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MICROBIOLOGY

Comparative Study of Actinomycete Communities Associated with *Lasius niger* and *Formica cunicularia* Ants and Their Nests

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Abstract—A comparative analysis of the abundance and biodiversity of actinomycete communities isolated from living ants *Lasius niger* and *Formica cunicularia*, as well as their anthills, has been carried out for the first time. The number of actinomycetes detected in *L. niger* ants is close to the number of actinomycetes in their anthills and one order is higher than that for *F. cunicularia*. Actinomycete communities of anthills and the intact soil are characterized by a high diversity, equitability, absence of severe dominants, and the presence of common species and differ by number and the range of species. Biodiversity of actinomycetes associated with living ants is considerably lower than in their nests and the surrounding soil and the range of actinomycetes is specific for both the species of ants.

Keywords: actinomycetes, ants, biodiversity, *Lasius niger, Formica cunicularia*

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INTRODUCTION

Ants belong to the "allogenic ecosystem engineers" type—organisms that change the properties of the environment by their vital activities and create new ecological niches [1]. It is known that soil-forming ants have a great influence on the chemical (due to accumulation and redistribution of organic matter) and physical (aeration and temperature) properties of the soil [2–3].

Ants *Lasius niger* (black garden ant) and *Formica cunicularia* (mining ant) are widely distributed in Middle Russia and in the south of Russia [6, 7]. There is less information on their soil-forming role as well as the associated microbial complexes, including actinomycetes.

Soil saprotrophe actinomycetes are aerobes, neutrophiles, temperature mesophiles, olygotrophes, and moderate xerophiles [8]. Soil nests of ants (nests and their populations are called anthills in Russian literature) have the conditions satisfying these requirements [9–11]. The concentration of chitin is higher in the nests than in the intact soil (due to the high abundance of insects) and the capacity to degrade chitin is quite common for actinomycetes [12]. Thus, soil anthills can serve an ecological niche for actinomycetes.

The aim of this work was to characterize actinomycete complexes of anthills—sites of natural abundance of mycelial prokaryotes.

MATERIALS AND METHODS

The objects of the study were samples of the upper layer of post urban sod podzolic soil [13] located at the field site (Ryazan oblast, Kasimovskii raion, upper bank of Unzh River), which was taken out of agricultural use more than 15 years ago, and samples of the above ground part of ants nests (anthills) and the ants *L. niger* and *F. cunucularia*.

The structure of actinomycete complexes of the nest material and the intact soil were studied by the sample plating method on Gauze's agar no.1 [14].

The "actinoflora" was isolated by means of the "washout" method: one living ant was placed into a plastic tube (Eppendorf) with 0.75 mL of sterile distilled water and vortexed for 1 min using a Vortex shaker. The suspension obtained was spread on an expanded set of nutrient media: Gauze's agar no.1, glucose peptone agar, and a chitin-containing medium [15].

For isolation of actinomycetes associated directly with ants, each "washed" insect was ground with

Table 1. Species structure of soil actinomycetes in control soil

Strain	Number, 10^3 CFU/g	Frequency occurrence, %	Mean abundance, %	Identified as
K_1	57.8	100	24.3	*S. olivochromogenes*
K_2	51.1	100	21.5	*S. violascens*
K_9	15.6	100	6.54	*S. varsoviensis*
K_{16}	6.7	33	2.8	*S. cinereoruber*
K_{11}	2.2	33	0.9	*S. roseoflavus*
K_{17}	15.6	67	6.5	*S. olivaceoviridis*
K_{21}	11.1	33	4.7	*S. hygroscopicus*
Micr	4.4	67	1.9	*Micromonospora* sp.
K_3	6.7	67	2.8	*S. albovinaceus*
K_5	8.9	67	3.7	*S. canus*
K_6	13.3	67	5.6	*S. endus*
K_7	4.4	67	1.9	*S. variabilis*
K_8	6.7	67	2.8	*Streptomyces* sp.
K_{14}	17.8	67	7.5	*Streptomyces* sp.
X	15.6	100	6.5	*Streptomyces* sp.

0.75 mL of sterile water, and the obtained homogenisate was inoculated on the same media.

To limit the growth of mycelial fungi and gram-negative bacteria, nistatine (10^3 units/mL) and nalidixic acid (7 μg/mL) were added into melted media. Incubation was carried out for 3 weeks at 28°C.

