Parameters of ecological niches of *Badister*, *Licinus* and *Panagaeus* (Coleoptera, Carabidae) species measured against eight ecological factors

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Brygadyrenko V. V. 2015. Parameters of ecological niches of *Badister*, *Licinus* and *Panagaeus* (Coleoptera, Carabidae) species measured against eight ecological factors. *Baltic J. Coleopterol., 15(2): 137 – 154.*

Based on the results of research conducted between 2001 and 2014 in five administrative regions in the south of Ukraine the abundance of 6 ground beetle species has been analysed in relation to 8 ecological factors. This analysis showed that the abundance of *Badister bullatus* (Schrank, 1798) reached its maximum in forests with a sparse herbaceous layer, thick litter, loamy and clay soil. *B. lacertosus* Sturm, 1815 is most abundant in areas with low soil salinity, on loamy soils. The abundance of *B. unipustulatus* Bonelli, 1813 reaches its maximum in hygrophilous moisture conditions. The abundance of *Licinus depressus* (Paykull, 1790) in forests of the steppe zone decreases on saline soils in conditions of increased insolation, in coniferous forests, in areas with no litter, on sandy soils and near ant-hills. The abundance of *Panagaeus bipustulatus* (Fabricius, 1775) reaches its maximum in forests with average tree crown density, with sparse grass cover, average litter thickness, with xeromesophilous and mesophilous moisture, on loamy soils with average salinity and low to average numbers of ants. The abundance of *P. cruxmajor* (Linnaeus, 1758) increases in areas of high tree crown density, on sandy soils with average salinity, low and average numbers of ants.

Key words: ecological niche; litter; moisture; soil salinity; tree crown density; herbaceous layer cover

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INTRODUCTION

The ecological niche of a particular species is assessed against a range of numerous ecological factors, some of which can have a limiting affect in one part of its range or a specific climatic zone, without limiting the distribution of the species in other areas (Hutchinson, 1957). When describing the ecological peculiarities of ground beetle species most works refer to the relationship of a species to moisture, soil salinity, and type of vegetational community as a whole. Few attempts have been made to characterize the ecological niche of particular ground beetle species because this requires multifactorial experimental research: some researchers reveal the influence of a complex of ecological factors upon a certain ground beetle species (Thiele, 1977; Turin et al., 2003); others assess the influence of a single ecological factor upon many species, comparing them with one another (Rossolimo, 1989; Brygadyrenko, 2005, 2006).

The evaluation of ecological niches (introducing a kind of passport system for a species' environmental requirements) is possible thanks to results of laboratory and field studies (Hutchinson, 1957; Thiele, 1977). Laboratory experiments help to improve the assessment of a species' potential tolerance for the extreme values of a particular factor, field observation of beetles' distribution in different types of ecosystems allow one to define an occupied ecological niche – the range of characteristics which a species favours the most in a given region (Shalamova et al., 2012).

The eight ecological factors studied here were selected in the context of their significance in the steppe zone of Ukraine. Within this zone, the type of forest (coniferous, deciduous, mixed) is determined by the specifics of soil texture, soil salinity, the effect of strong sunlight and by the water balance, which is chiefly determined by the quantity of rainfall, the rate of evaporation and the surface relief (Belgard, 1950). In each type of forest the most important ecological factors are tree crown density and density of the herbaceous layer, which together determine the thickness of the litter layer (Belgard, 1971). The interaction of the biotic and abiotic factors mentioned above determine the structure of the litter macrofauna in any given forest, which in Ukraine is invariably dominated from tree crown level to the soil, and especially in the litter, by ants (Rossolimo, 1989; Brygadyrenko, 2005, 2006, 2015). For this reason the the abundance of the six selected species of ground beetles was assessed in relation to the following eight important ecological factors: type of forest ecosystem (coniferous, mixed or deciduous forest), moisture conditions, soil texture, soil salinity, tree crown density, density of the herbaceous layer, litter depth and abundance of ants. Each of the analysed ecological factors has a different influence on the various ground beetle species, firstly, on the physiological level (for example, metabolic retardation or accumulation of toxins) and, secondly, on the level of survival in a given ecosystem (this can be related to the migration capacity of individuals within populations) (Thiele, 1977; Semenova, 2008). Insofar as physiological changes are difficult to evaluate, we have chosen for this study abundance as the more reliable indicator of the suitability of forest ecosystems for each selected ground beetle species.

The objective of this article is to assess the occupied ecological niches of six ground beetle species of the genera *Badister*, *Licinus* and *Panagaeus* in the conditions of the steppe zone of Ukraine measured against 8 ecological factors.

MATERIAL AND METHODS

The ground beetles were collected from natural forests and plantations of various vegetational composition in Dnipropetrov'sk, Zaporizja, Nikolaev, Donetsk and Kharkiv regions of Ukraine in 2001–2014. This article covers the analysis of the distribution of 6 ground beetles species in 836 forest ecosystems (sites). Each site was analyzed using the same methods: the characteristics of the soil and plant cover were assessed; the litter macrofauna was collected using pit-fall traps.

The geobotanical description for each site includes density of the tree shrub and herbaceous layers, and also phytocoenotic activity of each plant species separately. The thickness of the litter layer was analysed (the average taken for 10 measurements). The soil texture for a depth of 0–20 cm was classified according to 4 types (clay, loam, sandy loam, sand). The moisture of the soil was determined by the presence of indicator species of herbaceous plants according to the scale for the steppe zone suggested by Belgard (1950). The salinity of the soil was also characterized by the presence of indicator species of herbaceous plants according to a scale suggested by Belgard (1950). The number of ants at a particular site was assessed according to the monitoring of pitfall traps. A detailed description of the forest ecosystems of Ukraine's steppe zone, and also a description of the flora and soil cover of the area researched for this article can be found in Belgard's publications (1950, 1971). A fuller geobotanical characteristic of the sample plots is given in previous publications by the author (Brygadyrenko, 2004, 2005, 2015).

At each site 10 half-litre pitfall traps (with 20% solution of NaCl) were placed at a distance of least 2 m from one another. On average, the collection of invertebrates was made every 5 days (depending upon the weather conditions). Overall, 3-24 collections were taken from each site. The numbers of invertebrates were calculated on the basis of individuals per 10 trap-days. This article analyses the abundance of the 6 researched ground beetle species based on collections taken over 20 day periods in mid June (when the variety of macrofauna reaches its maximum). The data were analyzed by ANOVA using the package Statistica 8.0. Vertical bars (Fig. 1–6) denote 0.95 confidence intervals. The factual meaning of Fisher's F-criterion for a certain numerical degree of freedom, and also the reliability of variation between the different values of the factors loaded is shown above each diagram. The threshold of significance for differences in abundance of a species was set at $P = 0.05$. The abundance of the six species of ground beetle in 836 forest ecosystems was analysed by cluster analysis (Euclidean distance, single linkage) using the package Statistica 8.0.

