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Analysis of the Local Ant Fauna (Hymenoptera, Formicidae) in Southern Vietnam

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Abstract—The ant fauna of Nam Cat Tien in the southern part of the Cat Tien Biosphere Reserve (Dong Nai Prov., Southern Vietnam) was studied in 2007–2008. The zonal type of vegetation under study is closed deciduous tropical forests dominated by *Lagerstroemia* spp. in association with Dipterocarpaceae and Fabaceae. The local ant fauna comprises 272 species from 68 genera and 12 subfamilies. The maximum number of species was found in the genera *Polyrhachi*s (31), *Camponotus* (21), *Pheidole* (21), *Leptogenys* (17), and *Crematogaster* (13). Seven ant genera (*Echinopla* F. Sm., *Indomyrma* Brown, *Liomyrmex* Mayr, *Paratopula* Wheeler, *Proatta* For., *Protanilla* Taylor, and *Rotastruma* Bolton) are reported from Vietnam for the first time. The ecological pattern of the ant fauna in the main forest biotopes of the study area is considered. In the dipterocarp forests in the central part of the reserve, the complex of stratobiont species was the most diverse. In the bamboo forests, the stratobiont complex is less diverse but the fraction of dendrobionts is greater. The forests with similar layer structure occurring on sand and loamy soils were shown to differ in the species composition of ant assemblages. Repeated population inventories of ants were carried out in 8 model plots of 100 m^2 each during the dry and rainy season. The specificity of revealing species of different biomorphs is discussed in the seasonal aspect. The structure of the ant fauna of Nam Cat Tien is compared to that in other territories of the Oriental Region. The zoogeographic unity of the study area and some localities of the Indo-Malayan Subregion (Borneo, Java) is demonstrated.

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Ants are one of the most abundant insect groups in the tropics, constituting 10–15% of the animal biomass in different biotopes (Agosti et al., 2000). These social insects have a broad range of life forms and inhabit all the strata and layers of the tropical forest, from soil and litter to the crowns of tall trees. A high taxonomic diversity of tropical ants and at the same time, distinct biotopic association related to the specificity of settlement, makes this group a good object of monitoring studies. Such studies are especially important in the primary tropical forests of Southern Vietnam, since these territories were the target of extensive ecocide during the Second Indochina War, after which only small stands of dense tall rain forests had remained (Kuznetsov, 2003).

A necessary stage in studying tropical forest ant associations is obtaining representative faunistic lists. The fauna and taxonomy of ants in Vietnam in general are insufficiently studied (Ogata, 2005). Systematic researches have started only since 1997 on the basis of national parks and so far have embraced only the northern and partly central provinces of Vietnam (Bui, 2002; Yamane et al., 2002; Eguchi et al.. 2004). The local ant faunas in Northern Vietnam were found to include up to 160 species. As for the southern provinces, faunistic studies in them have been almost absent up till now. Before our work in the Cat Tien Biosphere Reserve, only a preliminary manuscript list of ants in this protected territory existed, compiled by C. Eguchi and T.V. Bui in 2005 based on the results of three-week collections and including 103 species, 44 genera, and 11 subfamilies. Incidentally, 5 new species have already been described based on these collections (Eguchi and Bui, 2005; Eguchi, 2008; Eguchi et al., 2006, 2008; Borowiec, 2009).

The purpose of the present communication is analysis of the local ant fauna in the Cat Tien Biosphere Reserve as a model area of tropical monsoon forests in Southern Vietnam. To achieve this goal the following tasks had to be fulfilled: obtaining the full faunistic list, assessment of the ecological range of the ant fauna in the main types of forest biotopes, assessment of the species diversity of ant communities, comparison of the results obtained with the published data on the local ant faunas in the Oriental Region.

