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Articles

The influence of ants on the environment and their relationship with ecosystem components

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Having a wide geographical distribution and, as an engineering species, actively transforming the landscapes they inhabit, ants have a significant impact on the environment, creating new biogenic landforms and changing a number of its parameters, including biotic ones. This review is devoted to the consideration of the diverse environment-forming activities of ants in different regions of the world. An analysis of the scientific literature carried out in this context revealed a clear disproportion between the fairly good knowledge of tropical regions and the insufficient knowledge of temperate latitudes. The environment-forming activity of ants actively populating grasslands removed from agricultural use: steppes, continental and floodplain meadows of temperate latitudes has been especially poorly studied, which determines the undoubted priority of this area of research.

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Introduction

In almost all terrestrial ecosystems of our planet, with the exception of the Arctic territories, ants are one of the dominant groups of invertebrate animals. Researchers have noted the important role of ants in the trophic networks of terrestrial ecosystems, their diverse social and consortial interactions with other organisms (Hölldobler, Wilson 1990; Wilson, Hölldobler 2005).

Being integral elements of forest, meadow and steppe biogeocenoses, ants, as colonial insects and “natural engineers”, actively participate in the creation of nano-forms of biogenic relief, the morphometric characteristics of which are very diverse, and depend on the species specificity, the characteristics of the ants’ habitat and the age of these zoogenic landforms (Leontiev, Tatarnikov 2013; Tiede et al. 2017; Wills, Landis 2018).

It is shown that the most significant changes during the historical development of land use have undergone grass ecosystems: steppe and meadow landscapes. A significant proportion of meadows in temperate regions has been transformed into agricultural landscapes, significant areas of which have ceased to be used in recent years and have become fallow lands (Kurganova, Kudeyarov 2012; Kurganova et al. 2018; Matasov et al. 2019; Ivanov et al. 2023). It is important to note that when human economic activity ceases (plowing, haymaking, grazing), meadow spaces are quickly occupied by ants, which is manifested in a significant increase in the density of ant nests in meadow areas.

As mass consumers of a variety of organic substrates, ants in temperate grasslands influence the diversity of invertebrates, plants, and soil microbes and potentially alter grassland productivity. Previous research has noted the importance of studying the role of ants in soil processes and how grassland fragmentation may influence community formation of ants and associated organisms. (Wills, Landis 2018; Ivanov et al. 2022).

Ants have a noticeable impact on a number of environmental parameters, such as: soil density and porosity, thermoregulation, temperature changes inside the anthill, nitrogen content, carbon content, composition and activity of microorganisms, phosphorus content, potassium content, acidity, CO_2 emission, CH_4 emission, N_2O emissions (Wills, Landis 2018; Golichenkov et al. 2019; Lei et al. 2021; Urbańczyk, Szulc 2023; Churilina et al. 2017; Wang et al. 2018; Mehring et al. 2021; Soper et al. 2019).

Based on the analysis of numerous publications (Dauber et al. 2006; Stebaev et al. 1968; Mordkovich 2014; Neustruev 1976), the authors propose to distinguish ecosystems inhabited by anthills into a special category of complex two-member ecosystems, consisting of a host background ecosystem (for example, a dense turf meadow) and numerous “islands” - interspersed with natural nanoecosystems in this background. Anthills, in fact, being disturbed areas of dense turf of the background meadow ecosystems that host them, form niches for various invertebrate consorts and alien and weed plants that are not able to colonize meadow ecosystems due to high competition from native meadow species (Dauber et al. 2006), which significantly increases mosaic and biodiversity of such complex two-membered meadow ecosystems.

Results

When ants occupied the territory, the appearance of the first nests indicates the beginning of intensive modification of the soil cover, which, as a rule, can go in two directions (Frouz, Jilkova 2008): firstly, it is transporting organic material from the surroundings to the nests as food or building material; secondly, it is bioturbation - mixing and accumulating soil material from different sources and horizons.

