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EFFECT OF CANOPY DENSITY ON LITTER INVERTEBRATE COMMUNITY STRUCTURE IN PINE FORESTS

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Abstract

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We investigated the structure of the litter invertebrate community in 141 pine (*Pinus sylvestris* Linnaeus, 1753) forest sites with five variants of canopy density (30–44, 45–59, 60–74, 75–89 and 90–100%) in the steppe zone of Ukraine. The total number of litter macrofauna specimens collected at each site decreased from an average of 84/100 trap-days in the sparsest stands (30–40% density) to 4–39 specimens/100 trap-days in the forests with a denser canopy. The number of macrofauna species caught in the pitfall traps does not vary significantly with different degrees of canopy density. The Shannon–Weaver and Pielou diversity indexes show increases corresponding to increasing stages of canopy density. The average share of phytophages in the trophic structure of the litter macrofauna does not vary with canopy density. The relative number of saprophages decreases from 54% in the forests with the sparsest canopy to 11–13% in the forests with denser canopies. The relative number of saprophages in pine forests (22%) is lower than that in deciduous forests (40%). The share of zoophages in the trophic structure of the litter macrofauna increases significantly with the increase in the pine forest canopy density (from 21% in the sparsest plots to 59% in the densest). The relative number of polyphages is highest (47–65%) when the canopy density is 45–89%. At canopy densities below or above this range, the share of polyphages in the community decreases to 20 and 24%, respectively. Regardless of canopy density, Formicidae and Lycosidae invariably rank amongst the first three dominant families. Nine families of invertebrates dominate in the pine forest stands with the highest density (90–100%), and 5–7 families dominate in the stands with lower density. For the pine forest litter macrofauna, we have observed an extreme simplification of the community size structure compared with natural and planted deciduous forests of the steppe zone of Ukraine.

Key words: trophic structure, biodiversity, saprophages, zoophages, polyphages, macrofauna.

Introduction

Litter macrofauna forms the part of the forest animal community and woody vegetation part of the plant subsystem of the forest ecosystem. The interaction between these two elements has been studied by many researchers, but their attention has usually been confined to specific interactions between selected populations of the plant and animal subsystems (Walsh, Linit, 1984; Zagatti et al., 1997; Smit et al., 2002). The litter macrofauna is one of the most varied species complexes in any type of terrestrial ecosystem, forests in particular. Its structure tends to be highly complex in a multi-species tree community and noticeably simplified in monodominant pine forest communities on oligotrophic sandy soils. The poverty of species composition and relative simplicity of their trophic nets make ecosystems dominated by *Pinus sylvestris* Linnaeus, 1753, attractive as a control for assessment of regional biodiversity.

Scots pine, with a vast geographical range and high tolerance of the effects of different environmental factors (especially humidity and salinity of the soil, its *pH*, its textural composition and extreme variations of temperature), exists in most steppe habitats in environments that are unsuitable for woody vegetation of the angiosperm group. For example, in the south of its natural range – in the steppe zone of Ukraine – Scots pine is common in the extreme conditions of arid tracts of river terraces with light-textured soils (Belgard, 1971). When pine forests of the steppe zone occupy more humid areas or soils rich in macroelements, the role of angiosperms (common oak, small-leaved linden, field maple, etc.) increases and a fairly diverse mixed forest vegetational community is formed. In this connection, phytocenoses of the Scots pine are a convenient object for evaluating the effect of the woody canopy, first of all its density, on the structure of the litter macrofauna. The effect of diversity and features of the phytocenosis on the composition of the invertebrate fauna is a very promising research topic in general; though for pine forests, it is practically unresearched (Teuben, Smidt, 1992; Stamps, Linit, 1997; Talbot et al., 2008; Dinnage et al., 2012).

Various aspects of the species composition of pine forest macrofauna have been studied in different climatic zones and for different species of genus *Pinus* (Rybalov et al., 1998; Hutchens, Wallace, 2002; Striganova, Poryadina, 2005; Robson et al., 2009; Gryuntal, 2009, 2010; Rybalov, Kamaev, 2011). A significant number of papers have been devoted to the structure of pine forest litter mesofauna, which is the basis of trophic links for macrofauna zoophages and polyphages (Kaneko et al., 1998). Many researchers have paid attention to one of the most important factors influencing pine forests in the south of their range – the factor of fires (Weber, Flannigan, 1997; Müller et al., 2007; Moroz et al., 2011; Boboulos, Purvis, 2012). Periodic burning of fallen dry needles prevents the regeneration of angiosperm species, so in the driest conditions of pine forests, denuded plots (devoid of herbaceous vegetation) or cryptogamous associations of mosses and lichens dominate (Sedia, Ehrenfeld, 2006).

