Oecologia (2005) 145: 76–86
DOI 10.1007/s00442-005-0107-3

PLANT ANIMAL INTERACTIONS

Laurence Gaume · Merry Zacharias
Vladimir Grosbois · Renee M. Borges

The fitness consequences of bearing domatia and having the right ant partner: experiments with protective and non-protective ants in a semi-myrmecophyte

Received: 7 October 2004 / Accepted: 15 March 2005 / Published online: 20 May 2005

Abstract The fitness advantage provided by caulinary domatia to myrmecophytes has never been directly demonstrated because most myrmecophytic species do not present any individual variation in the presence of domatia and the removal of domatia from entire plants is a destructive process. The semi-myrmecophytic tree, *Humboldtia brunonis* (Fabaceae: Caesalpinioideae), is an ideal species to investigate the selective advantage conferred by domatia because within the same population, some plants are devoid of domatia while others bear them. Several ant species patrol the plant for extra-floral nectar. Fruit production was found to be enhanced in domatia-bearing trees compared to trees devoid of domatia independent of the ant associate. However, this domatium effect was most conspicuous for trees associated with the populous and nomadic ant, *Technomyrmex albipes*. This species is a frequent associate of *H. brunonis*, inhabiting its domatia or building carton nests on it. Ant exclusion experiments revealed that *T. albipes* was the only ant to provide efficient anti-herbivore protection to the leaves of its host tree. Measures of ant activity as well as experiments using caterpillars revealed that the higher efficiency of *T. albipes* was due to its greater patrolling density and consequent shorter lag time in attacking the larvae. *T. albipes* also provided efficient anti-herbivore protection to flowers since fruit initiation was greater on ant-patrolled inflorescences than on those from which ants were excluded. We therefore demonstrated that caulinary domatia provide a selective advantage to their host-plant and that biotic defence is potentially the main fitness benefit mediated by domatia. However, it is not the sole advantage. The general positive effect of domatia on fruit set in this ant–plant could reflect other benefits conferred by domatia-inhabitants, which are not restricted to ants in this myrmecophyte, but comprise a large diversity of other invertebrates. Our results indicate that mutualisms enhance the evolution of myrmecophytism.

Keywords Myrmecophyte · Ant–plant mutualism · Biotic defence · Plant reproductive fitness · *Humboldtia brunonis* · *Technomyrmex albipes*

Introduction

Myrmecophytism is taxonomically widespread, having evolved almost exclusively in tropical areas in more than 100 genera (Heil and McKey 2003). Myrmecophytes are plants, which possess specialised structures, called (myrmeco)domatia, that facilitate ant nesting (Wheeler 1942; Beattie 1985) and thereby promote ant fidelity. Most myrmecophytes also feed ants through extrafloral nectaries, food bodies, or indirectly via honeydew of sap-sucking homopteran trophobionts (Davidson and McKey 1993; Heil and McKey 2003). Myrmecophytes are involved in a suite of relationships with ants ranging from parasitism (Yu and Pierce 1998; Gaume and McKey 1999; Izzo and Vasconcelos 2002; Gaume et al. 2005), conditional mutualism (Gaume et al. 1998; Gaume and McKey 2002; Trimble and Sagers 2004) to obligate mutualism (reviewed by Heil and McKey 2003). In mutualistic relationships, ants offer to myrmecophytes efficient protection against herbivores (e.g. Janzen 1967; Fiala et al. 1994; Gaume et al. 1997), fungi

Communicated by Christian Koerner

L. Gaume (✉)
Botanique et bioinformatique de l'architecture des plantes,
UMR CNRS 5120, TA 40/PS 2, Boulevard de la Lironde,
34398 Montpellier cedex 5, France
E-mail: lgaume@cirad.fr
Fax: +33-4-67615668

M. Zacharias · R. M. Borges
Centre for Ecological Sciences,
Indian Institute of Science, Bangalore 560 012, India
E-mail: renee@ces.iisc.ernet.in

V. Grosbois
Department of Biometry, CEFE-CNRS,
1919 route de Mende, 34293 Montpellier cedex 5, France

(e.g. Letourneau 1998), or competing plants (e.g. Janzen 1969; Morawetz et al. 1992), or supply them with nutrients (e.g. Sagers et al. 2000; Fischer et al. 2003). Protection mutualisms in ant–plant systems vary in degree of specialisation, being often conditional in multispecies or opportunistic systems and stronger in species-specific ones (McKey et al. 2005). Spatial or temporal heterogeneity easily explains conditional mutualisms (Thompson and Cunningham 2002; Nuismer et al. 2003) as well as species co-existence in ant–plant systems (Yu et al. 2001; Palmer et al. 2003).

While the selective advantage provided by domatia to their host-plant has been shown in other plant–arthropod systems (Agrawal and Karban 1997; Agrawal et al. 2000; Romero and Benson 2004), in ant–plant systems, this is only assumed (Fiala and Maschwitz 1992). Intrageneric comparisons of species presenting different degrees of myrmecophytism have offered indirect evidence that domatia provide a selective advantage to myrmecophytes (Fiala et al. 1994; Gaume 1998; Fiala et al. 1999; McKey 2000). However, selective pressures such as herbivory might differ between species. In addition, several studies, focused on ant-exclusion experiments, have shown the effect of ant presence on the fitness parameters of myrmecophytes (reviewed by Davidson and McKey 1993). But, although domatia mediate ant presence, the ant effect on domatia-bearing plants would not mimic a domatia effect. Indeed, while the benefit conferred by domatia to the plant is certainly linked to the ants, the cost to the plant of bearing domatia is not taken into account in the ant exclusion analyses although this cost might influence the fitness of the plant.

Therefore, the best way to show a fitness effect of domatia would be to compare fitness parameters of individuals with and without domatia within the same species. Such a comparison has never been made for two main reasons. Firstly, domatia removal is too destructive, particularly for myrmecophytes with caulinary domatia. Secondly, intra-population variation in domatia presence/absence is unusual. Ordinarily, domatia are expressed even without ant presence and are found to be inherited structures (Beattie 1985). It is only in the ant–plant *Vochysia vismiaefolia* that domatia were reported to be induced by ants (Blüthgen and Wesenberg 2001). Besides this case and other cases where domatia onset is dependent on plant ontogeny (Brouat and McKey 2000, 2001), in a population of a given myrmecophyte, all plants bear domatia. However, this is not true for the ant–plant *Humboldtia brunonis* (Caesalpinioideae) found in the tropical forest of southern India, which is polymorphic for the presence–absence of domatia.

