Ants at the border between the epigean and soil blocks of a forest coenosis

Муравьи на границе наземного и почвенного блоков лесного ценоза

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ABSTRACT. Litter plays a key role in shaping spatial and functional structure of ant and other soil invertebrate communities in temperate forest. Serving as a coenotic surface, it unites into a single space all structural elements of the forest and represents the main arena for all events to take place in ant populations. It is a boundary layer between the epigean and soil blocks of a forest coenosis, being traversed this or that way by the main mass of invertebrates, both macro- and mesofauna, that form there a *seasonal conveyer of food resources*. This conveyer provides a stable food supply to ants and other soil and litter predators. One-time sampling in the litter characterizes a stationary abundance of the predatory complex, yet revealing only the power of the flow of other invertebrates traversing this boundary interface. This makes direct comparisons of evaluations of various invertebrate groups incorrect.

РЕЗЮМЕ. Подстилка занимает ключевое место в пространственно-функциональной структуре сообществ муравьев и других почвенных беспозвоночных лесов умеренной зоны. Как ценотическая поверхность, она объединяет в единое пространство все структурные элементы леса и является основной ареной всех происходящих в поселениях муравьев событий. Это пограничный слой между наземным и почвенным блоками лесного ценоза, через который так или иначе проходит основная масса беспозвоночных — представителей мезофауны и микрофауны, образующих здесь сезонный *конвейер пищевых ресурсов*. Этот конвейер создает устойчивую кормовую базу для муравьев и других почвенно-подстилочных хищников. Единовременные учеты в подстилке характеризуют стационарную численность комплекса хищников, но выявляют лишь мощность проходящего через пограничный слой потока остальных беспозвоночных. Это делает прямое сопоставление оценок разных групп беспозвоночных некорректным.

Introduction

Due to the diversity of life-forms and other adaptations (morphological, physiological, behavioral and organizational), ants have managed to populate all terrestrial plant associations. Yet the most prominent role they appear to play in forest communities [Zakharov, 2004]. It is there that ants show the maximum levels of species diversity and population density. Thus, in humid tropical forest both ants and termites account for about 50% of all insect biomass [LaSalle, Gauld, 1993]. Just a single tree in Costa Rica selva yields about 90 ant species [Tobin, 1997]. The species diversity of ants in temperate forest is considerably lower, but even here ant populations often show high levels of stability in abundance and biomass, up to 11.5 million individuals, or 86 kg of live biomass, per hectare [Zakharov et al., 1983].

Forest provides for its inhabitants a favorable mosaic of living conditions and supplies them with food. In terrestrial ecosystems, two trophic blocks are clearly distinguished: epigean and soil [Rafes, 1980]. Forest as a many-tier community comprising clear-cut structural horizons and showing a complex parcel structure provides enough conditions to sustain species with very different requirements [Morozov, 1928].

Litter is particular in the structure of a forest coenosis. Both litter and the adjacent topsoil are characterized by the highest levels of concentration of soil invertebrates, this being documented by all soil zoological research. Forest litter for ants, its surface in particular, is the main foraging ground to provide the ant family with protein food. It is with litter that certain situations are related which appear to basically contradict some accepted rules of synecology.

Firstly, why, regardless of the population density of ants from the *Formica rufa* group, the consumption of soil and litter invertebrates fails to result in a decrease in prey diversity and biomass [Suvorov, 1987, 1994].

Secondly, why is it only in forest litter that, violating the rule of "trophic pyramids", soil invertebrate populations (macrofauna) are dominated by predators [Mineeva, 1978; Striganova, Poryadina, 2005].

In both cases, predators (ants and other predatory invertebrates) intensely and regularly remove large amounts of prey. Thus, to sustain a level of 11.5 million ants per hectare, the ant-hills must daily receive about 1 kg protein food per hectare [Zakharov et al., 1983]. One can suggest that both of these situations are related to certain properties that litter has and to the place it occupies in the spatial and functional structure of the forest.

Litter as a boundary layer between the epigean and soil blocks of a forest coenosis

The specificity of litter and its significance as a component of forest coenoses has repeatedly been emphasized by soil scientists [Vilensky, 1970], biogeocoenologists [Sukachev, 1964], forest researchers [Morozov, 1928] and forest entomologists [Vorontsov, 1963]. V.N. Sukachev [1964], analyzing the structure of forest biogeocoenoses, referred to forest litter as their special component, regarding it as a transitional stratum forming the interface between two topic blocks, epigean and soil one, of terrestrial coenoses. Litter renders a highly significant effect on the water, thermal and nutritional regimes of forest soils [Vilensky, 1970]. G.F. Morozov [1912] emphasized that "litter represents a new biological environment formed by forest", rendering "a paramount effect on the soil, the live cover and forest regeneration" [cited after: Morozov, 1928]. Litter provides favorable conditions for dwelling, for dormant phases' survival and for the hibernation of numerous forest insects [Vorontsov, 1963].