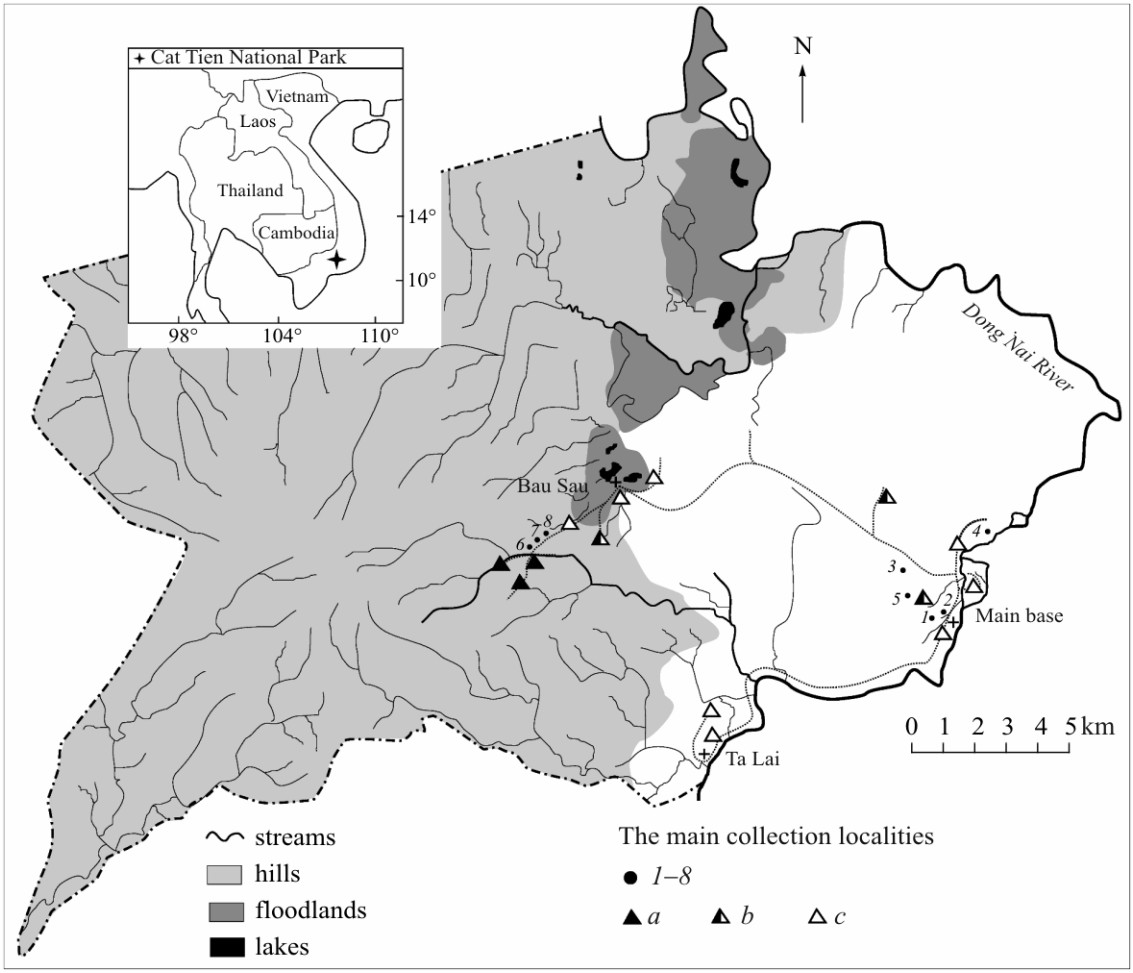

Fig. 1. A schematic map of the study area. The main localities of material collection in 2007–2008: model plots (*1–8*) and biotopes (*a*, dipterocarp forests on hills; *b*, *Lagerstroemia* forests on basalts; *c*, bamboo forests and open biotopes). The survey routes are shown by dotted lines.

MATERIALS AND METHODS

Studies were carried out in March–June 2007 and January–November 2008, in Nam Cat Tien (11°20′50″–11°32′13″N, 107°11′13″–107°28′20″E). This is a southern part of the Cat Tien Biosphere Reserve, located in Dong Nai Province, with an area of 38 202 ha, that can be subdivided into two parts according to its relief (Fig. 1). In the lowland eastern part the altitudes do not exceed 150 m above sea level, while the rest of the territory is hilly with heights 150–375 m above sea level.

The study area lies in the zone of the tropical monsoon climate with a distinct seasonal aspect. The bioclimatic type is monsoon tropical, with summer rains (Nguyen Khanh Van et al., 2000). The dry season lasts from December to April, the rainy season, from May to November. The mean annual precipitation is 2450 mm. The peak of the dry season is February–March, that of the rainy season, August–September (with monthly precipitation 400–450 mm). The relative air humidity normally exceeds 70%, with the mean annual temperature +25.4°C. During our work, the lowest night temperature of +17°C was recorded in November, and the highest shade temperature of +43°C, in April.

The study area lies in the zone of tropical monsoon semi-deciduous forests with prevalence of *Lagerstroemia* spp. in association with Dipterocarpaceae and Fabaceae (Blank et al., 2000). The area occupied by primary evergreen forests in Nam Cat Tien is only 1.8% of its territory, the total fraction of evergreen forests being 20.5%. The first place in area occupied is held by mixed forests with bamboo (30.8%) and bamboo forests proper (27.5%). The next place is occupied by semi-deciduous forests (13.3%), grasslands (2.9%), and shrubs (1.3%). The agricultural lands comprise only 0.2%.

The main biotopes and sample plots for studying ants were selected so as to embrace all the plant formations listed above. At the same time, emphasis was laid on evergreen and semi-deciduous forests with multilayer structure, where the highest species diversity of ants was observed. We distinguished the following main types of biotopes, which in a certain sense could be called generalized: I, crapemyrtle (*Lagerstroemia*) forests on basalts; II, dipterocarp forests on sandy soil; III, palm forest; IV, dipterocarp forests on hills; V, bamboo forests; and VI, forest edges and open biotopes.

The main work was conducted in 8 model plots 100 m^2 each laid in 4 types of biotopes. Plots 1–3 and 5 (generalized biotope I) were laid in forests with *Lagerstroemia calyculata* Kurz. with different codominant species: *Afzelia xylocarpa* (Kurz.) in 1, *Tetrameles nudiflora* R.Br. in 2, *Ficus* sp. in 3, and *Dipterocarpus alatus* Roxb. in 4. All these plots are characterized by loamy black soils with high organic content and abundant whinstone fragments on the surface. Plot 4 (generalized biotope II) on the riverbed bank of the river Dong Nai differs considerably in edaphic conditions and, as a consequence, in the animal population of its soil (Anichkin, 2008). The dominant tree species is *D. alatus*; the soils are sandy, formed by powerful river sediments (3–5 m). The ecotonic character of this biotope should be noted. In the central part of the reserve, 3 plots were laid in two types of biotopes; plots 6 and 7 (generalized biotope III) were located in forests derived from dipterocarp ones, with palms *Livistona saribus* (Lour.) and *Licuala* sp., plot 8 (generalized biotope V) was located in the mixed bamboo forest. The minimal drainage was observed on plot 6, where partial flooding occurred in the middle of the rainy season. The location of the main points of data collection, including the model plots, is shown in Fig. 1.

Several main methods for assessment of the ant population and inventory of the tropical ant fauna were suggested (Agosti et al., 2000; Hashimoto et al., 2001, etc.). Earlier, by the example of insular tropical ecosystems it was established that the species diversity of an ant association could be adequately characterized based on a 10 × 10 m plot in an undisturbed zonal landscape (Zakharov, 1994). Model plots of the same size were used in our research. Before carrying out inventories in each plot, they were marked out and mapped to a scale 1: 40. Surface carbohydrate feeders were used to reveal ant nests or sections of them and estimate the foraging activity of ants on the soil surface. Inventory was carried out simultaneously on 25–45 feeders exposed for 30–45 min. To reveal species which did not visit the feeders, the model plot was subdivided into squares with sides of 1–4 m and carefully examined square by square. In addition, underground feeders with carbohydrate and protein bait were used to estimate ant activity within the upper soil layer. The bait was placed in perforated plastic containers (d = 2.5 cm, h = 5 cm), which were buried at a depth of 5–10 cm along the perimeter of the plot for 24–72 h. Altogether, we performed 20 inventories at land feeders (100–225 feeders per plot) and 37 inventories using underground feeders (10 feeders per plot).

During the fauna inventories, ants were also collected manually from plants, tree trunks, under the bark, from hollows, in dead wood stumps and other wood debris, fallen fruit, and epiphytes. The soil and litter dwelling species were collected using soil sifters, while those occurring on plants were collected with entomological net. In field stations where electric light was available, winged ants attracted by light were regularly collected.