The non-specialised ant–plant *H. brunonis*, therefore, offers the opportunity to test for the selective advantage associated with domatia and to better understand the selective pressures leading to the origin of myrmecophytism. Besides other invertebrates (Rickson et al. 2003), *H. brunonis* is also associated with several ant species, which differ in their population dynamics and degree of symbiosis, leading to spatial and temporal heterogeneity in this ant–plant system (Gaume et al. 2005). Among these ants, *Crematogaster dohrni* and the tramp ant *Technomyrmex albipes* are the most common associates of *H. brunonis*. The present study has two main goals. The first one is to test whether domatia provide a selective advantage to *H. brunonis* by comparing the fruit set of trees with and without domatia growing in the same habitat. The second one is to test whether the selective advantage associated with domatia might vary with the ant occupant and to investigate the exact nature of the benefit mediated by domatia. We will experimentally investigate whether the main benefit of domatia could result largely from anti-herbivore protection conferred by ants. We will focus on the very populous ant colonies of *T. albipes* . The fitness effect of *T. albipes* on *H. brunonis* will be compared to that of the other ant associates and discussed at the meta-population scale. The ultimate purpose is to test whether the mutualistic nature of the ant–plant relationship is a necessary condition for myrmecophytism to spread.

Material and methods

Studied species

Humboldtia brunonis Wall. (Fabaceae: Caesalpinioideae) is an endemic understorey tree of the southern Western Ghats of India (Ramesh and Pascal 1997). The genus *Humboldtia* includes six species, three of which are myrmecophytes, possessing swollen internodes that form caulinary domatia and harbour ants. Compared to *H. laurifolia* Vahl, a true myrmecophyte in which all trees bear domatia (Krombein et al. 1999), *H. brunonis* is polymorphic for the presence of domatia. In the same population, some trees possess domatia, while others do not. Beside this, they do not differ in any other aspects. *H. brunonis* can thus be considered as a "semi-myrmecophyte". Saplings smaller than 1 m in height very rarely bear domatia (6 out of 296 were found to bear domatia). The domatia are swollen internodes (up to ca. 10 cm long, 1 cm wide) with excavated pith and self-opening entrance holes located opposite the point of leaf insertion. Domatia on *H. brunonis* are less abundant than on *H. laurifolia* and are not systematic: some branches of domatia-bearing trees can bear both inflated (up to five consecutive domatia) and non-inflated internodes. A large diversity of microfauna, including a number of ant species, inhabit the domatia of *H. brunonis* (Rickson et al. 2003). Most of the ant colonies that inhabit domatia are opportunistic species that, in addition to other non-nesting species, feed at the extrafloral nectaries (EFNs) found on the abaxial surfaces of leaflets (leaves are paripinnate and comprise four leaflets), on stipules and flower bracts. Nectaries are active only during the growth phase of the plant parts bearing them.

Technomyrmex albipes Smith (Formicinae: Dolichoderinae) is, with *C. dohrni* Mayr (Myrmicinae), one of the two major EFN-foragers and domatia inhabitants of *H. brunonis* (Gaume et al. 2005). Its colonies are patchily distributed in *H. brunonis* populations (Shenoy 2003). It is known to have a nomadic way of life coupled with extremely populous, polydomous and secondarily polygynous colonies (Yamauchi et al. 1991). Members of a single colony may nest on both domatia and non-domatia-bearing trees, because they can spread from tree to tree and they construct carton nests on the plant as well as under the plant's stipules. They competitively exclude any other ants from the tree they occupy (Gaume et al. 2005). The other EFN—visiting ants are the castration parasite *C. dohrni* (a nesting species, workers of which more often patrol inflorescence buds than young leaves and could also damage the flower buds) and other resident or non-resident ant species, which often co-occur on the same trees (Gaume et al. 2005). Except perhaps the minute ant *Vombisidris humboldticola* (Zacharias and Rajan 2004), none of the ants are specialist plant–ants and none are specifically associated with *H. brunonis*.

We studied the plant in March–April 1999 in Makut Reserve Forest, Coorg District, Karnataka State, in the Western Ghats (lat. 12°05N, longitude 75°44E, altitude 180 m, wet evergreen forest with an average rainfall of 5,000 mm and a dry season of 4–5 months). As most of the trees that fruited were in sunny habitats (along trails), we studied in such open areas 104 trees whose height was greater than or equal to 1 m.

Effect of presence of domatia and ant identity on the total fruit production of trees

We estimated tree height using a calibrated 3-m stick and counted the total number of fruits on the 104 trees. For each tree, we also noted presence/absence of domatia and the identity of ants observed patrolling both young leaves and inflorescences buds. Thirty-six of these trees were patrolled exclusively by *T. albipes* and 68 by other ants; most of the time, several species per tree (43 trees mostly but not exclusively by *C. dohrni*, a domatia-inhabitant, and 25 trees by ants other than *C. dohrni* and *T. albipes*). The other EFN-foraging ants were mostly opportunistic species found sporadically on EFNs: *Camponotus confucii, C. infuscus, C. angusticollis, Polyrhachis* sp., *Oecophylla smaragdina, Tapinoma melanocephalum*. Others were also nesting inside domatia: *C. wroughtonii, Cataulacus taprobanae, Monomorium monomorium, V. humboldticola* . The minute ant *V. humboldticola* was the only species to be both symbiotically and specifically associated with *Humboldtia*.

We first performed two logistic regressions in order to test whether both presence/absence of domatia and identity of ant occupant (*T. albipes*/others) were dependant on tree height.

We then performed two Poisson regressions in order to test for the effect of tree height (continuous covariate), of domatia presence/absence (categorical covariate) and of ant identity (categorical covariate) on the number of fruits produced. All the second order interactions and the third order interaction were included in the departure model. The first Poisson regression was conducted on the full data set, considering two categories for the ant identity covariate: *T. albipes* versus all other ants. The second regression was conducted on the data subset corresponding to trees patrolled by ants other than *T. albipes*. This second model aimed at testing whether the castrating ants *C. dorhni* have a different impact on fruit production compared to ants other than *C. dohrni* and *T. albipes*, and at measuring the magnitude of the hypothetical domatia effect for these categories of trees.

Ant-exclusion experiments and comparative effects of *T. albipes* versus all other ants on young leaf herbivory

On each of 20 randomly chosen trees, we selected two intact small young leaves (leaflets of ça. 4 cm length). One was left intact and served as control. At the base of the other one, we applied Tanglefoot glue to exclude ants. We previously recorded the identity of the ants patrolling the leaves of each tree. Five trees were occupied by *T. albipes* colonies, which actively patrolled their young leaves. Young leaves of the 15 other trees were occasionally patrolled by one or several ant species, including *C. dohrni* (eight trees), *C. confucii* (six trees), *M. monomorium* (three trees), *C. taprobanae* (two trees), *C. angusticollis* (two trees) and *T. melanocephalum* (one tree). Among these ants, only *C. dohrni, C. taprobanae* and *M. monomorium* were found nesting in *H. brunonis* domatia, while the others were non-resident ants attracted by the plant's EFN. Ten days later, we scored, for each of the four leaflets of each leaf, herbivory as 0 (intact) or 1 (damaged). We could thus calculate for each leaf the number of leaflets (out of a constant total of four) damaged by herbivores and analysed both the effects of ant-exclusion treatment and ant identity on herbivory using a Poisson regression.