Thus, a collection of actinomycete strains was obtained which mainly belonged to the genus *Streptomyces*; their primary identification was based on study of cultural and morphological features according to the Gauze's determiner [14].

The structure of actinomycete complexes was analyzed on the basis of evaluation of parameters of the species diversity; biodiversity indices and parameters were calculated for comparative characterization [16].

RESULTS AND DISCUSSION

Representatives of the genus *Streptomyces* dominated in actinomycete complexes of nests that is characteristic for soils of the forest zone. Moreover, representatives of the genus *Micromonospora* were isolated from samples of nests in small amounts (Tables 1–3). They occur in the soil layer of forest and meadow biomes of the humic zone comprising the minor component of the soil actinomycete complex. But they often associated with plant substrate, such as sod, litter, mosses, peat at al [17].

The studied anthills were formed on the soil of the light granulometric composition; therefore, the percentage of micromonospores in them does not exceed 10%. Certain rise in the number of micromonospores was observed in the anthill of *F. cunicularia* (10^5 CFU/g) as compared to the control soil (4.7×10^4).

The total number of actinomycetes in the nests under study differed from that in the intact (control) soil (Fig. 1). In the nest of *F. cunicularia*, the quantity of actinomycetes (CFU/g) twice exceeds the number in the intact soil. Likewise, in the nest of *L. niger* this value is higher by order than one in control soil. The increased number of actinomycetes in samples of nests occurred mainly due to common for all the considered complexes and most abundant members of the genus *Streptomyces*.

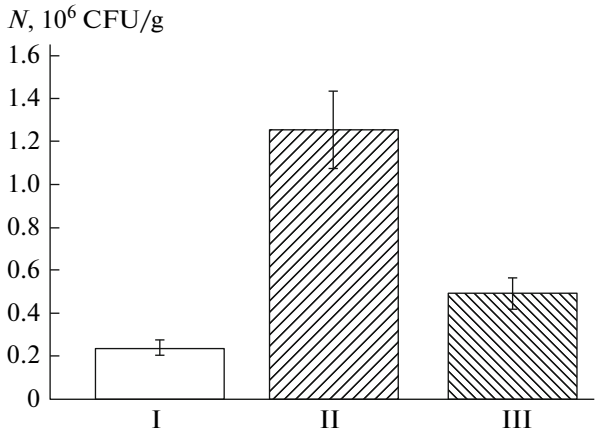

Fig. 1. Total number of actinomycete complexes in nest of (II) *L. niger*, (III) *F. cunicularia* and (I) control soil: (*N*) number of colony forming units of actinomycetes in gram of substrate. Error bars correspond to the value of the relative error.

Table 2. Species structure of actinomycete complex of *L. niger* nests

Strain	Number, 10^3 CFU/g	Frequency occurrence, %	Mean abundance, %	Identified as
L_5	200	100	15.9	*S. olivochromogenes*
L_3	302	100	24.1	*S. violascens*
L_2	262	100	20.9	*S. varsoviensis*
L_{10}	64.4	67	5.1	*S. cinereoruber*
K_{11}	4.4	33	0.4	*S. roseoflavus*
K_{17}	11.1	67	0.9	*S. olivaceoviridis*
L_1	31.1	67	2.5	*S. roseolilacinus*
Micr	8.9	67	0.7	*Micromonospora* sp.
L_4	44.4	33	3.6	*S. resistomycificus*
L_6	82.2	67	6.6	*S. pseudogriseolus*
L_7	37.8	67	3.0	*S. sporoclivatus*
L_9	66.7	67	5.3	*S. nashvillensis*
L_9''	13.3	33	1.1	*S. carpaticus*
L_{11}	26.7	67	2.1	*S. ambofaciens*
L_{16}	37.8	67	3.0	*S. albus*
L_{17}	4.4	33	0.4	*S. durhamensis*
Micr-1	55.6	33	4.4	*Micromonospora* sp.

