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BIODIVERSITY OF MYRMECOPHYTES IN EASTERN INDIA

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ABSTRACT

The biologically interesting ant-plant association, myrmecophytism, occurs in tropical areas in more than 100 genera belonging to 40 plant families. These myrmecophytic species are predominantly distributed in South East Asia, especially the Malaysian region, with comparatively few species in India *Acacia cornigera, Acacia catcheu, Acacia auriculiformis, Acacia mangium, Acacia nilotica, Ipomea-pes-caprae* (Convolvulaceae), *Loranthus longifolia* (Loranthaceae), *Mangifera indica* (Anacardiaceae), *Paveta indica* (Rubiaceae), *Pterospermum sp* (Sterculiaceae), *Shorea robusta* (Dipterocarpaceae), *Citrus sp* (Rutaceae), *Manikara achras* (Sapotaceae) etc. Myrmecophytes have evolved repeatedly in plant groups those possess structures that can be used by ants with little or no modification and those plants have modified structure in which ant colonies nest. Host plant species represented two different strategies. High-reward hosts produced significantly more extrafloral nectar, food bodies, and nesting space than low-reward hosts, even when being inhabited by the same species of ant mutualist (Facultative and Obligate mutualism). High-reward hosts were more effectively defended against herbivores and exploited to a lower extent by non defending ants than low-reward hosts. Ants regularly nest in a variety of plant-derived structures but few species nest in living plants, and fewer still modify living plants for their own use as domatia. These cavities are found primarily in the stem, leaves and spine of plant. Myrmecophytism showed that the comparative morphology of the different myrmecophytes with domatia and their relatives that have varying degrees of association with ants.

KEYWORDS: Myrmecophytes, Domatia, Food bodies, extra floral nectarines (EFNs), Ants, Pollinators, Seed dispersal, Defence, Weaver ant, eastern India

INTRODUCTION

The relationships between ants and myrmecophytes are still viewed by many as unique and curious phenomena, unrelatedto mainstream evolutionary ecology. However, as argued by McKey (1988), renewed interest in these relationships is leading to the discovery of both pattern and complexity resembling that found in other ecological system. First, certain unifying principles of plant defence theory may be generalized to ant-protection mutualisms (McKey, 1984 &1988). In addition, symbiotic ant-plant relationships are likely to be products of selection based on complex networks of direct and indirect interactions, the outcome of which can be modified by variation in the physical environment (Schemske and Horvitz, 1988; Davidson and Epstein, 1989; Davidson et al., 1990). Given these parallels with other ecological systems, symbiotic ant-plant associations may have a unique role to play in elucidating the determinants of evolutionary specialization. Both myrmecophytes and plant-ants vary in their degree of specialization and this variation can be quantified explicitly by experiment, and related to present day selection environments. Myrmecophytic systems are widespread and ecologically well described, but the chemical ecology of the various interactions, among ants and plants is still poorly understood. Antsinhabiting Macarangaor Central American, Acacia myrmecophytes are generally believed to make no use of attacked arthropods or other potential prey as an additional food sources, but only discard them from the plant (Janzen

1974, Fiala & Maschwitz, 1990). There are over 100 different genera of myrmecophytes (Speight *et al.*, 2008). These plants possess structural adaptations that provide ants with food and/or shelter. These specialized structures include domatia, food bodies, and extrafloralnectaries (Speight *et al.*, 2008). In exchange for food and shelter, ants aid the myrmecophyte in pollination, seed dispersal, gathering of essential nutrients, and/or defense (*Speight et al.*, 2008). Specifically, domatia adapted to ants may be called myrmecodomatia (Wilson, 1971).

