyzing the abundance of a given invertebrate species across dozens or hundreds of sites (Brygadyrenko, 2004, 2006). Up to now, research of this kind has not been conducted for ground beetles.

In the steppe zone of Ukraine over 80% of the territory is given over to agriculture, with forest habitats occupying no more than 10% of the territory (Belgard, 1971). Forests in this zone are characterized by the exteme phytogenic variety of both natural and cultivated species, with the number of dominant tree species amounting to over 30 (Brygadyrenko, 2015). Forest ecosystems in the south of Ukraine are subject to the contrasting, often hostile, conditions of their surrounding environment, and in many cases have a strongly steppe phytocenosis. For this reason, a detailed study of the distribution of particular ground beetle species in these habitats is a convenient method of conducting research at the maximum level of detail into their potential ecological niches.

In Europe the subfamily Platyninae Bonelli, 1810 (www.faunaeur.org) is represented by the tribes Omphreini, Platynini and Sphodrini. The first of these includes a single genus *Omphreus*, the second by 13 genera (*Agelaea*, *Agonum*, *Anchomenus*, *Atranus*, *Cardiomera*, *Galaicodytes*, *Limodromus*, *Olisthopus*, *Oxypselaphus*, *Paranchus*, *Platynus*, *Pseudanchomenus* and *Sericoda*), the third by 19 genera (*Amaroschema*, *Gomerina*, *Paraeutrichopus*, *Platyderus*, *Pseudomyas*, *Pseudoplatyderus*, *Calathus*, *Synuchidius*, *Anchomenidius*, *Dolichus*, *Calathidius*, *Hystricosphodrus*, *Laemostenus*, *Licinopsis*, *Pseudotaphoxenus*, *Sphodropsis*, *Sphodrus*, *Taphoxenus* and *Synuchus*). Only 38 species of Platynini and 20 species of Sphodrini inhabit Ukraine, and the variety of species of these subfamilies is much lower in the steppe zone than in the forest-steppe and forest zones (Brygadyrenko, 2003a; Putchkov, 2011, 2012).

Species belonging to the ground beetle subfamily Platyninae differ sharply in their ecological preferences, especially with regard to habitat type, moisture, character of the soil, and peculiarities of the plant cover (Hůrka, 1996; Brygadyrenko, 2003a). Some species favour xerophilous ecosystems, though most inhabit mesophilous and hygrophilous habitat types (Lindroth, 1985). The variety of their habitat requirements, the wide distribution and high abundance of many of these species make the subfamily Platyninae a convenient object for study of ecological niches.

The aim of this research is thus the assessment of the potential ecological niches of 8 species of ground beetle of the Platyninae subfamily, dominant in forests in the steppe zone of Ukraine, measured against the background of 8 ecological factors.

Material and methods

The counting of the ground beetles was conducted in five regions (Dnepropetrovsk, Zaporozhye, Nikolayev, Donetsk and Kharkov) of Ukraine from 2001 to 2014 in natural and planted forests of various types and ages. In this report ground beetles from 836 forest sites are analysed. The same methodology was applied at each site: the soil and vegetational conditions were evaluated and the ground beetles were collected in soil traps; a standard geobotanical description was made (the crown density of the tree layer and the density of the herbaceous layer were measured both as a combined total and also for every plant species separately); the litter depth was measured (taken as the average of ten measurements); the soil texture was noted (clay, loam, sandy loam, sand); the soil humidity was assessed (using indicator species of the herbaceous layer, according to the scale devised for the steppe zone by Belgard (1950)); the soil texture was assessed (using indicator species of the herbaceous layer, according to Belgard's (1950) scale); the abundance of ants was determined (using soil traps). A detailed description of the forest ecosystems of the steppe zone of Ukraine, giving details for different plant species, can be found in Belgard's (1950, 1971) works on forestry in this zone. A more detailed geobotanical description of the research plots can be found in our earlier publications (Brygadyrenko, 2005, 2014, 2015; Brygadyrenko and Solovjov, 2007).

The count of ground beetles in the litter was conducted using standard methods: at each site 10 half litre soil traps (with 20% NaCl solution) were placed at least two metres from each other. The traps were checked on average every 5th day (depending on the weather conditions), and, overall, 3–24 collections were made for every sample plot. The abundance of each ground beetle species was calculated from specimens collected per 10 trap-days, subjected to standard anova methods in the package Statistica 8.0. The diagrams (Figs 1–8) show the average number of each species (specimens/10 trap-days), vertical bars denote 95% confidence intervals. Above every graph is shown the factual value of the Fisher criterion for a specified degree of freedom, and also the reliability of differences between different abundance values for the ground beetles. Differences in the abundance of species were considered significant at $p < 0.05$. We considered that insignificant differences at $0.05 < p < 0.10$ represented only a tendency.

Results

Calathus ambiguus (Paykull, 1790), as a eurybiont species, tends to be at its most abundant in xeromesophilous and mesophilous conditions (Fig. 1e), with average abundance of ants (Fig. 1h) and in pine forests (Fig. 1b). Its frequency is 3.7%, average abundance – 0.014 ± 0.101 specimens/10 trap-days and 0.276% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

The abundance of *Calathus erratus* (C.R. Sahlberg, 1827) is significantly greater in xeromesophilous moisture conditions (Fig. 2e), with an average abundance of ants (Fig. 2h). In comparison with *C. ambiguus* (Fig. 1) this species is more xerophilous and favours plots with lower numbers of ants. Its frequency is 3.0%, average abundance – 0.009 ± 0.068 specimens/10 trap-days and 0.169% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

Calathus fuscipes (Goeze, 1777) is a steppe species, frequently found on fields, in anthropogenically transformed ecosystems, where it is numerically dominant in the litter macrofauna. Against the background of 6 of the 8 analysed ecological factors the abundance of *C. fuscipes* varies significantly. It reaches its maximum abundance at

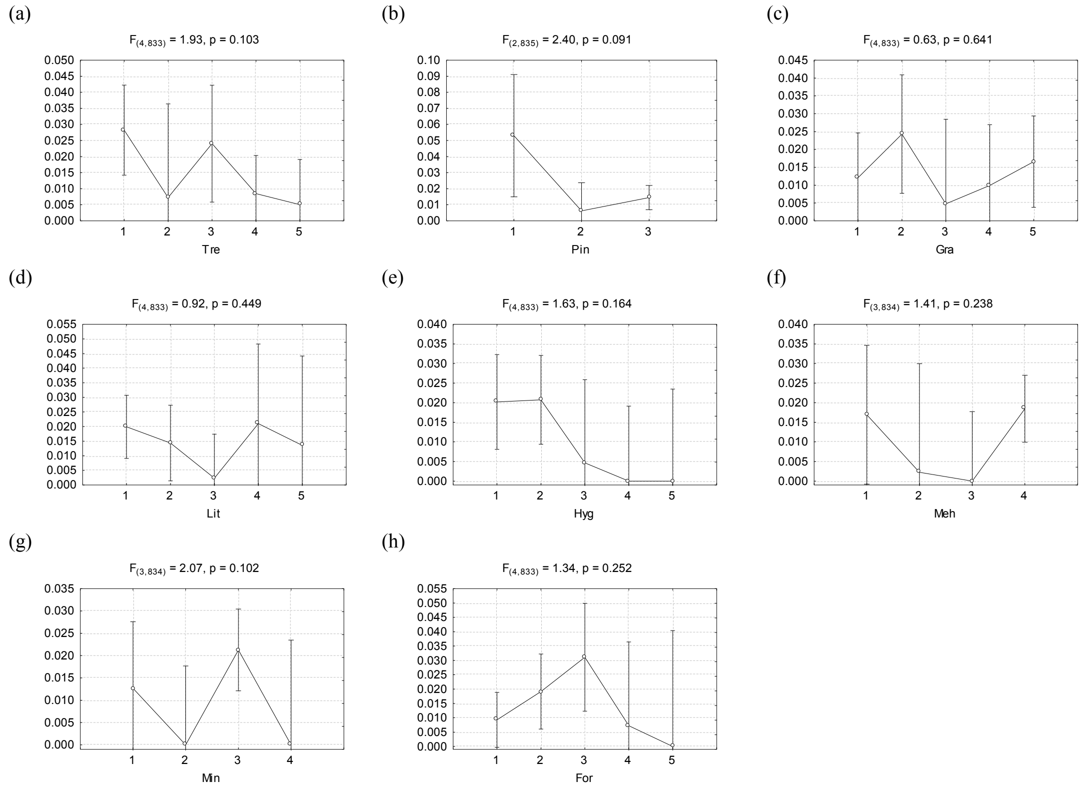

Fig. 1. Influence of conditions in forest ecosystems on *Calathus ambiguus* (Paykull, 1790): abscissa Tre – tree crown density (1 – <20%, 2 – 21–40%, 3 – 41–60%, 4 – 61–80%, 5 – >81%); Pin – type of forest ecosystem (1 – pine, 2 – mixed, 3 – broad-leaved forest); Gra – density of herbaceous layer cover (1 – <20%, 2 – 21–40%, 3 – 41–60%, 4 – 61–80%, 5 – >81%); Lit – thickness of the litter (1 – <10 mm, 2 – 11–20, 3 – 21–30, 4 – 31–40, 5 – >41 mm); Hyg – moisture conditions (1 – xeromesophilous, 2 – mesophilous, 3 – hygomesophilous, 4 – mesohygrophilous, 5 – hygophilous); Meh – soil texture (1 – sandy, 2 – sandy loam, 3 – loam, 4 – clay); Min – soil salinity (1 – trophotopes AB, B, C, 2 – Dc, Dac, 3 – Dn, 4 – De, E); For – abundance of ants (1 – <4, 2 – 5–16, 3 – 17–64, 4 – 65–256, 5 – >256 specimens/10 trap-days); ordinate – number of ground beetles, specimens/10 trap-days.