Activity of ants, herbivores and nectar production on young leaves over a 24-h cycle

Rhythms of EFN production and of insect activity on young leaves were recorded concurrently during a 24-h period beginning at 1100 h. On each of the twelve randomly chosen trees, we selected two young leaves of similar size. At the base of one young leaf, we applied Tanglefoot glue in order to exclude ants, and counted the total number of nectaries. Nectar droplets were wiped off every 2 h, after counting the total number of EFN droplets produced. On the other young leaf, we recorded the number of ants every 2 h. The number of herbivorous insects were counted every 2 h on both leaves. Three leaves (trees) were patrolled by *T. albipes* while the other nine leaves (trees) were patrolled by other ant species sometimes several on the same tree. Those ants included diurnal species such as *C. taprobanae* ($n = 1$ leaf), *C. confucii* ($n = 1$), nocto-diurnal species such as *C. dohrni* ($n = 4$), and nocturnal ones such as *C. infuscus* ($n = 2$) and *C. angusticollis* ($n = 3$). We performed a Poisson regression in order to examine how ant activity (ant number) on young leaves varies with ant identity (*T. albipes*/other ants pooled together). In order to account for any systematic circadian pattern of variation in ant activity, we included in the departure model a linear and a quadratic effect of the continuous covariate time of day (denoted as t, and taking values ranging from 1 to 12 indicating the position of the record in the sequence of 12 observations undertaken in the course of the 24 h cycle starting at 1100 h). In this starting model, we also included the effect of the continuous covariate ant number$_{t\text{-}1}$ ($\log[x + 1]$-transformed to fit with the log-link function) on ant number$_t$ in order to factor out any temporal autocorrelation remaining after systematic circadian variation has been accounted for. We also included the interactions ant × t, ant × t^2 and ant number$_{t\text{-}1}$ × ant.

Behavioural reaction of *T. albipes* to caterpillars deposited on young leaves and inflorescence buds

Fifteen trees patrolled by *T. albipes* were selected. Two young leaves per tree were chosen and one distal leaflet of each of these was selected for herbivore–plant experiments. Ant density on the leaflet was estimated as the "number of ants/length of the focal leaflet". We deposited a caterpillar (length < 2 cm) freshly collected from other *H. brunonis* trees on the abaxial surface of the experimental leaflet. The caterpillars belonged to the Noctuidae and Geometridae and were frequently found eating young leaves or flowering buds of *H. brunonis*. The behaviour of the ants was then observed for 10 min (time sufficient for ants to find the larva). We noted the time elapsed until the first ant-caterpillar contact as well as the ant reaction towards the larva. Using GLM, we examined how the time to discovery of the larva was related to tree identity and to ant density on the leaf (with $\log[x + 1]$-transformation of the variable "ant density"). We then investigated the relationship between ant density and leaflet length (with log-transformation of the variable "leaflet length"). For comparison, a similar experiment using caterpillars was then carried out on a total of 36 inflorescence buds (IBs: inflorescences whose flowers are still in the bud stage) chosen from 12 other *Technomyrmex* patrolled-trees (three inflorescences per tree).

Effect of *Technomyrmex* exclusion from inflorescences on fruit initiation

We chose 16 pairs of intact IBs of comparable size (ça. 2.5 cm long) on 16 trees patrolled by *T. albipes*. For each pair, one IB was left intact with patrolling *Technomyrmex* workers, whereas ants were excluded from the other by Tanglefoot. After 10 days, we recorded the number of fruits initiated (assessed by a clear swelling of the basal portion of the style) on both ant-patrolled and ant-excluded inflorescences. To control for any abortion of initiated fruits, we recorded the number of fruits produced on each IB 8 days later. We compared the number of fruits initiated and the number of matured fruits on ant-patrolled and ant-free inflorescences, using the Wilcoxon test for paired samples.

Statistical analyses were carried out using the software package SAS v.6.2, taking into account errors of type 3 for the general linear models. The logistic and Poisson regressions were carried out using procedure GENMOD. For these two types of regressions, the test statistics were corrected for over-dispersion when necessary using as an over-dispersion parameter the square root of the ratio of Pearson χ^2 over the residual number of degrees of freedom, which will thereafter be referred to as $\hat{c}$. A $\hat{c}$ close to one indicates that the model adequately fits the data whereas a $\hat{c}$ substantially greater than one indicates over-dispersion. As a rule of thumb, we applied the over-dispersion parameter when $\hat{c}$ exceeded 1.2. For model selection, backward procedures were adopted starting with the removal of the non-significant highest order interactions.

Results

No effect of tree height on the presence of domatia and of *Technomyrmex* ants

From analysis of the 104 studied trees (1 m $<$ height $<$ 12 m), domatia presence on trees appears to be independent of their height (Logistic regression, no over-dispersion: $\hat{c} = 1.02$; effect of height: $\chi^2 = 0.21$, $df = 1$, $P = 0.65$). Therefore, larger trees are not more likely to bear domatia. Larger trees are also not more likely to harbour *T. albipes* (Logistic regression, no over-dispersion: $\hat{c} = 1.02$; effect of height on ant identity: $\chi^2 = 0.84$, $df = 1$, $P = 0.36$).

Effect of tree height, presence of domatia and ant identity on fruit production

Fruit production significantly increased with tree height. There was a global and highly significant effect of domatia presence as well as of ant identity on fruit production (Poisson regression on the full data set [$n = 104$], Table 1). Fruit production was highest for trees occupied exclusively by *T. albipes*, and the positive effect of domatia presence on fruit production was most conspicuous for this group (Fig. 1 drawn from the estimates obtained from the common slope but different intercepts given by the Poisson regression model presented in Table 1). There was no significant

Table 1 Poisson regression models testing for the effect of tree height, domatia (presence vs. absence) and ant identity on the number of fruits produced. The tests are corrected for over-dispersion (respectively $\hat{c} = 2.42$ and $\hat{c} = 2.26$), therefore F instead of χ^2 values are provided

Covariate	*ndf*	*ddf*	*F*	*P*	Estimate	SE
Poisson regression on the full data set						
Height	1	100	46.32	0.0001		
Ant (*T. albipes* vs. all others)	1	100	28.65	0.0001		
Domatia	1	100	18.13	0.0001		
Parameter						
Common slope for the height effect					0.25	0.04
Intercept for domatia = 1, ant = *T. albipes*					0.98	0.35
Intercept increment for domatia = 0					−0.85	0.20
Intercept increment for ant = all others					−1.07	0.20
Poisson regression on the data subset corresponding to trees associated with ants other than *T. albipes*						
Height	1	64	14.14	0.0004		
Ant (*C. dohrni* vs. other ants)	1	64	0.15	0.6968		
Domatia	1	64	3.18	0.0744		
Parameter						
Common slope for the height effect					0.21	0.06
Intercept for domatia = 1, ant = others					0.21	0.58
Intercept increment for domatia = 0					−0.56	0.31
Intercept increment for ant = *C. dohrni*					−0.13	0.32