Bioturbation has a beneficial effect on plant growth, which has a positive effect on the rate of restoration of disturbed areas (Dostál et al. 2005). Bioturbation of ants and its impact on the environment also largely depends on the respective species of ants and the features of the construction of anthills (Frouz, Jilkova 2008). The number of ant nests in the territory is the most important factor to explain the differences in soil bioturbation turnover in different habitats (Lobry de Bruyn, Conacher 1994). The above ground volume and mass of soil in anthills may indicate the degree of soil turnover as a result of the construction activity of ants (Nkem et al. 2000).

In addition to the number of anthills on the territory, traces of foraging ants – "feeding paths", namely their number and length, are considered to be an equally important factor. The importance of the foraging tracks of ants is related to their ability to move through territories that are subjected to land use at various degrees, which contributes to the collection of heterogeneous material for anthills (Nkem et al. 2000). At the same time, in the territories themselves, which are under the influence of permanent land use (for example, plowing), anthills spread to a lesser extent (Lobry de Bruyn, Conacher 1994). Considering that the land use system has changed significantly in recent years – significant territories are being withdrawn from agricultural circulation and become fallow (for example, huge floodplain areas of the Ob River) (Mikhaleiko et al. 2023), ants have more available space for the construction of anthills (Ivanov et al. 2022), as a result of which new inhabited areas territories can undergo significant transformation due to the high activity of ants (Khazan et al. 2020), which emphasizes the importance of studying the vital activity of ants in fallow territories.

The fact of soil mixing is confirmed by the discovery of an increased content of clay, silt, sand, as well as foreign material of anthropogenic origin and organic substances in the composition of anthills compared to the background soil, both horizontally and vertically, however, there are no unambiguous trends in this property – everything depends, apparently, on the specific type of ants and their habitats (Wiken et al. 1976; Lobry de Bruyn, Conacher 1994; Drager et al. 2016; Robins, Robins 2011).

Ant mounds with a higher percentage of slope will contribute more to the redistribution of soil material after the anthill is subjected to erosion (Nkem et al. 2000). The processes of slope erosion of anthills are considered an important factor in increasing the level of nutrients in the soil around anthills (Eldridge, Myers 1998).

It is known that ants are ectothermal organisms – they largely depend on the external temperature (Jørgensen et al. 2022). As the temperature increases, the ants' burrowing activity increases. Colonies exposed to higher temperatures dig nests of a larger size and depth than those living in an environment with milder temperatures (Ibarra et al. 2024).

Nevertheless, the importance of ant bioturbation in global terms is currently a debatable issue (Viles et al. 2021). Studies in cold-temperate latitudes have shown that earthworms have a greater bioturbation effect in some ecosystems (Taylor et al. 2019). On the other hand, there is a more significant influence of ants in tropical zones (Tschinkel, 2015; Wilkinson 2009). The authors of the above-mentioned study noted that, despite the well-known bioturbation of ants, the structure and properties of the biopores they form remain relatively poorly understood, especially compared to earthworms (Ibarra et al. 2024).

As noted above, ants are ectothermal organisms, therefore air temperature is an important environmental factor for their existence. There are many illustrative examples of how ants thermoregulate in anthills, for example, the nests of fire ants (*Solenopsis* spp.) are asymmetric, and their shape changes depending on the season – the surface area that is directly exposed to the sun changes (Vogt et al. 2008). *Acromyrmex heyeri* avoids overheating during the day and cooling at night due to covering with straw and fragments of anthill plants, which have lower thermal conductivity (Bollazzi, Roces 2010). *Atta vollenweideri* nests are thermoregulated using a ventilation system consisting of air outflow through central tunnels and inflow through peripheral tunnels (Kleineidam et al. 2001). In addition, ants are able to change their circadian rhythm by foraging at a cooler time of day (Lei et al. 2021), or even move to a cooler microenvironment (Penick & Tschinkel 2008).