Throughout the investigation, 24 inventories of the ant population in the model plots were carried out, about 380 trees were examined, on average, up to the height of 2–3 m, of which 150 trees belonged to the first sublayer, and about 80 bamboo stems; 108 butts of big trees and palms, 34 dry trees, 102 stumps at different stages of decomposition, about 200 m of lianas were studied. The total material studied, together with collections made by our colleagues (2004–2008), comprised 42.7 thousand individuals (41 800 workers, 545 females, and 366 males).

Identification of material was carried out using all the sources available, including original descriptions. The system of subfamilies and genera of ants mainly follows that of Bolton (2003).

Comparison of the structure of local ant faunas in the Oriental Region was done using published data and internet resources on 8 localities: the Northern Vietnamese national parks Hoang Lien Son (Bui and Eguchi, 2003), Cuc Phuong (Yamane et al., 2002), Ba Vi, and Tam Dao (Eguchi et al., 2004); the Malaysian (Borneo) national parks Poring (www.antbase.net/literature-pdf/ants-of-poring-2005.pdf) and Tawau (http://homepage.mac.com/aenictus/tawl.html); the Bogor Botanical Garden, Java (Ito et al., 2001); and Sinharaja Rain Forest Reserve, Sri Lanka (Ganawar-

dene et al., 2008). The analysis also includes the author's unpublished data on the local ant fauna of the Bi Dup-Nui Ba National Park on the Da Lat Plateau, Southern Vietnam. Comparison was made at the genus level since many species remained unidentified. First, the species abundance of each genus in the structure of local ant faunas was determined, in order to eliminate the influence of different volumes of the faunistic lists. After this, we performed cluster analysis of calculated parts using the Czekanowski–Sørensen coefficient (Pesenko, 1982) with construction of a similarity dendrogram by the neighbor-joining method. The zoogeographic subdivision of the Oriental Region was borrowed from the latest synopsis of Asian ants (Ogata, 2005).

RESULTS AND DISCUSSION

The Fauna and Biotopic Distribution of Ants

The ant fauna of the Indochinese Subregion of the Oriental Region, which traditionally includes the entire territory of Vietnam, counts 89 genera (Ogata, 2005). For Southern Vietnam, according to our calculations, 75 genera have been reported so far. Proceeding from these numbers, one can suggest that the local ant fauna of Nam Cat Tien, including 68 genera, representatively reflects the regional ant fauna. The composition of the ant fauna and the species diversity in the generalized biotopes of the study area are shown in Table 1. The table does not include 3 genera (*Leptanilla* Em., *Myopopone* Rog., and *Mystrium* Rog.) listed in the preliminary synopsis of Nam Cat Tien ants but not found by the author, and the species collected only in light traps. If these ants were taken into account, the total number of the species found in 2007–2008 would be 272. The following genera are the best represented in the local fauna: *Polyrhachis* (31 species), *Camponotus* and *Pheidole* (21 species each), *Leptogenys* (17), *Crematogaster* (13), and *Tetramorium* (10); 20 genera include 3–9 species each, and 41 genera are represented in the study area by 1–2 species each. The number of species reported here is not final and may change in the course of additional collections and further processing of the material.

Most part of the species are typical forest inhabitants. Several species were found only in open biotopes, such as grasslands, floodlands, and agricultural lands: *Camponotus parius* Em., *Cerapachys* cf. *hewitti* (Wheel.), *Iridomyrmex anceps* (Reg.), *Lepisiota rothneyi* (For.), *Polyrhachis* cf. *zopyra* F. Sm., and *Solenopsis geminata* (F.). Some of them, for instance, *C. parius* and *L. rothneyi*, may also inhabit peripheral forest areas, extending there along wide forest paths. The introduced species *Anoplolepis gracilipes* (F.Sm.), *Cardiocondyla nuda* (Mayr), *C. wroughtonii* (For.), *Monomorium destructor* (Jerd.), *M. floricola* (Jerd.), *M. pharaonis* (L.), *Nylanderia bourbonica* (For.), *Paratrechina longicornis* (Latr.), *Tapinoma melanocephalum* (F.), and *Technomyrmex albipes* F.Sm. prefer forest edges or disturbed forests with a thinned canopy.

The ant fauna of dipterocarp forests on hills is the most representative. This can be accounted for by a considerable distance from the forest edge and buildings and a lower anthropogenic pressure. However, one should also consider the specific state of vegetation in this cenosis, namely the preserved patches of the old dipterocarp forest on zonal red-yellow ferralitic soils. These particular habitats include the core of the geo- and stratobiont ant complex in Nam Cat Tien, which is represented by a number of genera and species rare in the region. This applies, first of all, to the genus *Acropyga*. These ants are specialized trophobionts collecting honeydew from root mealybugs of the subfamily Rhizoecinae (Terayama et al., 2002). Three species of this genus have been reported so far from the Oriental Region and 6, from the Indo-Australian Region (La Polla, 2004). The revealed fauna of Nam Cat Tien includes *A. acutiventris* Rog., *A. butteli* For., *A.* cf. *oceanica* Em., *A. pallida* (Donist.), and 2 presumably new species, considerably supplementing data on the arealogy of the genus. The generalized biotope in question has all the *Pachicondyla* and *Pseudolasius* species known in the region, most species of Dacetini and *Carebara* (6 each), and 4 species of *Hypoponera*. Such ants as *Acanthomyrmex humilis* Eg. et al., *Anochetus princeps* Em., *Cryptopone testacea* (Motsch.), *Discothyrea* sp. 2, *Gnamptogenys costata* (Em.), *Indomyrma* sp., *Pristomyrmex* spp., *Tetramorium* sp. 2, and *Vollenhovia* sp. 2 were found only in this biotope.