Litter, being situated at the border between two main blocks of a forest, carries out two functions important to our study. On the one hand, it represents the basal coenotic surface of a forest community. On the other hand, it is the boundary layer (BL) through which both epigean and soil blocks of a forest coenosis constantly exchange information and energy.

The roles the soil surface (litter) plays as a coenotic surface lie primarily in consolidating the elements of the epigean topic block into a single system and in forming a territorial continuum as an integrated space used by ants and other non-flying herpetobiotic invertebrates (as well as non-flying vertebrates).

The border between the epigean and soil coenotic blocks serves as an arena of the main events for ants as well, i.e. the formation of a system of foraging grounds and protected areas, of anthill interactions and their dispersal [Zakharov, 2004]. The significance for ants of such a coenotic surface that bonds the elements of the epigean topic block into a single space is revealed in rigid systems of territorial division that is realized in ant communities of various types and complexity levels [Seima, 2003, 2008]. In forests of the temperate zone a consolidating role of the litter (soil) surface becomes the best expressed. Indeed, in contrast to, e.g., the selva, where parallel ant communities are being formed at each tier, all ants in our woodlands are more or less strongly related to the soil [Zakharov, 2002].

Litter as a boundary layer in forest coenoses appears to be the main place of interactions between invertebrates that populate various forest strata. Numerous plant-eating insects utilize the litter and topsoil for development, hibernation and/or as shelter [Vorontsov, 1963]. In the course of vertical migrations soil-dwellers reach litter and get upon its surface [Ghilarov, Chernov, 1975]. It is through litter that the bulk of invertebrates, both macro- and mesofauna, move this or that way. Energy and information flows binding different topic forest blocks also pass there. It is there as well that contacts between the inhabitants of various strata and environments take place. Some thereby are predators, some others their prey. Ants actively use the food resources provided by the litter and soil, taking up macrofauna representatives, as well as mesofauna microarthropods.

A "food conveyer" in the boundary layer

Based on the amount of time spent in this boundary layer (BL), as well as on the specifics of its utilization, several ecological groups of invertebrates can be distinguished. The foundations of such a division were laid as far back as the works of M.S. Ghilarov [1939, 1949] and K. Forsslund [1944] in their ecological classification of the soil population. According to this classification, the following arthropod groups are delimited: *geobionts*, in which the entire life cycle is restricted to the soil; *geophiles*, which pass only certain phases of their life history in the soil; and *geoxenes*, for which the soil serves only as shelter during their imaginal diapause or physiological dormancy [Striganova, 2006]. Following the above principles, three ecological groups can be distinguished as applied to the inhabitants of the boundary layer (BL) alone [Zakharov, 1987]:

A — obligate BL inhabitants (users);

B — facultative BL inhabitants feeding actively there in the larval stage (imagines feeding in the epigean block) or mainly feeding within the BL, but moving down into the lower soil horizons;

C — facultative BL inhabitants represented by epigean arthropods which pass their dormancy phases or overcome adverse environmental conditions in the BL, or use the BL as a temporary shelter.

Representatives of groups *B* and *C* spend in the BL only some part of their life cycle, of the vegetation season or day. However, due to superimposing the population densities of various species showing differ-

ent phenologies and activity cycles, the BL appears to be steadily exposed to total invertebrate abundance levels high for particular conditions. Indeed, the numbers of each of the constituent species referred to the above groups are projected to the BL in certain life stadia. So the bulk of invertebrates, both macro- and mesofauna, do traverse the BL this or that way, forming a "*seasonal conveyer of food resources*". It is this conveyer that provides a stable nutritive base for the soil-litter predatory complex operating in and mostly confined (group *A*) to the BL. This complex is primarily composed of the predatory Carabidae and Staphylinidae beetles, of the ants hunting in the litter and on the soil surface, of the Chilopoda centipedes, of the spider families Linyphiidae, Theridiidae etc. The same layer also accumulates the predatory larvae of the beetle family Elateridae and of a number of Diptera families such as Rhagionidae, Asilidae, Therevidae or Empididae, all referred to group *B*.

The plentiful and diverse potential prey must have predetermined the rich fauna of litter-soil predatory invertebrates, primarily obligate BL-dwellers. Even discarding the ants which are traditionally ignored by standard soil zoological sampling techniques and in subsequent data analyses, predatory invertebrates prevail numerically in soil macrofauna of spruce, pine and small-leaved taiga woodlands [Mineeva, 1978; Striganova, Poryadina, 2005]. The BL of a spruce forest of the Uchinsky Park Forestry, Moscow Region yielded more than 130 predatory species of litter-soil macrofauna alone, mostly representing group *A*. With the average annual population density being 12.932 individuals per sample (0.0625 sq. m), similar data for individual years failed to differ by more than 19.6%. Some other characteristics of the litter-soil predatory complex were relatively stable as well, such as the index of species saturation, size and temporal structure etc. [Zakharov et al., 1989]. In contrast, the bulk of the species forming the herpetobiotic (= grass-dwelling) invertebrate complex are plant-eaters, or phytophages [Chernov, Rudenskaya, 1975].