sites where tree crown density is 40–80% (Fig. 3a), in broad-leaved forests (Fig. 3b), herbaceous cover density 20–40% (Fig. 3c), the litter layer is 10–40 mm (Fig. 3d), with clay soil (Fig. 3e), in the trophotope Dn (Fig. 3g). A lower abundance was observed (on the level of a tendency) at sites where ants were abundant (over 64 specimens/10 trap-days, Fig. 3h). Its frequency was 11.7%, average abundance – 0.26 ± 1.62 specimens/10 trap-days and 4.95% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

Calathus melanocephalus (Linnaeus, 1758) was significantly more abundant in forests of the steppe zone at sites with a thick litter layer (30–40 mm, Fig. 4d) and with soils of average salinity (Fig. 4g). Other factors analysed influence *C. melanocephalus* only at the level of tendency: abundance was greater in mesohygrophilous and hygrophilous moisture conditions (Fig. 4e) and sites with low numbers of ants (Fig. 4h). Its frequency was 3.8%, average abundance – 0.012 ± 0.083 specimens/10 trap-days and 0.237% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

The abundance of *Dolichus halensis* (Schaller, 1783) was significantly higher at sites with a low tree crown density (Fig. 5a), in trophotope Dn (Fig. 5g). Its abundance was slightly higher (at the level of a tendency) at clay soil sites (Fig. 5f) and low numbers of ants (Fig. 5h). Its frequency was 6.0%, average abundance – 0.080 ± 0.594 specimens/10 trap-days and 1.53% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

The abundance of *Anchomenus dorsalis* (Pontoppidan, 1763) was significantly greatest at forest sites with a low crown density (Fig. 6a), maximum level of herbaceous cover (Fig. 6c), mesophilous moisture conditions (Fig. 6e) and low abundance of ants (<16 specimens/10 trap-days, Fig. 6h). Its frequency was – 1.8%, average abundance – 0.056 ± 1.090 specimens/10 trap-days and 1.08% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

Limodromus krynickii (Sperk, 1835) is a forest meadow species of ground beetle, which in forest ecosystems varies significantly in abundance in relation to 2 of

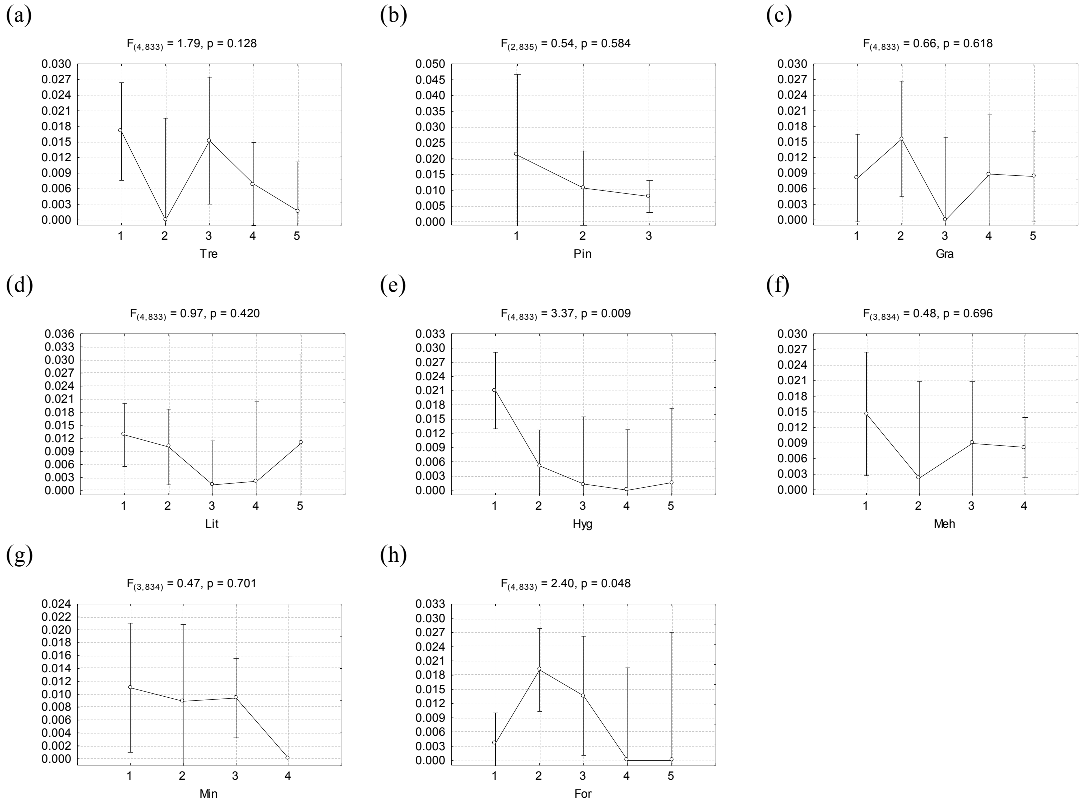

Fig. 2. Influence of forest ecosystem conditions on *Calathus erratus* (C.R. Sahlberg, 1827).
For explanation see key to Fig. 1.

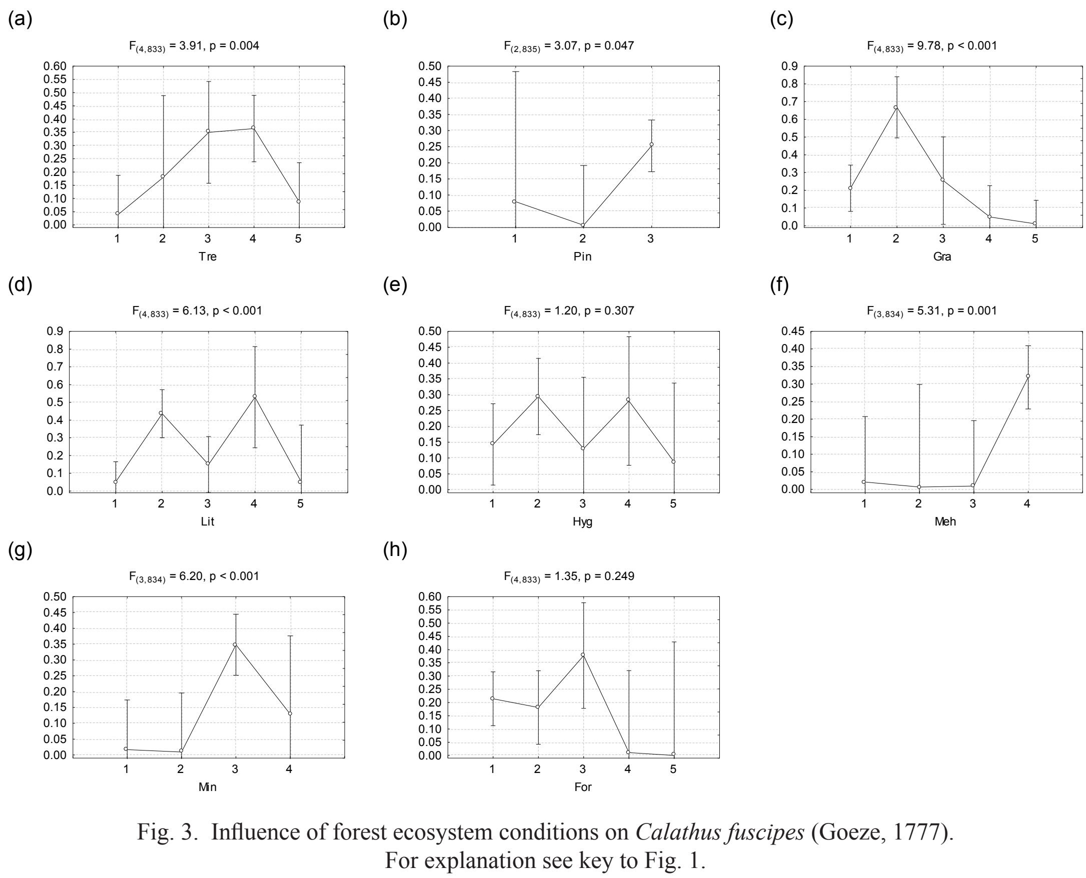

Fig. 3. Influence of forest ecosystem conditions on *Calathus fuscipes* (Goeze, 1777).
For explanation see key to Fig. 1.