The effect of the phytocenosis composition of pine forests on invertebrate fauna has up to now been insufficiently studied (Durant, Fox, 1966; Bangert et al., 2005; Dinnage et al., 2012; Eliav, Yael, 2013). The majority of papers on this theme have been devoted to the study of controlling pine pests belonging to the litter fauna population (Uetz, 1979; Ozanne et al., 2000; Fondren, McCullough, 2005). The harshest hydrothermal conditions in the pine forests of the steppe zone are created in the dry summer period when most of the shoots and young pine trees die (Fioretto et al., 1998; Lingua et al., 2008; Dulamsuren et al., 2009). At this time, most of the litter invertebrate species migrate to the deeper layers of the soil in areas where aspen and birch phytocenoses are concentrated (Loza, Brygadyrenko, 2007).

Pine synthesises intensively the substances (lignin, terpenes, tannins and other phenol compounds) that slow down the disintegration of plant litter (Breymeyer et al., 1997; Berg, Laskowski, 1997; Zagatti et al., 1997; Garnett et al., 2004; Nierop, Verstraten, 2006; Yankelevich et al., 2006). On the soil surface, a thick layer of litter is formed, which negatively effects the development of the litter macrofauna through the chemical compounds it contains

(Bjorkman, 1997; Whiles, Wallace, 1997). Litter in the pine forests prevents the germination of seeds of flowering plants, insulates the soil from moisture loss and prevents nutrient leaching by rainwater, thus contributing to the retention of nutrients in the ecosystem (Jack et al., 1977; Rafferty et al., 1997; Gholz et al., 2000; Finzi, Schlesinger, 2002; Smit et al., 2002; Guo et al., 2004; Berg et al., 2010). The litter creates habitat for litter invertebrates and provides them with a food substratum. In the arid southern pine forests, the preservation and integrity of the litter horizon play a primary role in maintaining the structure of the litter macrofauna and the stability of the ecosystem as a whole (Liski et al., 2003; Moroz et al., 2011).

Until now, the pine forest litter macrofauna in the steppe zone of Ukraine has only received fragmentary attention study (Brygadyrenko, Komarov, 2008). Most attention has been directed to pine forests in protected areas (Loza, Brygadyrenko, 2007; Fedorchenko, Brygadyrenko, 2008; Moroz et al., 2011) or to the species composition of certain taxonomic groups (Brygadyrenko, 2003). Changes in the structure of the litter macrofauna under the influence of the changes in the structure of plant communities as a whole has remained unexplored for the pine forests of the steppe zone of Ukraine.

Material and methods

Litter macrofauna was gathered in natural forests of 50-to-200-year-old *P. sylvestris* and 20-to-80-year-old pine plantations on the territory of Dnipropetrovsk, Zaporizhzhya, Nikolayev, Donetsk and Kharkiv regions of Ukraine in the years 2001–2013. For each site, a geo-botanical description according to the standard methods was carried out, taking into account the density of each vegetational layer and the percentage of cover for every species of plant separately.

Hundred and forty-one forest plots where *P. sylvestris* was the dominant plant were involved in the study. Each site was homogenous in its vegetational composition and measured approximately 200 x 250 meters. The minimum distance between adjacent sites was 1 kilometer. The sites were classified under the following moisture conditions: mesoxerophilous, 30; xeromesophilous, 51; mesophilous, 21; hygromesophilous, 25; mesohygrophilous, 14.

The trial sites differed in tree canopy density: 30–44% in 17 trial sites, 45–59% in 43 sites, 60–74% in 28 sites, 75–89% in 25 sites and 90–100% in 28 sites. The trial sites where tree layer density exceeded 50% were more often not characterised by mixed woodland dominated by pine and oak. In decreasing order of frequency, the most common tree species in the pine forests studied were *Betula pubescens* Ehrh., *Populus tremula* L., *Populus nigra* L., *Tilia cordata* Mill., *Quercus robur* L., *Salix alba* L., *Acer campestre* L., *Acer tataricum* L., *Robinia pseudoacacia* L., *Ulmus laevis* Pall., *Ulmus carpinifolia* Rupp. ex G. Suckow, *Fraxinus excelsior* L.