Studies naturally indicate lower temperatures inside ant complexes compared to the background soil (Vogt et al. 2008; Bollazzi, Roces 2010; Kleineidam et al. 2001; Penick, Tschinkel 2008; Lei et al. 2021; Golichenkov et al. 2019; Dainenko, Rusakov 2012). It was noted that pedobiont ants live in more thermostatically controlled conditions than ants, which mainly live in mounds (Golichenkov et al. 2019).

The construction of tunnels both above ground in the embankment and underground increases macroporosity and reduces the bulk density of the soil (Frouz, Jilkova 2008; Golichenkov et al. 2019; Cammeraat et al. 2002; Zhou et al. 2023; Leal et al. 2007). Reduced soil bulk density can contribute to increased aeration and soil water permeability (McCahon, Lockwood 1990).

A two-way effect of ants' vital activity on soil water permeability was noted (Cammeraat et al. 2002; Green et al. 1999): on the one hand, ant nests increase water infiltration in humid conditions; on the other hand, ant nests reduce the level of water infiltration in arid conditions. The humidity of an ant nest often differs significantly from the humidity of the background soil and can be either lower (Mc- Cahon, Lockwood 1990) or higher (Coenen-Stass et al. 1980). Humidity values can vary even within a single species (Froz 2000). In addition, the soil moisture of ant nests is influenced by organic substances (Zhou et al. 2023). The presence of ants in the soil increases the content of organic matter, which contributes to an increase in soil hydrophobicity (Domisch et al. 2008).

Ants are capable of changing chemical properties in soils in the zone of their influence (Yang et al. 2022; Nkem et al. 2000, Yang et al. 2021), however it all depends on the specific type and characteristics of the environment.

Increased nitrogen content compared to background soils was observed in most of the analyzed works (Wagner, Jones 2006; Eldridge, Myers 1998; Zhou et al. 2023; Urbańczyk, Szulc 2023;), except for one (Dostál et al. 2004). Ants’ activity can enhance the release of nitrogen from plant residues; splitting organic matter, ants contribute to soil mineralization inside the anthill (Churilina et al. 2017; Wagner, Jones 2006; Yang et al. 2021; Nkem et al. 2000; Kristiansen, Amelung 2001). It is observed that the accelerated turnover rate of nitrogen compounds is typical for humid environments (Cammeraat, Risch 2008).

Soils affected by ants are mainly characterized by increased carbon concentrations in their chemical composition compared to the background soil (Eldridge, Myers 1998; Nkem et al. 2000; Dainenko, Rusakov 2012; Cammeraat et al. 2002; Zhou et al. 2023; Urbańczyk, Szulc 2023), but in two studies the carbon values in the chemical composition of anthill soils were lower compared to the background soil (Dostál et al. 2004; Dainenko, Rusakov 2012). It was noted that the difference in the amount of carbon between the anthill dome and the background soil may become smaller as the age of the ant colony increases (Lane, Bassirad 2005).

With an increase in the carbon and nitrogen content in anthills, the biomass level increases (Kotova et al. 2015; Churilina et al. 2017; Kotova et al. 2013; Jílková et al. 2016). A characteristic feature of the composition of the bacterial complex of anthills is the dominance of actinomycetes in it, the relative abundance of which often exceeds 50% (Churilina et al. 2017). Actinomycetes, in turn, are known for their ability to nitrogen fixation, antibiotic production and chitin destruction, but nitrogen fixation in anthills is considered understudied (Kotova et al. 2015; Kotova et al. 2013). Otherwise, the composition of the bacterial complex of anthills may differ both from the characteristics of a particular ant species and from the habitat in which the colony lives (Bringhurst et al. 2022).

Higher phosphorus concentrations are observed everywhere in anthills compared to controls (Nkem et al. 2000, Frouz et al. 2003; Urbańczyk, Szulc 2023; Dostál et al. 2004; Eldridge, Myers 1998; Dainenko, Rusakov 2012; Cammeraat et al. 2002; Zhou et al. 2023), however, approximately the same phosphorus content was noted in the soil of anthills and controls (Leal et al. 2007).