Myrmecophytes share a mutualistic relationship with ants, benefiting both the plants and ants. This association may be either facultative or obligate (Koptur, 1991). In obligate mutualisms, both of the organisms involved are interdependent; they cannot survive on their own. An example of this type of mutualism can be found in the Macaranga genus of plants. All species of this genus provide food for ants in various forms, but only the obligate species produce domatia (Speight et al., 2008). Some of the most common species of myrmecophytic Macaranga interact with ants in the Crematogaster genus. C. borneensis have been found to be completely dependent on its partner plant, not being able to survive without the provided nesting spaces and food bodies. In laboratory tests, the worker ants did not survive away from the plants, and in their natural habitat they were never found anywhere else (Fiala, Maschwitz & Pong 1991) Facultative mutualism is a type of relationship where the survival of both parties (plant and ants, in this instance), is

not dependent upon the interaction. Both organisms can survive without the other species. Facultative mutualisms most often occur in plants that have extra floralnectaries but no other specialized structures for the ants (Koptur, 1991). These non-exclusive nectaries allow a variety of animal species to interact with the plant (Koptur, 1991). Facultative relationships can also develop between nonnative plant and ant species, where co-evolution has not occurred. For example, World legumes that were introduced to North America can be protected by ants that originated from a different region (Koptur, 1991)

MATERIAL & METHODS Plant material and study sites

Selected 14 plants for study in the different area of West Bengal, India and the phenomenon have been observed by the repeated visit. The name of plant, family name, habit, habitats, place of collection has been described in the table no. 1. Simultaneously the different types of fluid, visited ants and food bodies has also been collected for chemical analysis under light microscope Leica DM 1000 with photography attachment. Selected plant material, family, habit, habitats and study area (Table: 1).

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Sl. No.	Scientific name	Family	Habitats	Habit	Place of collection /observation
1.	Acacia cornigera	Mimosaceae	Terrestrial	Tree	Belurmath, West Bengal
2.	Acacia catcheu	Mimosaceae	Terrestrial	Tree	PaschimMedinipur, West Bengal
3.	Acacia auriculiformis	Mimosaceae	Terrestrial	Tree	PurbaMedinipur, West Bengal
4.	Acacia mangium	Mimosaceae	Terrestrial	Tree	PurbaMedinipur, West Bengal
5.	Acacia nilotica	Mimosaceae	Terrestrial	Tree	PurbaMedinipur, West Bengal
6.	Citrus sp	Rutaceae	Terrestrial	Shrubs	PurbaMedinipur, West Bengal
7.	Ipomea-pes-caprae	Convolvulaceae	Mangrove	Climber	PurbaMedinipur, West Bengal
			associated		
8.	Loranthus longifolia	Loranthaceae	Terrestrial	Aerial herbs	PurbaMedinipur, West Bengal
9.	Mangifera indica	Anacardiaceae	Terrestrial	Tree	PurbaMedinipur, West Bengal
10.	Paveta indica	Rubiaceae	Terrestrial	Tree	Purulia, West Bengal
11.	Pterospermum sp	Sterculiaceae	Terrestrial	Tree	PaschimMedinipur, West Bengal
12.	Manikara achras	Sapotaceae	Terrestrial	Tree	PurbaMedinipur, West Bengal
13.	Shorea robusta	Dipterocarpaceae	Terrestrial	Tree	PaschimMedinipur, West Bengal
14.	Swetenia mahogany	Meliaceae	Terrestrial	Tree	PurbaMedinipur, West Bengal

TABLE 1: Selected plant material, family, habit, habitats and study area.

Feeding experiments

All items were presented on the rachis or blade of young, FB-producing leaves (ten replicates per type of item and shrub). Ant behaviour was observed for the following 5 min, and six different types of behaviour were distinguished: (a) not found, (b) ignored [physical contact by at least one ant, yet not removed], (c) carried [FB taken up by an ant and then carried to another part of the plant], (d) removed [actively discarded from the plant], (e) collected (carried into a domatium, *i.e.*, thorn), (f) attacked [visibly attacked by biting and stinging]. In case that several different behaviours took place [*e.g.*, resident ants first attacking an insect and then discarding the dead insect from the plant], the last defined behaviour was used for evaluation.