RESULTS

Badister bullatus (Schrank, 1798) inhabits meadows, steppes, agrocoenoses, forests, and is often seen on anthropogenically-transformed territories and populated areas. The species reaches its maximum abundance at sites with low to average herbaceous layer cover (up to 60% cover, Fig. 1c), thick litter layer (30–40 mm, Fig. 1d), loamy soils and clay soils (Fig. 1f). It has a tendency to decrease in numbers where ants are numerous (more than 64 individuals/10 trap-days) (Fig. 1h). Moisture conditions (Fig. 1e), type of forest ecosystem (Fig. 1b), tree crown density (Fig. 1a) and soil salinity (Fig. 1g) do not significantly influence the abundance of this zoophage species. The frequency of occurrence (percentage of sites at which this species was recorded) was 6.6%, with an average number of 0.045 ± 0.227 individuals/10 trap-days.

B. lacertosus Sturm, 1815 is predominantly a meadow species. In the conditions of forest ecosystems of steppe zone its abundance significantly increases at sites with low soil salinity (Fig. 2g) and loamy soil (Fig. 2f). The tendency was observed for higher numbers in deciduous forests than in mixed and coniferous forests (Fig. 2b) in conditions of average litter thickness (Fig. 2d) and low numbers of ants (Fig. 2h). Its frequency of occurrence was 2.9%, the average number was 0.045 ± 0.227 individuals/10 trap-days.

B. unipustulatus Bonelli, 1813 is a riparian species. It reaches maximum abundance in hygrophilous moisture conditions (Fig. 3e). *B. unipustulatus* does not significantly vary in abundance in response to tree crown density (Fig. 3a), herbaceous plant cover (Fig. 3c) or numbers of ants (Fig. 3h) and in deciduous forests (Fig. 3b), on sandy soils (Fig. 3f). In the conditions of thick litter layer (with thickness more than 30 mm, Fig. 3d) the abundance of the species tends to increase. Frequency of occurrence was 0.7%, with an average number of 0.003 ± 0.051 individuals/10 trap-days.

Licinus depressus (Paykull, 1790) is a forest species, which is also often common in meadows. In forests of Ukraine's steppe zone the abundance of the species significantly varies in response to herbaceous plant cover (maximum in conditions of low herbaceous layer cover, Fig. 4c) and litter capacity (maximum with thickness of about 30–40 mm, Fig. 4d). Moisture conditions (Fig. 4e), abundance of ants (Fig. 4h), crown density (Fig. 4a) or soil texture (Fig. 4f) do not significantly influence *L. depressus*. Frequency of occurrence was 8.4%, the average number was 0.049 ± 0.214 individuals/10 trap-days.

The abundance of the forest species *Panagaeus bipustulatus* (Fabricius, 1775) significantly varies in response to 6 out of the 8 considered ecological factors. It is most abundant at 20–80% tree crown density (Fig. 5a), poorly developed herbaceous layer (less than 20% cover, Fig. 5c), average litter thickness (20–40 mm, Fig. 5d), xeromesophilous moisture (Fig. 5e), loamy soils (Fig. 5f), average level of salinity (trophotopes Dc and Dac, Fig. 5g), low and average abundance of ants (up to 64 individu-

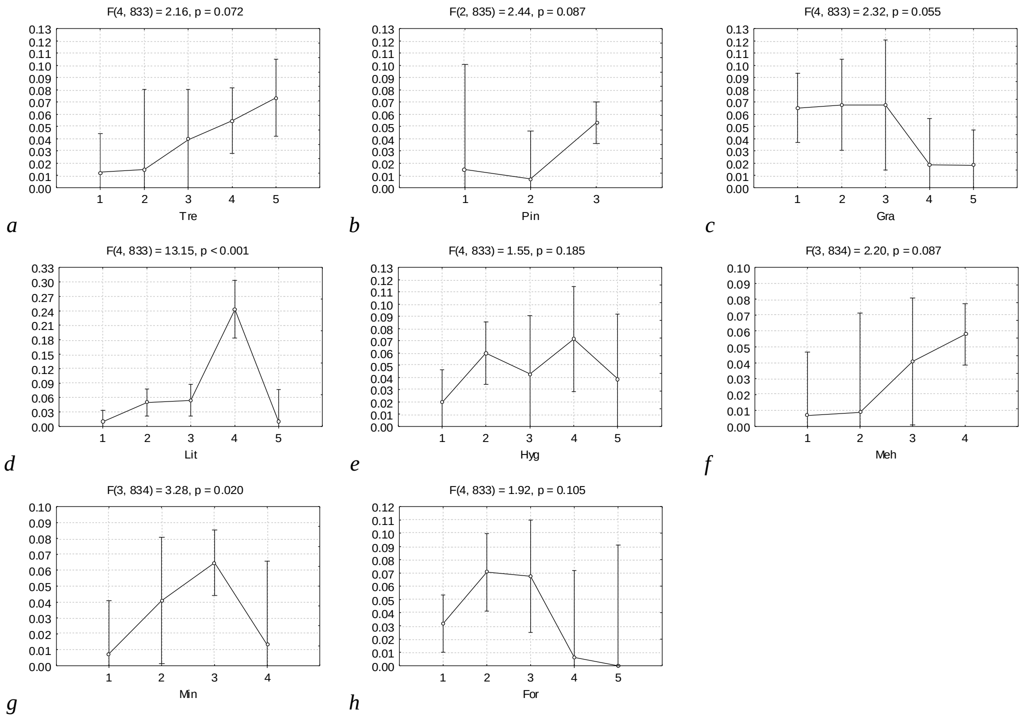

Fig. 1. Influence of conditions of forest ecosystem on *Badister bullatus* (Schrank, 1798):
a: Tre – tree crown density (1 – <20%, 2 – 21–40%, 3 – 41–60%, 4 – 61–80%, 5 – >81%);
b: Pin – type of forest ecosystem (1 – coniferous, 2 – mixed, 3 – deciduous forest);
c: Gra – density of the herbaceous layer (1 – <20%, 2 – 21–40%, 3 – 41–60%, 4 – 61–80%, 5 – >81%);
d: Lit – litter depth (1 – <10 mm, 2 – 11–20, 3 – 21–30, 4 – 31–40, 5 – >41 mm);
e: Hyg – moisture conditions (1 – xeromesophilous, 2 – mesophilous, 3 – hygromesophilous, 4 – mesohygrophilous, 5 – hygrophilous);
f: Meh – soil texture (1 – sandy, 2 – sandy loam, 3 – loam, 4 – clay);
g: Min – soil salinity (1 – trophotopes ŔÂ, Â, Ń, 2 – Dc, Dac, 3 – Dn, 4 – De, Ĺ);
h: For – abundance of ants (1 – <4, 2 – 5–16, 3 – 17–64, 4 – 65–256, 5 – >256 individuals/10 trap-days);
ordinate – loading of factor

als/10 trap-days, Fig. 5h). A tendency was observed for *P. bipustulatus* to increase in abundance in deciduous forests in comparison to mixed and coniferous forests (Fig. 5b). Frequency of occurrence was 8.0%, the average abundance was 0.11 ± 0.54 individuals/10 trap-days.