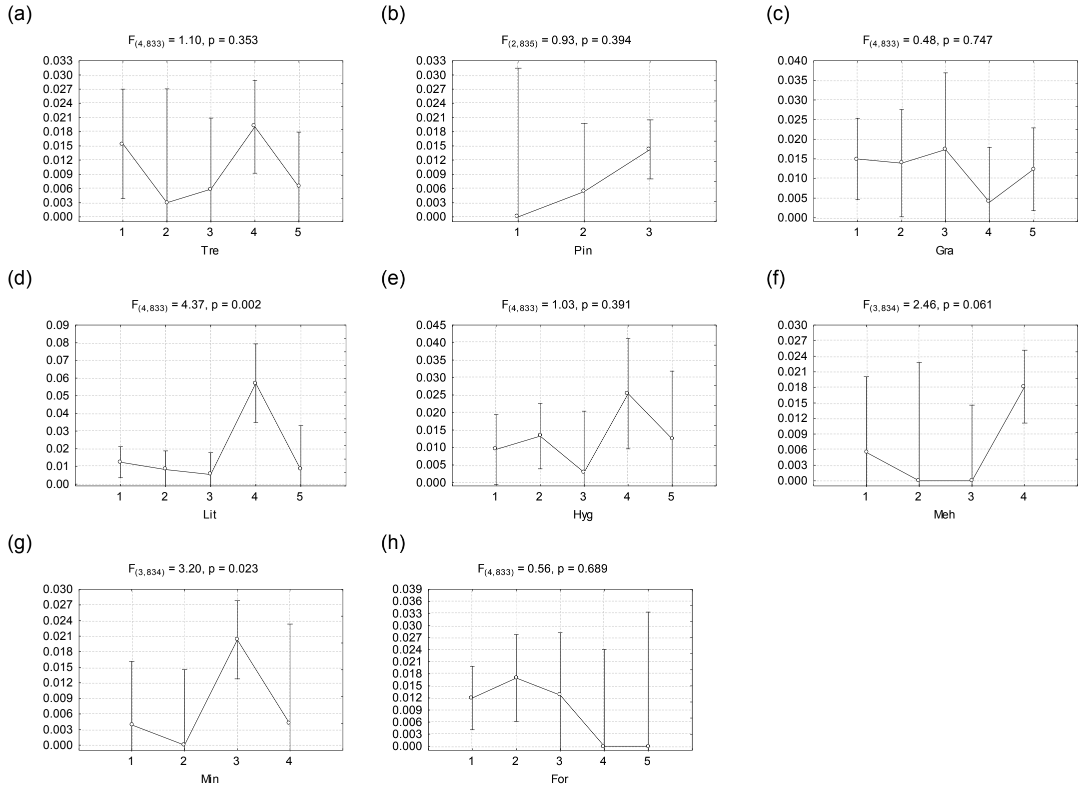

Fig. 4. Influence of forest ecosystem conditions on *Calathus melanocephalus* (Linnaeus, 1758).
For explanation see key to Fig. 1.

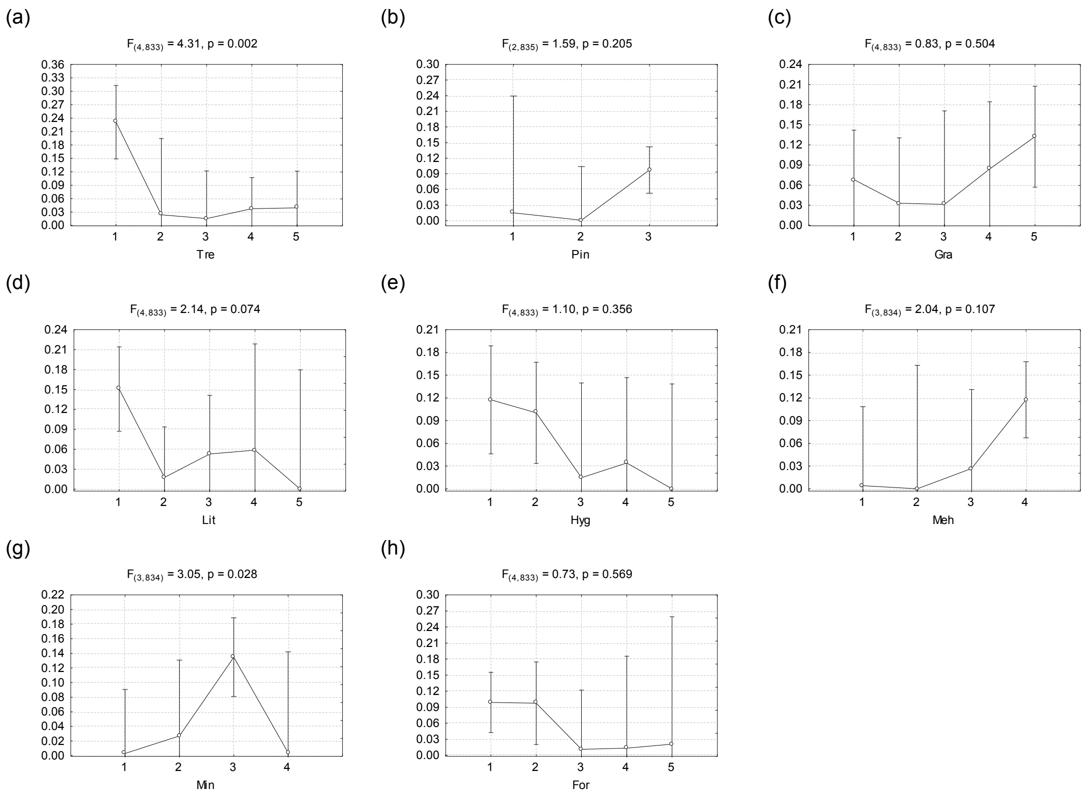

Fig. 5. Influence of forest ecosystem conditions on *Dolichus halensis* (Schaller, 1783).
For explanation see key to Fig. 1.

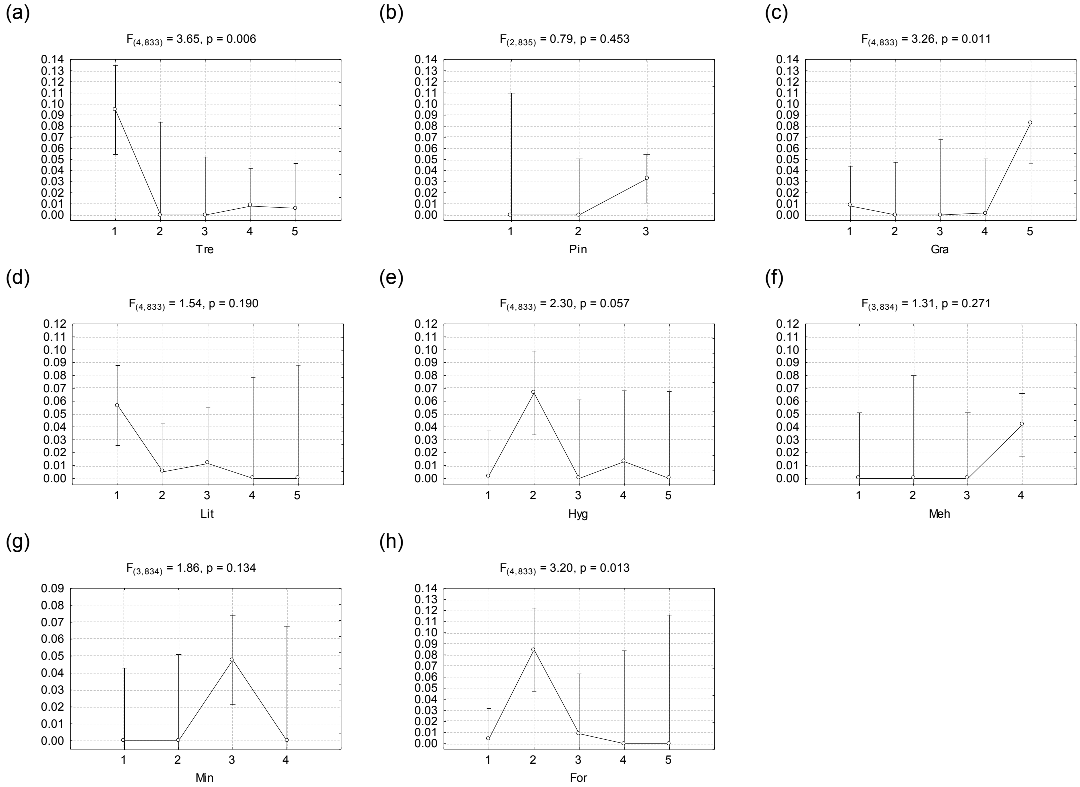

Fig. 6. Influence of forest ecosystem conditions on *Anchomenus dorsalis* (Pontoppidan, 1763).
For explanation see key to Fig. 1.