Table 3. Species structure of actinomycete complex of *F. cunicularia* nests

Strain	Number, 10^3 CFU/g	Frequency occurrence, %	Mean abundance, %	Identified as
F_2	42.2	100	8.6	*S. ovilaceus*
F_8	33.3	100	6.8	*S. violascens*
F_3	171	100	35	*S. varsoviensis*
F_1	100	100	20.5	*S. cinereoruber*
F_5	22.2	67	4.5	*S. noboritoensis*
F_9	15.6	67	3.2	*S. olivaceoviridis*
F_4	15.6	100	3.2	*S. hygroscopicus*
Micr	2.2	33	0.5	*Micromonospora* sp.
F_6	33.3	100	6.8	*S. chromofuscus*
F_7	6.7	33	1.4	*Steptomyces* sp.
F_{10}	8.9	33	1.8	*S. globisporus*
F_{11}	37.8	67	7.7	*S. violaceoruber*

In the anthill of *L. niger*, species *S. olivochromogenes, S. violascens, S. varsoviensis*, and *cinereoruber* contributed to the increased abundance in the nest (Tables 1, 2). The most numerous species that we identified conventionally as *S. violascens* (it had a number of differences from the type species described in [14]) was found in all the samples. In the nest of *L. niger*, its number reached the absolute maximum (3×10^5 CFU/g) being one order higher than in the nest material of *F. cunicularia* (3×10^4 CFU/g) and control soil (5×10^4CFU/g). The species *S. olivochromogenes* in the intact soil was counted to be 5.78×10^4 CFU/g and that in the nest of *L. niger* to 2×10^5 CFU/g (Tables 1–3).

In the nest material of *F. cunicularia*, the increased abundance was due to species *S. varsoviensis* and *S. cinereoruber* (Tables 2–4). Representatives of the species *S. varsoviensis* in the anthill of *F. cunicularia* were one order higher (1.7×10^5 CFU/g) than in the intact soil (1.5×10^4 CFU/g) and in the hill of *L. niger* (2.6×10^4 CFU/g). The number of *S. cinereoruber* in the nest of the mining ants comprised 10^5 CFU/g,

which was two orders higher than in the control soil (6.7×10^3 CFU/g) and one order higher than in the nest material of black garden ants (6.4×10^4 CFU/g).

Species that did not occur in the control soil contributed additionally to the increased number of actinomycetes in ants' nests (Tables 1–3).

Therefore, the number of actinomycetes is higher in the samples of nest material than in the intact soil, which is especially characteristic for *L. niger* anthills. One can suppose that this was the activity of the black garden ants that led to the increased number of streptomycetes in the soil.

The objects under study were characterized by a similar range of the species composition of actinomycetes: we selected 15 phenotypes from samples of the intact soil—somewhat higher from nest material of *L. niger* and from *F. cunicularia*: 12 phenotypically different strains.

In order to evaluate the significance of the species in the community, occurrence frequency and relative abundance criteria are used (Table 4). The occurrence frequency describes the regularity and irregularity in the distribution of a species in a complex. It is calculated as a percent ratio of the number of samples wherein the species occurs to the total number of examined samples. The relative abundance is the percentage occupied by the species in the complex of a considered object.

The comparison of actinomycete complexes of the studied objects showed the absence of obvious dominants—species whose percentage exceeds 36%. Grouping of subdominant (16–36%) and typical species comprised almost one half. These are the common species; due to these species, the number of streptomycetes in ant nests was significantly higher than in the control soil.

A part of the complex represented by minor species was specific for each of the studied habitats. It included both frequent and rare species, and their relative abundance did not exceed 16% (Table 4).

Therefore, in streptomycete complexes of *L. niger* and *F. cunicularia* nests, about one half of the number is made of species inherited from the "parental" soil and the other half is made of a specific set of species.

When assessing the diversity within a habitat [18], it is necessary to know the number of species on a certain area and how equally by abundance the species are distributed in a community. For assessment of parameters of the α-diversity of actinomycete complexes isolated from the control soil and nests of *L. niger* and *F. cunicularia*, indices of dominance (*D*), diversity (*H*), evenness (*E*), and similarity (*S*) were calculated, which are known to general ecology [19] and represent mathematical expression of dependence between the number of species and their significance [20].