P. cruxmajor (Linnaeus, 1758), which is morphologically close to the species mentioned above, has a wider range of tolerance for the studied ecological factors: its abundance varies significantly in response to 6 of the 8 analysed factors. The abundance of *P. cruxmajor* was found to be significantly higher in conditions of 60–100% tree crown density (Fig. 6a), loamy soil (Fig. 6f), average soil salinity (trophotopes Dc and Dac, Fig. 6g), low and average abundance of ants (up to 16 individuals/10 trap-days, Fig. 6h). Measured against these characteristics, *P. cruxmajor* does not differ in abundance from *P. bipustulatus*. As with the previous species a tendency was observed for its abundance to increase in deciduous forests in comparison with mixed and coniferous forests (Fig. 6b). Unlike *P. bipustulatus*, *P. cruxmajor* is stable in abundance in relation to different levels of herbaceous layer cover (Fig. 6c) and moisture of the soil (more hygrophilous spesies, Fig. 6e). Frequency of occurrence was 8.8%, with an average number of 0.17 ± 0.85 individuals/10 trap-days.

Thus, in the steppe zone of Ukraine 4 of the 6 species of ground beetles belonging to the Licinini and Panagaeini tribes vary significantly in abundance in response to moisture of the soil, 4 species in response to salinity of the soil, 3 in response to texture of the soil, 3 in response to litter thickness, 2 in response to herbaceous layer cover, 2 in response to tree crown density, 2 in response to type of forest ecosystem (coniferous, mixed or deciduous forest) and 1 in response to abundance of ants (Table 1).

Cluster analysis of the distribution of the species researched in forest ecosystems of the steppe zone of Ukraine shows that species belonging to the genera *Badister* and *Licinus* have collectively the greatest similarity in their environmental requirements (Fig. 7). The two species of the *Panagaeus* genus differed greatly from each other and from the *Badister* and *Licinus* in their ecological patterns.

DISCUSSION

B. bullatus

This is a European-Central Siberian species (Kryzhanovskij et al., 1995; Hurka, 1996; Freudĺ et al., 2004); distributed from West Europe to West Siberia, North Iran, the Caucasus, and North Africa; records for North America should be referred to other, closely related species (Lindroth, 1986). Frĺudĺ et al. (2004) mentions *B. bullatus* for the territory of countries of Central Europe. *B. bullatus* has been recorded throughout the territory of Bulgaria (Hieke, Wrase, 1988), in 8 out of 23 regions of Spain (Serrano, 2003). Putchkov (2011, 2012) mentions *B. bullatus* as occurring throughout Ukraine.

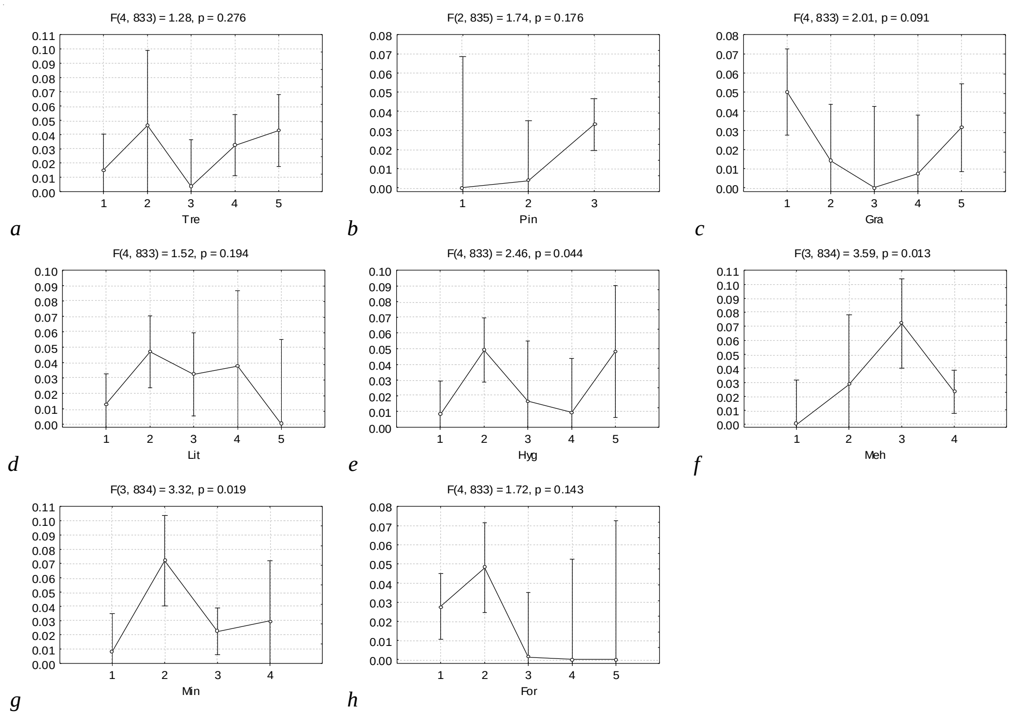

Fig. 2. Influence of conditions of forest ecosystem on *Badister lacertosus* Sturm, 1815: explanations see Fig. 1

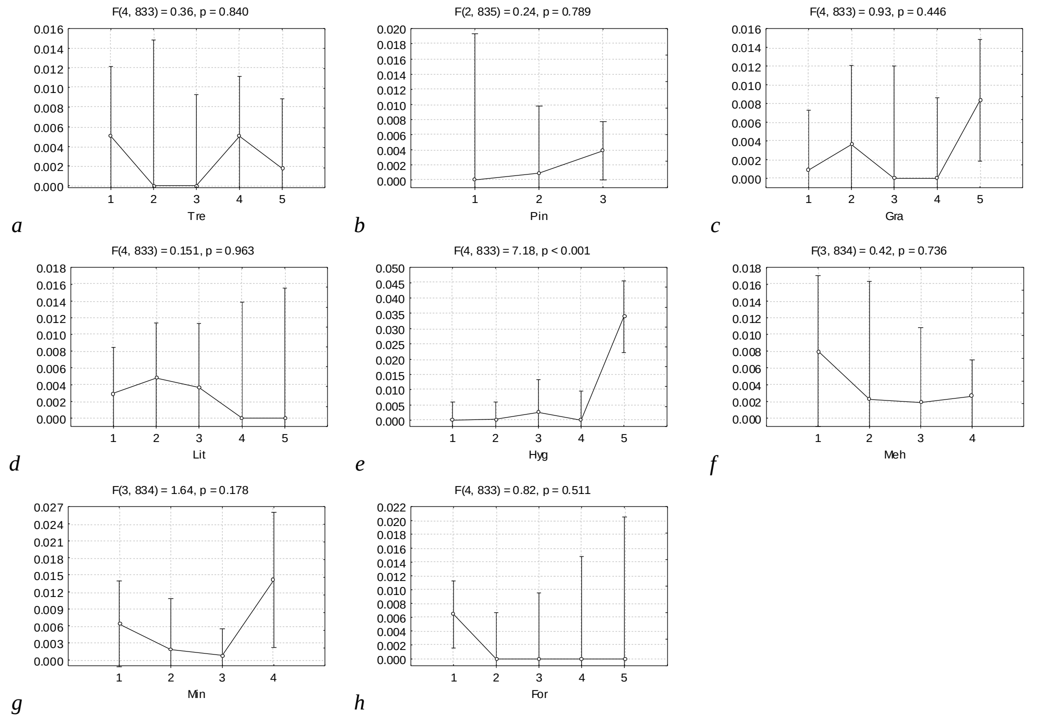

Fig. 3. Influence of conditions of forest ecosystem on *Badister unipustulatus* Bonelli, 1813: explanations see Fig. 1

According to Lindroth (1986), *B. bullatus* is in Fennoscandia and Denmark "the most eurytopic *Barister*, occurring in dry as well as in rather moist habitats, both in open country and in somewhat shaded sites. It is particularly subdominant in open deciduous forest and forest edges, on moderately dry soil with thick layer of litter; also on open, sandy grassland". Lindroth (1974) states that in Great Britain *B. bullatus* occurs "in open as well as in somewhat shaded, places, e.g. under bushes and in open forests; common". Luff (1992) writes that *B. bullatus* "occurs throughout much of Britain and Ireland on open, dry and often sandy soils, usually at low altitudes. In Scotland it is almost exclusively coastal, being found on sand dunes, sandy coastal grasslands. The species flies readily, and breeds in the spring".