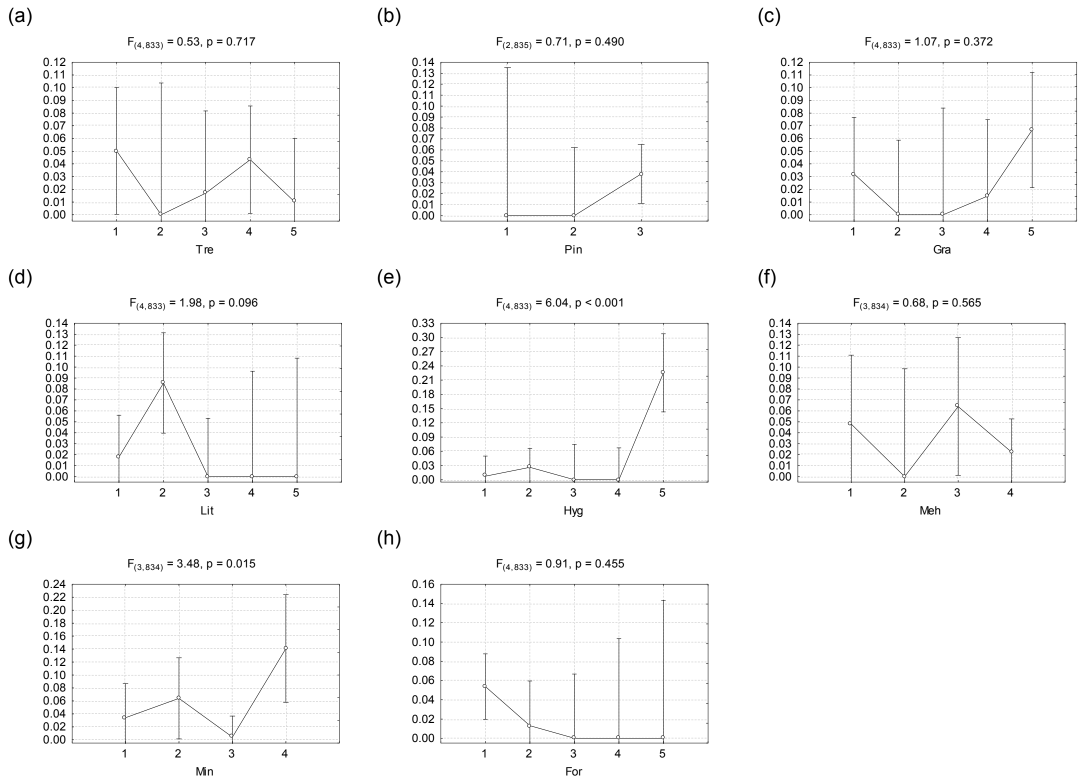

Fig. 7. Influence of forest ecosystem conditions on *Limodromus krynickii* (Sperk, 1835).
For explanation see key to Fig. 1.

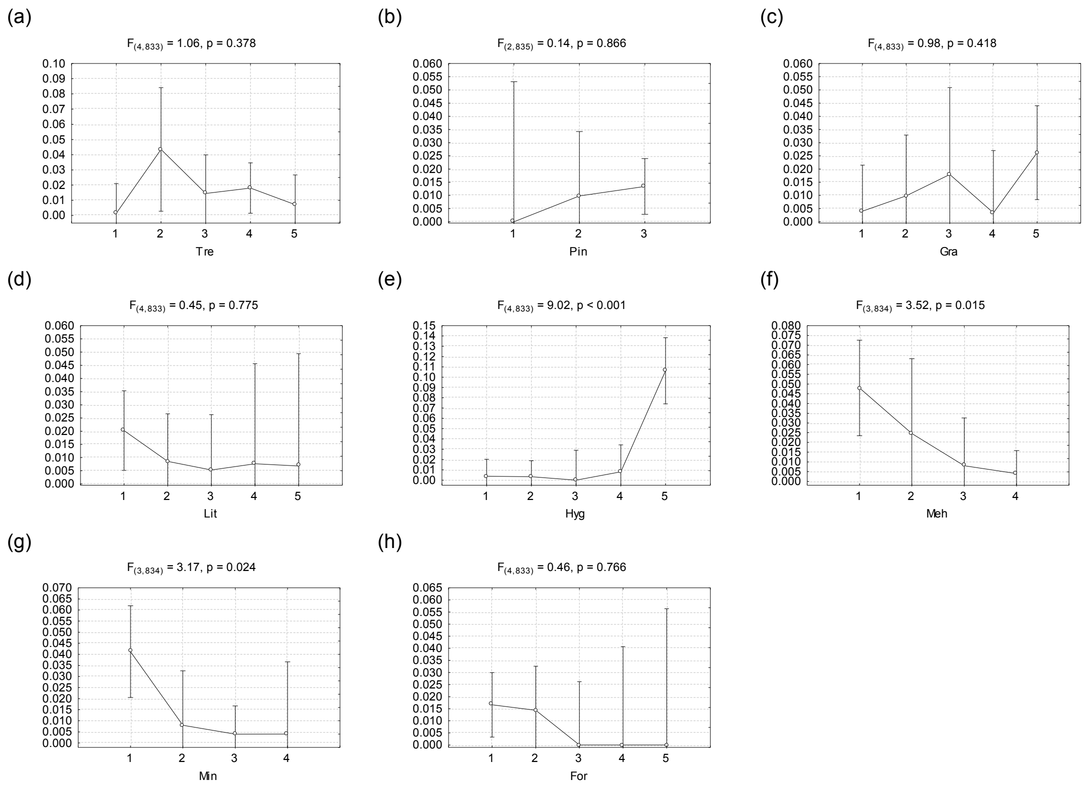

Fig. 8. Influence of forest ecosystem conditions on *Oxypselaphus obscurus* (Herbst, 1784).
For explanation see key to Fig. 1.

the 8 analysed ecological factors. Its abundance reaches its maximum in hygrophilous moisture conditions (Fig. 7e) and in trophotypes De, E (Fig. 7g). It was noted that it tended to be more numerous at sites with a low abundance of ants (Fig. 7h), on plots with a thin litter layer (10–20 mm, Fig. 7d). Its frequency was – 1.2%, average abundance – 0.031 ± 0.358 specimens/10 trap-days and 0.592% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

Oxypselaphus obscurus (Herbst, 1784) is a hygrophilous forest meadow species of ground beetle, which in the steppe zone significantly varies in abundance in relation to 3 of the 8 ecological factors analysed. Its abundance reaches its maximum in hygrophilous moisture conditions (Fig. 8e), on sandy soils (Fig. 8f), in trophotypes AB, B and C (Fig. 8g). Abundance of ants (Fig. 8h), tree crown density (Fig. 8a) or density of herbaceous cover (Fig. 8c) did not significantly influence the abundance of *O. obscurus*. Its frequency was 1.9%, average abundance – 0.012 ± 0.140 specimens/10 trap-days and 0.237% of the total number of carabid beetles collected in forests of the steppe zone of Ukraine.

According to the results of our research, the abundance of only one of the species studied, *C. ambiguus*, was not significantly influenced by any of the factors (Table 1). The abundance of *C. erratus* was influenced by only one factor, *C. melanocephalus*, *L. krynickii* and *D. halensis* significantly varied in relation to two factors, *A. dorsalis* and *O. obscurus* in relation to three factors. The abundance of *C. fuscipes* varied significantly in response to six factors.

Soil salinity influences significantly 5 of the 8 selected ground beetle species belonging to the Platyninae subfamily. Soil moisture and tree crown density influence 3 species. Litter depth, density of herbaceous cover and soil texture influence 2 species. Type of forest ecosystem and abundance of ants influence 1 species (Table 1).

The results of our cluster analysis for the distribution of the species studied on the sample plots show the greatest degree of similarity in the patterns for *C. melanocephalus*, *C. erratus* and *C. ambiguus* (Fig. 9). The lowest degree of similarity in distribution of these species was shown for *O. obscurus*, *L. krynickii* and *D. halensis*. The xerophilous *A. dorsalis* and *C. fuscipes* present a second species cluster showing a low level of distributional similarity.

Discussion

Phylogenetic similarity and ecological adaptability of species in the genus *Calathus*

The genus *Calathus* consists of 177 species classified into 10 subgenera (Gañán et al., 2008). Ruiz et al. (2012) state that the genera *Calathus* and *Dolichus* split at the boundary of the Eocene and Oligocene (about 34 million

Table 1. Relationship between the studied ground beetle species of the subfamily Platyninae and the influence of eight ecological factors in forest ecosystems in the steppe zone of Ukraine (based on the analysis of 836 collections from soil traps)

Species	Tre	Pin	Gra	Lit	Hyg	Meh	Min	For
Calathus ambiguus (Paykull, 1790)	–	–	–	–	–	–	–	–
Calathus erratus (C. R. Sahlberg, 1827)	–	–	–	–	+	–	–	–
Calathus fuscipes (Goeze, 1777)	+	+	+	+	–	+	+	–
Calathus melanocephalus (Linnaeus, 1758)	–	–	–	+	–	–	+	–
Dolichus halensis (Schaller, 1783)	+	–	–	–	–	–	+	–
Anchomenus dorsalis (Pontoppidan, 1763)	+	–	+	–	–	–	–	+
Limodromus krynickii (Sperk, 1835)	–	–	–	–	+	–	+	–
Oxypselaphus obscurus (Herbst, 1784)	–	–	–	–	+	+	+	–

Tre, tree crown density; Pin, type of forest ecosystem; Gra, density of herbaceous layer cover; Lit, thickness of the litter; Hyg, moisture conditions; Meh, soil texture; Min, soil salinity; For, abundance of ants; "+" and "–" – significant ($p < 0.05$) and insignificant ($p > 0.05$) influence of the ecological factor.