The shrub layer at the majority of trial sites was composed (in decreasing order of frequency) of *Sambucus racemosa* L., *Euonymus verrucosa* Scop., *Euonymus europaea* L., *Amorpha fruticosa* L., *Lonicera tatarica* L., *Swida sanguinea* (L.) Opiz, *Crataegus monogyna* Jacq., *Salix cinerea* L., *Salix pentandra* L., *Frangula alnus* Mill., *Corylus avellana* (L.) H. Karst., *Rosa canina* L. On most trial sites, the density of the shrub layer ranged between 10 and 35%.

On more xerophilous areas, the grassy tracts were dominated by *Calamagrostis epigeios* (L.) Roth, *Dactylis glomerata* L., *Ballota nigra* L., *Chelidonium majus* L., *Hieracium pilosella* L., *Potentilla arenaria* Borkh., *Sedum telephium* L., *Thymus pallasianus* Heinr. Braun, *Chamaecytisus austriacus* (L.) Link, *Viola lavrenkoana* Klokov, *Betonica officinalis* L., *Origanum vulgare* L., *Achillea micrantha* Willd., *Hypericum perforatum* L. and others. In mesophilous conditions, the species composition of herbaceous plants in the pine forests was enriched by *Convallaria majalis* L., *Glechoma hederacea* L., *Polygonatum odoratum* (Mill.) Druce, *Ajuga genevensis* L., *Fragaria viridis* Weston, *Hierochloë odorata* (L.) P. Beauv., *Aristolochia clematitis* L., *Pteridium aquilinum* (L.) Kuhn, *Galium aparine* L., *Pulsatilla nigricans* Storck., *Leonurus quinquelobatus* Gilib., *Stachys sylvatica* L. The density of the grass cover on the trial sites ranged widely from 0 to 100%: 0–9% in 46 trial plots, 10–29% in 20 sites, 30–49% in 21 sites, 50–69% in 15 sites, 70–89% in 18 sites and 90–100% in 21 sites.

The sites (plots) researched were classified according to trophotope (Belgard, 1971), a trophotope being an index of the mineralization of the soil ranging from A to E, where A indicates extreme poverty of nutrients and E indicates extreme salinity. The sites were classified as follows: AB, 58 trial plots; B, 52 plots; BC, 14 plots; C, 14 plots.

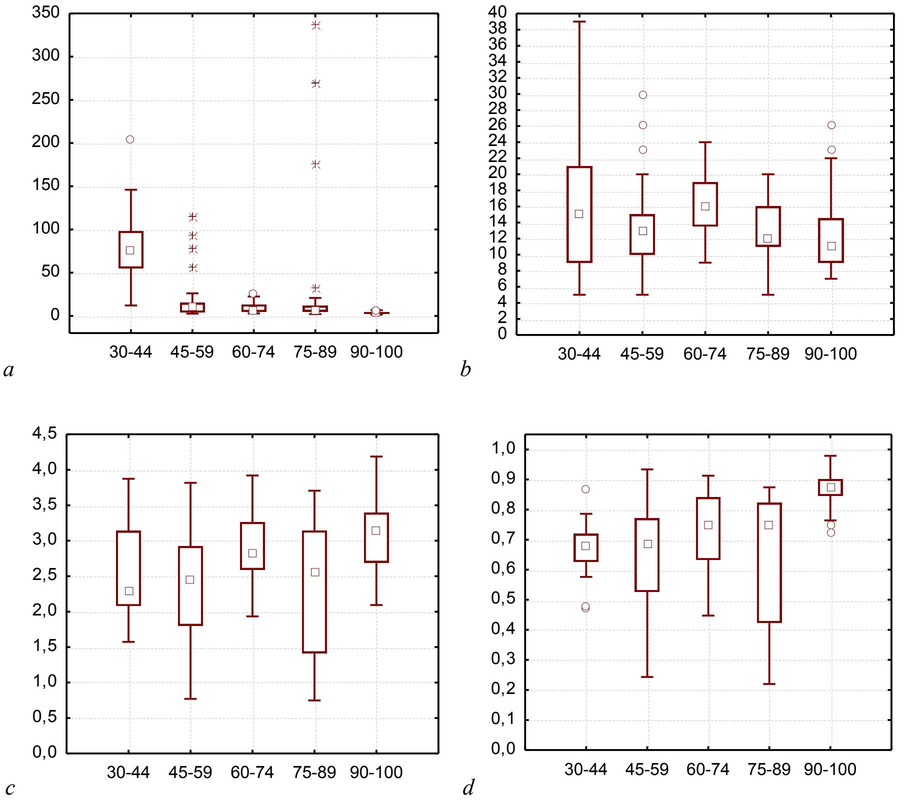


Fig. 1. Main characteristics of litter invertebrate communities of the pine forests of the steppe zone of Ukraine: (a) the total number (samples/100 trap-days), (b) the number of species, (c) Shannon index (bit), (d) Pielou index (bit); abscissa, canopy density (%); ordinates, the characteristics values.