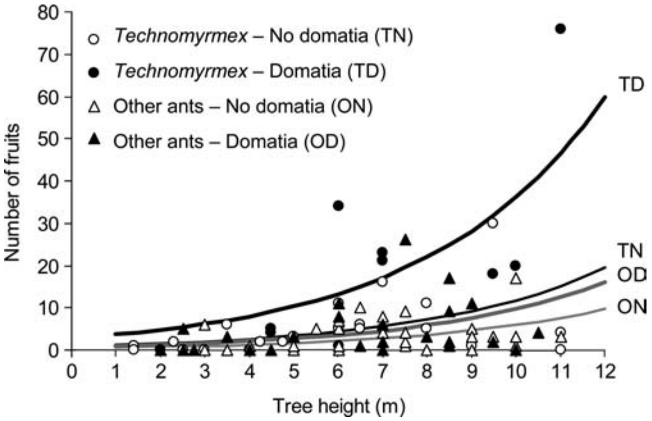

Fig. 1 Fruit-set advantage provided by domatia. Effect of tree height and domatia presence for trees associated with *Technomyrmex albipes* or other ants. Estimations of the log-linear regression lines provided by the Poisson regression model were added for each category of trees

effect of the third order interaction between ant identity, domatia presence and height on fruit production and also of the 2 second order interactions involving tree height, indicating that the slopes of the regression of fruit production against tree height, for the four categories defined by the ant and domatia covariates, were equal on a logarithmic scale (i.e. parallel regression lines). The effect of the second order interaction between ant identity and domatia presence was not significant implying that the presence of domatia increased fruit production both for trees occupied exclusively by *T. albipes* and for trees occupied by other ant species. These results remained unchanged after the removal of two possible outliers (trees of 6 m and 11 m occupied by *T. albipes*, which produced a comparatively greater number of fruits).

Fruit production significantly increased with tree height for the 68 trees patrolled by all ants other than *T. albipes*, but the positive effect of domatia presence was only marginally significant (Table 1b). Moreover, fruit production was not significantly lower for trees mostly patrolled by the castrating species *C. dohrni* than for trees patrolled by ants other than *C. dohrni* (Table 1b). This justified the fact that in the first analysis, we pooled together these two categories of ants into only one category that was examined against *T. albipes*. In this second model, all the interactions effects were, as previously, non-significant.

To summarise, domatia presence was found to be independent of tree size in this semi-myrmecophyte. For trees of comparable sizes, domatia conferred a global benefit on the host-plant in terms of fruit production irrespective of the ant species occupying the tree. In addition, fruit production was greater on trees associated with *T. albipes* as compared to trees associated with other ants.

Effect of ant exclusion and ant identity on leaf herbivory

In the 20 randomly chosen trees, identity of the ant associate had a highly significant effect on leaf herbivory (number of leaflets damaged in young leaves), while the effect of the ant exclusion treatment was only marginally significant (Poisson regression model, effect of ant identity: $\chi^2 = 18.22$, $P = 0.0001$; effect of treatment: $\chi^2 = 3.09$, $P = 0.079$; no over-dispersion: $\hat{c} = 0.96$). Whatever the treatment (ants excluded or not), herbivory damage to leaves was globally far less for *Technomyrmex*-patrolled trees than for others (Fig. 2). The exclusion treatment did not affect the two kinds of trees

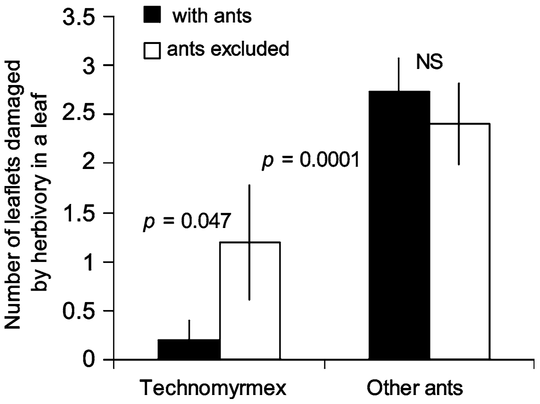

Fig. 2 Mean (± SE) young leaf herbivory (number of leaflets damaged out a total of four) in 20 trees compared for leaves patrolled by *T. albipes* ($n = 2{\times}5$) and leaves patrolled by other ants ($n = 2{\times}15$) and for leaves with ants ($n = 20$) and leaves where ants were excluded ($n = 20$)

in the same manner (significant ant identity × treatment interaction: $\chi^2 = 4.29$, $P = 0.038$). Indeed, taking into account only the five *Technomyrmex*-patrolled trees, there was a significant effect of the exclusion treatment on leaf herbivory (Poisson regression on the data subset corresponding to *Technomyrmex*-patrolled trees; no over-dispersion: $\hat{c} = 1.1$; effect of treatment: $\chi^2 = 3.96$, $p = 0.046$). The leaves from which *Technomyrmex* ants were excluded suffered greater herbivory than control leaves (Fig. 2). On the contrary, for the 15 trees patrolled by other ants, there was no significant difference of herbivory between control and ant-excluded leaves (Poisson regression on the data subset corresponding to trees patrolled by other ants; no over-dispersion: $\hat{c} = 0.93$; effect of treatment: $\chi^2 = 0.32$, $P = 0.569$).

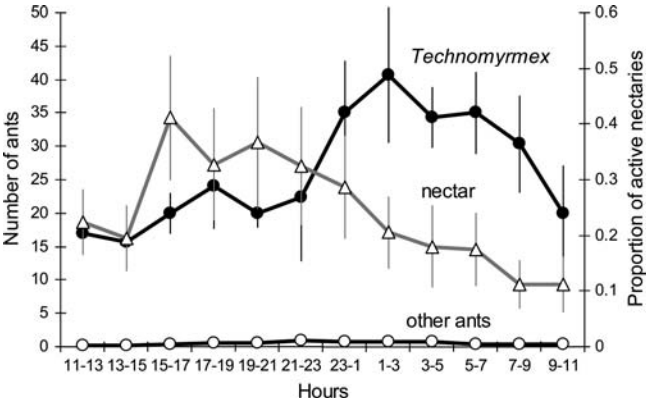

Fig. 3 Mean (± SE) ant and nectar (Δ) activity on young leaves from trees patrolled by *T. albipes* ((*filled circle*), $n = 3$) and trees patrolled by other ants ((*open circle*), $n = 12$)

Nectar production and ant activity on young leaves of *H. brunonis*

The circadian pattern of variation in ant activity on young leaves was well described by a quadratic relationship with time of the day (for example, the equation predicting the circadian pattern of activity of *T. albipes* was: $\log y = 2.3 + 0.3t - 0.02t^2$) showing an increase during the night until ça. 0300 hours then a progressive decrease (Fig. 3, Table 2). Both kinds of ants showed such a trend in circadian activity rhythm on young leaves (neither the interaction ant*t nor the interaction ant*t^2 was significant in the model). But the activity of *T. albipes* was far greater (up to 50 times greater) than that of other species, which was both sporadic and reduced (Table 2, Fig. 3). As a consequence, no herbivorous insect was observed on leaves patrolled by *T. albipes*, while three beetles of two species (both Curculionidae) and one undetermined caterpillar species were sporadically seen chewing the leaves during the day and the night on 3 of the 12 leaves patrolled by other ant species.