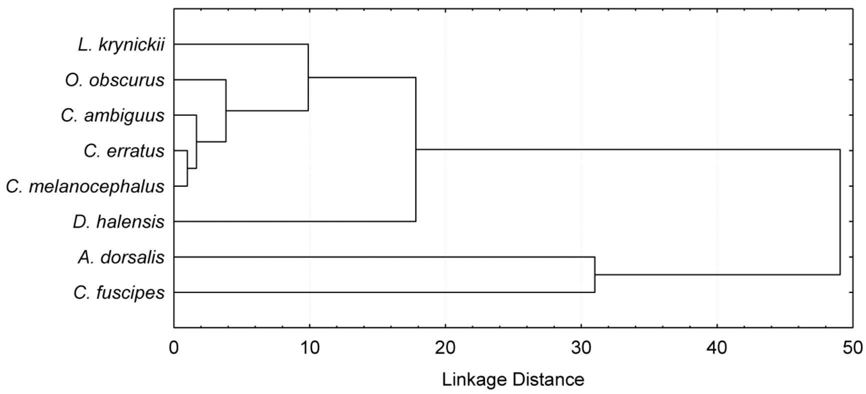

Fig. 9. Results of cluster analysis of the distribution of the ground beetle species studied in forest ecosystems in the steppe zone of Ukraine.

years ago). Following this, one of the youngest groups of the *Calathus* genus appeared, the group of species related to *C. fuscipes*, with the greatest intensity of species development occurring in the mountain ranges of Southern Europe during periods of glaciations, when small populations remained in the southern Pyrenees, the Apennines and the Balkan Peninsula (Ruiz et al., 2009, 2010, 2012). In Central Europe the number of species belonging to the genus *Calathus* is not high, and is dominated by species with a wide range and a fairly high level of ecological adaptability (Vereschagina, 1984).

Study of the biological variety of *Calathus* ground beetles has been conducted most fully in Spain: both from the perspective of territorial distribution in particular areas and that of occupation of ecological niches by particular species (Gañán et al., 2008). Negre (1969) was the first to make a detailed analysis of the distribution of *Calathus* species on the Iberian Peninsula, recording 13 species of this genus (the greatest number of species being in the foothills and the mountains of the Pyrenees). In the Iberian Peninsula, there are now known to be 23 species present, 14 (70%) of which are endemic to the peninsula (Gañán et al., 2008). According to Serrano (2013) 27 taxa at the level of species and subspecies inhabit Spain. Analysis of the distribution of *Calathus* species on seven of the Canary Islands (colonization and diversification) using Polymerase Chain Reaction Amplification and Sequencing allowed Emerson et al. (2000) to identify the routes and timing of the colonisation of these islands from continental Europe.

It is well known that various species of this genus are well able to thrive in agricultural landscapes (Kromp, 1999; Lang et al., 1999; Magura, 2002; Kutasi et al., 2004). *C. fuscipes*, *C. erratus* and *C. melanocephalus* (Schwerk and Szyszko, 2012) form the dominant ground beetle fauna on abandoned agricultural land in Poland. Błaszkiewicz and Schwerk (2013), in their research in west Poland (Wałecki district), an area composed of various forests, agricultural and post-agricultural areas at different stages of succession, found that *C. erratus* composed 3.3%, *C. fuscipes* – 3.9%, *C. melanocephalus* – 1.5% of the Carabid population. Ground beetles of the genus *Calathus* are one of the faunal components of agrocenosis and are fairly common in eastern Latvia: *C. fuscipes* – 0.26%, *C. erratus* – 0.45%, *C. ambiguus* – 0.44%, *C. melanocephalus* – 0.13% of the Carabid population (Bukejs and Balalaikins, 2008). However, despite sharing an ability to survive in the extreme conditions of agricultural activity, *Calathus* species differ in their range and ecological niches.

C. ambiguus

A West Palaearctic species, ranging to West Siberia and Central Asia (Hůrka, 1996). In the former Soviet Union *C. ambiguus* is distributed across the whole of its European territory, eastwards to the Altai, the southern limit of its range being in to Iran and Afghanistan (Vereschagina, 1984; Kryzhanovskij et al., 1995). Putchkov (2012) mentions that it occurs throughout the territory of Ukraine.

Vereschagina (1984) states that *C. ambiguus* favours open, dry steppe habitat. According to Lindroth (1985), in Fennoscandia *C. ambiguus* is a "rather stenotopic species, living in open, dry country on sandy or gravelly, sometimes clay-mixed soil with sparse vegetation, notably on southern slopes. Also in agricultural land on sandy fields. The species is often found together with *C. erratus*". Lindroth (1974) states that in Great Britain *C. ambiguus* shares the same habitat preference as *C. erratus*, with which it is often associated; also occurring in chalk pits. In the Czech and Slovak Republic *C. ambiguus* is "common in dry and warm unshaded habitats: fields, steppe; lowlands to hills" (Hůrka, 1996). In Spain *C. ambiguus* is common, occurring in 11 of the 23 regions Serrano (2013), while it is also included in the fauna of Turkey (Kesdek and Yildirim, 2004).

Sigida (1993) considers *C. ambiguus* to be a polytopic mesophile, typical of natural steppe areas and pastureland, bairaks (ravine forest) and floodplain forest, salines and areas of high salinity, semi-desert areas, agricultural and urban landscapes. In Moldova *C. ambiguus* is a mesoxerophilic steppe species, not often found in cultivated fields, vinyards and gardens (Karpova and Matalin, 1993). In the Non-Chernozem Area of Russia small numbers of specimens of *C. ambiguus* have been collected from fields sewn with winter wheat and maize (Soboleva-Dokuchaeva, 1995).

C. erratus

A Eurosiberian species (Hůrka, 1996). In the former USSR *C. erratus* extends as far as the Primorski Kray, ranging in the north beyond the Arctic Circle (Vereschagina, 1984; Kryzhanovskij et al., 1995). Putchkov (2012) states that it occurs throughout Ukraine.

Lindroth (1985) states that in Fennoscandia *C. erratus* is "xerophilous, usually occurring on dry, sandy or gravelly soil poor in humus and with sparse vegetation. Predominantly in open country, for instance on *Calluna*-heath, in dunes, and in dry meadows and grassland; also in thin forests. It is frequently encountered on agricultural land on light soil, notably in root crop fields". Lindroth (1974) mentions that in Great Britain *C. erratus* occurs on dry, usually sandy ground with sparse vegetation. The northern population of *C. erratus* in Fennoscandia is macropterous, on the shores of the Baltic brachypterous specimens predominate (Lindroth, 1979). In the Non-Chernozem Area of Russia *C. erratus* inhabits forest ecosystems (Soboleva-Dokuchaeva, 1995). In the south of the Baikal region *C. erratus* inhabits mesophilous and steppe type meadows, forest clearings, slopes of ravines, fallow and wasteland (Shilenkov, 1978). In the Czech Republic and Slovakia *C. erratus* is "common in dry, unshaded habitats: fields, forests, *Calluna*-heath; lowlands to mountains, frequent in hills" (Hůrka, 1996).

It is rarer in the southern part of its range, being mainly associated with forest ecosystems. Sigida (1993) considers *C. erratus* to be a polytopic mesophile, typical of natural steppe areas and pastures, bairak and floodplain forests. *C. erratus* occurs in only one of the 23 regions of Spain researched by Serrano (2013). It has not been recorded in Moldova (Karpova and Matalin, 1993).

C. fuscipes

A West Palaearctic species, introduced in North America (Hůrka, 1996). Common across the entire European part of the former USSR, the southern limit of its range is in North Africa and Iran (Vereschagina, 1984; Kryzhanovskij et al., 1995). In Ukraine *C. fuscipes graecus* (Dejean, 1831), (Putchkov, 2012) occurs in the southern subzone of the steppe zone (right bank of the Dnieper, westwards) and in the Crimean peninsula, *C. fuscipes fuscipes* (Goeze, 1777) occurs throughout the rest of Ukraine.

In Fennoscandia according to Lindroth (1985) *C. fuscipes* is a "eurytopic species, predominantly occurring in open country on rather dry, notably sandy or clay soil more or less rich in humus, e.g. in meadows and grassland; often on cultivated soil and also in light forests". Lindroth (1974) states that in Great Britain *C. fuscipes* occurs "in moderately dry meadows and grassland, often on cultivated soil; also in thin forests". In the Czech and Slovak Republics *C. fuscipes* is "very common, in unshaded, rather dry habitats: meadows, fields, steppe; lowlands to mountains" (Hůrka, 1996). According to Serrano (2013) *C. fuscipes* occurs throughout almost all of Spain.