Both groups *B* and *C* are dominated by plant-eating animals, in which the probability of falling prey to epigean or litter-dwelling predators correlates positively with the duration of their stay in the BL. It is by effectuating seasonal and/or diurnal vertical migrations that they provide for regular supplies of prey into the BL and BL-associated predators. I.V. Stebaev et al. [1993] described the situation as follows: "The predatory pressure in the litter horizon is mainly due to… Carabidae and Staphylinidae, the larvae of which hunt largely inside the crevices of two lower subhorizons while the adults move actively around on the surface, attacking both the imago emerging after metamorphosis and the larvae entering for dormancy and metamorphosis. So they control both flows at once, using the border position of the entire litter horizon".

The specificity of the spatio-temporal dynamics of invertebrates in the border layer and the prevalence of unspecialized predators in the composition in its constant inhabitants are also of importance to ants. On the one hand, ants utilize the "food conveyer" of the border layer to the maximum extent in order to supply their families with protein food. It is from there that anthills regularly get the bulk of protein prey [Gösswald, 1990]. Importantly, in order to effectively use the border layer's food resources it is only there that ants are fully capable of realizing their group and collective forms of hunting large-sized prey. This also means that the importance of substrates as arenas of ant foraging activities basically remains underestimated. For example, the development of group forms of hunting in ants seems to be directly related to that of complex forms of behavior, as well as of the capacities for coordinated actions and mutual education of foragers. In its turn, this preconditions community growth and its better organization.

On the other hand, concentrations in the border layer alone of the other predatory invertebrates so different in appearance, behavior and size, but using the same food resources create a real problem of competition, a solution of which is of considerable importance to ant life. It is noteworthy that almost all obligate predatory species in the BL are generalists capable of consuming a wide range of prey the seasonal conveyer supplies, thus representing serious competitors to forest ants. As demonstrated by soil zoological surveys in spruce stands in the Moscow Region [Suvorov, 1987, 1994; Zakharov et al., 1989], the total numbers and biomass of litter-soil predators appear to be comparable to those of a multispecies ant community with the participation of a strong federation of *Formica aquilonia* [Zakharov et al., 1983].

Ants successfully compete with other predatory herpetobiotic invertebrates as spiders, ground beetles and rove beetles [Cherix, Bounre, 1980]. Interactions between them and ants show their own specific features: while an anthill is small, those predators go on hunting in the ant foraging territory, but larger ant families gradually oust the competitors from their foraging grounds [Suvorov, 1994; Rybalov et al.., 1998; Hawes et al., 2002]. The larger species of competitors are expelled first, some of them even falling prey to ants, whereas most leave ant territories, failing to withstand their hosts' growing pressure. Smaller species are more successful in avoiding contacts with ants, often surviving at the periphery of ant foraging territories [Gridina, 1990; Rybalov, 2005].

A combined pressure of ants and other litter-soil predators might seem to render a serious effect on the numbers and structure of litter populations. Yet this is not so, albeit ants do affect the size and spatial structure of the entire invertebrate complex [Suvorov, 1994]. Ants as unspecialized predators remove primarily mass prey species, thus promoting the conservation of rarer species in the stands and maintaining a diversity of forest invertebrates [LaSalle, Gauld, 1993]. A conspicuous drop in abundance and biomass in the territories

controlled by wood ants has only been documented for earthworms [Laakso, 1999; Rybalov, 2005]. These data have been strongly corroborated by special studies on the effect of litter-soil predators on pests. The maximum "tributes" the ants receive from particular forest pests (sawflies, moths) pupating in taiga litter amount to some 7–9% [Pleshanov, 1982].

These two situations seem best to be accounted for by soil zoological sampling evaluations of litter predators and other invertebrates being characterized by profoundly different results. As regards predators constantly confined to the border stratum, we really obtain their stationary abundance values. Their stability in a particular place through a number of years is also evidence of that [Zakharov et al., 1989]. Similar results concern ants as well, with stable multiyear surveys of their populations in normal conditions being thoroughly documented [Gösswald, 1990]. Hence, our estimates of the numbers of these two groups can basically be considered as absolute. However, with respect to ecological groups *B* and *C* we actually evaluate only the rate of the flow traversing the litter. Combined estimates of the numbers, biomass and production of all of the invertebrates that take part in the food conveyer of the border stratum require special, quite laborious studies. A real potential for the use of combined characteristics of the litter-soil predatory complex is thereby retained for unbiased comparisons of the production and condition of various forest communities.

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