There is reason to suppose that dipterocarp forests on hills are refugium for geo- and stratobiont species which disperse from there to the surrounding biotopes. This is distinctly confirmed by the ant fauna of the adjoining palm forest which is similar to that of dipterocarp forests by more than 75%. These biotopes have two common species from each of the genera *Acropyga*, *Pachycondyla*, and *Pyramica*, and also *Cerapachys* cf. *coecus* (Mayr) and *Mayriella granu-*

Table 1. The ant fauna composition and species diversity in the principal (generalized) biotopes of Nam Cat Tien

Subfamily	Genus	Biotopes						Total
		I	II	III	IV	V	VI	
Amblyoponinae	*Amblyopone* Erichson	2	1	0	0	0	0	2
Aenectinae	*Aenictus* Shuckard	1	3	1	2	0	2	6
Cerapachyinae	*Cerapachys* F. Smith	5	3	3	4	2	2	9
Dolichoderinae	*Dolichoderus* Lund	3	2	3	3	2	1	5
	Iridomyrmex Mayr	0	0	0	0	0	1	1
	Philidris Shattuck	1	1	1	1	1	1	1
	Tapinoma Foerster	2	2	1	1	1	1	2
	Technomyrmex Mayr	3	4	4	4	1	2	7
Dorylinae	*Dorylus* Fabricius	0	1	1	1	0	0	1
Ectatomminae	*Gnamptogenys* Roger	2	2	1	1	2	1	3
Formicinae	*Acropyga* Roger	0	0	2	6	0	0	6
	Anoplolepis Santschi	1	1	0	1	1	1	1
	Camponotus Mayr	9	10	8	9	10	7	19
	Cladomyrma Wheeler	1	0	0	0	0	0	1
	Echinopla F. Smith*	0	1	0	0	0	0	1
	Lepisiota Santschi	0	0	0	0	0	1	1
	Nylanderia Emery	2	3	2	4	3	2	5
	Oecophylla F. Smith	1	1	0	1	1	1	1
	Paratrechina Motschoulsky	1	0	0	0	0	1	1
	Paraparatrechina Donisthorpe	2	2	1	1	0	0	2
	Polyrhachis F. Smith	10	8	7	12	17	10	26
	Prenolepis Mayr	1	1	0	1	0	0	2
	Pseudolasius Emery	1	2	1	3	0	0	3
Leptanillinae	*Protanilla* Taylor*	1	0	0	0	0	0	1
Myrmicinae	*Acanthomyrmex* Emery	0	0	0	1	0	0	1
	Calyptomyrmex Emery	0	1	0	0	0	0	1
	Cardiocondyla Emery	1	1	0	1	0	2	4
	Carebara Westwood	4	4	4	5	0	1	7
	Cataulacus F. Smith	1	1	1	1	1	1	1
	Crematogaster Lund	4	7	3	3	10	6	13
	Dilobocondyla Santschi	0	1	0	0	0	1	1
	Indomyrma Brown*	0	0	0	1	0	0	1
	Liomyrmex Mayr*	1	0	0	0	0	0	1
	Lophomyrmex Emery	1	1	1	0	0	0	1
	Mayriella Forel	0	0	1	1	0	0	1
	Monomorium Mayr	4	4	2	3	3	4	6
	Myrmecina Curtis	1	0	0	0	0	0	1
	Myrmicaria Saunders	0	0	0	2	0	0	2
	Paratopula Wheeler*	1	0	0	0	0	0	1
	Pheidole Westwood	11	14	11	10	8	5	20
	Pheidologeton Mayr	1	2	2	0	1	2	3

Table 1 (Contd.)

Subfamily	Genus	Biotopes						Total
		I	II	III	IV	V	VI	
	Pristomyrmex Mayr	0	0	0	2	0	0	2
	Proatta Forel*	1	1	0	1	0	0	1
	Pyramica Roger	0	1	2	2	0	0	3
	Rotastruma Bolton*	1	0	0	0	0	0	1
	Solenopsis Westwood	0	1	1	1	0	1	2
	Strumigenys F. Smith	1	2	3	4	0	0	5
	Tetramorium Mayr	6	5	5	5	3	5	9
	Vollenhovia Mayr	1	1	1	2	0	0	2
	Solenopsidini gen. sp.	1	1	0	1	0	0	1
Ponerinae	*Anochetus* Mayr	3	0	1	3	0	0	5
	Centromyrmex Mayr	1	1	0	1	0	0	1
	Cryptopone Emery	0	0	0	1	0	0	1
	Diacamma Mayr	2	2	3	2	3	3	3
	Harpegnathos Jerdon	1	0	0	0	0	0	1
	Hypoponera Santschi	3	3	4	4	2	1	5
	Leptogenys Roger	13	9	6	5	6	7	17
	Odontomachus Fatreille	0	0	1	1	1	1	2
	Odontoponera Mayr	1	1	1	1	1	1	1
	Pachycondyla F. Smith	4	6	7	8	2	0	8
	Platythyrea Roger	1	1	1	2	1	1	2
	Ponera Fatreille	1	2	0	1	0	0	3
Proceratiinae	*Discothyrea* Roger	0	1	0	1	0	0	2
	Probolomyrmex Mayr	1	0	0	0	0	0	1
Pseudomyrmicinae	*Tetraponera* F. Smith	3	4	3	1	3	4	7
Total genera		47	45	36	47	25	32	65
Total species		124	126	100	132	86	80	257

Notes: Generalized biotopes: I, *Lagerstroemia* forests on basalts; II, dipterocarp forest on sandy soil; III, palm forest; IV, dipterocarp forests in the hills; V, bamboo forests; VI, forest edges and open biotopes (not counting species collected in light traps).
* Reported for the first time from Vietnam.

lata Dluss. et Rad., which were not found in other localities.

Some difference in the geo- and stratobiont ant diversity is to be observed between generalized biotopes I and II, which is determined by different soil conditions. Here one may speak about ecological vicariance at the level of species and even genera. For example, species of the genus *Anochetus* are common in the geo- and stratobiont ant complex of biotope I but absent in biotope II. Approximately the same situation is observed with the genus *Amblyopone*. The ant *A. quadrata* (Kar.) is rather common in crapemyrtle forests on basalts but almost never occurs in the dipterocarp forest on sandy soil. Species of the genus *Pseudolasius*, mainly *P. silvestrii* Wheel., clearly prevail in terms of density in the dipterocarp forest on sand soil. The genera *Carebara*, *Cerapachys*, and *Ponera* also include species associated only with one of the biotopes in question. Such ants as *Myrmecina* sp., *Tetramorium inglebyi* For., and *Tetramorium* sp. 1 are also specific for generalized biotope I. The species list of this biotope also included *Liomyrmex gestroi* (Em.), *Probolomyrmex vieti* Eg. et al., *Protanilla* sp. 1, and 3 litter-dwelling species of *Leptogenys*. Such ants as *Calyptomyrmex rectopilosus* Dluss. et Rad., *Discothyrea* sp. 1, and *Pyramica* cf. *emeswangi* Bolton were found in biotope II. It should be emphasized that many