Studies indicate an increase in potassium concentration in anthills (Urbańczyk, Szulc 2023; Drager et al. 2016; Frouz et al. 2003; Dostál et al. 2004; Eldridge, Myers 1998; Dainenko, Rusakov 2012; Cammeraat et al. 2002), and in some studies there was no significant difference in potassium content in anthills and control soil (Nkem et al. 2000; Leal et al. 2007).

There is an increased content of magnesium, calcium and sodium cations in the soils of anthills compared with the control (Urbanczyk, Szulc 2023), while it is noted that the content of the above-mentioned element cations in agroecosystems is lower than in any other ant habitat (Farji-Brener, Werenkraut 2017).

Trends in changes in the level of soil acidity in anthills by ants are noted, mainly cases of pH shift towards a neutral value are shown (Urbańczyk, Szulc 2023; Churilina et al. 2017; Froz et al. 2003; Dostal et al. 2004; Cammeraat et al. 2002). The decrease in pH can be explained by the increased carbon level in the anthill, which contributes to soil alkalinization (Cammeraat, Risch 2008), however, no specific patterns of changes in the acidity level by ants have been identified at the moment (Churilina et al. 2017).

Different ant species are known to be able to accumulate heavy metals from the environment (Yang et al. 2021; Skaldina et al. 2018). A case of a decrease in the level of heavy metals – chromium, lead, copper, nickel in anthills by ants has been recorded (Shi et al. 2023). It is assumed that ants accumulate heavy metals from the soil of the anthill, and then die outside the anthill, which helps to reduce the level of heavy metals in the nest (Shi et al. 2023).

Anthills can be natural sources of greenhouse gases. Greenhouse gas emissions from anthills are associated not only with the respiration and construction activities of ants, but also with the activity of microorganisms, which ants influence when changing the structure of the soil and its biogeochemical processes (Berberich et al. 2018; Jílková, Froz 2014; Jílková et al. 2016).

Ant respiration and decomposition of organic matter are direct sources of CO_2 (Römer et al. 2018; Caiafa et al. 2023). Since ant nests are a closed environment, ants control the concentration of CO_2 inside the anthill, for example, by swarming ventilation paths that provide the anthill gas exchange and maintain microclimatic conditions inside the nest (Jílková et al. 2016; Caiafa et al. 2023).

It was noted that the specificity of ant species is not related to CO_2 emissions, variability in CO_2 flux values may be more related to abiotic factors, for example, temperature (Jílková et al. 2016; Caiafa et al. 2023). With increasing temperature, oxygen consumption increases and the metabolism of ants and microorganisms in the anthill accelerates, which in turn increases CO_2 production (Ibarra et al. 2024; Jílková et al. 2016). Anthills and surrounding soil areas are able to emit 15-60% more CO_2 than soil areas that do not belong to anthills (Fernandez-Bou et al. 2019; Wang et al. 2018; Mehring et al. 2021; Wu et al. 2015; Fernandez-Bou et al. 2019; Jílková et al. 2016).

Ants can be both a source and a sink of methane: CH_4 production is often observed in the upper part of anthills due to the decomposition of organic matter with a high nutrient content by microorganisms (Berberich et al. 2018; Caiafa et al. 2023), while CH_4 consumption by methanotrophic soil bacteria occurs deep in the anthill (Jílková et al. 2016). It is noted, that CH_4 emission from anthills is probably the result of a combination of microbial activity and abiotic CH_4 emission associated with gas emissions through soil pores that pass through anthill nests (Berberich et al. 2018; Mehring et al. 2021).