RESULT

Domatia are internal plant structures that appear to be specifically adapted for habitation by ants (Janzen, 1966). These cavities are found primarily in the stems, leaves, and spines of plants. Many different genera of plants offer domatia. It is shown that the relationship between the woody cross-sectional area of the solid and hollow parts of internodes is negatively allometric at the beginning of the secondary growth and nearly isometric later on. Thus, in hollow stems, the first phase of slow secondary growth compensates for the 'overconstruction' of the ring of wood during primary growth. Moreover, the cumulative production cost of a domatium estimated as the additional volume of wood required for a hollow stem compared with a solid one is very high at the beginning of secondary growth and then quickly tends to zero. Plants of the Acacia genus have some of the most widely recognized forms of domatia and offer some of the best examples of ant-plant obligate mutualism (Janzen, 1966). Different species of *Acacia* provide a variety of resources needed for their codependent counterparts. One of these resources is the need for shelter. *Acacia* have enlarged thorns on their stems that are excavated by ants for use as housing structures. Since the tree contains their nest, these aggressive ants react strongly to any disturbance of the tree, providing the myrmecophyte with defense from grazing herbivores and encroaching vines.

Domatia can also be found within the tubers of certain plants ((Jebb, 1991). Tubers form when the hypocotyls of a seedling swell to form a hollow, chambered structure that can become inhabited by ants. The Rubiaceae family ofplants Paveta indica (Fig-1) contains the most commonly known tuberous myrmecophyte, Myrmecodia, literally meaning "ant-house" (Fig. 2). The Shorearobusta (Fig. 3), Mangiferaindica (Fig. 4) are formed building up leaf domatia. The rolling pattern of leaf domatia in Pterospermum sp (Fig. 5) and the complete leaf domatiaon a hemi parasitic angiosperm (Lorenthus longifolia) in Manikara plant species (Fig-10). In the interesting, hanging like leaf domatia found in Swetenia mahogany (Fig-7). Some plants produce food bodies for use by other organisms. These small epidermal structures contain a variety of nutrients that are removed and consumed by foragers (Rico-Gray & Oliveira, 2007). Food bodies are identified by the main nutrient they contain and by the genus of plant producing them (Rico-Gray & Oliveira 2007). Early observation indicated that food bodies can have high nutritive values. Beltian bodies are found on the leaflet tips of Acacia plants and have relatively high protein content Heil et al. (2004). Beccarian bodies are found on young leaves of the Macaranga genus and are especially rich in lipids. Lipids are also the main nutrient

found in Pearl bodies, found on the leaves and stems of *Ochroma* plants. Most ant inhabitants of *Cecropia* plants harvest the last type of food body, as their primary food source. Remarkably these Müllerian bodies, found on the

stalk of the leaf, are primarily glycogen. Glycogen is the principal storage carbohydrate found in animals and is extremely rare in plants (Rico-Gray & Oliveira 2007), (Table No. -2).

TABLE 2: Nutrient content of various food bodies						
Food Bodies	Main Nutrient Contained	Plant Genus	Location on Plants			
Beltian bodies	Protein	Acacia	Leaflet tips			
Beccarian bodies	Lipids	Macaranga	Young leaves			
Pearl bodies	Lipids	Ochroma	Leaves and stems			
Müllerian bodies	Glycogen	Cecropia	Petiole of the leaf			





FIGURE 1: The leaf domatia on *Pavetaindica* in the family Rubiaceae

FIGURE 2: Ant-house in Paveta indica



FIGURE 3: The building up leaf domatia in *Shorea robusta*.



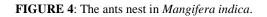




FIGURE 5: The rolling pattern of leaf domatia in *Pterospermum* sp.

The three main nutrient classes in plant-derived cellular ant rewards. Ant-acacias (also called "swollen thron"



FIGURE 6: The hemiparasitic(*Lorenthus longifolia*) leaf domatia.

acacias) occur both in Africa and in central America and apparently all *Acacia* ants live ins enlarged throns and feed

on extrafloral nectar secreted by foliar nectaries as a sources of carbohydrates and water. Each *Acacia* plant species can be inhabited by different plant species, ants of the *Pseudomyrmex ferrugineus* group and their host acacias have obviously experienced coevolution rather than strict cospeciation (Ward, 1993). The ants continiously patrol the surface of their host plant and protected it from depend on this protection and grow poorly in the absence of their ant partner. Ant-plant

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FIGURE 7: The hanging like leaf domatia in *Swetenia* mahogany



FIGURE 9: The liquid fluid exchange between two ants in *Impatiens balsamia*.

interation often is mediated by extra floral nectar (EFN) composition that may influence plant visitation by ants. Extra floral nectarines are found outside the flower structure of plants. Plants in some 300 genera produce EFN to attract ants as a means of indirect defence and are most commonly associated with vegetative structure that normally do not have nectarines, such as leaves, stems, and twings (Koptur, 1991).