Hurka (1996) writes that in the Czech and Slovak Republics *B. bullatus* is common "in dry to wet habitats, indifferent to shade: steppe, meadows, overgrown edges of waters, swamps; lowlands to mountains, mostly in hills". FrÍudÍ et al. (2004) place the species in the planar-montane group, noting that "in Central Europe, widespread and common. Unlike the other species even in relatively dry habitats, both in the forest as in open areas. From the lowlands to subalpine layers".

In Denmark, Sweden and Norway, *B. bullatus* inhabits anthropogenic habitats, probably with a preference for naturally open, dry habitats, woodland (Andersen, 2000). In Denmark, *B. bullatus* has been observed 5 times more frequently in urbanized ecosystems than in natural forests (Elek, Lövei, 2005). In the Mazurian Lakes (Mamry Lake) in Poland, *B. bullatus* were sampled in 8 lake islands from 17 study sites (Ulrich, Zalewski, 2006). In Brest region of Belarus, the species has been recorded in oak plantations in meadows, comprising 1.3% of the overall ground beetle population and 1.1% in ash plantations with a meadowsweet understorey (Derunkov, 2009). According to Tóthmérész et al. (2014) in Hungary, *B. bullatus* inhabits edge, forest and grassland ecosystems. In Bałcyny (Northern Poland), *B. bullatus* has been recorded on old fal-

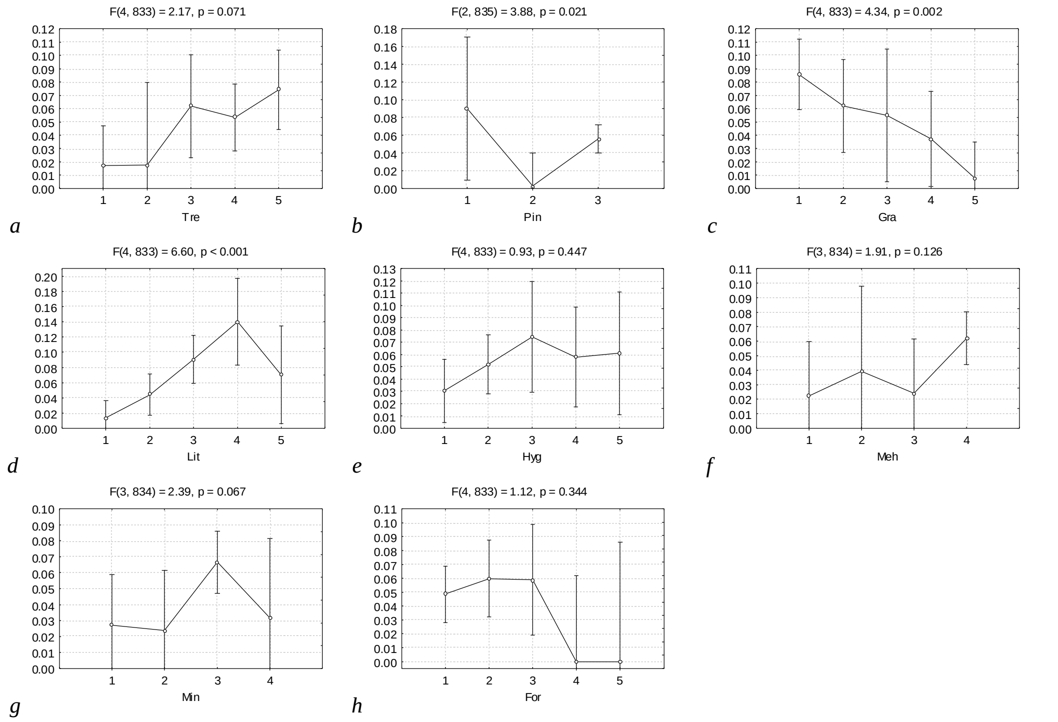

Fig. 4. Influence of conditions of forest ecosystem on *Licinus depressus* (Paykull, 1790): explanations see Fig. 1

low (Sądej et al., 2012), in the Białowieża primaeval forest (Northern Poland) the abundance of this species came to 0.05% of the overall ground beetle population (Skłodowski, 2006). The species is common in floodland habitats of the Polessia area of Ukraine (Kirichenko, 2000). *B. bullatus* is rare in the Po Plain (Lombardy, Italy), inhabiting open habitats (Pilon et al., 2013). In city parks of Nizhniy Tagil (Western Siberia), *B. bullatus* has disappeared following recreational impact despite the survival of many other ground beetle species there (Semenova, 2008). However, in Gomel' city *B. bullatus* is constantly observed (Halinouski, Krytskaya, 2014).

In the south of its range in the Ciscaucasus (Sigida, 1993), *B. bullatus* is considered to belong to the polytopic, mesophilic group, inhabiting the plakor complex, it is typical of natural steppe areas and pastures, ravine forests and bottomland forests, agricultural landscapes. *B. bullatus* is quite often seen in Volgograd and Astrakhan regions and in Kalmykia (Kaljuzhnaja et al., 2000). In Moldova (Karpova, Matalin, 1993), it flies at night towards ultraviolet light. Komarov (1991) points out that *B. bullatus* "in comparison with other species prefers less moist habitats, especially in the northern parts of its range. It is common in meadows, edges of deciduous and mixed forests, and sometimes is seen in agrocoenoses.

According to our data, *B. bullatus* is the most drought-resistant species of its genus in Ukraine's steppe zone, sometimes being found even in xeromesophilous moisture conditions (Brygadyrenko, 2003), often recorded in cities, in woodland belts by highways (Brygadyrenko, Chernysh, 2003). The abundance of the species is greatest in sparse herbaceous vegetation, in thick litter, on loamy and clay soil. Other ecological factors did not influence the abundance of *B. bullatus*.

***B. lacer**tosus*

A transpalaearctic species (Kryzhanovskij et al., 1995; Hurka, 1996). Freude et al. (2004) consider *B. lacertosus* to be distributed in all countries of central Europe. The species is distributed throughout Bulgaria (Hieke, Wrase, 1988), but is absent in Spain (Serrano, 2003) and Great Britain (Lindroth, 1974). Putchkov (2011, 2012) states that *B. lacertosus* is distributed in the forest and forest-steppe zones of Ukraine.