Table 2. The ecological spectrum of ant fauna in generalized forest biotopes of Nam Cat Tien

Life form	Biotopes									
	I		II		III		IV		V	
	S	%	*S*	%	*S*	%	*S*	%	*S*	%
Geobionts	12	9.7	13	10.3	9	9.0	19	14.4	1	1.2
Stratobionts	23	18.5	17	13.5	19	19.0	33	25.0	5	5.8
Herpetobionts	54	43.5	53	42.1	41	41.0	46	34.9	37	43.0
Dendrobionts	32	25.8	35	27.8	26	26.0	30	22.7	40	46.5
Legionaries	3	2.4	8	6.3	5	5.0	4	3.0	3	3.5
Total	124	100	126	100	100	100	132	100	86	100

Note: The generalized biotopes are designated with *Roman numerals* as in notes to Table 1. For each biotope, the number of species (*S*) and the fraction (%) of each biomorph in the ant fauna are specified.

geo- and stratobiont species present in the dipterocarp forest on sandy soil prefer to settle in wood residues. This may be related to the risk of soil nests being destroyed during the rainy season but may be also accounted for by the azonal character of the soil.

The biotopic distribution of herpetobiont and dendrobiont ants is more uniform though it also reveals certain specificity. Rather demonstrative is the distribution of ants of the genus *Odontomachus*, which are the key species in ant associations. These ants are present only in the central part the Nam Cat Tien National Park, *O. rixosus* F.Sm. being associated with generalized biotopes III and IV, and *O. simillimus* F.Sm., with generalized biotopes V and VI. The limits of distribution of these species in the study area mark the boundary between peripheral and indigenous forests.

The dipterocarp forest on sandy soil is characterized by the highest diversity of the genus *Pheidole*; the recently described *Ph. aspidata* Eg. et Bui and *Ph. tumida* Eg. were found only in this biotope. It is interesting that several species of *Pheidole* are confined to the central part of the National Park (*Ph.* cf. *acantha* Eg., *Ph. laevithorax* Eg., *Ph.* sp. E, *Ph.* cf. *sauberi* For., and *Ph.* sp. 8), the latter two of them being background species in the ant associations of biotopes III and IV. Thus, ecological vicariance can be also observed in this case. The numbers of the subfamily Dolichoderinae increase considerably in these biotopes, while that of *Crematogaster* spp. decreases, indicating a low level of disturbance (Agosti et al., 2000).

Among dendrobiont ants, such species as *Cladomyrma* sp. (associated with the liana *Sphenodesma pierri* from the family Verbenaceae), *Crematogaster sewardi* For., *Rotastruma* sp. (nr. *recava*) and some others are characteristic of crapemyrtle forests. The dendrobiont species typical of dipterocarp forests are *Camponotus rufifemur* Em., *C. saundersi* Em., *Dolichoderus sulcaticeps* Mayr, *Myrmicaria arachnoides* (F.Sm.), and *Polyrhachis bellicosa* F.Sm.

Among forest biotopes, various kinds of bamboo forests are special as concerns their ant fauna. They have a completely different structure of the ant complex (Table 2), determined by a very small part of geo- and stratobionts. At the same time, the complex of dendrobiont and herpetobiont ants inhabiting bamboos is larger. It includes *Cataulacus granulatus* (Latr.), *Diacamma rugosum* (Le Guill.), *Platythyrea parallela*, some species of *Camponotus*, *Polyrhachis*, and *Crematogaster*. Ants of the last two genera achieve the highest diversity in bamboo forests in the study area. Several species of *Polyrhachis* were found to settle only in bamboo (Liefke et al., 1998). Among the species present in Nam Cat Tien, these are *P. arachne* Em. and *P. schellerichae* Dor.

One should specially consider the interpretation of the "legionary" biomorph used in this communication. This biomorph usually includes representatives of doryline subfamilies ("true" legionary or army ants) which have colonies numbering 10^5–10^6 adults and are characterized by the nomadic way of life and group hunting of social insects (Wilson, 1958, cited after Gotwald, 1982). However, these characters are also observed in some species of other ant subfamilies, first of all Ponerinae. Witte (2001) suggested that legionary ants should be determined by combination of the nomadic way of life and mass hunting ("Massenjagd," term of Witte), which consists of collective search,

Table 3. Distribution of relative abundance (%) of background ant species according to the surveys at feeders (generalized data)

Species	SF	Plots	Species	UF	Plots
Anoplolepis gracilipes (F. Sm.)	20.4	1–5	*L.* cf. *birmanus*	37.8	1–6
Odontoponera transversa (F. Sm.)	13.2	1–5	*Carebara* cf. *bouvardi* (San.)	15.0	1–4, 6, 7
Lophomyrmex cf. *birmanus* Em.	11.1	1–6	*Pseudolasius silvestrii* Wheel.	14.1	1, 4, 5
Nylanderia picta Wheel.	7.8	1–7	*Tetramorium inglebyi* For.	3.9	2
Pheidole sp. 8	4.2	6, 7	*Carebara* sp. B2	3.8	2, 3, 5–7
Pheidole planifrons San.	2.3	1–5	*Pheidole* sp. 8	3.3	6, 7
Diacamma ?*geometricum* (F. Sm.)	2.2	1–5, 7, 8	*Philidris laevigata* (Em.)	2.5	3
Pheidole cf. *taipoana* Wheel.	2.0	1, 2, 4, 5	*Dorylus orientalis* Westw.	2.5	4
Pheidole binghamii For.	1.7	3, 4, 6, 7	*Pheidologeton affinis* (Jerd.)	2.3	2
Pheidole cf. *sauberi* For.	1.7	6, 7	*Pheidole* cf. *saubery*	2.2	7

Note: SF is the mean abundance of the species per 100 surface feeders (n = 20); UF—the same, per 10 underground feeders (n = 37).

attack, and transport of prey. Of principal importance is formation of a column of hunters before contact with prey and a fast increase in the number of ants, or "recruitment overrun," upon contact, ensuring successful capture. According to this interpretation, 13 species from the genera *Aenictus*, *Dorylus*, *Leptogenys*, and *Pheidologeton* present in Nam Cat Tien should be assigned to the legionary group. The most common among them are *L. processionalis* (Jerd.) and *Ph. diversus* (Jerd.). The distribution of legionary ants reveals their preference for ecotonic associations.