C. fuscipes Sigida (1993) is a forest mesophile, occurring in bairak and floodplain forests, agricultural and urban landscapes. In Moldova *C. fuscipes* is a mesophile, belonging to the meadow-field group, being uncommon only on sewn perennial grassland (Karpova and Matalin, 1993). According to Klausnitzer (1987) *C. fuscipes* is one of the most abundant species of ground beetle in urban habitats, occurring in the sports stadiums, lawns and airports of Warsaw and Keln; the author considers the species to be a eurytopic mesophile of open ground, dominating on fields. According to KOCOUREK et al. (2013), in the Czech Republic *C. fuscipes* comprised 0.8% of the total of carabid beetles collected from maize fields at the Prague-Ruzyně site (Central Bohemia), and 11.1% of the total of carabid beetles collected at the same time at the Ivanovice na Hane site (Central Moravia). In Hungary, in a lowland oak forest-grassland complex (TÓTHMÉRÉSZ et al., 2014) *C. fuscipes* proved to be one of the most reliable indicators of grassland as opposed to edge and forest ecosystems.

C. melanocephalus

A Palaearctic species, probably introduced in North America (HŮRKA, 1996). *C. melanocephalus* is common all over Europe in lowland habitats and alpine areas up to the middle alpine region (LINDROTH, 1985). VERESCHAGINA (1984) states that in the former USSR *C. melanocephalus* is one of the most abundant and eurybiont species. PUTCHKOV (2012) mentions that it occurs throughout Ukraine. SERRANO (2013) states that *C. melanocephalus* inhabits practically all regions of Spain.

According to LINDROTH (1985), in Fennoscandia *C. melanocephalus* is a "commonly distributed species which usually lives in open country on different kinds of moderately dry ground with sparse vegetation, achieving its greatest abundance on sandy soil. It is a common inhabitant of dry meadows, grassland, dunes and heath; also on agricultural land and in thin forests, mainly of *Pinus*. It is frequent in the fjelds up to the lower alpine region." The species is nocturnal and its reproductive period is mainly August–September in Scandinavia (NYLUND, 1991). LINDROTH (1974) states that in Great Britain *C. melanocephalus* occurs on all kinds of open moderately dry soil with grass, meadow or weed vegetation.

In the Czech Republic and Slovakia *C. melanocephalus* is "very common, mainly in unshaded or moderately shaded habitats: fields, steppe; lowlands to mountains" (HŮRKA, 1996). *C. melanocephalus* SIGIDA (1993) is a polytopic mesophile, typical of natural steppe areas and pastureland, bairak and floodplain forest, salines and areas of high salinity, and agricultural landscapes. In Moldova *C. melanocephalus* is a mesophile, belonging to the meadow-field group, common on fields in floodplains and dry interfluves, rare in isolated forest blocks (KARPOVA and MATALIN, 1993). In the Non-Chernozem Area of Russia *C. melanocephalus* comprises on average 2.3% of the total number of ground beetles; on fields of winter wheat – 7.5%, in forest ecosystems – 4.9%, on sewn beetroot – 3.6%, clover – 2.4%, barley – 1.1% (SOBOLEVA-DOKUCHAEVA, 1995).

The age structure of *C. melanocephalus* populations can vary in different ecosystems (VAN DIJK, 1972). Some specimens can live longer than usual, which can lead to higher populations in particular ecosystems. The results of laboratory experiments of VAN DIJK (1994) showed that the average number of eggs laid by a female *C. melanocephalus* increased from 50.9 to 73.8 and 142.5 eggs for one female when the beetle's food consumption was increased from 1 to 2 and 5 mg/day respectively.

Various species in the genus move exclusively on the surface of the soil, for many, for example *C. melanocephalus* (AUKEMA, 1990), short wings are the dominant trait, while long wings are a recessive trait. The expression of genes for long wings could be modified by environmental factors such as temperature and food supply (AUKEMA, 1991). It is possible that prolonged summer migrations account for the presence of small numbers this species in unsuitable habitat.

D. halensis

A Palaearctic species, reaching the southern Kuril Islands, Japan and South China (HŮRKA, 1996). In the former USSR *D. halensis* does not extend as far north as the other species of *Calathus* discussed above; the range of *D. halensis* extends as far east as Primorski Kray (VERESCHAGINA, 1984; KRYZHANOVSKIJ et al., 1995). PUTCHKOV (2012) states that it occurs throughout Ukraine. It is significantly less common in the south of its range: according to SERRANO (2013) *D. halensis* was found only in 2 of Spain's 23 regions, KESDEK and YILDIRIM (2004) consider *D. halensis* a rare species in Turkey.

The species is highly abundant in the Far East. At nine sites of three forest types selected in order to examine the effects of forest habitat in the Japanese red pine of Naju City, South Korea *D. halensis* comprised 17.4% of the total numbers of ground beetles trapped (DO and JOO, 2013). DO et al. (2014) in their study at Eulsukdo Island landfill (Republic of Korea) found that *D. halensis* comprised 30.8% of over 92,000 ground beetle specimens trapped. Despite these high figures, the abovementioned authors consider this flightless species which breeds in autumn to belong to the group which dominates in grassland and not forest ecosystems.

Research conducted in Busan Metropolitan City (Republic of Korea) showed that in parks *D. halensis* comprised over 40.8% of the total number of ground beetles, at closed landfill sites – 35.5%, in restored urban wetlands – 47.4%, in unmanaged grasslands – 44.1%, in forest parks – 4.1% (DO et al., 2014). At the same time, the species was completely absent from a brown field derelict area, gardens inside the interchange, and urban roadsides (DO et al., 2014). These variations in abundance could be connected either with anthropogenic activity or with natural ecological factors (biotic and abiotic). No attempt was made to distinguish these factors.

In Fennoscandia LINDROTH (1985) mentions that the species occurs "on open, often cultivated fields, usually on clayey soil. It is a common species in agricultural regions of Eastern Europe and is a pronounced steppe element in our fauna." In the Czech Republic and Slovakia it is "common to sporadic on dry to moderately dry, unshaded habitats: fields; lowlands to hills" (HŮRKA, 1996). SIGIDA (1993) considers *D. halensis* to be a polytopic mesophile, characteristic of natural steppe and pastureland, bairaks and floodplain forest, agricultural and urban landscapes. In Moldova *D. halensis* is a mesophile, belonging to the meadow-field group, abundant on fields in floodplains and dry interfluvials, uncommon in vinyards and nut orchards (KARPOVA and MATALIN, 1993).

A. dorsalis

A West Palaearctic, eurytopic species, reaching eastward to Central Asia (HŮRKA, 1996). The species occurs across almost the entire territory of the former USSR, except for the northern taiga and tundra zones (KRYZHANOVSKIJ et al., 1995). PUTCHKOV (2012) mentions that it occurs throughout Ukraine. SERRANO (2013) states that *A. dorsalis* occurs in 20 of the 23 regions of Spain, KESDEK and YILDIRIM (2004) include it in the fauna of Turkey.

LINDROTH (1974) states that in Great Britain *A. dorsalis* "is the least hygrophilous of all *Agonum*, occurring in open meadows and grassland, usually on gravelly or clayish, often chalky soil. Somewhat local but often abundant; often large aggregations under stones in spring". In Fennoscandia according to LINDROTH (1985) "the least hygrophilous of all *Agonum*, occurring in open meadows and grassland, usually on gravelly or clayey, often limestone soil. Also on arable land, particularly in winter crops on heavy soil." In the Czech Republic and Slovakia it is "very common in unshaded, dry to moderately moist habitats; fields, steppe, pastures, edges of small woods; from lowlands to mountains, often gregariously" (HŮRKA, 1996).

In the Caucasus SIGIDA (1993) considers *A. dorsalis* to be a polytopic mesophile, typical of bairak and floodplain forest. In Moldova *A. dorsalis* is a mesophile, belonging to the meadow-field group, occurring infrequently on fields in floodplains and dry interfluvials, in vinyards and cherry orchards, isolated forest blocks (KARPOVA and MATALIN, 1993). In the Non-Chernozem Area of Russia single specimens of *A. dorsalis* were caught in barley crops, winter wheat, beetroot and in forest ecosystems (SOBOLEVA-DOKUCHAEVA, 1995).

A. dorsalis was found by KNAPP and UHNAVA (2014) in drier open areas such as arable fields, meadows, dry grasslands (steppes), and gardens. According to KOCOUREK et al. (2013), *A. dorsalis* comprised 8.7% of the total number of carabid beetles collected from maize fields at the Prague-Ruzyně site (Central Bohemia), and 0.5% at Ivanovice na Hane site (Central Moravia). According to BARANOVSKA et al. (2014), in the Czech Republic *A. dorsalis* occurs in open habitats and is common even in intensively managed agricultural landscapes. *A. dorsalis* is an important generalist predator feeding on aphids and other arthropod crop pests (WRATTEN and VICKERMAN, 1985; BILDE and TOFT, 1994) and is thus considered a beneficial organism with biocontrol potential.

L. krynickii

A West Palearctic species, ranging from the Elbe River to the Urals and Central Asia (HŮRKA, 1996). In the former Soviet Union the range of *L. krinickii* extends across the European part, eastwards to the Altai (KRYZHANOVSKIJ et al., 1995). In Ukraine PUTCHKOV (2012) states that it occurs in the forest zone, the broad-leaved forest zone and the forest-steppe zone. *L. krynickii* has not been recorded in Moldova (KARPOVA and MATALIN, 1993).