Behavioural reaction of *T. albipes* to deposited caterpillars

In 58 cases (24 out of 30 from leaves and 34 out of 36 from buds), larvae were removed within the 10 min of

Table 2 Poisson regression model testing for the effect of time of day and ant identity (*T. albipes* vs. others) on ant number. The effect of ant number at $t-1$($\log[x+1]$-transformed variable) on ant number at t was also tested to factor out any temporal autocorrelation in ant activity. The non-significant interactions were removed from the model. The tests were corrected for over-dispersion ($\hat{c} = 1.39$)

	ndf	*ddf*	*F*	*P*	Estimate	SE
Covariate						
Ant identity	1	126	40.39	0.0001		
(Number of ants)$_{t\text{-}1}$	1	126	30.39	0.0001		
t	1	126	12.84	0.0005		
t^2	1	126	12.82	0.0005		
(Number of ants)$_{t\text{-}1}$ × ant identity	1	126	9.98	0.0016		
Parameter						
Intercept for ant = all others					−2.26	0.41
Intercept for ant = *T. albipes*					1.01	0.41
t					0.3	0.90
t^2					−0.02	0.01
(Number of ants)$_{t\text{-}1}$ for ant = all others					1.37	0.27
(Number of ants)$_{t\text{-}1}$ for ant = *T. albipes*					0.41	0.13

the experiment. In eight cases (six from leaves and two from buds), the larvae were not removed. The 58 cases of removal corresponded to six cases where the larva was found and eaten, 46 cases where the larva was bitten and evicted (but in 23 out of these 46 cases, the larva managed to hang on the plant by a silk thread) and 6 cases where the larva escaped. The eight cases of non-removal corresponded to two cases where the larva was not found within the 10 min (on buds) and six cases where it was attacked and bitten by ants, which did not succeed in removing it (on leaves).

On the leaves, the time to discovery of the larva by *T. albipes* averaged 61.6 s ± 85.6 (Fig. 4). This time response showed no significant dependence on tree identity ($F_{14,14} = 2.31$, $P = 0.15$) but a significant decrease with the logarithm of density of ants on the leaf (GLM from log(x + 1)-transformed data: $F_{1,28} = 14.4$, $P = 0.0007$; intercept = 169.36 [SE = 31.20] significantly different from zero: $T = 5.43$, $P = 0.0001$; slope = −115.67 [SE = 30.48] significantly different from zero: $T = -3.79$, $P = 0.0007$). The residuals were normally distributed (Shapiro statistic, $W = 0.98$, $P = 0.81$). Ant density was itself a negative function of leaf size (regression from log(x)-transformed data: $F_{1,28} = 9.02$, $P = 0.005$; intercept = 4.48 [SE = 0.92] significantly different from zero: $T = 4.86$, $P = 0.0001$; slope = −1.24 [SE = 0.41] significantly different from zero: $T = -3.00$, $P = 0.005$). This means that the younger and, thus, the more tender the leaf (young leaves are devoid of mechanical protection against herbivores), the higher was the patrolling activity by ants, potential agents for biotic defence.

Technomyrmex—exclusion experiment on inflorescences

Technomyrmex albipes were present in large numbers on control inflorescences, where they patrolled young, initiated fruits. Nectaries on bracts subtending these fruits continued to produce some nectar. Control inflorescences initiated significantly more fruits than did the experimental inflorescences from which ants were excluded (Wilcoxon test for matched pairs: $Z = 2.03$, $P = 0.04$, $n = 16$). On the 16 inflorescences from which *Technomyrmex* were excluded, only 2 fruits were initiated, while 13 fruits were initiated on 6 (min = 1, max = 4 fruits per inflorescence) of the 16 control inflorescences. All initiated fruits aborted in the following days except two, which were produced by control inflorescences patrolled by *T. albipes*.

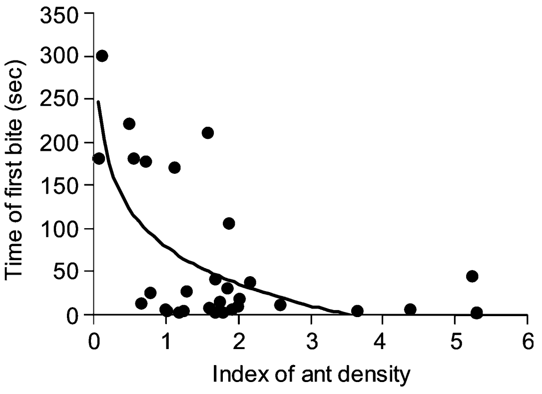

Fig. 4 Time of larva discovery by *T. albipes* as a logarithmic function of ant density (expressed as number of ants divided by leaflet length in cm, $n = 30$)

Discussion

Humboldtia brunonis is characterised by the production of a great number of flowers and a very low ratio of fruits/flowers both because of a low pollination efficiency and because of a high rate of fruit abortion. The precise reasons for such a pattern are not yet elucidated. The high abortion rate of initiated fruits might be explained by early herbivory on flowers and young fruits (Gaume et al. 2005) that might be caused by beetles against which ants are quite inefficient. Despite such a globally low fruit set, our results show that for trees of comparable height and habitat, those which bore domatia, produced more fruits than those devoid of domatia, irrespective of the identity of ants associated with the tree. However, this trend was more conspicuous for trees associated with *T. albipes*. Our results further show that, in contrast with other opportunistic ants, the tramp ant *T. albipes* provided significant anti-herbivore protection to *H. brunonis* and that fruit production was consequently enhanced for all trees patrolled by this species compared to others. These data raise three important questions for the evolution of myrmecophytism. (1) Does the presence of domatia, by increasing ant density, confer a selective advantage on the individual plant? Or, alternatively, are domatia and fruit production only correlated because they both characterise plants that have more resources for reasons independent of ant association? (2) Why is a polymorphism for domatia presence maintained in the populations of *H. brunonis*? (3) Does the mutualistic nature of the ant–plant relationship enhance the evolution of myrmecophytism? Despite the nomadic habits of its colonies, does *T. albipes* confer a long-term protective benefit to its host-plant, that is able to maintain positive selection on domatia?

Do domatia really confer a selective advantage on the myrmecophyte? If so, what is the exact nature of this advantage?

Our results clearly show that plants associated with domatia produced more fruits than plants devoid of them. But these are correlative data and not a demonstration *sensu stricto* of the selective advantage provided by domatia to their hosts. Plants that benefit from more resources may simply produce larger numbers of both fruits and domatia. Direct availability of resources such as light could explain patterns in both domatia and fruit production in *H. brunonis*. In their study of *H. laurifolia*, Krombein et al. (1999) reported that trees that bore more numerous domatia were located in sunny habitats, which are also habitats where fruiting may most probably occur. However, our sample of trees was carefully selected in homogeneously sunny environments, along trails. Therefore, all sampled trees would have benefited from similar light regimes. In the present study, heterogeneity of domatia production therefore did not reflect heterogeneity of light availability. We thus believe that greater fruit production by plants with domatia is a direct result of benefits conferred by their occupants. The fact that the extent of these benefits depend on the ant occupant strongly supports this hypothesis.