Lindroth (1986) writes that in Fennoscandia and Denmark *B. lacertosus* shares the same habitat preferences and sometimes occurs together with *B. unipustulatus*, inhabiting “moist, rather shaded sites, usually in mull-rich deciduous forest, for instance of ash, alder and beech, often in forest swamps. It dwells among moss and leaves”. Hurka (1996) states that in the Czech and Slovak Republics *B. lacertosus* is common in “water edges with vegetation, swamps, moist meadows; lowlands to hills”. Freude et al. (2004) place the species in the planar-montane group and write that “in Central Europe, widespread, prefers humid, shady sites, rich in humus (sometimes with *B. unipustulatus* together)”. Komarov (1991) writes that in habitat preferences *B. lacertosus* “differs significantly from *B. bullatus*. Throughout its range it inhabits deciduous and mixed forests while *B. bullatus* prefers open habitats”.

Tóthmérész et al. (2014) point out that in Hungary *B. lacertosus* is a reliable indicator species for edge and forest as opposed to grassland ecosystems. Kirichenko (2000) refers to *B. lacertosus* as a common species in floodland habitats of the Polessia area of Ukraine. In the Biaiowieïa primaeval forest (Northern Poland), the species makes up 0.11% of the overall total of ground beetles (Skiodowski, 2006), in Baicyny *B. lacertosus* was found in eight-year and twelve-year fallow (S№dej et al., 2012). The abundance of the species amounted to 0.49% of the overall total of ground beetles in humid forest habitats of Puszcza Knyszyńska forest (North-eastern Poland) (Kwiatkowski, 2011). The species was found in cities and suburban areas: in Belarus in Gomel’ city (Halinouski, Krytskaya, 2014) and in Hungary in Debrecen it has been classified as a species that prefers suburban areas (Magura et al., 2004). In Brest region (Belarus) it dominates in oak

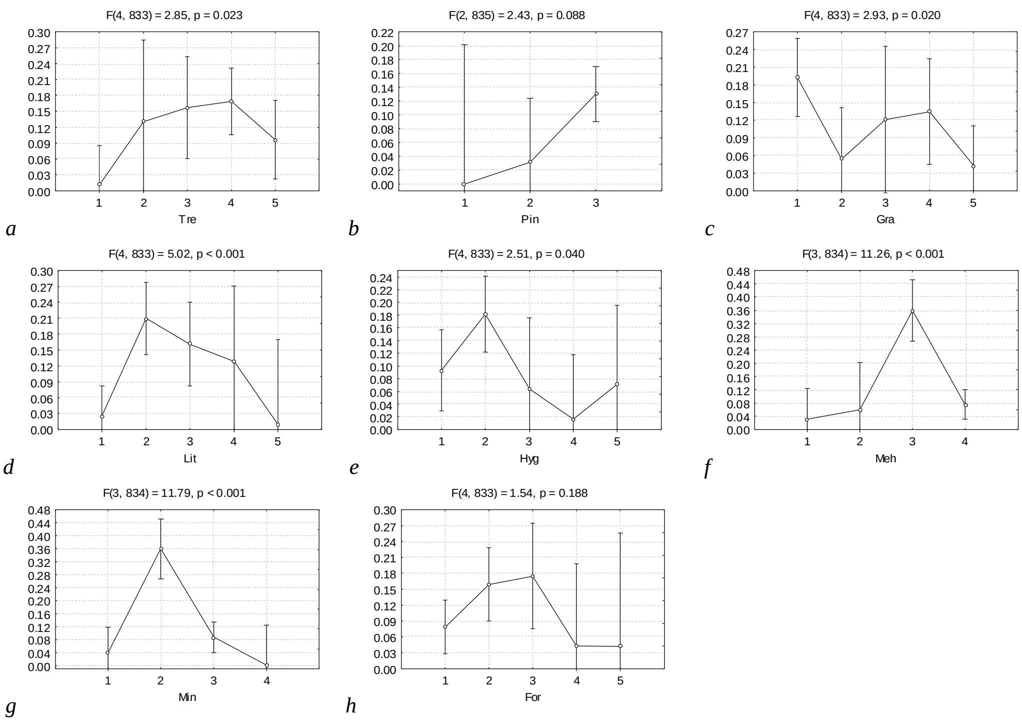

Fig. 5. Influence of conditions of forest ecosystem on *Panagaeus bipustulatus* (Fabricius, 1775): explanations see Fig. 1

plantations on former meadows, making up 2.2% of total ground beetle numbers, in an area of ash with a meadowsweet understorey 2.2%, and in Gomel' region in an oak grove with a bracken understorey 4.0% (Derunkov, 2009).

In Ukraine's steppe zone, the species is abundant on reservoir shores, including shores of forest reservoirs (Loza, Brygadyrenko, 2007). On the shores of salt-water lakes, this species is less abundant than others of the genus *Badister* (Brygadyrenko, 2000). *B. lacertosus* shows a greater hygrophilous affinity compared to *B. bullatus* (Brygadyrenko, 2003). In forests of steppe zone, the species is more numerous in conditions of low soil salinity, on loamy soils with low numbers of ants.

B. unipustulatus

A West Palaearctic species (Kryzhanovskij et al., 1995; Hurka, 1996), distributed from Western Europe to Asia Minor, the Caucasus and West Siberia (Lindroth, 1986). Freude et al. (2004) state that *B. unipustulatus* is distributed in all central European countries. *B. unipustulatus* is distributed throughout Bulgaria (Hieke, Wrase, 1988), and only in 3 out of 23 regions of Spain (Serrano, 2003). Putchkov (2011, 2012) considers *B. unipustulatus* to be distributed throughout Ukraine. Ganglbauer (1892) does not mention the habitats preferred by *B. unipustulatus*', restricting himself to the word "seldom".

Lindroth (1986) writes that in Fennoscandia and Denmark *B. unipustulatus* is a very rare "stenotopic species, occurring on moist, warm, mull-rich clay soil, in rather shaded sites, usually near stagnant water. It is especially typical of forest swamps under deciduous trees and bushes, e.g. alder and birch. The beetles occur among moss and leaves; in winter under bark of trees". In Great Britain, *B. unipustulatus* lives "among leaves and moss on moist, shaded places, usually near pools; local" (Lindroth, 1974). Luff (1992) mentions that in Great Britain this species "occurs in fens and wet, marshy woodlands, usually in litter near standing water or