The Shannon index (*H*) values for actinomycete complexes of all the studied objects were close and allowed us to characterize diversity as relatively high

Table 4. Criteria of species significance in the complex of soil actinomycetes

Frequency occurrence, %	Degree of toxicity	Relative abundance (p_i), %	Degree of dominance
according to [22]		according to [23]	
≥60	typical	≥36	dominant
30–60	frequent	16–36	subdominant
<30	rare	<16	minor

Table 5. Values of indices of dominance (*D*), diversity (*H*), equitability (*E*) and similarity (*S*) for complexes of actinomycetes isolated form control soil and nests of *L. niger* and *F. cunicularia*

Parameter	Control soil (I)	Anthill *Lasius niger* (II)	Anthill *Formica cunicularia* (III)
H	2.95	2.80	2.70
E	0.86	0.83	0.85
D	0.13	0.14	0.19
S	I–II 0.48	II–III 0.38	I–III 0.37

(Table 5). Generally, the *H* values lied within the range from 1.5 to 3.5: the higher the Shannon index, the higher the species diversity of a community [16]. A high value was calculated for control soil, and a lower value for nests of *F. cunicularia*.

The evenness index (E) (Pielow index) characterizes the equitability of abundance distribution by taxa, its value is maximum at equal abundance of all the species. Of the studied communities, the highest *E* value was noted for the intact soil (0.86).

Therefore, values of the *H* and *E* indices for all the studied actinomycete complexes were close and showed a high biodiversity and equitability that characterizes them to be mature and stabile. The maximum values were observed for the intact soil (Table 5).

The least value of the Simpson dominance index (*D*) was observed for the control soil, and the highest for nests of *Formica* (the diversity decreases with increasing *D*). This parameter is a quite sensitive indicator of dominance of one species or several species and weakly depends on the species richness [16]. There is a species with a high abundance index (35%) in the actinomycete complex of *Formica*—*S. varsoviensis* (Table 5).

To assess degrees of similarity or differences between the complexes of actinomycetes isolated form nest material and the intact soil (β-diversity or diversities between habitats), the Sørensen similarity coefficient (S) was used. The value of this parameter corre-

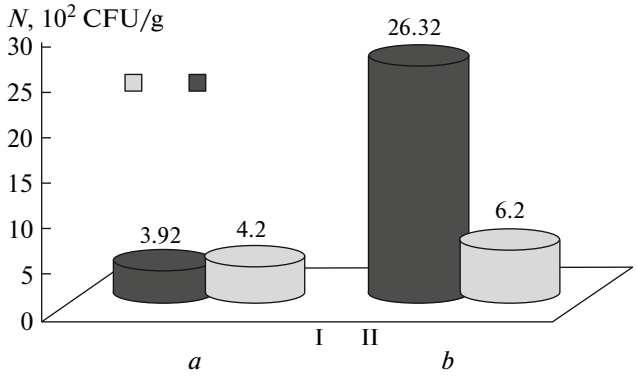

Fig. 2. Mean number of actinomycetes associated with ants (I) *L. niger* and (II) *F. cunicularia* (II): (*a*) washout, (*b*) homogenisate. (*N*) number of colony-forming units of actinomycetes isolated from one ant.

sponds to the range of probabilities of the absolute dissimilarity to compete coincidence of the structure of the considered communities. The S coefficient calculated for control soil and nest material of *Lasius* comprised 0.48; i.e., similarities and differences are approximately equal. The S index was almost the same in the pairs of control–*Formica* and *Formica*–*Lasius*: 0.37 and 0.38; the complex of actinomycetes of the nest of *Formica* was similarity distant from the control soil and from the complex of the *Lasius* nest. β-Diversity can be characterized as high.

Thus, structures of actinomycete complexes of *L. niger* and *F. cunicularia* nest material were similar with intact soil by diversity and equitability, but clearly differed by the number and the range of species.

The influence of ants on the diversity of actinomycetes is most completely determined as the result of changes in the soil properties during construction and arrangement of a nest. There are examples in literature of a striking mutualistic interaction between ants and actinomycetes, including symbiosis between leaf-cutting ants from the tribe *Attini* and actinomycetes of the genus *Pseudonocardia* inhabiting the surface of their bodies. These actinomycetes have specific antibiotic activity in relation to a micromycetes *Escovopsis* sp., which infests the fungal gardens cultivated by ants. Ants, in turn, afford actinomycetes with a unique ecological niche, provide their distribution, and supply them with nutrient substances [21].