The Species Diversity of Ant Communities

The species diversity of ant communities reaches its maximum in the tropics. The main parameter of diversity is species density (saturation) of the association, which normally exceeds 30 species per 100 m^2. The complexes of geo- and stratobiont species and those associated with the above-ground layers exist rather independently from each other (Zakharov, 1984), each of them contributing to the total species diversity. Threshold values of ant species density have been established for different tropical regions. In the subtropical forests of Northern Vietnam it constitutes 25–30 species, in the Australian bush, 30–35, and in the Peruvian selva, 40–45 species (Zakharov and Sablin-Yavorskii, 1998). According to the results of our studies, the average density of ant species in monsoon tropical forests of Southern Vietnam is 33 species per 100 m^2. However, this value varies rather strongly depending on the type of the biotope, collection methods, and the season of study.

Using all the above methods, we revealed 170 species of ants in 8 model plots, i.e., considerably more than half of all the local ant fauna. Of them, 165 species were found by active collection by means of an aspirator and soil sifters. Unique findings were made in each model plot. In other words, active collection methods proved to be much better for revealing the species diversity of ants. Surveys and collection of ants at feeders revealed fewer species (74), but allowed the structure of the ant population to be characterized in terms of relative abundance. The total number of species varied from 37 in underground feeders to 60 on the soil surface, only 6 of them showing a relative abundance above 10% (Table 3). On plots 3–5, *Anoplolepis gracilipes* and *Odontoponera transversa* clearly prevailed during the surveys. The role of the former species in ant assemblages should be considered in greater detail.

As noted above, *A. gracilipes* typically occurs in forest edges and disturbed forests, which accounts for its prevalence in plots positioned near the national park station. The social basis of the prevalence of this species is its supercolony organization, probably representing the secondary federation (Zakharov, 1991). By the example of ecosystems of the Indian Ocean islands, it has been shown that "supercolonies" of *A. gracilipes* may occupy up to 10 thousand ha (Abbott, 2006), significantly reducing the species diversity of ants (Lester et al., 2009). However, another study carried out on several Pacific islands demonstrated that the colonies of *A. gracilipes* had different haplotypes and depending on this, varied in the degree

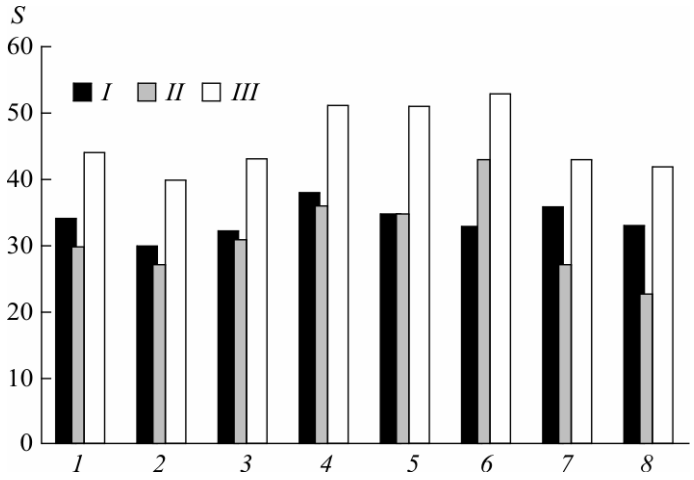

Fig. 2. Species diversity of ants (*S*) in model plots (*1–8*): *I*, in dry season; *II*, in rainy season (for plot 8, beginning and end of rainy season, respectively); *III*, total number of species found.

of aggressiveness and influence on native associations (Abbott et al., 2007). It was concluded that "old invaders" were less aggressive and did not reduce the overall species diversity of ant associations. According to our results, the prevalence of *A. gracilipes* on the soil surface is of a wave-like nature; it has virtually no effect on the species density of ants but does change the activity of other herpetobiont species.

Interesting in this respect is the status of *Lophomyrmex* cf. *birmanus*, occurring in most ant associations in the study area. This species is less abundant than *A. gracilipes* and *O. transversa* at carbohydrate surface feeders, but clearly prevails according to the underground feeder data (Table 3). The activity of *L.* cf. *birmanus* in the upper soil layer can be explained by its biological specificity: members of this genus belong to the group of "tunneling ants" (Moffett, 1986). However, they are quite active on the soil surface as well. Surveys at surface feeders showed that foragers of *L.* cf. *birmanus* were subject to aggression on the part of most of other herpetobiont species, first of all *O. transversa* and *A. gracilipes*. Activity of *L.* cf. *birmanus* on the soil surface may be limited by these species. The density of *L.* cf. *birmanus* was also found to decrease in areas with high abundance of *Pheidole* species (plot 4).

Inventories carried out by the same methods during the dry and rainy seasons mostly give similar estimates of ant species diversity in model plots. At the same time, the chances of revealing rare species vary considerably, which affects the resultant values of species diversity (Fig. 2). This may be accounted for by different reasons. First of all, activity of the geo- and stratobiont species considerably increases at the beginning of the wet season, which was recorded by surveys using underground feeders and by during collections from the upper soil layer (Zryanin, 2008). Another reason for the above differences may be the mosaic pattern of ant distribution. For example, in plot 6, at the beginning of the wet season, 9 species were collected from a single log about 2 m long and 15–20 cm in diameter, whereas a total of 19 species were found in all the logs within this plot during the rainy season. Increasing soil humidity may force the ants to settle more actively in the wood substrate. On the other hand, a number of dendrobiont ants from the genera *Dolichoderus*, *Camponotus*, *Polyrhachis*, and *Tetraponera* were more often recorded on the soil surface or in the coppice layer during the dry season. At that time, abundant leaf fall takes place in the upper tree sublayer and unfavorable conditions arise. The situation changes with the onset of the rainy season and activity of many dendrobionts may be shifted to the crowns. Thus, under the conditions of the study area the seasonal dynamics of different species complexes may considerably affect their observed diversity.