Soils with a sandy texture (trophotopes AB and B) as well as sandy loams (BC and C) prevailed. The trial sites also varied in the degree of plant litter accumulation. The thickness of the litter in the different pine forests researched ranged from 2 to 70 mm: 0–9 mm in 28 trial sites, 10–24 mm in 19 sites, 35–39 mm in 47 sites, 40–55 mm in 19 sites, >55 mm in 28 sites.

The pitfall traps (500 ml volume with fixative solution of 20% NaCl) were checked every 5–7 days for 20–185 days (from 3 to 24 pitfall traps for each plot). For the comparison of community structure, 20-day time periods (mid-June) were analysed for each trial site. The data collected for other months was not used for this investigation.

The diversity of macrofauna communities (Shannon, Weaver, 1949; Pielou, 1977) was assessed by the relative number of species in the pitfall traps over a 20-day period. In the analysis of the taxonomic structure, groups comprising over 3% of the total composition of the community were considered dominant. The statistical analysis of the results was performed using the program package Statistica 8.0. The diagrams show median, 25–75% quartiles and the selected outlier data points: ° – outliers * – extremes. The text gives only average values of the discussed features. To compare the samples, analysis of variance (ANOVA) was used. The differences between the values of different moisture gradation characteristics were considered reliable at $P < 0.05$.

Results

Basic characteristics of communities

The total number of the pine forest litter macrofauna individuals collected (Fig. 1a) significantly decreased from 84 specimens/100 trap-days in the sparsest tree stands (30–44% canopy density) to 4–39 specimens/100 trap-days in the sites with a denser tree canopy. Certain test areas had particularly high numbers of *Formica cinerea* Mayr, 1853, *Formica fusca* Linnaeus, 1758 and *Formica glauca* Ruzsky, 1896. According to the results of our studies on the effect of canopy density on litter macrofauna in deciduous forests of the steppe zone of Ukraine, a nonsignificant decrease in the number of litter macrofauna individuals was noted as canopy density increased, from 217 (20–49% density) to 128 individuals per 100 trap-days (90–100% tree canopy density).

The average number of macrofauna species caught in the pitfall traps during the 20-day period of their exposure (Fig. 1b) did not change significantly, ranging from 13 to 17 for varying degrees of the tree canopy cover. In the natural broadleaf forests of the steppe zone, the number of species for equivalent degrees of the tree canopy density varies between 17 and 24. Thus, there is a practically constant number of macrofauna species in the litter regardless of the tree canopy density, but for broadleaf forests, it is 42% higher than that for pine forests (21 and 14 species for the 20-day period of the soil traps exposure, respectively). Pine tree canopy density strongly influences hygrothermal conditions in pine forests and the resulting changes in environmental micro-climatic conditions are reflected in changes in the taxonomic structure of the litter community at the species level, though the average number of species remains unchanged.

The Shannon–Weaver diversity index (Fig. 1c) increases significantly when less dense tree stands (2.38 and 2.56 bits for 30–44% and 45–59% density) give way to denser stands (up to 3.11 bits for 90–100% density). In the broadleaf forests of southern Ukraine with similar gradations of canopy density, significant changes in the Shannon–Weaver index (from 1.92–2.07 to 3.09 bits, respectively) can also be witnessed. Thus, the index average value for pine and deciduous forests is not different (2.64 bits for pine forests and 2.57 bits for broadleaf forests).

The Pielou diversity index (Fig. 1d) of the litter macrofauna also increases significantly from 0.650 and 0.665 bits for 45–59% and 30–44% density, respectively, to 0.868 bits for 90–100% density. In the broadleaf forests, it is also possible to witness an increase of the Pielou index from 0.461 to 0.743 bits with an increase of canopy density of up to 100%. The average level of the Pielou index for pine forests is significantly higher ($P < 0.001$) than that for broadleaf forests (0.708 bits for pine forests and 0.605 bits for broadleaf forests). Thus, the proportion of common species in the structure of domination of the pine forest litter macrofauna is lower than that in broadleaf forests.