In Fennoscandia according to the data of LINDROTH (1985) the species is very rare in Denmark, and also in Sweden, where it is restricted to the southeast of the country. The species does not occur in Norway or East Fennoscandria. In Europe it is distributed as far as the Elbe and Central Italy in the west, and Leningrad region in the north, extending eastward into Siberia. The species is "decidedly stenotopic, being confined to dark and marshy habitats in mull-rich deciduous forests. The species typically occurs in rich vegetation, e.g. of *Filipendula ulmaria*. The species can be found in litter and undermoss and bark of tree stumps, etc, often together with *A. assimile*."

HŮRKA (1996) states that it is absent in Bohemia, rare to very rare in Moravia, rare to sporadic in the Slovak Republic, "a local; hygrophilous species of shaded borders of waters with rich vegetation in floodplain forests; lowlands." In the Caucasus *L. krynickii* according to SIGIDA (1993) is a forest mesophile, occurring in bairak and floodplain forest, agricultural and urban landscapes.

O. obscurus

A Holarctic species (HŮRKA, 1996). It is common in the European part of the former Soviet Union and Western Siberia, extending as far east as Lake Baikal (KRYZHANOVSKIJ et al., 1995). According to PUTCHKOV (2012), in Ukraine it inhabits the forest and forest-steppe zones, and also the Crimean Mountains and their foothills (along with the south-eastern coastal strip). *O. obscurus* has not been recorded in Moldova (KARPOVA and MATALIN, 1993). SERRANO (2013) mentions that *O. obscurus* inhabits only 5 of Spain's 23 regions.

LINDROTH (1974) states that in Great Britain *O. obscurus* occurs "in damp deciduous forests and in densely vegetated marshes, among leaves and mosses". In Fennoscandia according to LINDROTH (1985) the species occurs "predominantly in deciduous and mixed forests, living in damp, shaded sites among litter and moss. It is particularly numerous in stands of alder and ash in forest swamps, occurring among wet leaves around trees and stumps. Less abundant in peaty woods between pillows of *Sphagnum*. Also in densely vegetated marshes in open country".

In the Czech Republic and Slovakia it is "common in floodplain forests and among dense vegetation of edges of marshes and waters, from lowlands to hills" (Hůrka, 1996). In the Non-Chernozem Area of Russia *O. obscurus* has been recorded (scattered specimens) only in forest ecosystems (Soboleva-Dokuchaeva, 1995). In the Caucasus *O. obscurus* Sigida (1993) is considered part of the stagnophilous, hygrophilous complex, being a typical inhabitant of marshes and waterlogged, open floodplains. In Hungary, in a lowland oak forest-grassland complex (Tóthmérész et al., 2014) *O. obscurus* proved to be a highly reliable indicator of edge ecosystems. This ground beetle species swims well, having been observed to survive for up to 22 days on the surface of water (Kolesnikov et al., 2012). This feature of its biology enables it to survive in floodplain rivers, far from the banks. Investigations in the north of its range, on Oland island situated in the Baltic Sea, showed that *O. obscurus* is one of the most abundant species of ground beetle, both in forest and meadow habitat (Andersen, 2011). In the steppe zone of Ukraine *O. obscurus* is at its most numerous in broad-leaved forests, in moist, shady areas with a deep litter layer and acid sandy soil.

Fine differences in the habitat preferences of species can be assessed not only by the average value for a species in relation to a specific factor. It is also important to assess the range of tolerance of a species in relation to that particular factor. The presentation of data in this paper in graph form can be used both for comparison of ecological preferences of different species of ground beetle and for assessment of general tolerance of species groups sharing the same ecosystem and for comparisons between ecosystems (Brygadyrenko, 2003b).

Adoption of the research methods used for this article allows a clear multiple level assessment to be made of the ecological niches of different species of ground beetle. The results of a quantitative assessment of the ecosystemic preferences of different species can vary under the influence of climatic zone.

Conclusions

In the forests of the steppe zone of Ukraine *C. ambiguus* is a typical mesophile, with a slight preference for pine forests. *C. erratus* is at its most numerous in xeromesophilous moisture conditions with an average abundance of ants. *C. fuscipes* favours broad-leaved forests with 40–80% tree crown density, a sparse herbaceous layer, and clay soil with high salinity. *C. melanocephalus* is at its most numerous in forests with a deep litter layer with average soil salinity. *D. halensis* is often found in forests with of low crown density and favours areas with high salinity. *A. dorsalis* favours plots with scattered trees, thick grass, mesophilous moisture conditions and low abundance of ants. *L. krynickii* inhabits forests with a thin litter layer, hygrophilous moisture conditions and soils with low salinity. *O. obscurus* inhabits moist areas of forests with acid, sandy soil.

References

Andersen, J., 2011. Winter quarters of wetland ground beetles (Coleoptera, Carabidae) in South Scandinavia. *Journal of Insect Conservation*, 15: 799–810.

Aukema, B., 1990. Wing-length determination in two wing-dimorphic Calathus species (Coleoptera: Carabidae). *Hereditas*, 113: 189–202.

Aukema, B., 1991. Fecundity in relation to wing-morph of three closely related species of the melanocephalus group of the genus Calathus (Coleoptera: Carabidae). *Oecologia*, 87: 118–126.

Baranovská, E., Knapp, M., Saska, P., 2014. The effects of overwintering, sex, year, field identity and vegetation at the boundary of fields on the body condition of Anchomenus dorsalis (Coleoptera: Carabidae). *European Journal of Entomology*, 111: 608–614.

Belgard, A.L., 1950. *Lesnaja rastitel'nost' jugovostoka USSR* [The forest vegetation of the southeast of the Ukrainian Soviet Socialist Republic]. Kiev: Kiev University Press. 256 p.

Belgard, A.L., 1971. *Stepnoe lesovedenie* [Steppe forestry]. Moscow: Lesnaja promyshlennost'. 336 p.

Bilde, T., Toft, S., 1994. Prey preference and egg production of the carabid beetle Agonum dorsale. *Entomologia Experimentalis et Applicata*, 73: 151–156.

Błaszkiewicz, M., Schwerk, A., 2013. Carabid beetle (Coleoptera: Carabidae) diversity in agricultural and post-agricultural areas in relation to the surrounding habitats. *Baltic Journal of Coleopterology*, 13 (1): 15–26.

Brygadyrenko, V.V., 2003a. Fauna zhuzhelitc (Coleoptera, Carabidae) Dnepropetrovskoj oblasti [Fauna of ground beetles (Coleoptera, Carabidae) of Dnipropetrovsk region]. *Problems of Ecology and Environmental Protection in the Technogenic Region*, 3: 78–88.

Brygadyrenko, V.V., 2003b. Ispol'zovanie topologicheskih spektrov v zoologicheskoj diagnostike pochv na primere semejstva zhuzhelic (Coleoptera, Carabidae) [Using topological spectrums in zoological diagnostics of soils with the family Carabidae (Coleoptera) as an example]. *Ecology and Noospherology*, 13 (1): 119–130.

Brygadyrenko, V.V., 2004. Vozdejstvie uslovij sredy na sostav zhivotnogo naselenija podstilki i fitocenoz lesnyh ekosistem stepnoj zony Ukrainy [The influence of environmental conditions on the litter animals and phytocoenosis in the forest ecosystems of the Steppe zone of Ukraine]. *Forestry and Agroforestry*, 106: 77–83.

Brygadyrenko, V.V., 2005. Ekologicheskie aspekty vzaimodejstvija murav'ev (Hymenoptera, Formicidae) s podstilochnymi bespozvonochnymi v uslovijah stepnyh lesov [Environmental aspects of the interaction of ants (Hymenoptera, Formicidae) with litter invertebrates in steppe forest]. *Question of Steppe Forestry and Forest Land Reclamation*, 9: 181–192.

Brygadyrenko, V.V., 2006. Vozmozhnosti ispol'zovaniya napochvennyh bespozvonochnyh dlya indikacii gradaciy uvlazhneniya edafotopa v lesnyh ekosistemah [The possibility of using soil invertebrates to indicate soil moisture gradations in forest ecosystems]. *Visnyk of Dnipropetrovsk University. Biology, Ecology*, 14: 21–26.

Brygadyrenko, V.V., 2014. Influence of soil moisture on litter invertebrate community structure of pine forests of the steppe zone of Ukraine. *Folia Oecologica*, 41: 8–16.

Brygadyrenko, V.V., 2015. Vplyv umov zvolozhennja ta mineralizacii' g'runtovogo rozchynu na strukturu pidstylkovoi' mezofauny shyrokolystjanyh lisiv stepovoi' zony Ukrai'ny [Influence of moisture conditions and soil salinity on structure of litter macrofauna of the deciduous forests of Ukraine steppe zone]. *Visnyk of Dnipropetrovsk University. Biology, Ecology*, 23: 50–65.

Brygadyrenko, V.V., Solovjov, S.V., 2007. Vplyv pervynnogo g'runtoutvorennja u zaplavnyh lisah Dniprovs'ko-Oril's'kogo pryrodnogo zapovidnyka na strukturu gerpetobiju [Effect of initial soil in floodplain forests of the Dnieper-Oril's'ke Nature Reserve on the community structure of litter invertebrates]. *Pynannia Bioidycacii ta Ecologii*, 12 (1): 34–45.

Bukejs, A., Balalaikins, M., 2008. Ground beetles (Coleoptera: Carabidae) of wheat agrocenosis in Latvia. *Acta Zoologica Lituanica*, 18: 134–138.