Soils are one of the main sources of nitrogen oxides, which is mainly formed as a result of microbial processes: nitrophication and denitrification (Majeed et al. 2018; Caiafa et al. 2023). Ants, as a result of their activities, can contribute to the development of communities of microorganisms in the soil of the anthill that carry out the processes of nitrophication and denitrification (Kotova et al. 2015; Churilina et al. 2017). Research results suggest that anthills can indeed contribute to N_2O emissions into the atmosphere, probably mainly due to the stimulation of nitrophication and denitrification processes (Majeed et al. 2018; Soper et al. 2019; Caiafa et al. 2023; Wu et al. 2015), however, currently Research is more focused on the study of CO_2 emissions, which is reflected in the study of nitrogen oxide emissions.

Generalized data on the influence of ants on a number of indicators of the condition of nests and surrounding substrates are shown in the Table 1.

Some ant species are capable of spreading plant seeds (Drager 2016; Philpott et al. 2009; Fernandes et al. 2024; Oliveira et al. 2024). As a rule, biotic and abiotic factors influence the spread of seeds. Among biotic factors, the distribution of seeds is influenced by vegetation structure, species composition and size of ants, density of ant nests and competition for resources, among abiotic factors are temperature and drying of seeds (Philpott et al. 2009; Leal et al. 2015).

The involvement of ants in the seed propagation process is explained by the presence in many flower seeds of a lipid–rich appendage, the elaiosome, which attracts ants (Oliveira et al. 2024; Leal et al. 2015). The mechanism of seed propagation consists in transferring the seed to an ant nest, in which the ants eat the elaiosome, and then throw the seed into an external landfill, which is enriched with organic substances, which promotes germination and seed growth (Oliveira et al. 2024; Leal et al. 2015).

In addition, in the process of eating the eliosome, ants can disinfect seeds with an antimicrobial substance produced by their exocrine glands, however, the chemical composition of antimicrobial substances secreted by ant glands varies greatly among species (Fernandes et al. 2024).

The largest ant species show the greatest efficiency in the seed distribution process, since it is easier for them to collect and transport seeds (Oliveira et al. 2024; Fernandes et al., 2024). An increase in anthropogenic influence on ants negatively affects the seed propagation process (Oliveira et al. 2024). On the other hand, the effects of physical and chemical manipulations of ants on seeds are poorly understood, given that not all seed-spreading ants bring unambiguous benefits to myrmecochore plants (Fernandes et al. 2024).

Anthills, in fact, being disturbed areas of dense turf of the background meadow ecosystems that host them, form niches for drift and weeds that are unable to populate meadow ecosystems due to high competition from native meadow species (Dauber et al. 2006), which significantly increases the mosaic and biodiversity of such complex binomial meadow ecosystems, consisting of a background ecosystem and numerous "islands" – inclusions of natural nanoecosystems into this background.

Parameters	The influence of ants	Species	Region	Source
Soil density and porosity	The soil in anthills is less dense and more porous than in the background soil	Lasius niger, Lasius flavus, Formica cunicularia	Russia (Rjazan)	Golichenkov et al. 2019
		Messor bouvieri	Spain (Rambla Onda)	Cammeraat et al. 2002