To assess the species diversity during the rainy season, a complete inventory of ant nests was carried out in August 2008 within the entire areas of model plots 2 and 4 subdivided into squares 1 × 1 m. As a result, 255 nests of 32 species were found in plot 2 and a total of 38 species were recorded during mapping; inventory of plot 4 revealed 324 nests of 46 species, with the total species diversity of 56 species. It is essential

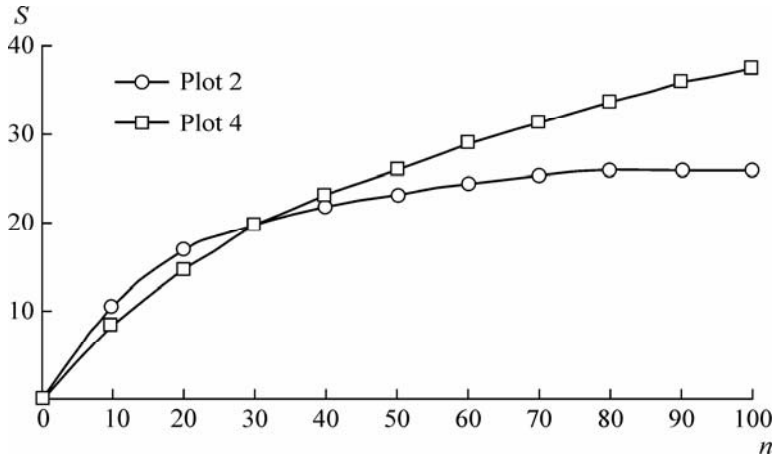

Fig. 3. Cumulative curves of the number of ant species according to the results of nest inventory in two model plots in the middle of rainy season. *S* is species diversity (not counting mass species), *n* is the number of 1 × 1 m squares examined.

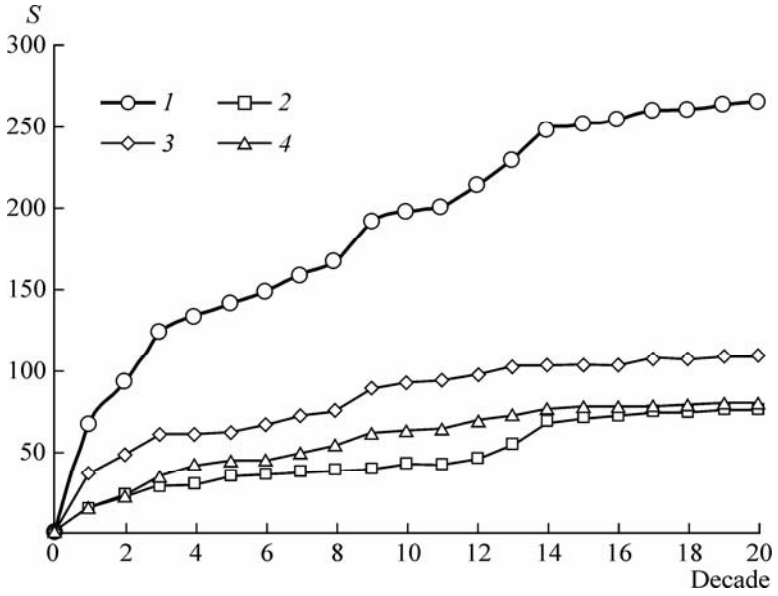

Fig. 4. Cumulative curves of the number of ant species found in Nam Cat Tien in 2007–2008 (*S*), by decades: total number (*1*), geo- and stratobionts (*2*), herpetobionts and legionaries (*3*), and dendrobionts (*4*).

that more than a half of all the nests (sections) belonged to only 3 species. On plot 2 these were *Nylanderia picta*, *O. transversa*, and *L.* cf. *birmanus*, and on plot 4, the first two species and *Hypoponera* sp. 1. Species with low settlement density (1–2 nests per plot with comparatively small colonies) comprised 35–45% of the species composition of these associations. The chances of their discovery would strongly depend on the sample volume. As can be seen from Fig. 3, the sample volume might be smaller for the ant association in plot 2, but even in this case no less than a third of the plot would need to be carefully examined to reveal 75% of rare species. During the dry season a larger sample would be required to reveal a similar fraction of species.

In the low and medium mountain forests of Northern Vietnam, it was possible to collect 150–200 ant species in 10–20 days (Eguchi et al., 2004). Since our work began in the middle of the dry season in peripheral forests, a similar number of species was recorded within 60 days. Analysis of the cumulative curves (Fig. 4) reveals at least 2 key stages. The first stage (between the 8th and 10th decades), the beginning of the work in the central part of the National Park, coincided with the end of the dry period. The growth of the species number during that period was determined by finding new herpeto- and dendrobionts in the new territory examined. The second stage (11–14th decades) coincided with the middle of the rainy season and was characterized by the prevalent growth of the

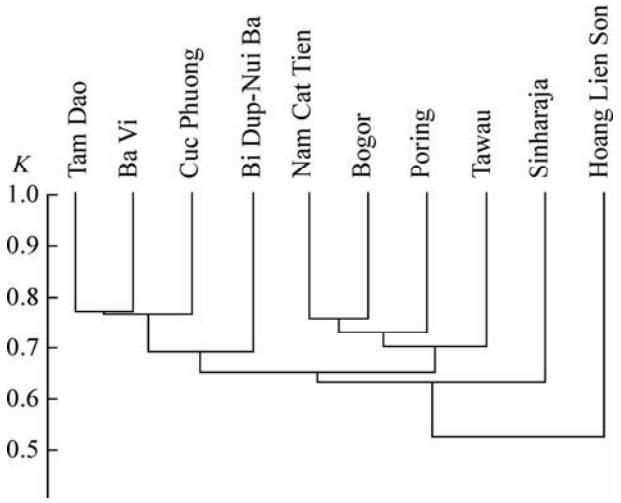

Fig. 5. Comparison of structure of local ant faunas of ants of the Oriental Region. *C* is the Czekanowski–Sørensen coefficient.

number of geo- and stratobionts revealed, intensive collections having been carried out in dipterocarp forests in the hills. As a result, the relative abundance of biomorphs reached the final proportion characterizing the local ant fauna in the study area, and the cumulative curves flattened out. Thus, two factors are important for revealing the complete species diversity of ants: coverage of the territory, including primary forests, and seasonality. The first factor appears to be more significant as regards herpetobionts and dendrobionts, and the second one, as regards the geo- and stratobionts.