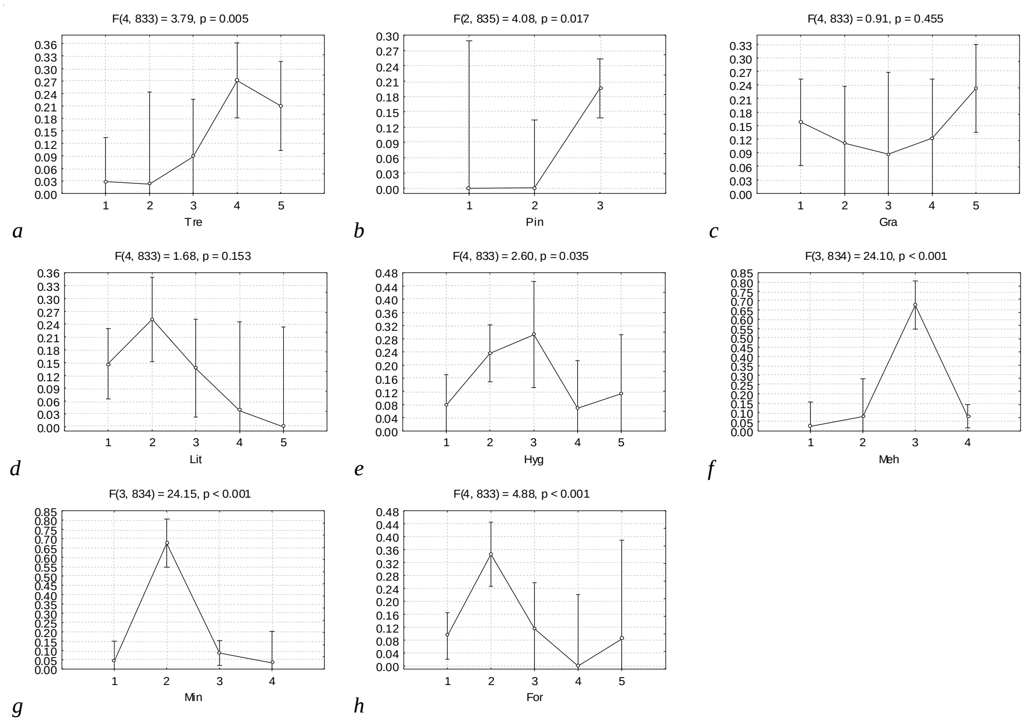

Fig. 6. Influence of conditions of forest ecosystem on *Panagaeus cruxmajor* (Linnaeus, 1758): explanations see. Fig. 1

hibernating under bark. *B. unipustulatus* is winged, and possibly breeds in summer, rather later than other *Badister* species".

Hurka (1996) writes that in the Czech and Slovak Republics *B. unipustulatus* is sporadic in "wet, overgrown edges of waters and swamps; lowlands". Fråudå et al. (2004) mention that *B. unipustulatus* belongs to the planar-montane species group "in Central Europe widespread, but only locally common. Often on the edge of ponds in forests, but also in open terrain on trenches with richly developed herbaceous layer, often on clay soils". Komarov (1991) writes that *B. unipustulatus* "within its range is seen in highly moist littoral formations with dense vegetation. Flies towards ultraviolet light". In the Białowieża primaeval forest (Northern Poland), the species does not exceed 0.008% of the total number of ground beetles (Skłodowski, 2006). In Brest region (Belarus), it is found on floodplain meadows in glades of oak-alder-bottomland, making up 5.7% of the total number of ground beetles (Derunkov, 2009). *B. unipustulatus* is typical in floodland habitats of the Polessia area of Ukraine (Kirichenko, 2000).

In Ciscaucasia and the northern slopes of the Central Caucasus, it is considered to belong to the rheophilic group of the hygrophilous invertebrate complex: in lowland areas *B. unipustulatus* is characteristic of marshland, unforested floodplains and urban landscapes, while in mountain areas it is characteristic of mountain rivers and streams. In Moldova *B. unipustulatus* is uncommon on floodplain fields and flies at night towards ultraviolet light (Karpova, Matalin, 1993). In the Republic of Adygheya (North Caucasus), it is "very common. On the banks of rivers in the plains or foothills in waterside habitats it is often found on periodically flooded sites. Occurs on agrocoenoses. Flies towards light." (Zamotajlov, Nikitskiy, 2010). *B. unipustulatus* is ubiquitous and very common in the Lower Volga area (Kaljuzhnaja et al., 2000).

Our data show that in the steppe zone of Ukraine it is common on the banks of reservoirs, including saline water bodies (Brygadyrenko, 2000), has a strongly hygrophilous preference, reaching its maximum abundance in ultrahygrophilous moisture conditions (Brygadyrenko, 2003). Its abundance is greatest in deciduous forest, near shore-lines, on sandy soils with low salinity. *B. unipustulatus* can be found equally in forests and in open country, at sites with minimal to average litter depth, on shores covered with herbaceous vegetation and on unvegetated shores, and at sites with varying numbers of ants.

L. depressus

A Palaearctic species (Kryzhanovskij et al., 1995; Hurka, 1996), commonest from West Europe to the Caucasus and West Siberia (Lindroth, 1986). Fråudå et al. (2004) state that *L. depressus* occurs "in al-

Table 1. Relationship between studied species of ground beetles of the tribes Licinini and Panagaeini and the influence of eight ecological factors in forest ecosystems in the steppe zone of Ukraine (based on the distribution in 836 samples from soil traps)

Species	Tre	Pin	Gra	Lit	Hyg	Meh	Min	For
Badister bullatus (Schrank, 1798)	–	–	–	+	–	–	+	–
B. lacertosus Sturm, 1815	–	–	–	–	+	+	+	–
B. unipustulatus Bonelli, 1813	–	–	–	–	+	–	–	–
Licinus depressus (Paykull, 1790)	–	+	+	+	–	–	–	–
Panagaeus bipustulatus (Fabricius, 1775)	+	–	+	+	+	+	+	–
P. cruxmajor (Linnaeus, 1758)	+	+	–	–	+	+	+	+

Notes: Tre – tree crown density, Pin – type of forest ecosystem (coniferous, mixed or deciduous forest), Gra – density of the herbaceous layer, Lit – litter depth, Hyg – moisture conditions, Meh – soil texture, Min – soil salinity, For – abundance of ants; "+" – influence of ecological factor is considered significant at $P < 0.05$, "–" – influence of ecological factor is considered insignificant at $P > 0.05$.

most all parts of Central Europe, but only detected locally". The species has been recorded throughout the territory of Bulgaria (Hieke, Wrase, 1988), but is recorded only in one out of 23 regions of Spain (Serrano, 2003). *L. depressus* is recorded infrequently in the Lower Volga area (Kaljuzhnaja et al., 2000). Putchkov (2011, 2012) states that *L. depressus* is distributed throughout Ukraine, Kirichenko (2000) mentioning that the species is more common in floodland habitats of the Polessia area of Ukraine.

Lindroth (1986) states that in Fennoscandia and Denmark *L. depressus* "is a xerophilous species, living on dry, sandy or gravelly soil, often mixed with clay or chalk. The species prefers somewhat shaded sites in open grassland. In Central Europe also in dry forest". In Great Britain, *L. depressus* lives "on dry sand, gravel or chalk; local and rare" (Lindroth, 1974). Luff (1992) concretizes the distribution and biology of the species: *L. depressus* "is a snail-feeder, occurring on dry, usually calcareous soils, in grassland or woodland, also in chalk and gravel pits. It is brachypterous and autumn-breeding in Britain".

Hurka (1996) writes that in the Czech and Slovak Republics *L. depressus* is sporadic and rare "in drier, unshaded habitats: steppe, elevated, not flooded water edges with sparse vegetation; lowlands to foothills". In Denmark, Sweden and Norway, this species occurs in anthropogenic habitats, with a probable preference for naturally open, dry habitats (Andersen, 2000). Fråudå et al. (2004) characterizes the species as planar-subalpine, resident in "dry, warm and richly structured habitats, often on calcareous or sandy soil, locally also in forests. From the lowlands to subalpine in height". In the Bia³owie¿a primaeval forest (Northern Poland), the abundance of the species does not exceed 0.007% of the total count of ground beetles (Sk³odowski, 2006).