FIGURE 8: The ant collected liquid from extra floral nectari gland. (Mutualistic relationship between plant & animals).



FIGURE 10: Theextrafloralnectaries on the petiole in *Ipomeapes-caprae*.



FIGURE 11: Sterozoom microscopic picture of EFN of *Cassia occidentalis*; EFN on petiole.



FIGURE 12: Sterozoom microscopic picture of EFN of Acacia catechu; EFN on middle of the leaf branching.



FIGURE 13: Sterozoom microscopic picture of EFN of *Coccina sp*; EFN on lower part of the leaf.

between owns (Fig-9). Resulting benefits for plants include pollination in the case of floral nectar and protection from herbivores through the attraction of carnivores in the case of extrafloral nectar (EFN; Koptur 1992; Heil, 2007 & 2008). EFN is usually secreted outside the flowers, and in contrast to floral nectar-it is not

Nectar is an aqueous solution of substances that mainly comprise primary metabolites such as sugars and amino acids and generally serves the attraction of mutualistic animals to the plants (Fig-8) (Baker and Baker 1975; Baker *et al.*, 1978).The ant collect liquid from the EFN gland and sometimes these ant species exchange liquid involved in pollination (Bentley, 1977; Koptur, 1992). The EFN in the species Ipomeapes-caprae belonging to the family Convolvulaceae. The plants have a pair of extra floral nectaries on the petiole of each leaf near the point of blade attachment, which produce nectar (Fig. 10). Red nectaries at the base of young leaves have been found to produce more nectar and attract ants and other visitors. The EFNs of I. pes-caprae were found to be visited by many foraging ants as well as many non ant visitors like beetles wasps, jumping spiders and flies. Ants visited the EFNs of I. pes-caprae on a round the clock basis patrolling the upper and the lower leaf surface and stem (Mondal et al. and Chakraborty, 2013). Also found EFNs in different plant species outside the flower, some examples of sterozoom microscopic picture of EFN of (a) Cassia occidentalis; EFN on petiole (b) Acacia catechu;



FIGURE 14: Sterozoom microscopic picture of EFN of Passiflora vitifelia; pair of EFN on petiole.



FIGURE 16: Ants defense the herbivores activity in Cassia



FIGURE 18: The workers ant construct nest by weaving together leaves and flower in *Manikara sp.*

Myrmecochory, literally translated as "ant-dispersal," is the collection and dispersal of seeds by ants. Ants disperse more than 30% of the spring-flowering herbaceous plants EFN on middle of the leaf branching (c) *Coccina sp*; EFN on lower part of the leaf (d) *Passiflora vitifelia* ; pair of EFN on petiole (e) *Ipomea cornia* ; secretion the liquid from EFN on two sides of the petiole. (Fig - 11, 12, 13, 14, 15)

The effectiveness of ants as pollinators was analyzed by assessing (1) their quantitative importance at flowers; (2) there effect on host plant seed production; (3) their effect on the performance of the host plant progeny, estimated as seed germination, seedling emergence, seedling survival to flowering. The ant species producing significantly more seeds than flowers visited by only winged insects did not differ from self-pollination. Ant-pollinated flowers produced seeds with a germination rate comparable to the other treatments. Moreover, seedlings from these seeds emerged as fast, and survived at the same rate as controls.



FIGURE 15: Sterozoom microscopic picture of EFN of *Ipomea cornia*; secretion the liquid from EFN on two sides of the petiole.



FIGURE 17: The workers ants produced the nest using larval silk in *Citrus sp.*



FIGURE 19: Ants feeding the storage food inside the leaf domatia.

in eastern North America (Rico-Gray & Oliveira, 2007). Both the plant and the ant benefit in this scenario. The ants are provided with an elaiosome, a detachable food body found on the surface of the seed. Myrmecochorous plant seeds have nutrient rich appendages, elaiosomes, which induce some ant species to carry the seeds back to their nest where the elaiosome is consumed and the seed is discarded unharmed. The benefits to plants of dispersal of their seeds in this way have been well documented, but the benefits to the ants from consuming the elaiosomes have rarely been measured and are less clear.