What is the exact nature of these benefits? Anti-herbivore protection is probably the main potential benefit mediated by domatia. If not, we would not have found a greater effect of domatia on fruit production for trees associated with the protective ant, *T. albipes*, than for other trees. However, our data suggest that anti-herbivore protection is not the sole benefit mediated by domatia. Indeed, even trees that were occupied by non-protective ants tended to produce more fruits when they bore domatia. Why? It is firstly possible that the other ants, most of which are opportunistic species, would have earlier provided their domatia-bearing hosts with some significant anti-herbivore protection, although their positive effect in terms of biotic defence was not detectable during the time of the study. Earlier anti-herbivore protection, during a period of higher young leaf production for example, would thus explain the present enhanced reproductive output. Benefits associated with opportunistic ants are highly variable in time and space because of a number of factors linked to both ants and herbivores (Di Giusto et al. 2001) and this mainly explains the existence of conditional mutualisms (Cushman and Addicott 1991; Bronstein 1994). The anti-herbivore hypothesis for opportunistic ants might hold but this would not explain why even the domatia-bearing trees that were occupied by non-protective ants or castrating ants such as *C. dohrni*, also tended to produce more fruits than trees devoid of domatia. Another hypothesis should be raised. Via isotopic analyses of N and C, more and more studies tend to show the existence of a nutritional benefit conferred by symbiotic ants on their host-plant through their waste products (Fischer et al. 2003; Sagers et al. 2000; Treseder et al. 1995; Trimble and Sagers 2004). As *H. brunonis* harbours not only ants but also a diversity of other invertebrates (e.g. earthworms, bees, wasps, centipedes, and roaches) inside their domatia (Rickson et al. 2003; Michener et al. 2003), we would not be astonished to discover nutrient exchanges between ants or other invertebrates and their host-plant.

The fitness effect of domatia is enhanced when the ant partner offers a substantial reciprocal benefit to the plant such as anti-herbivore protection. Hence, plants that bear domatia are especially advantaged when they are associated with the right ant partner. Therefore, the mutualistic nature of the ant–plant relationship seems to be essential for myrmecophytism to spread.

Why is a polymorphism for domatia presence maintained in the populations of *H. brunonis*?

The question remains why trees without domatia are still present in the populations of *H. brunonis*. A simple explanation would be that ants induce domatia, such as in *Vochysia vismiaefolia* (Blüthgen and Wesenberg 2001). But in *H. brunonis*, domatia occur prior to occupancy by ants since they are formed during the development of internodes and are self-opening, and are often also inhabited by a multitude of other animals (Rickson et al. 2003). We rather think that domatia are heritable characters. What determines such a polymorphism? Despite the benefits conferred by domatia, there may be a structural cost associated with them. Domatia can weaken stem stability (Moog et al. 2002) or they can suffer from structural injuries due to destructive predation by birds in search of ants (personal observation). We believe that because of the opportunistic (and sometimes castrating) characteristics of the ant associates of *H. brunonis*, sometimes costs of producing domatia may overlay the benefits and would result in maintaining the polymorphism in *H. brunonis* populations. *H. brunonis* populations are characterised by a mosaic of ant–plant relationships, which are more or less specialised, and whose opportunistic character should lead to time- and space-dependent outcomes. Selection on domatia will be certainly all the more intense if the ant–plant mutualism is durable.

Is the tramp ant *T. albipes* implicated in a mutualistic and durable relationship with *H. brunonis*?

In our studied population, *T. albipes* provided *H. brunonis* trees with effective protection against herbivorous insects. Trees that were patrolled by this species invariably suffered lower herbivore damage to leaves than other trees. Moreover, *T. albipes* also protected inflorescences of *H. brunonis*, since inflorescences deprived of ants initiated significantly fewer fruits than control ones. Although *H. brunonis* seems to be characterised by a low rate of fruit/flower production, the positive effect of *T. albipes* is marked. The indirect effects (increased photosynthetic activity via protection from herbivores), and the direct effects (protection of young fruits) we documented could easily explain the enhanced reproductive output of trees associated with this ant species compared to others.

The effectiveness of *T. albipes* appears to be due to three characteristics of the ant. First, the very populous colonies of this ant (Yamauchi et al. 1991) provide a great advantage to the host-plant since they permit a consistently high patrolling activity on its young leaves, which results in deterrence of any potential herbivores. The effect is enhanced by the presence of domatia that *de visu* increase the occupation rate of the ant species. Herbivores also avoid entire trees patrolled by *T. albipes* since even leaves from which *T. albipes* were excluded suffered lower herbivory than leaves on trees patrolled by other ants.

Secondly, the high degree of territoriality and associated aggression in *T. albipes* also contribute to efficient biotic defence in this ant. *T. albipes* is the only associate of *H. brunonis* that can competitively exclude any other ant occupant from the tree. Moreover, the ants systematically attack caterpillars they encounter but most of the time did not attempt to prey on them and therefore seemed to offer completely free service to the plants. Caterpillar eviction by *T. albipes* might be a simple consequence of the aggressive defence by these ants of a principal food source, the carbohydrate-rich EFN of *H. brunonis*, which is avidly sought after by several other arthropods (Gaume et al. 2005).

The habit of feeding on plant exudates (Blüthgen et al. 2003; Carver et al. 2003; Davidson et al. 2003, 2004) fulfils the third characteristic mediating the protection mutualism between *T. albipes* and *H. brunonis*. *T. albipes* patrols both flower buds and young leaves in search of EFN. We showed that their activity was most important during the night although the activity of nectar secretion was lower on young leaves during this period. This paradox is easily explained by the fact that EFN activity on inflorescences is itself enhanced during the night and is correlated with the general activity pattern of *T. albipes* (Gaume et al. 2005). Although this ant is often a pest tending harmful homopterans on plants (Nechols and Seibert 1985; Carver et al. 2003), colonies on *H. brunonis* rarely tended homopterans, except on a few bud inflorescences from a couple of plants. Perhaps, the plant's EFNs distract ants from tending homopterans, as proposed by Beccera and Venable (1989) and thus confer a selective advantage to the plant in terms of biotic defence. Indeed, as in many other EFN-bearing plants (e.g., Di Giusto et al. 2001), EFNs of *H. brunonis* are only active on growing organs, which are devoid of mechanical defence and which presumably most benefit from biotic defence. On young leaves, EFN secretion and ant activity are permanent while both do not occur on mature leaves. We showed that ant density was greater on the youngest leaves and that higher ant densities induce more effective protection against caterpillars.

These local populations of *T. albipes* are therefore involved in a protection mutualism with *H. brunonis*. Moreover, *T. albipes* appeared to be the sole ant that protects *H. brunonis* against herbivores. Its positive effect on the reproductive output of the plant might counterbalance the effects of a cheating species such as *C. dohrni*, which nests in the tree, feeds at EFNs but does not protect the young leaves and castrates the flowers of its host-plant (Gaume et al. 2005). This could also explain the persistence of such a parasite in the ant–plant system.