		Iridomyrmex anceps	China (Wetland Park, Shanghai)	Zhou et al. 2023
		Camponotus blandus, Dorymyrmex brunneus, Dinoponera quadricieps, Pheidole sp., Solenopsis sp., Trachymyrmex sp.	Brazil (The San Francisco River in the Sergipe State area)	Leal et al. 2007
Thermoregulation, temperature change inside the anthill	An increase or decrease in temperature in anthills directly depends on the conditions of the habitat, ants use different methods of thermoregulation, the temperature on the surface is often higher than inside the anthill. The temperature inside the anthill is lower than in the background soil	Solenopsis invicta	USA (Mississippi)	Vogt et al. 2008
		Acromyrmex heyeri	Uruguay (Juanico)	Bollazzi, Roces 2010
		Atta vollenweideri	Argentina (Formosa)	Kleineidam et al. 2001
		Solenopsis invicta	USA (Tallahassee)	Penick, Tschinkel 2008
		Solenopsis invicta	China (Guangzhou)	Lei et al. 2021
		Lasius niger, Lasius flavus, Formica cunicularia	Russia (Arkhangelsk region)	Golichenkov et al. 2019
		Lasius niger	Russia (Yaroslavl and Leningrad regions)	Daineko, Rusakov 2012
Nitrogen content	Increased nitrogen content compared to background soil	Pogonomyrmex rugosu	USA (Boulder City, Kane Spring)	Wagner, Jones 2006
		Aphaenogaster barbigula	Australia (Yetong Nature Reserve)	Eldridge, Myers 1998
		Iridomyrmex anceps	China (Wetland Park, Shanghai)	Zhou et al. 2023
		Formica rufa	Poland (Idzbark)	Urbańczyk, Szulc 2023
	Nitrogen content in anthills is lower compared to background soil	Lasius flavus	Slovakia (Cape Obrubovanets)	Dostál et al. 2004
Carbon content	The carbon content in anthills is higher compared to the background soil	Aphaenogaster barbigula	Australia (Yetong Nature Reserve)	Eldridge, Myers 1998
		Iridomyrmex greensladei	Australia (New South Wales)	Nkem et al. 2000
		Lasius niger	Russia (Yaroslavl and Leningrad regions)	Daineko, Rusakov 2012
		Messor bouvieri	Spain (Rambla Onda)	Cammeraat et al. 2002
		Iridomyrmex anceps	China (Wetland Park, Shanghai)	Zhou et al. 2023
		Formica rufa	Poland (Idzbark)	Urbańczyk, Szulc, 2023
	The carbon content in anthills is lower compared to the background soil	Lasius flavus	Slovakia (Cape Obrubovanets)	Dostál et al. 2004
		Lasius niger	Russia (Yaroslavl and Leningrad regions)	Daineko, Rusakov 2012
Microorganisms	In anthills, the biomass level is higher, nitrogen-fixing bacteria dominate in the bacterial complex	Lasius niger, Lasius flavus, Formica cunicularia, Tetramorium caespitum	Russia (Rjazan)	Kotova et al. 2015
		Lasius niger, Formica sp., Myrmica sp.	Russia (Arkhangelsk region)	Churilina et al. 2017
		Lasius niger, Lasius flavus, Formica cunicularia, Tetramorium caespitum	Russia (Rjazan)	Kotova et al. 2013
		Formica aquilonia	Czech Republic (Mount Crate)	Jílková et al. 2016
Phosphorus content	Increased phosphorus content compared to the background soil	Iridomyrmex greensladei	Australia (New South Wales)	Nkem et al. 2000
		Lasius niger	Czech Republic,	Frouz et al. 2003