Trophic structure

The average share of phytophages in the trophic structure of the litter macrofauna (Fig. 2a) does not significantly change with increasing canopy density and remains at a low level

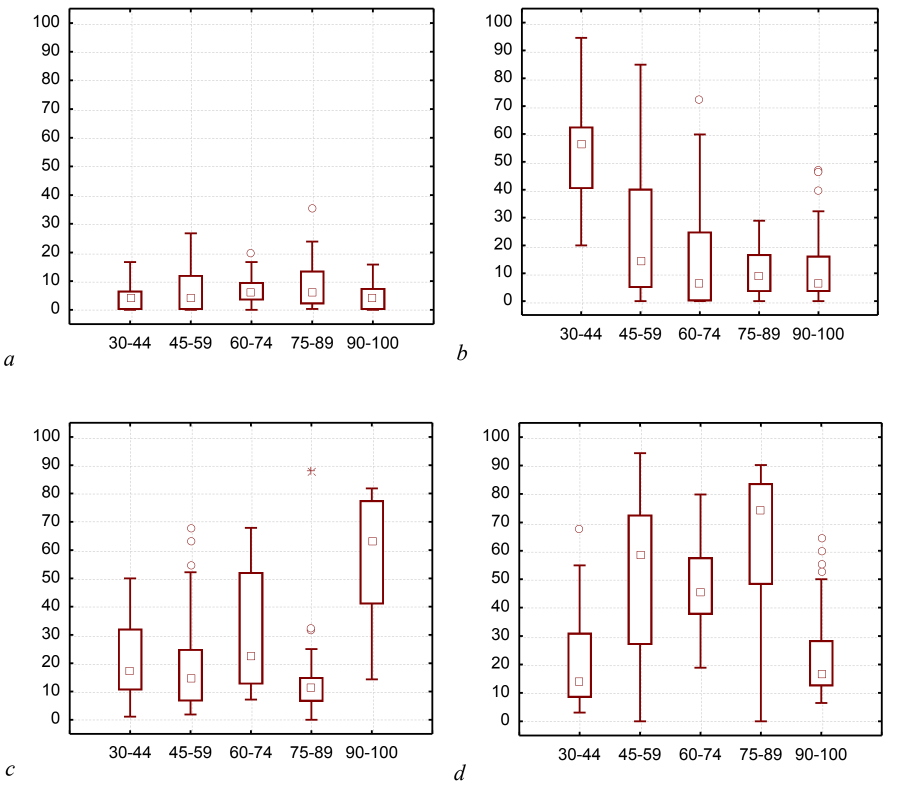


Fig. 2. Trophic structure of litter invertebrate's communities of the pine forests of the steppe zone ofUkraine: (a) phytophages, (b) saprophages, (c) zoophages, (d) polyphages; abscissa, canopy density (in %), ordinates, share of the trophic group in numbers (in %).

(4–9%). The share of phytophages in the litter macrofauna of deciduous forests is also low (2–7%) and does not have any definite tendency to change.

The relative number of saprophages (Fig. 2b), when one compares forests with the sparsest canopy (30–40%) with denser tree stands, falls dramatically from 54% to 11–13%. A similar tendency is not observed in natural broadleaf forests of the steppe zone of Ukraine: the average number of saprophages fluctuates from 24% to 47% with no apparent correlation with canopy density. The relative number of saprophages in pine forests (22%) is lower than in broadleaf forests (40%). The average number of saprophage species in pine forests of different canopy densities also falls dramatically from 3–10 at 30–44% density to 1–2 at 90–100% canopy density.

The relative number of zoophages significantly rises (Fig. 2c) when the pine forest canopy density increases (from 21% at 30–44% density to 59% at 90–100% density). In broadleaf forests, the share of zoophages on an average is significantly lower (by 77%) and does not have a definite tendency to change with differences in canopy density (fluctuating within the range of 8–20%). The average number of zoophage species in the pine forest litter macrofauna does not change significantly.

The relative number of polyphages reaches its maximum at a canopy density of 45–89% (Fig. 2d) and makes up 47–65% of the litter macrofauna on an average. With the decrease or increase in canopy density beyond this range, the share of polyphages in the community decreases dramatically by up to 20.5% or 24.1%, respectively. The number of polyphage species in the litter mesofauna does not change. At equivalent canopy densities in broadleaf forests, the average proportion of polyphages is at the same level but it fluctuates within a considerably narrower range (28–62%).