How can a tramp ant be a faithful partner of a host-plant? First, the nomadic ant *T. albipes*, native to the Indo-Pacific area (McGlynn 1999), was recorded in the earliest accounts of ant diversity in India (Forel 1895). It seems to be involved in some specific association with the genus *Humboldtia* since in addition to *H. brunonis* (Rickson et al. 2003; this study), it is also a very common occupant of *H. decurrens* in South India (Merry Zacharias, pers. obsv.) and of *H. laurifolia* in Sri Lanka (Krombein et al. 1999). Moreover, *T. albipes* might be locally faithful to populations of *H. brunonis* at a non-negligible time scale. Indeed, the *Technomyrmex* population studied from the Makut Forest Reserve during the dry season of 1999 was seen in the same locality during the following rainy season. It was not seen 4 years later in this locality but in other ones separated by a few kilometres during a 3-year period (M. Shenoy and R. Borges, personal observation). We thus believe that, at the study site, *T. albipes*, which can migrate from one locality to the other, is a faithful mutualistic partner at the meta-population scale. Its nomadic way of life is not detrimental to individual plants and can instead be an advantage. Indeed, individual plants do not support the populous colonies (several thousand workers) during their entire life but only during shorter periods and then gain in reproductive output at a lower investment cost than for an obligate ant symbiont. Although the dynamics of the plant–ant interaction might be geographically and temporally structured as in other intricate plant–insect interactions (Thompson and Cunningham 2002), this environmental heterogeneity might locally lead to rapid adaptation and 'coevolutionary' change between the two partners (Thompson 1999). In that sense, we further believe that selection for myrmecophytism (domatia production) could be maintained in *H. brunonis* partly because of the high benefit provided by some ants such as this nomadic but faithful partner at the meta-population scale.

In conclusion, domatia provide a selective advantage to *H. brunonis*, which can vary with the identity of the occupant. This advantage is most conspicuous with *T. albipes* implicated in a mutualism of protection with its host-plant. This advantage should, therefore, mostly come from anti-herbivore protection of ant inhabitants but could additionally come from other cryptic benefits, such as myrmecotrophy. Isotopic analyses will permit us to test this last hypothesis. Although the selective advantage conferred by domatia was demonstrated in other plant–arthropod systems (Agrawal and Karban 1997; Romero and Benson 2004), in ant–plant systems, this is the first time that it is confirmed. Some studies, focused on the ant's fitness, reported that nesting space provided by domatia appears to be the most important factor for the evolution of obligate myrmecophytism (Fiala and Maschwitz 1992; Fonseca 1999). But up to now, no study has focused on the fitness effect of domatia on individual plants. Our study thus contributes to a better understanding of how selection on the plant partner has shaped myrmecophytism. It also stresses the key role played by mutualistic ant–plant interactions in the evolution of myrmecophytism.

Acknowledgments The research was funded by a "Romain Rolland" post-doctoral fellowship of the French Ministry of Foreign Affairs, and by the Ministry of the Environment and Forests, Government of India. We thank the Forest Department of Karnataka for permission to carry out research in the field, as well as Raghavan, Eerappan and Salaam for their cordial field assistance. Dr. T.M. Musthak Ali and Dr. K. Chandrashekara (University of Agricultural Sciences, GKVK, Bangalore) and B. Bolton (London Museum of Natural History) are thanked for their taxonomic determinations of insects. This manuscript was greatly improved by stimulating discussions with Megha Shenoy, Carine Brouat and Doyle McKey as well as by the highly constructive contribution of four anonymous referees.

References

Agrawal AA, Karban R (1997) Domatia mediate plant–arthropod mutualism. Nature 387:562–563

Agrawal AA, Karban R, Colfer RG (2000) How leaf domatia and induced plant resistance affect herbivores, natural enemies and plant performance. Oikos 89:70–80

Beattie AJ (1985) The evolutionary ecology of ant–plant mutualisms. Cambridge University Press, Cambridge

Beccera JXI, Venable DL (1989) Extrafloral nectaries: a defence against ant-Homoptera mutualisms? Oikos 55:276–280

Blüthgen N, Wesenberg J (2001) Ants induce domatia in a rain forest tree (*Vochysia vismiaefolia*). Biotropica 33:637–642

Blüthgen N, Gebauer G, Fiedler K (2003) Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. Oecologia 137:426–435

Bronstein JL (1994) Conditional outcomes in mutualistic interactions. Trends Ecol Evol 9:214–217

Brouat C, McKey D (2000) Origin of caulinary ant domatia and timing of their onset in plant ontogeny: evolution of a key trait in horizontally transmitted ant–plant symbioses. Biol J Linnean Soc 71:801–819

Brouat C, McKey D (2001) Leaf-stem allometry, hollow stems, and the evolution of caulinary domatia in myrmecophytes. New Phytol 151:391–406

Carver M, Blüthgen N, Grimshaw JF, Bellis GA (2003) *Aphis clerodendri* Matsumura (Hemiptera: Aphididae), attendant ants (Hymenoptera: Formicidae) and associates on *Clerodendrum* (Verbenaceae) in Australia. Aust J Entomol 42:109–113

Cushman JH, Addicott JF (1991) Conditional interactions in ant–plant-herbivore mutualisms. In: Huxley CR, Cutler DF (ed) ant–plant interactions. Oxford University Press, Oxford, pp 92–103

Davidson DW, McKey D (1993) The evolutionary ecology of symbiotic ant–plant relationships. J Hymenoptera Res 2:13–83

Davidson DW, Cook SC, Snelling RR, Chua TH (2003) Explaining the abundance of ants in lowland tropical rainforest canopies. Science 300:969–972

Davidson DW, Cook SC, Snelling RR (2004) Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. Oecologia 139:255–266

Di Giusto B, Anstett M-C, Dounias E, McKey CB (2001) Variation in the effectiveness of biotic defense: the case of an opportunistic ant–plant protection mutualism. Oecologia 129:367–375

Fiala B, Maschwitz U (1992) Domatia as most important adaptations in the evolution of myrmecophytes in the paleotropical tree genus *Macaranga* (Euphorbiaceae). Plant Syst Evol 180:53–64

Fiala B, Rabenstein R, Maschwitz U, Linsenmair KE (1994) Diversity of ant–plant interactions: protective efficacy in *Macaranga* species with different degrees of ant-association. Oecologia 97:186–192

Fiala B, Jacob A, Maschwitz U, Linsenmair KE (1999) Diversity, evolutionary specialization and geographic distribution of a mutualistic ant–plant complex: *Macaranga* and *Crematogaster* in South East Asia. Biol J Linnean Soc 66:305–331

Fischer RC, Wanek W, Richter A, Mayer V (2003) Do ants feed plants? A 15N labelling study of nitrogen fluxes from ants to plants in the mutualism of *Pheidole* and *Piper*. J Ecol 91:126–134

Fonseca CR (1999) Amazonian ant–plant interactions and the nesting space limitation hypothesis. J Trop Ecol 15:807–825