			Slovakia, Germany	
		Formica rufa	Poland (Idzbark)	Urbańczyk, Szulc 2023
		Lasius flavus	Slovakia (Cape Obrubovanets)	Dostál et al. 2004
		Aphaenogaster barbigula	Australia (Yetong Nature Reserve)	Eldridge, Myers 1998
		Lasius niger	Russia (Yaroslavl and Leningrad regions)	Daineko, Rusakov 2012
		Messor bouvieri	Spain (Rambla Onda)	Cammeraat et al. 2002
		Iridomyrmex anceps	China (Wetland Park, Shanghai)	Zhou et al. 2023
	The phosphorus content in anthills and background soil is approximately at the same level	Camponotus blandus, Dorymyrmex brunneus, Dinoponera quadricieps, Pheidole sp., Solenopsis sp., Trachymyrmex sp.	Brazil (The San Francisco River in the Sergipe State area)	Leal et al. 2007
Potassium content	Increased potassium content compared to the background soil	Formica rufa	Poland (Idzbark)	Urbańczyk, Szulc 2023
		Formica subsericea	USA (University of Kansas Field Station)	Drager et al. 2016
		Lasius niger	Czech Republic, Slovakia, Germany	Frouz et al. 2003
		Lasius flavus	Slovakia (Cape Obrubovanets)	Dostál et al. 2004
		Aphaenogaster barbigula	Australia (Yetong Nature Reserve)	Eldridge, Myers 1998
		Lasius niger	Russia (Yaroslavl and Leningrad regions)	Daineko, Rusakov 2012
		Messor bouvieri	Spain (Rambla Onda)	Cammeraat et al. 2002
	The potassium content in anthills and background soil is approximately at the same level	Iridomyrmex greensladei	Australia (New South Wales)	Nkem et al. 2000
		Camponotus blandus, Dorymyrmex brunneus, Dinoponera quadricieps, Pheidole sp., Solenopsis sp., Trachymyrmex sp.	Brazil (The San Francisco River in the Sergipe State area)	Leal et al. 2007
pH	Acidity in anthills shifts towards a neutral value in comparison with the background soil	Formica rufa	Poland (Idzbark)	Urbańczyk, Szulc 2023
		Lasius niger, Formica sp., Myrmica sp.	Russia (Arkhangelsk region)	Churilina et al. 2017
		Lasius niger	Czech Republic, Slovakia, Germany	Frouz et al. 2003
		Lasius flavus	Slovakia (Cape Obrubovanets)	Dosta´l et al. 2004
		Messor bouvieri	Spain (Rambla Onda)	Cammeraat et al. 2002
CO_2 emissions	Anthills are able to emit more CO_2 than soils that do not belong to anthills	Odontoponera transervsa, Pheidologeton affinis	China (Xishuangbanna-Dai Botanical Garden)	Wang et al. 2018
		Atta cephalotes	Costa Rica (La Selva Biological Station)	Fernandez-Bou et al. 2019
		Formica aquilonia	Czech Republic (Mount Crate)	Jílková et al. 2016
		Atta cephalotes	Costa Rica (La Selva Biological Station)	Mehring et al. 2021
CH_4 emission	Anthills are both sources and sinks of CH_4, CH_4 emission can be biotic and abiotic in nature	Formica aquilonia	Czech Republic (Mount Crate)	Jílková et al. 2016
		Formica polyctena	Germany (Neuwied)	Berberich et al. 2018
		Atta cephalotes	Costa Rica (La Selva Biological Station)	Mehring et al. 2021
N_2O emission	It is assumed that	Atta mexicana,	Mexico (Xalapa)	Majeed et al. 2018

	nitrification and denitrification processes are the main sources of N_2O production in anthill soils, and therefore anthills can emit more N_2O than the background soil	Solenopsis geminate		
		Atta colombica	Costa-Rica (Osa Conservation Piro Biological Station)	Soper et al. 2019
		Lasius niger, Lasius flavus, Formica candida	China (Sanjiang Mire Wetland Experimental Station)	Wu et al. 2015

Table 1. *The influence of ants on the physical and chemical parameters of the environment*

Ants belong to one of the few animal groups in which the coexistence of many species of living organisms is possible (Reznikova 1999; Stebaeva et al. 1977). In the communities of these insects, interspecific relationships will include both antagonistic forms such as predation, competition and parasitism, as well as mutually beneficial relationships, for example, mutualism and trophobiosis (Reznikova 1999; Stebaeva et al. 1977).

The old anthills are especially rich in a variety of roommates (Stebaeva et al. 1977). A wide variety of arthropods live together with ants and benefit from the fact that ant communities are well-protected habitats with a stable microclimate. Concentrated brood and accumulated food in ant nests represent valuable resources that are easily used by associated organisms (Hölldobler, Wilson 1990). The mechanisms of some interactions between ants and myrmecophiles, which can be called “symbioses” due to the close spatial relationship, are well studied, and there is significant progress in the ecological understanding of ant colonies as supra–organizational formations. The sociobiological characteristics of an ant colony are of paramount importance to answer the question of whether a myrmecophile can successfully infiltrate an ant colony. Pre-adaptation to penetration differs in colonies of the same species, since some signs may be optional. In addition, the frequency of colony movement, colony size, habitat choice, and nesting materials may be variables that affect the suitability of an ant colony for a particular myrmecophile. (Geiselhardt et al. 2007).