Size structure

In the pine forest litter, it is possible to observe a simplification of the size structure of the macrofauna (Fig. 3). Invertebrates with a length of 4–7 mm dominate (73–75% of the total numbers of all mesofauna at 45–89% tree canopy density). At equivalent levels of canopy density in broadleaf forests, the percentage of the litter invertebrate community occupied by this size group is much lower, fluctuating between 27% and 64%.

The proportion of the population of the size groups exceeding 20 mm in body length reaches its maximum (33%) in the sparsest pine forest stands (Fig. 3a). It decreases sharply to 1–4% in the denser pine stands.

The average share of the smallest size group in the invertebrate community with a body length of less than 4 mm increases gradually from 9% in the sparsest pine stands to 20% in the denser pine forest sites. In broadleaf forests of the steppe zone, the share of this size group is significantly higher (7–52% for equivalent levels of stand density, a definite tendency to change is absent). Unfavourable hygrothermal conditions of the litter in sparse pine forests are responsible for the low share of the smallest (measured by body length) size group of the macrofauna in the litter invertebrate population.

Additional peaks for the size groups of 12–15 and 16–19 mm (in contrast to individual examples from broadleaf forests) are absent on the size structure diagram.

The community size structure measured by the number of species is even more leveled in comparison with the structure as measured by the absolute number of individuals in each group. It is worth noting in conclusion that in pine forest ecosystems, the most extreme variants of simplification of the litter invertebrate population concern the size structure, in contrast to the situation in natural and planted broadleaf forest ecosystems as well as steppe and meadow ecosystems in the steppe zone of Ukraine.

Taxonomic structure

In the litter of the sparsest tree stands (30–40% density) in the pine forests of the steppe zone of Ukraine, the dominant taxa are (Fig. 4a) Julidae (average percentage of dominance by number, 31%), Lycosidae (15%), Formicidae (15%), Isopoda (12%), Carabidae (4%) and Lygaeidae (4%).