Myrmecotrophy, meaning "ant-fed," is the ability of plants to absorb nutrients from debris piles left by ant nests or, in the case of Nepenthes bicalcarata, from ant egesta (Bazile et al. 2012). The tropical tree Cecropiapeltata obtains 98% of its nitrogen from the waste deposited by its ant counterparts (Benzing, 1991). Since plants provide essential resources for ants, the need to protect the plant and those resources is extremely important. Many myrmecophytes are defended from both herbivores (Fig-16) and other competing plants by their ant counterparts (Rico-Gray & Oliveira, 2007) Acacia cornigera, for example, is thoroughly guarded by its obligate ant partner, Pseudomyrmex ferruginea. A single colony of P. ferruginea may contain more than 30,000 ants, and can tend multiple Acacia trees (Rico-Gray & Oliveira, 2007). The soldier ants are extremely aggressive, patrolling the trees twenty-four hours a day. Any disturbance to the tree alerts ants, who then recruit more workers from inside the horn domatia. These ants defend the Acacia by biting, violently stinging, and pruning any trespassers. The ants keep the plant free from other insects and vertebrate herbivores, but also from invading fungi and other plants (Rico-Gray & Oliveira, 2007).

Weaver ants or Green ants (genus Oecophylla) are eusocial insects of the family Formicidae (order Hymenoptera). Weaver ants are obligately arboreal and are known for their unique nest building behaviour where workers construct nests by weaving together leaves using larval silk (Fig. 17,18). Colonies can be extremely large consisting of more than a hundred nests spanning numerous trees and contain more than half a million workers. Like many other ant species, weaver ants prey on small insects and supplement their diet with carbohydraterich honeydew excreted by small insects (Hemiptera). Oecophylla workers exhibit a clear bimodal size distribution, with almost no overlap between the size of the minor and major workers. The major workers are approximately eight to ten millimeters in length and the minors approximately half the length of the majors. There is a division of labour associated with the size difference between workers. Major workers forage, defend, maintain, expand the colony whereas and storage the food for future inside the leave domatia (Fig-19). Minor workers tend to stay within the nests where they care for the brood and 'milk' scale insects in or close to the nests. Oecophylla weaver ants vary in color from reddish to yellowish brown dependent on the species.

CONCLUSION

Food bodies and extrafloral nectar are the only plantderived food sources of ants resident inmyrmecophytes. These ants apparently do not make use of external food sources. Physiological constraints appear to affect FB construction and composition of the different species investigated in the present study. However, most aspects

of FB composition, as well as the similarities and dissimilarities with the composition of FBs, could most posibly be explained as adaptations to the FBs' functional role as important ant food. The both types of host strategies coexist because of variable net outcomes of different investment-payoff regimes and that the effects of exploiters on the outcome of mutualisms can, thus, increase the diversity within the taxa involved. So, Plant mutualistic relationships with animals are very important as they play a vital role in ecological system; both benefit by increasing their reproductive output. Human-induced changes are killing off species of plant and animals, depleting the earth's biodiversity. And as we have seen, all organisms are linked to one another in more ways than one. So, loss of a species sets off a chain reaction. This type of study should be needed for sustainable biodiversity conservation. Life did not take over the planet by combat but by networking.

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REFERENCES

Bazile, V., Moran, J.A., Moguédec, G. Le, Marshall, D.J., Gaume, L. (2012) A carnivorous plant fed by its ant symbiont: a unique multi-faceted nutritional mutualism". *PLoS ONE* 7 (5) 36179.

Beattie, Andrew J., Hughes, Lesley (2002) Ant-plant interactions. In Pellmyr, Olle. *Plant-Animal Interactions*. Malden, MA: Blackwell Publishing 211–235.