Do, Y., Joo, G.J., 2013. The effect of fragmentation and intensive management on carabid beetles in coniferous forest. *Applied Ecology and Environmental Research*, 11: 451–461.

Do, Y., Kim, J.Y., Kim, G.-Y., Joo, G.-J., 2014. Importance of closed landfills as green space in urbanized areas: Ecological assessment using carabid beetles. *Landscape and Ecological Engineering*, 10: 277–284.

Do, Y., Lineman, M., Joo, G.-J., 2014. Carabid beetles in green infrastructures: The importance of management practices for improving the biodiversity in a metropolitan city. *Urban Ecosystems*, 17 (3): 661–673.

Emerson, B.C., Oromi, P., Hewitt, G.M., 2000. Interpreting colonization of the Calathus (Coleoptera: Carabidae) on the Canary Islands and Madeira through the application of the parametric bootstrap. *Evolution*, 54: 2081–2090.

Gañán, I., Baselga, A., Novoa, F., 2008. Diversity patterns in Iberian Calathus (Coleoptera, Carabidae: Harpalinae): Species turnover shows a story overlooked by species richness. *Environmental Entomology*, 37: 1488–1497.

Hůrka, K., 1996. *Carabidae of the Czech and Slovak Republics*. Zlín, Czech Republic: Kabourek. 565 p.

Hutchinson, G.E., 1957. Concluding remarks. *Cold Spring Harbor Symposia on Quantitive Biology,* 22: 415–427.

Karpova, E.V., Matalin, A.V., 1993. Annotirovannyj spisok zhuzhelic (Coleoptera, Carabidae) juga Moldovy [An annotated check list of carabids (Coleoptera, Carabidae) of Moldova]. *Entomologičeskoe Obozrenie*, 72: 570–585.

Kesdek, M., Yildirim, E., 2004. Contribution to the knowledge of Carabidae fauna of Turkey. Part 2 Platynini (Coleoptera, Carabidae). *Linzer Biologische Beiträge*, 36 (1): 527–533.

Klausnitzer, B., 1987. *Ökologie der Großstadtfauna*. Jena: VEB Gustav Fischer Verlag. 246 p.

Knapp, M., Uhnava, K., 2014. Body size and nutrition intake effects on fecundity and overwintering success in Anchomenus dorsalis (Coleoptera: Carabidae). *Journal of Insect Science*, 14 (240): DOI: 10.1093/jisesa/ieu102

Kocourek, F., Saska, P., Řezáč, M., 2013. Diversity of carabid beetles (Coleoptera: Carabidae) under three different control strategies against European corn borer in maize. *Plant Protection Science*, 49: 146–153.

Kolesnikov, F.N., Karamyan, A.N., Hoback, W.W., 2012. Survival of ground beetles (Coleoptera: Carabidae) submerged during floods: Field and laboratory studies. *European Journal of Entomology*, 109: 71–76.

Kromp, B., 1999. Carabid beetles in sustainable agriculture: A review on pest control efficacy, cultivation impacts and enhancement. *Agriculture, Ecosystems and Environment*, 74 (1–3): 187–228.

Kryzhanovskij, O.L., Belousov, I.A., Kabak, I.I., Kataev, B.M., Makarov, K.V., Shilenkov, V.G., 1995. *A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae)*. Sofia: Pensoft Publishers. 271 p.

Kutasi, C., Markó, V., Balog, A., 2004. Species composition of carabid (Coleoptera: Carabidae) communities in apple and pear orchards in Hungary. *Acta Phytopathologica et Entomologica Hungarica*, 39 (1–3): 71–89.

Lang, A., Filser, J., Henschel, J.R., 1999. Predation by ground beetles and wolf spiders on herbivorous insects in a maize crop. *Agriculture, Ecosystems and Environment*, 72 (2): 189–199.

Lindroth, C.H., 1974. *Coleoptera, Carabidae. Handbooks for the identification of British insects.* Vol. 4, part 2. London: Royal Entomological Society. 148 p.

Lindroth, C.H., 1979. The theory of glacial refugia. In Erwin, T.L., Ball, G.E., Whitehead, D.R., Halpern, A.E. (eds). *Carabid beetles*. The Hague: Dr. W. Junk bv Publishers, p. 385–394.

Lindroth, C.H., 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica*, 15 (2): 233–497.

Magura, T., 2002. Carabids and forest edge: Spatial pattern and edge effect. *Forest Ecology and Management*, 157 (1–3): 23–37.

Negre, J., 1969. Los grandes Calathus de la Península Ibérica. *Miscellània Zoològica*, 2 (4): 7–32.

Nylund, L., 1991. Metabolic rates of Calathus melanocephalus (L.) (Coleoptera, Carabidae) from alpine and lowland habitats (Jeloy and Finse, Norway) and Drenthe, the Netherlands. *Comparative Biochemistry and Physiology*, 100A (4): 853–862.

Putchkov, A.V., 2011. Ground beetles of the Ukraine (Coleoptera, Carabidae). *ZooKeys*, 100: 503–515.

Putchkov, A.V., 2012. Faunisticheskij obzor karaboidnyh zhukov (Coleoptera, Caraboidea) Ukrainy [A review of the caraboid-beetles (Coleoptera, Caraboidea) of Ukraine]. *Ukrai'ns'kyj Entomologichnyj Zhurnal*, 2 (5): 3–44.

Ruiz, C., Bjarte, J., Serrano, J., 2009. Molecular phylogeny of the tribe Sphodrini (Coleoptera: Carabidae) based on mitochondrial and nuclear markers. *Molecular Phylogenetics and Evolution*, 50: 59–73.

Ruiz, C., Jordal, B.H., Emerson, B.C., Will, K.W, Serrano, J., 2010. Phylogeny of the subtribe Calathina (Coleoptera: Carabidae: Sphodrini) in the Holarctic region based on nuclear and mitochondrial markers. *Molecular Phylogenetics and Evolution*, 55: 358–371.

Ruiz, C., Bjarte, J.H., Serrano, J., 2012. Diversification of subgenus Calathus (Coleoptera: Carabidae) in the Mediterranean region – glacial refugia and taxon pulses. *Journal of Biogeography*, 39: 1791–1805.

Schwerk, A., Szyszko, J. 2012, Variation in epigeic carabid fauna (Coleoptera: Carabidae) on differently-treated post-agricultural land. *Baltic Journal of Coleopterology*, 12 (1): 39–48.

Serrano, J., 2013. *New catalogue of the family Carabidae of the Iberian Peninsula (Coleoptera)*. Murcia: Ediciones Universidad de Murcia. 192 p.

Shilenkov, V.G., 1978. Osobennosti biologii massovyh vidov zhuzhelic (Coleoptera, Carabidae) fauny juzhnogo Pribajkal'ja [Peculiarities of biology of abundant ground-beetles (Coleoptera, Carabidae) in the south of the Baikal region]. *Entomologičeskoe Obozrenie*, 57 (2): 290–301.

Sigida, S.I., 1993. Landshaftno-biotopicheskoe raspredelenie i jekologicheskaja harakteristika zhuzhelic (Coleoptera, Carabidae) Predkavkaz'ja i severnyh sklonov Central'nogo Kavkaza [Landscape and biotopic distribution and ecological characteristic of carabids (Coleoptera, Carabidae) of Ciscaucasia and northern slopes of the Central Caucasus]. *Entomologičeskoe Obozrenie*, 72 (1): 11–38.

Soboleva-Dokuchaeva, I.I., 1995. Osobennosti formirovanija fauny zhuzhelic (Coleoptera, Carabidae) agrocenozov Nechernozem'ja pri kontakte s lesom [Peculiarities of formation of ground-beetles fauna (Coleoptera, Carabidae) in agrocoenoses neighbouring forests in the non-Chernozem area]. *Entomologičeskoe Obozrenie*, 74 (3): 551–567.

Thiele, H.U., 1977. *Carabid beetles in their environments*. Berlin: Springer-Verlag. 369 p.

Tóthmérész, B., Nagy, D.D., Mizser, S., Bogyó, D., Magura, T., 2014. Edge effects on ground-dwelling beetles (Carabidae and Staphylinidae) in oak forest-forest edge-grassland habitats in Hungary. *European Journal of Entomology*, 111 (5): 686–691.

van Dijk, T.S., 1972. The significance of the diversity in age composition of Calathus melanocephalus L. (Col., Carabidae) in space and time at Schiermonnikoog. *Oecologia*, 10: 111–136.

van Dijk, T.S., 1994. On the relationship between food, reproduction and survival of two carabid beetles: Calathus melanocephalus and Pterostichus versicolor. *Ecological Entomology*, 19: 263–270.

Vereschagina, T.N., 1984. Zhuzhelicy roda Calathus Bon. (Coleoptera, Carabidae) fauny SSSR [Carabids of the genus Calathus Bon. (Coleoptera, Carabidae) of the fauna of the USSR]. *Entomologičeskoe Obozrenie*, 63 (4): 751–766.

Wratten, E.S.D., Vickerman, G.P., 1985. Foraging by the carabid Agonum dorsale in the field. *Ecological Entomology*, 10: 181–189.

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