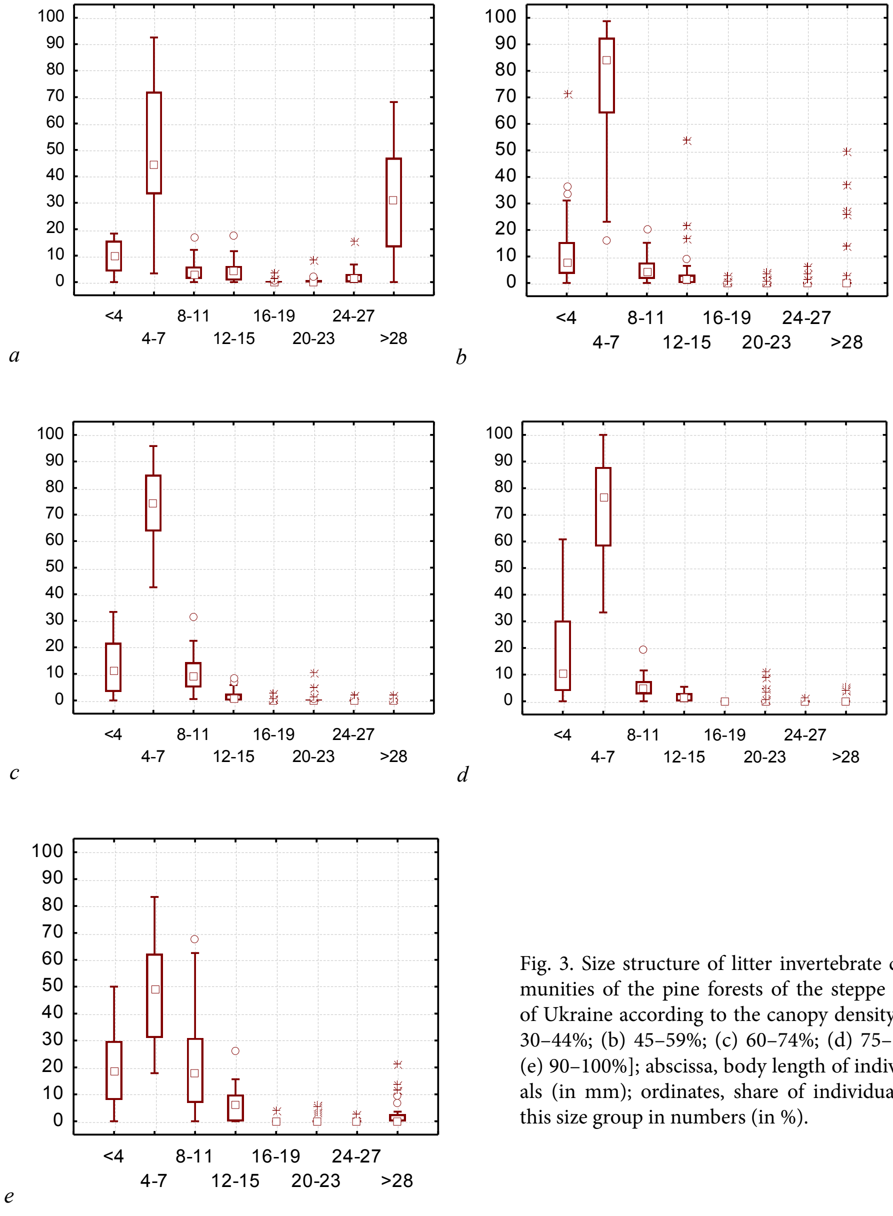
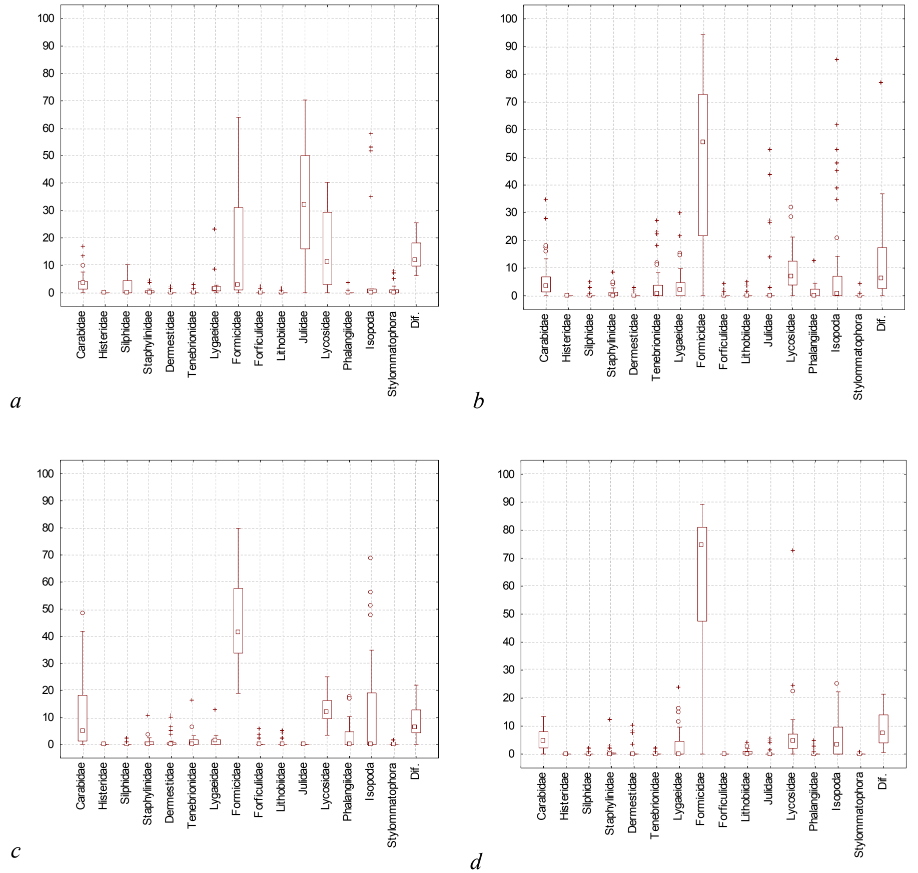


Fig. 3. Size structure of litter invertebrate communities of the pine forests of the steppe zone of Ukraine according to the canopy density [(a) 30–44%; (b) 45–59%; (c) 60–74%; (d) 75–89%; (e) 90–100%]; abscissa, body length of individuals (in mm); ordinates, share of individuals of this size group in numbers (in %).

In the pine forest stands of medium canopy density (45–59%), the dominant taxa in the litter macrofauna (Fig. 4b) are Formicidae (48%), Isopoda (10%), Lycosidae (9%), Carabidae (6%), Lygaeidae (4%), Julidae (4%) and Tenebrionidae (4%).