Comparison of the Local ant Faunas of the Oriental Region

According to the accepted zoogeographical division of the Oriental Region (Ogata, 2005), the localities chosen for comparison are situated in three subregions. Hoang Lien Son, Cuc Phuong, Ba Vi, Tam Dao, Bi Dup-Nui Ba, and Nam Cat Tien lie in the Indochinese Subregion; Poring, Tawau, and Bogor, in the Indo-Malayan Subregion; Sinharaja, in the Ceylon Subregion. However, comparison of the structure of ant faunas shows distinct differences between localities of the Indochinese Subregion (Fig. 5).

Among them, Hoang Lien Son, located in the mountains of Northern Vietnam at 1100–2200 m above sea level, distinctly stands out. A considerable fraction of its ant fauna is constituted by species of the genera *Myrmica* Latr. and *Aphaenogaster* Mayr (Table 4). They should be supplemented by the Holarctic genus *Lasius* F. which was not found in other localities. According to the latest views (Radchenko and Elmes, 2009), the most ancient species of *Myrmica* are distributed in the Himalayas, South and Southeast Asia, but there they inhabit only mountain forests and

Table 4. Fractions (%) of genera prevailing in the number of species in local ant faunas of the Oriental Region

Genus	Localities									
	Hoang Lien Son	Cuc Phuong	Tam Dao	Ba Vi	Bi Dup-Nui Ba	Nam Cat Tien	Poring	Tawau	Bogor	Sinharaja
Pheidole	13.8	6.9	11.3	13.9	6.8	7.7	5.2	10.9	6.5	11.3
Camponotus	8.0	6.9	6.0	6.6	8.1	7.7	11.6	3.5	6.0	5.2
Polyrhachis	1.1	5.6	6.0	2.0	9.5	11.4	6.5	9.1	11.6	5.2
Tetramorium	4.6	5.6	3.3	6.0	4.1	3.7	4.9	4.3	4.7	11.3
Leptogenys	5.7	6.9	4.0	5.3	8.1	6.3	2.3	3.0	2.8	4.1
Pachycondyla	6.9	4.4	4.6	4.6	5.4	2.9	3.1	3.5	3.3	2.6
Crematogaster	3.4	1.9	4.6	1.3	2.7	4.8	5.4	3.0	2.8	4.6
Hypoponera	1.1	3.1	1.3	2.0	2.7	1.8	3.7	6.1	3.7	2.6
Cerapachys	1.1	1.3	1.3	3.3	4.1	3.3	2.3	0.9	1.9	7.7
Dolichoderus	–	2.5	5.3	1.3	1.4	1.8	1.8	0.9	1.9	1.0
Aphaenogaster	6.9	1.3	1.3	1.3	1.4	–	0.2	–	–	–
Myrmica	5.7	–	–	–	–	–	–	–	–	–
Total: genera	33	49	50	47	36	67	75	56	60	56
Total: species	87	160	151	151	74	272	649	230	215	194

meadows. Species of *Myrmica* have not been observed in Ba Vi and Tam Dao (Northern Vietnam), positioned at altitudes below 1200 m. This genus was also missing in the mountains of Southern Vietnam (Bi Dup–Nui Ba) at altitudes up to 2200 m. The separate position of Hoang Lien Son in terms of its ant fauna also results from the minimal part of the genera *Cerapachys*, *Hypoponera*, and *Polyrhachis*, which are typical of the Oriental tropical forests.

The Sinharaja rainforest reserve occupies an intermediate position between Hoang Lien Son and the rest of the localities as regards its ant fauna. The three leading genera in this case are *Pheidole*, *Tetramorium*, and *Cerapachys*. Several more genera were not found in other localities: *Aneuretus* Em., the genus of the subfamily Aneuretinae, endemic to Ceylon Subregion, and also *Forelophilus* Kut., *Rhopalothrix* Mayr, *Rogerina* Em., and *Tyrannomyrmex* Fernand.

The rest of the localities form two clusters in the similarity dendrogram. The first cluster contains the local ant faunas of Northern Vietnam which the fauna of the Da Lat Plateau adjoins; the second includes the faunas of Java, Borneo, and Nam Cat Tien. The clusters differ considerably in the number of genera (33–50 in the first cluster and 56–75 in the second). The genera *Polyrhachis*, *Crematogaster*, and *Hypoponera* have the largest shares in the localities of the Indo-Malayan Subregion; the fractions of *Anochetus*, *Carebara*, *Strumigenys*, and *Technomyrmex* are also much greater. It was previously assumed that the Da Lat Plateau might have served as a barrier preventing the ant species of plain tropical forests from expanding to the north (Eguchi et al., 2004). This hypothesis is supported by processing of ant collections from the Bi Dup-Nui Ba National Park. The ant fauna of Nam Cat Tien, situated 150 km to the southwest, already has a typical Indo-Malayan aspect. A similar picture can be observed in other groups of insects, such as Lepidoptera Rhopalocera (Monastyrskii, 2003).

CONCLUSION

When comparing the volume of local ant faunas of Oriental Region, one can notice a certain trend. The ant fauna of plain and low-mountain forests of Northern Vietnam includes 150–160 species. A similar number of species (75–90) was found in the uplands (more than 1000 m above sea level) of Northern (Hoang Lien Son) and Southern Vietnam (Bi Dup-Nui Ba). In all the local ant faunas of the Indo-Malayan Subregion the number of genera exceeds 55, the number of species, 200.

According to changes in the key species in the association, the local ant fauna of Nam Cat Tien may contain two specific faunas (see Chernov, 1975): one located near the base and the other, in the central part of the National Park. Each of them includes over 200 species. Similar values of ant species diversity were recorded at the landscape level. In the indigenous forests of the study area it is estimated at 170–180 species, and in individual types of forests (generalized biotopes) at 120–130 species. In derived forests the ant species diversity is naturally reduced to 89–100 species. At the same time, species density (the number of species per 100 m^2) at the level of model plots remains sufficiently high due to changes in the structure of the association.

Our study has shown that previous estimates of 50–60 genera (Ho and Ogata, 2002) and 250–300 species (Dlussky and Radchenko, 1990) for the whole of Vietnam are evidently underrated. The presently known ant fauna of Vietnam includes 87 genera. As for species diversity, it must exceed 500 species. A detailed analysis of ant fauna in different territories of Vietnam is hampered by a large number of unidentified species many of which may be new to science. Such species constitute 55–60% in the local ant faunas of Northern Vietnam (Eguchi et al., 2004) and about 40% in the fauna of Nam Cat Tien. It is therefore necessary to focus on the taxonomic aspect of ant studies.

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