In the south of its range in Ciscaucasia (Sigida, 1993), *L. depressus* is a steppe mesophilic species that lives in ravine forests and bottomland forests, agricultural and urban landscapes. In the Republic of Adygheya it is a rare steppe mesophilic species, which can be also seen in agrocoenoses (Zamotajlov, Nikitsky, 2010). In Moldova (Karpova, Matalin, 1993) it is sometimes seen on fields in floodplains and is also recorded in Lucerne crops.

In a laboratory experiment conducted by the author (Brygadyrenko, Korolev, 2006) *L. depressus* was very seldom eaten by *Pterostichus melanarius* (Illiger, 1798). In a repeated study we compared the differences in consumption by *P. melanarius* of live and dead prey items: it is interesting that *P. melanarius* consumed only 7% more dead than live specimens of *L. depressus*, while 50–80% more dead than live specimens were eaten of other ground beetle species which are also consumed by *P. melanarius* at a low rate. This, perhaps, is connected with the presence of poisonous substances in the haemolymph of *L. depressus*, which are possibly obtained through the species' consumption of molluscs (Korolev, Brygadyrenko, 2012).

According to our data, in the steppe zone *L. depressus* is more abundant and tolerant to shade and soil salinity soil than *L. cassideus* (Fabricius, 1792) (Brygadyrenko, 2003). *L. depressus* is one of the species that is common in aspen forests on sandy terraces of steppe rivers (Loza, Brygadyrenko, 2007), local in city parks and along roads in woodland shelterbelts (Brygadyrenko, Chernysh, 2003).

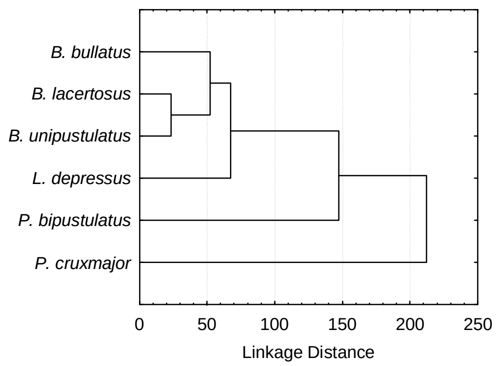

Fig. 1. Results of cluster analysis of the distribution of the groundbeetles of the tribes Licinini and Panagaeini in forest ecosystems in the steppe zone of Ukraine

P. bipustulatus

Distributed from West Europe to the Caucasus and Estonia (Kryzhanovskij et al., 1995; Lindroth, 1986). Fråudå et al. (2004) mentions that *P. bipustulatus* occurs in all central European countries; Hieke and Wrase (1988) mention that it occurs in Bulgaria, Serrano (2003) that it occurs in Spain (in 5 out of 23 regions), Putchkov (2011, 2012) that it occurs throughout Ukraine except for the Crimean peninsula.

Lindroth (1986) writes that in Fennoscandia and Denmark *P. bipustulatus* is "more xerophilous than *P. ńruxmajor*, living in dry, sun-exposed grassland, on sandy, gravelly or chalky soil. The species is usually found under stones, in dry moss, or under bushes of *Sarothamnus* and *Juniperus*". Lindroth (1974) writes that in Great Britain *P. bipustulatus* is "almost xerophilous, on open, sandy or gravelly ground with short meadow vegetation; often in chalky districts. The two species are never found together; local and rare". Luff (1992) concretizes that in Great Britain this species "is a local species of dry, sandy or calcareous grasslands and dunes, found also in sand, chalk and gravel pits".

In the Czech and Slovak Republics (Hurka, 1996), *P. bipustulatus* is sporadic to rare, "preferably in drier, unshaded or partly shaded habitats: steppe, shrubby hill-sides, gardens; lowlands, hills to foothills". Freude et al. (2004) places *P. bipustulatus* in the planar-montane group and writes that it is widespread but infrequent in Central Europe "to the north is very rare. Preferably, fresh to moist habitats, meadows, marshes, and water banks. Overwinters as imago under bark or at the foot of willows and poplars". Ganglbauer (1892) claims that *P. bipustulatus* is "more seldom than *P. cruxmajor*, lives at dry, sandy places".

In Belgium (van Looy et al., 2007) *P. bipustulatus* inhabits open medium-wet grassland; dry gravel, sand substrate. Van Looy et al. (2007) consider the species to belong to the modestly stenotope, xerophilic ecological group. In Denmark, Sweden and Norway (Andersen, 2000) *P. bipustulatus* inhabits anthropogenic habitats; with a probable preference for naturally open, dry habitats. Halinouski and Krytskaya (2014) recorded this ground beetle species in Gomel' city. In Northern Poland, the species inhabits eight-year and twelve-year old fallows (S№dej et al., 2012), in the Biaiowieïa primaeval forest the abundance of the species does not exceed 0.007% of the overall number of ground beetles (Skiodowski, 2006).

In Ciscaucasia, *P. bipustulatus* (Sigida, 1993) belongs to the group of polytopic mesophiles of the upland complex and is a typical inhabitant of natural steppe areas and pastures. In Tatarstan the species lives "in dry places, and is very rare" (Zherebcov, 2000). In the Republic of Adygheya, *P. bipustulatus* "is quite rare. It is seen in river floodplains and marshy areas." *P. bipustulatus* is comparatively common in the Lower Volga area (Kaljuzhnaja et al., 2000).

In Ukraine's steppe zone, *P. bipustulatus* is one of mesophilous ground beetle species and is characteristic for different types of forests (Brygadyrenko, 2004). According to the results of our previous studies, *P. bipustulatus* is more tolerant of high numbers of ants than *P. cruxmajor* (Brygadyrenko, 2005). In a laboratory experiment (Brygadyrenko, Korolev, 2006) *P. bipustulatus* was often eaten by *Pterostichus melanarius* (Illiger, 1798). In aspen-birch stands with common reeds in Ukraine's northern steppe zone *P. bipustulatus* is the most abundant species of ground beetles, reaching up to 20% of their total population (Loza, Brygadyrenko, 2007). The species is often seen in roadside woodland belts, tolerating the effects of a complex of anthropogenic factors and comprises 6–33% of the total population of ground beetles (Brygadyrenko, Chernysh, 2003).

P. cruxmajor

A Palaearctic species (Kryzhanovskij et al., 1995; Hurka, 1996; Fråudå et al., 2004), distributed from West Europe to North Africa, Asia Minor, North Iran and East Siberia (Lindroth, 1986; Kesdek, 2012). Fråudå et al. (2004) mentions that the species inhabits all Central European countries. *P. cruxmajor* is distributed throughout Bulgaria (Hieke, Wrase, 1988), in 10 out of 23 regions of Spain (Serrano, 2003). Putchkov (2011, 2012) states that it occurs throughout Ukraine.

Ganglbauer (1892) states that *P. cruxmajor* "lives in marshy places". In Fennoscandia and Denmark (Lindroth, 1986), *P. cruxmajor* is "a hygrophilous species, occurring at the margin of lakes and slowly running rivers, as well as in wet meadows; usually on soft, clayey soil with rich vegetation". In Sweden, *P. cruxmajor* is "hygrophilous, associated with open habitats in an early successional stage, occurs also in gravel- or clay pits and other man-made ruderal habitats" (Ljungberg, 2002).