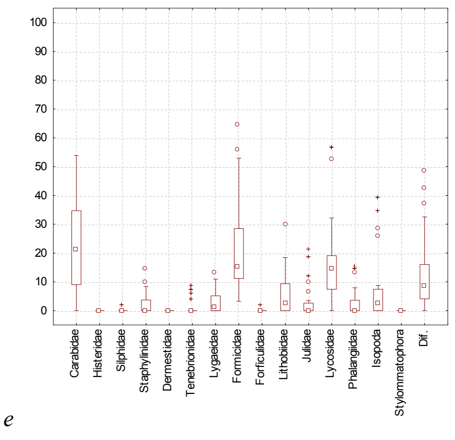


Fig. 4. Taxonomic structure of litter invertebrate communities of the steppe zone of Ukraine according to the canopy density [(a) 30–44%; (b) 45–59%; (c) 60–74%; (d), 75–89%; (e), 90–100%]; abscissa, dominant taxonomic groups; ordinates, share of this taxonomic group in the community in numbers (%); Dif., species of other taxonomic groups.

In the denser tree stands (60–74% density), Formicidae (45%), Lycosidae (13%), Carabidae (12%), Isopoda (12%) and Phalangiidae (3%) dominate (Fig. 4c).

In the mixed forest plots with a 75–89% tree canopy density (Fig. 4d), the dominant taxa in the litter macrofauna are Formicidae (63%), Lycosidae (9%), Isopoda (7%), Carabidae (5%) and Lygaeidae (4%).

The fauna of the densest (90–100%) plantation and natural pine forests differs greatly from those characterised earlier. It can be distinguished by polydominance (Fig. 4e): Carabidae (23%), Formicidae (22%), Lycosidae (16%), Isopoda (8%), Lithobiidae (6%), Julidae (3%), Staphylinidae (3%), Lygaeidae (3%) and Phalangiidae (3%).

Thus, regardless of the density of the pine forest canopy, two families of the first three dominant taxonomic groups are always the same – these are Formicidae and Lycosidae. In the densest (90–100%) pine forest stands, nine invertebrate families dominate, while in sparser variants of the stands, five to seven families dominate. When Formicidae make up 45–63% of the total number of macrofauna (at tree canopy densities of 45–89%), only a few species of Lycosidae, Isopoda, Carabidae, Julidae and Lygaeidae that are resistant to predation from ants survive. In the sparsest stands, the ants do not find a favorable trophic base (which is typically formed by Homoptera which suck plant sap). Ants find optimal conditions in denser stands. When the canopy density is close to 100%, more favorable conditions are formed for ground beetles and other zoophages that can prey on Formicidae. Changes in the species composition of ants can also be observed here.

Discussion

The increase in the gradations of tree canopy density in the pine forests of the steppe zone forms the most natural analogue to the transition from the psammophilous steppe ecosystem, which is typical of arena terraces of steppe rivers to the broadleaf forest ecosystem with a dense tree canopy. In this polymorphous ecotone, it is possible to observe the combination of a complex set of gradients. By isolating the effect of tree canopy density from a large amount of factual data, we obtained the characteristic of the changes in the litter macrofauna as a complex ecological system. For the majority of the studied characteristics of this system, no significant changes were found to correlate with increases in the tree canopy density in the pine forests of the steppe zone. In other words, some species are gradually replaced with others when the density of the stand increases. This change is relatively gradual, though, and it has little effect on the size, trophic and taxonomic structure of the community. When a forest begins its formation in the steppe zone, forest species are introduced into a practically steppe (zonal) community of the litter macrofauna, which is the characteristic of sparse pine forests. As the canopy density increases, these forest species selectively substitute the corresponding steppe species in size and trophic specialization. Gradually, this process leads to the formation of a forest litter macrofauna community that receives in outline the characteristic features of its size, trophic and taxonomic structure.

In many cases, one single gradation in canopy density shows a sharp deviation from other gradations of canopy density in its trophic structure. This shows how important other factors, not only tree canopy density, are for the litter macrofauna. The same feature is manifested in many other studied factors (moisture, soil texture, litter thickness, the percentage of herbaceous plant cover) that influence the litter invertebrate community.

Trophic links between individual populations of invertebrates are of paramount importance for the litter macrofauna community structure. In one type of pine forests, we found macrofauna communities that varied greatly in composition. The analysis of correlations between individual taxonomic groups of invertebrates showed that invertebrate populations have closer links between themselves than to other subsystems of the forest ecosystem (phytocenosis, soil, microbocenosis and microclimate). The litter macrofauna of the pine forests of the steppe zone is a multilevel fragment of a branched trophic net of a forest ecosystem as a whole and requires further detailed study.

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