Forel A (1895) Les Formicides de l'empire des Indes et de Ceylan. Bombay Nat Hist Soc 9:453–472

Gaume L (1998) Mutualisme, parasitisme et évolution des symbioses plantes-fourmis: le cas de *Leonardoxa* (Légumineuse) et de ses fourmis associées. PhD Thesis. ENSA.M. & University Montpellier 2

Gaume L, McKey DB (1999) An ant–plant mutualism and its host-specific parasite: activity rhythms, young leaf patrolling, and effects on herbivores of two specialist plant–ants inhabiting the same myrmecophyte. Oikos 84:130–144

Gaume L, McKey DB (2002) How identity of the homopteran trophobiont affects sex allocation in a symbiotic plant–ant: the proximate role of food. Behav Ecol Sociobiol 51:197–205

Gaume L, McKey D, Anstett M (1997) Benefits conferred by "timid" ants: active anti-herbivore protection of the rainforest tree *Leonardoxa africana* by the minute ant *Petalomyrmex phylax*. Oecologia 112:209–216

Gaume L, McKey D, Terrin S (1998) Ant–plant-homopteran mutualism: how the third partner affects the interaction between a plant-specialist ant and its myrmecophyte host. Proc R Soc Lond B 265:569–575

Gaume L, Zacharias M, Borges RM (2005) Ant–plant conflicts and a novel case of castration parasitism in a myrmecophyte. Evol Ecol Res 7:435–452

Heil M, McKey D (2003) Protective ant–plant interactions as model systems in ecological and evolutionary research. Annu Rev Ecol Evol Syst 34:425–453

Izzo TJ, Vasconcelos HL (2002) Cheating the cheater: domatia loss minimizes the effects of ant castration in an Amazonian ant–plant. Oecologia 133:200–205

Janzen DH (1967) Interaction of the bull's-horn acacia (*Acacia cornigera* L.) with an ant-inhabitant (*Pseudomyrmex ferruginea* F. Smith) in eastern Mexico. Kans Univ Sci Bull 47:315–558

Janzen DH (1969) Allelopathy by myrmecophytes: the ant *Azteca* as an allelopathic agent of *Cecropia*. Ecology 50:147–153

Krombein KV, Norden BB, Rickson MM, Rickson FR (1999) Biodiversity of the domatia occupants (ants, wasps, bees, and others) of the Sri Lankan myrmecophyte *Humboldtia laurifolia* Vahl (Fabaceae). Smithsonian Contrib Zool 603:1–33

Letourneau DK (1998) Ants, stem-borers, and fungal pathogens: experimental tests of a fitness advantage in *Piper* ant–plants. Ecology 79:593–603

McGlynn TP (1999) The worldwide transfer of ants: geographical distribution and ecological invasions. J Biogeogr 26:535–548

McKey DB (2000) *Leonardoxa africana* (Leguminosae: Caesalpinioideae): a complex of mostly allopatric subspecies. Adansonia 22:71–109

McKey DB, Gaume L, Brouat C, Di Giusto B, Pascal L, Debout G, Dalecky A, Heil M (2005) The trophic structure of tropical ant–plant-herbivore interactions: community consequences and coevolutionary dynamics. In: Burslem D, Pinard M, Hartley S (eds) Biotic interactions in the tropics. Cambridge University Press, Cambridge (in press)

Michener CD, Borges RM, Zacharias M, Shenoy M (2003) A new parasitic bee of the genus *Braunsapis* from India (Hymenoptera: Apidae: Allodapini). J Kans Entomol Soc 76:518–522

Moog J, Feldhaar H, Maschwitz U (2002) On the caulinary domatia of the SE Asian ant–plant *Zanthoxylum myriacanthum* Wall. ex Hook. f. (Rutaceae), their influence on branch statics, and the protection against herbivory. Sociobiology 40:547–574

Morawetz W, Henzl M, Wallnöfer B (1992) Tree killing by herbicide producing ants for the establishment of pure *Tococa occidentalis* populations in the Peruvian Amazon. Biodivers Conserv 1:19–33

Nechols JR, Seibert TF (1985) Biological control of the spherical mealybug, *Nipaecoccus vastator* (Homoptera: Pseudococcidae): assessment by ant exclusion. Environ Entomol 14:45–47

Nuismer SL, Gomulkiewicz R, Morgan MT (2003) Coevolution in temporally variable environments. Am Nat 162:195–204

Palmer TM, Stanton ML, Young TP (2003) Competition and coexistence: exploring mechanisms that restrict and maintain diversity within mutualist guilds. Am Nat 162:64–79

Ramesh BR, Pascal J-P (1997) Atlas of endemics of the Western Ghats (India). Distribution of tree species in the evergreen and semi-evergreen forests. Department of Ecology, French Institute of Pondicherry, Pondicherry

Rickson FR, Rickson MM, Ghorpade K, Norden BB, Krombein KV (2003) Invertebrate biodiversity (ants, bees and others) associated with stem domatia of the Indian myrmecophyte *Humboldtia brunonis* Wallich (Magnoliophyta: Fabaceae). Proc Entomol Soc Wash 105:73–79

Romero GQ, Benson WW (2004) Leaf domatia mediate mutualism between mites and a tropical tree. Oecologia 140:609–616

Sagers CL, Ginger SM, Evans RD (2000) Carbon and nitrogen isotopes trace nutrient exchange in an ant–plant mutualism. Oecologia 123:582–586

Shenoy M (2003) An examination of a network of interactions. The myrmecophyte *Humboldtia brunonis* (Fabaceae) and its invertebrate associates. Master's Thesis, Indian Institute of Science

Thompson JN (1999) Specific hypotheses on the geographic mosaic of coevolution. Am Nat 153:1–14

Thompson JN, Cunningham BM (2002) Geographic structure and dynamics of coevolutionary selection. Nature 417:735–738

Treseder KK, Davidson DW, Ehleringer JR (1995) Absorption of ant-provided carbon-dioxide and nitrogen by a tropical epiphyte. Nature 375:137–139

Trimble ST, Sagers CL (2004) Different host use in two highly specialized ant–plant associations: evidence from stable isotopes. Oecologia 138:74–82

Wheeler WM (1942) Studies of neotropical ant–plants and their ants. Bull Am Museum Comp Zool 90:1–251

Yamauchi KT, Furukawa T, Kinomura K, Takamine H, Tsuji K (1991) Secondary polygyny by inbred wingless sexuals in the dolichoderine ant *Technomyrmex albipes*. Behav Ecol Sociobiol 29:313–319

Yu DW, Pierce NE (1998) A castration parasite of an ant–plant mutualism. Proc R Soc Lond B 265:375–382

Yu DW, Wilson HB, Pierce NE (2001) An empirical model of species coexistence in a spatially structured environment. Ecology 82:1761–1771

Zacharias M, Rajan PD (2004) *Vombisidris humboldticola* (Hymenoptera: Formicidae), a new arboreal ant species from an Indian ant plant. Curr Sci 87:1337–1338