Benzing, David H. (1991)Myrmecotrophy: origins, operation, and importance. In Huxley, Camilla R.; Cutler, David F. *Ant-Plant Interactions*. New York, NY: Oxford University Press. pp. 353–373. ISBN 0-19-854639-4

Davidson, D.W., McKey, D. (1993) The evolutionary ecology of symbiotic ant-plant relationships. J Hym Res 2: 13-83

Fiala, Brigitte, Maschwitz, Ulrich, Pong, Tho Yow (1991) The association between *Macaranga* trees and ants in South-east Asia.In Huxley, Camilla R., Cutler, David F. *Ant-Plant Interactions*. New York, NY: Oxford University Press. pp. 263–270. ISBN 0-19-854639-4.

Gonzalez-Teuber, Marcia, M. Heil (April 2009) The Role of Extrafloral Nectar Amino Acids for the Preferences of Facultative and Obligate Ant Mutualists. *Journal of Chemical Ecology* 35 (4): 459–468.

Gonzalez-Teuber, M., Heil, M. (2009) The Role of Extrafloral Nectar Amino Acids for the Preferences of Facultative and Obligate Ant Mutualists. *Journal of Chemical Ecology* 35: 459–468.

Heil, M.B. Baumann, R. Kruger, K.E. Linsenmair (2004) Main nutrient compounds in food bodies of Mexican Acacia ant-plants. *Chemoecology* 14 (1): 45–52.

Heil, M., Rattke, J., Boland W. (April 2005). *Science* 308 (5721): 560–563

Heil, M., Baumann, B., Kruger, R., Linsenmair, K.E. (2004) Main nutrient compounds in food bodies of Mexican Acacia ant-plants. *Chemoecology* 14: 45–52.

Heil, M., Rattke, J., Boland, W. (2005) Postsecretory hydrolysis of nectar sucrose and specialization in ant/plant mutualism.*Science* 308: 560–563.

Janzen, D.H. (1966) Coevolution of mutualism between ants and acacias in Central America.*Evolution* 20: 249–275.

Jebb, Matthew (1991) Cavity structure and function in the tuberous Rubiaceae. In Huxley, Camilla R., Cutler, David F. *Ant-Plant Interactions*. New York, NY: Oxford University Press. pp. 374–389. ISBN 0-19-854639-4.

Jose M. Gomez (2000) Effectiveness of ants as pollinators of *Lobularia maritime*: effects on main sequential fitness components of the host plant. Springer-Verlag 122: 90-97.

Jose, M. Gomez Regino Zamora Jose A. Hodar Daniel Garcia (1996) Experimental study of pollination by ants in Mediterranean high mountain and arid habitats. Springer-Verlag105: 236-242.

Koptur, Suzanne (1991) Extrafloral nectarines of herbs and trees: modeling the interaction with ants and parasitoids. In Huxley, Camilla R., Cutler, David F. *Ant-Plant Interactions*. New York, NY: Oxford University Press. pp. 213–230. ISBN 0-19-854639-4.

Martin Heil, Birgit Baumann, Ralf Kruger and Eduard Linsenmair, K. (2004) Main nutrient compounds in food bodies of Mexican *Acaia*ant plants. Chemoecology 14:45-52

Mondal A.K. (Parui) M. S. Chakrabotry, T. (2013) Ant foraging on extrafloralnectaries (EFNs) of *Ipomeapes-caprae* (Convolvulaceae) in the dune vegetation: Ants as potential antiherbivore agents. Indian Journal of Geo-Marine Sciences, 42(1) 67-74.

Peakall Rod, Handel, Steven N., Beattie, Andrew J. (1991) The evidence for and importance of ant pollination.In Huxley, Camilla R., Cutler, David F. *Ant-Plant Interactions*. New York, NY: Oxford University Press. pp. 421–429. ISBN 0-19-854639-4.

Rico-Gray, Victor Oliveira, Paulo, S. (2007) *The Ecology and Evolution of Ant-Plant Interactions*. Chicago, IL: University of Chicago Press. pp. 42–51, 101–109.

Speight, Martin, R., Hunter, Mark D., Watt, Allan D. (2008) *Ecology of Insects* (2nd ed.). West Sussex, UK: Wiley Blackwell Publications. pp. 212–216.