Lindroth (1974) states that in Great Britain *P. cruxmajor* is "strongly hygrophilous, occurring at the margin of standing or slowly running waters, where the soil is soft and the vegetation rich; very local". In Britain, it is classified as an endangered (Red Data Book 1) species, and there are only three recent British records (Hyman, Parsons, 1992). Its ecology in Ireland is described as hygrophilous occurring on well vegetated, muddy shores of lakes and rivers, and muddy turloughs. In Britain, it has been recorded in lush vegetation on soft soils or mud at the margins of standing or slowly running water, as well as fens, dune slacks and coastal salt marshes (Shirt, 1987; Hyman, Parsons, 1992; Luff 1992; Moran et al., 2003). The specimens were sieved from "tussocks" of *Sphagnum*, not far from the roadside, in the floodplain of loughs. Luff (1992) writes that "this rare species used to occur locally in marshes and fens throughout south and east England and in Ireland, but there are only four recent records. Habitats include the area around a dune slack pond, and coastal saltmarsh grassland".

Hurka (1996) writes that in the Czech and Slovak Republics *P. cruxmajor* is sporadic, occurring "rather in moist, unshaded or partly shaded habitats: meadows near water, grassy water edges; lowlands to hills". *P. cruxmajor* is a stenotopic fauna element of marshes and moors in Western Germany (Wagner, Wagner, 2009). In the Mazurian Lakes in Poland, specimens of *P. cruxmajor* were sampled only from one lake island from 17 study sites (Ulrich, Zalewski, 2006). In the Białowieża primaeval forest (Northern Poland), the abundance of the species does not exceed 0.022% of the total count of ground beetles (Skłodowski, 2006).

FrĺudĺÍ et al. (2004) places the species in the planar-coline group and writes that "in Central Europe spread, but rarely. To the north it is very rare. Prefers warm, dry habitats, dry slopes, dry meadows and pastures. Only in the mountains and on humid surfaces". In Brest region of Belarus, the species accounts for 2.2% of the ground beetle population in ash forest with meadowsweet understorey (Derunkov, 2009). In floodland habitats of the Polessia area of Ukraine, *P. cruxmajor* is fairly common (Kirichenko, 2000). Pilon et al. (2013) consider *P. cruxmajor* to be a hygrophilous species, with a preference for open habitats, recorded in herbaceous buffer strips only in the Po Plain in Italy. Whitehead (1993) considers *P. cruxmajor* to be "an important species with a high conservation value, declining in many parts of its range. A primary wetland indicator, usually amongst helophytes in Balearic Islands". According to Halinouski and Krytskaya (2014), the species has a tolerance for the influence of a complex of anthropogenic factors in Gomel' city.

In Ciscaucasia, in the southern part of its range, Sigida (1993) places *P. cruxmajor* in the stagnophile group, writing that this is a characteristic species of marshes and unforested, flooded river valleys. In Moldova (Karpova, Matalin, 1993), it occasionally flies at night towards ultraviolet light. In Tatarstan, it is observed in damp, shady locations (Zherebcov, 2000). In the Republic of Adygheya, it is "very common. Often found on the banks of standing water bodies and in waterlogged areas. It is attracted to light" (Zamotajlov, Nikitsky, 2010). *P. cruxmajor* is common in the Don floodplain, in Kalmykia and in the Lower Volga area (Kaljuzhnaja et al., 2000).

Our data for the steppe zone of Ukraine show that *P. cruxmajor* is often found in deciduous and coniferous woodland in the northern part of the steppe zone (Brygadyrenko, 2004). In aspen-lime forests in this zone *P. cruxmajor* is one of the most abundant species, making up abīut 15% of the total ground beetle population (Loza, Brygadyrenko, 2007). In general, this species is more hygrophilous in character than *P. bipustulatus* (Brygadyrenko, 2003), although our previous research on 29 forest sites failed to show a significant hygrophilous preference in either species (Brygadyrenko, 2006). The species has a strong tolerance for anthropogenic pressure, comprising up to 21–29% of the total number of ground beetles in roadside shelterbelts (Brygadyrenko, Chernysh, 2003).

Cluster analysis

The results of the cluster analysis show that *P. bipustulatus* and *P. cruxmajor* have a great linkage distance from the other four species. This complements the data (Table 1), which shows that these two *Panagaeus* species are each influenced by six factors while each of the other four *Licinus* and *Badister* species are influenced by only one to three factors. This may be an indirect effect of the analysed ecological factors, being mediated through diet because the *Licinus* and *Badister* species feed mainly on tiny molluscs while the *Panagaeus* species are predatory polyphages with a trophic spectrum which still awaits research (our unpublished data). Thus result of the cluster analysis underlines the need to study the trophic preferences of *P. bipustulatus* and *P. cruxmajor*.

CONCLUSIONS

The data drawn from our research cannot be directly compared with the data of the literature for other regions of the Palearctic because ecological factors interact with each other differently in specific and complex ways in each geographic region. As far as is known to the author, despite the existence of detailed atlas work for the United Kingdom (Luff, 1992), the Fennoscandia and Denmark (Lindroth, 1986), etc., equivalent large scale research on the influence of a range of ecological factors on ground beetles, covering hundreds of separate sites, has not yet been conducted.

This analysis showed that in the steppe zone of Ukraine the abundance of *B. bullatus* was greatest in forests with a thin herbaceous layer, thick litter, loamy and clay soil. *B. lacertosus* is most abundant on sites with low soil salinity and loamy soils. The abundance of *B. unipustulatus* is greatest in hygrophilous moisture conditions. The abundance of *L. depressus* diminishes on saline soils in conditions of raised insolation, in coniferous forests, on sites devoid of litter, on sandy ground and near ant-hills. The abundance of *P. bipustulatus* reaches its maximum in forests with average tree crown density, sparse herbaceous cover, average litter depth, xeromesophilous and mesophilous moisture, on loamy soils of average salinity and low to average abundance of ants. The abundance of *P. cruxmajor* is greatest on sites with high tree crown density, on sandy soils of average salinityand low to average numbers of ants.

The use of the ecological scale shown in this article for assessing the degree of any given ecological factor allows one to make a clear and quantitative assessment of a ground beetle species' habitat requirements in forests in the steppe zone. In this article the main emphasis was on the ecological requirements of six common ground beetle species, each species taken separately. However, analysis of the combined requirements of the dominant ground beetle species inhabiting a particular ecosystem may allow one to make a quantitative assessment of their common (the average for the given group of species) tolerance for the influence of a particular ecological factor. We suppose, though this remains to be proved, that if all the analysed species in an ecosystem have a narrow range of preference for the level of a given ecological factor, then the ecosystem is stable, it is at the climax stage of its development. Conversely, we suppose that if the proportion of "ubiquitousness" of species is high in relation to a given ecological factor, then the ecosystem is at a successional stage on the approach to the climax condition. Further development of the ecological scale presented in this article can help deepen our understanding of the patterns of formation of species communities and the principles of development of species complexes in natural and anthropogenically disturbed ecosystems.

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Received: 20.09.2015
Accepted: 12.12.2015