It is customary to distinguish myrmecophiles, which ants care for only occasionally (optional interaction), from those who invariably depend on ants, at least at some stages of life (obligate association). Beetles, hymenoptera, bedbugs, and diptera are the most represented among insects by the number of myrmecophila species (Zakharov and Yanushev 2019). Ants have diverse and complex relationships with representatives of the mesofauna living in their nests, which can be individualized: Some myrmecophiles use anthills only as shelters, others eat up the remains of ant food, and others feed on the brood of ants (Zakharov, Yanushev 2019).

One of the most complex and mysterious forms of ant behavior is considered to be trophobiosis with various species of equidopteran proboscis insects, in particular aphids. It is known that due to cooperation with ants, the survival rate of myrmecophilic aphids can increase, since ants protect them from adverse effects, and in return "milk" them by collecting pad (Novgorodova 2012; Reznikova 1998).

Myrmecophilic staphylinids have succeeded in developing niches inside ant colonies, which specialize in colony life due to behavioral, anatomical and chemical changes (Naragon et al. 2022; Pliskevich 2016). These changes can be strikingly convergent (Pliskevich 2016). It is noted that ants build different relationships with different species of staphylinidae – from indifference to aggression, for example, there are insects that ants do not pay special attention to, which insects use and eat other arthropods, plant remains and fungal spores on the territory of the anthill (Pliskevich 2016).

In general, the nests of highly developed species of eusocial ants can be considered ecological islands with a variety of ecological niches, which are inhabited not only by ants and their brood, but also by many other organisms adapted to certain niches. Myrmecophilic behavior and exocrine glands allow myrmecophilic staphylinids to live in close contact with their host ants (Hölldobler, Kwapich 2019).

Conclusions

The analysis of numerous scientific papers devoted to the environmental activity of ants in different regions of the world has shown that ants have a diverse impact on the environment: they create new forms of nano-relief, change the chemical and physical properties of the soil, are a natural source of greenhouse gases, promote the spread of plant seeds, create a specific habitat for their consorts – diverse species of animals, plants and microorganisms with which various interspecific relationships are built.

Despite the large volume of scientific papers devoted to the study of the influence of ants on the environment, numerous unresolved issues remain, for example, about the importance of bioturbation activity of ants, about the mechanisms of soil acidity changes, about the role of ants in seed propagation and greenhouse gas emissions, and in general about the role of ant colonies in changing the structure of the landscape. To date, the role of ants and their companions in the transfer of matter and energy in ecosystems remains unclear. Taking into account the widespread and huge number of these insects, which, due to their individual characteristics, are able to have a diverse impact on the environment, their role as ecosystem transformers cannot be underestimated.

With an increase in the nutrient content in anthills, the activity of microorganisms and the biodiversity of their accompanying invertebrate consort animals increases, and the aboveground part of the anthills, being a disturbed turf layer, is populated by plant species not peculiar to this ecosystem, which are unable to spread in the background environment due to high competition. Taking into account the above facts, anthills can be considered separate nanoecosystems and nodal clusters of biota (Dauber et al. 2006; Stebaev et al. 1968; Mordkovich 2014; Neustruev 1976) interspersed with the background host ecosystem.

In general, the study of the engineering role of ants in the transformation of natural and anthropogenic disturbed ecosystems seems to be a promising topic for further research. At the same time, special attention should be paid to the study of the environmental activity of ants in the dynamically changing landscapes of floodplains of the Great Siberian Rivers, both in operation and decommissioned from agricultural circulation, which have a noticeable impact on the global carbon cycle, including an assessment of the impact of ants on fertility and sequestration potential of floodplain lands.

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