In less specialized ants, this mutualism can manifest as a surface associated or internal actinoflora, which is capable, for example, to protect the ants from entomopathogens. Therefore, at the next stage, we studied the complex of prokaryotes directly associated with ants *L. niger* and *F. cunicularia*. The numbers and species diversity of actinomycete complexes detected in platings of washout and suspensions of washed ants

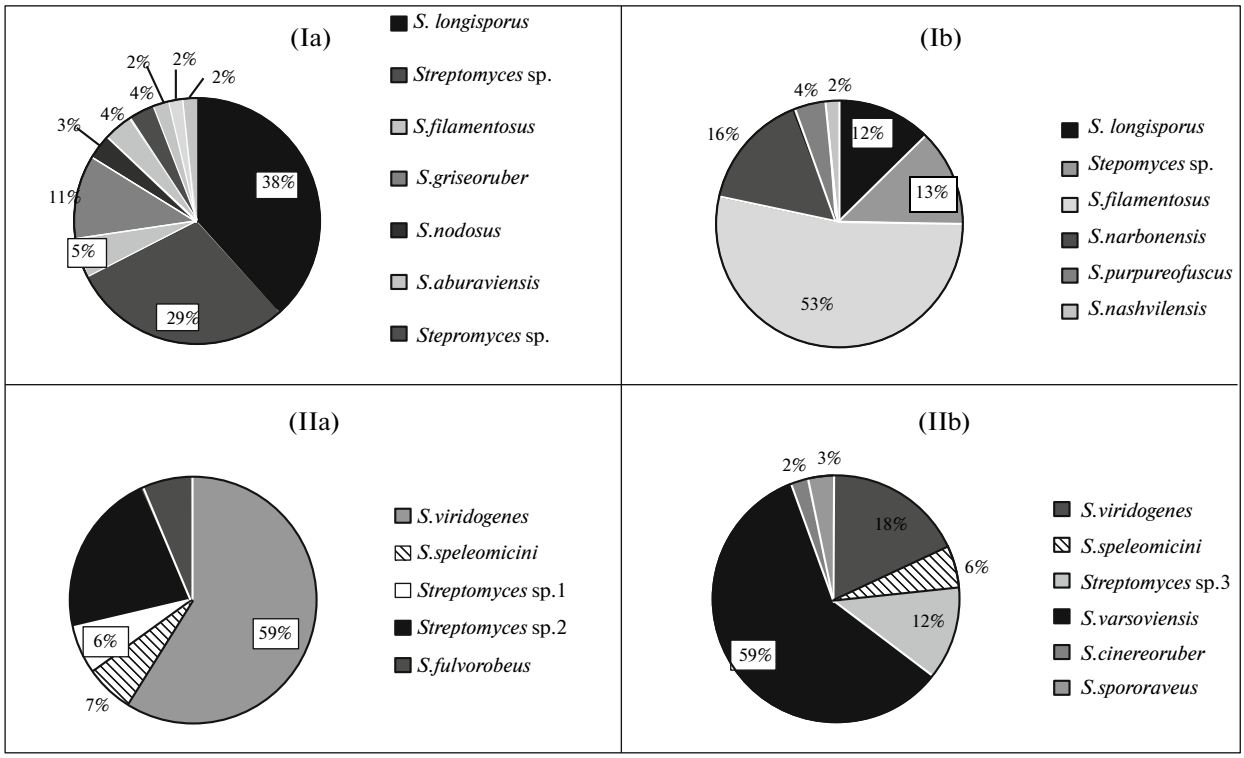

Fig. 3. Species structure of streptomycete complexes associated with ants (I) *L. niger* and (II) *F. cunicularia*. (a) washout, (b) homogenisate. The percentage of the species in the community (%).

Table 6. Values of indices of dominance, diversity, equitability and similarity for complexes of streptomycetes associated with ants *L. niger* and *F. cunicularia*

Parameters	*Lasius niger*		*Formica cunicularia*	
	washout	hogogenisate	washout	hogogenisate
Shannon index (*H*)	2.65	1.95	1.69	1.97
Pielow index (*E*)	0.80	0.76	0.73	0.70
Simpson index (*D*)	0.26	0.33	0.41	0.38
Sørensen index (*S*)	0.21		0.26	
	0			

L. niger and *F. cunicularia* were assessed. We suppose that organisms unstably associated with the surface of the ant, either accidentally or with adhered to particles of soil, enter into the washout, while actinomycetes adhering to covers and/or possible endosymbionts are present in homogenisate.

In platings of *L. niger* homogenisates, the number of actinomycetes comprised 2.6×10^6 CFU/g specimens, and that in the nest hill of *L. niger* comprised 1.26×10^6 CFU/g of soil. In suspension of *Formica*, the number of actinomycetes was 6.2×10^5 CFU/g of specimens, and that in the nest was 4.9×10^5 CFU/g soil. Since the weight of ants comprises several mg, it turns out that the number of actinomycetes in ants (hundreds of CFU/g) and their nests was almost similar when calculated to grams (Figs. 1 and 2). In washout of both ants, the number was estimated to be 4×10^5 CFU/g specimens, which is comparable with the control soil—2.3×10^5 CFU/g of soil.

The number of actinomycetes isolated from homogenisate of black garden ants was significantly higher than in platings of suspensions of mining ants (Fig. 2) although the latter are larger (on average, the weight of the ant *Formica* more than three times exceeds that of worker ant *Lasius*). The quantity of actinomycetes growing from washout wasn't directly proportional the size of an ant.

By the species range width, the *Lasius*–washout dominated; ten phenotypes were detected in this variant, identified as *Streptomyces*. Washout from *Formica* allowed us to detect only five species of streptomycetes. In platings of homogenisates of both species, six phenotypes also classified to the genus *Streptomyces* were detected.

Two common species for washout and homogenisate of *L. niger* were found—*S. filamentosus* and *S. longisporus* (Fig. 3). In platings of homogenisate, *S. filamentosus* dominated (53%) and it became minor in the plating of washout (5%). In contrast, *S. longisporus* dominated in washout (38%) and was subdominant (12%) in homogenisate of *L. niger* (Fig. 3).

In streptomycete complexes associated with ants *F. cunicularia*, two common species were also noted—*S. speleomicini* and *S. viridogenes* (Fig. 3). *S. viridogenes* dominated in washout (59%) and it was subdominant in the suspension (18%). The percentage of *S. speleomicini* in washout and suspension comprised 6–7%, which characterizes it as a minor species. In platings of *F. cunicularia* homogenisates, *S. varsoviensis* (59%) dominated, which was not detected in platings of surface washout (Fig. 3).

Hence, the structural characteristics of actinomycete complexes associated with ants depend on method techniques used for their isolation: dominants and subdominants change and sets of minor species differ. We believe that the species isolated from suspensions are more promising for the search of possible symbiotic actinomycetes.

The differences detected between the streptomycete complexes associated with ants are clearly demonstrated by α-diversity parameters (Table 6).

The highest value of the *H* diversity index was noted for *Lasius* washout, and the least was noted for washout from *Formica* ants; homogenisates had almost the same values. The above stated can be repeated for the evenness index E, since this parameter is directly proportional to the Shannon index.

A minimal value of D dominance index was noted for the washout from *Lasius*. In complexes of streptomycetes associated with *Formica*, dominants were more abundant (Fig. 3); the maximum D value was calculated for the washout variant (Table 6).

In the pair of washout and homogenisate for streptomycete complexes associated with *F. cunicularia* and *L. niger*, similarity of the species composition (coefficient Sørensen) comprised 21 and 26%, respectively (Table 5). Common species for ants *Lasius* and *Formica* were not isolated—S equals null.

CONCLUSIONS

A larger number of actinomycete species is isolated from the nest material of ants than during inoculation from homogenized ants or washout. This observation is quite expected since the soil from which nests are composed of is a natural bank of microorganisms, in particular, actinomycetes. A limited number of species are likely able to exist in associations with animals.

Complexes of streptomycetes isolated using living ants are significantly less diverse and less equitable and dominant species are more manifested in them as compared to communities isolated from their nests (Tables 5, 6).

Due to the almost complete washout of actinomycete communities of ants and nest material, β-diversity can be considered very high. For ants *F. cunicularia* and their nests, one common species was detected, *S. cinereoruber*, minor in homogenisate and subdominant in samples of the anthill. Common species for actinomycete community of ants *L. niger* and their nests were not detected.

The similarities between communities of actinomycetes in the intact soil are higher than between groups of actinomycetes associated with living ants. This allows us to assume that, despite the direct influence on actinomycetes by transformation of the soil, ants form unique complexes directly contacting with actinomycetes. The mechanisms, associations, and mutual benefit of these relationships undoubtedly require further study.

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