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Jérôme Orivel, Luc Lambs, Pierre-Jean G. Malé, Céline Leroy, Julien Grangier, et al.. Dynamics of the association between a long-lived understory myrmecophyte and its specific associated ants. *Oecologia*, 2011, 165 (2), pp.369-376. 10.1007/s00442-010-1739-5 . hal-00955375

HAL Id: hal-00955375

<https://hal.science/hal-00955375>

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Eprints ID : 11094

To link to this article :

DOI:10.1007/s00442-010-1739-5

URL : <http://dx.doi.org/10.1007/s00442-010-1739-5>

To cite this version :

Orivel, Jérôme and Lambs, Luc and Malé, Pierre-Jean G. and Leroy, Céline and Grangier, Julien and Otto, Thierry and Quilichini, Angélique and Dejean, *Alain Dynamics of the association between a long-lived understory myrmecophyte and its specific associated ants*. (2011) Oecologia, vol. 165 (n° 2). pp. 369-376. ISSN 0029-8549

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Dynamics of the association between a long-lived understory myrmecophyte and its specific associated ants

Jérôme Orivel · Luc Lambs · Pierre-Jean G. Malé ·
Céline Leroy · Julien Grangier · Thierry Otto ·
Angélique Quilichini · Alain Dejean

Abstract Myrmecophytic symbioses are widespread in tropical ecosystems and their diversity makes them useful tools for understanding the origin and evolution of mutualisms. Obligate ant–plants, or myrmecophytes, provide a nesting place, and, often, food to a limited number of plant–ant species. In exchange, plant–ants protect their host plants from herbivores, competitors and pathogens, and can provide them with nutrients. Although most

studies to date have highlighted a similar global pattern of interactions in these systems, little is known about the temporal structuring and dynamics of most of these associations. In this study we focused on the association between the understory myrmecophyte *Hirtella physophora* (Chrysobalanaceae) and its obligate ant partner *Allomerus decemarticulatus* (Myrmicinae). An examination of the life histories and growth rates of both partners demonstrated that this plant species has a much longer lifespan (up to about 350 years) than its associated ant colonies (up to about 21 years). The size of the ant colonies and their reproductive success were strongly limited by the available nesting space provided by the host plants. Moreover, the resident ants positively affected the vegetative growth of their host plant, but had a negative effect on its reproduction by reducing the number of flowers and fruits by more than 50%. Altogether our results are important to understanding the evolutionary dynamics of ant–plant symbioses. The highly specialized interaction between long-lived plants and ants with a shorter lifespan produces an asymmetry in the evolutionary rates of the interaction which, in return, can affect the degree to which the interests of the two partners converge.

Keywords *Allomerus decemarticulatus* · *Hirtella physophora* · Lifespan · Mutualism · Myrmecophyte

Communicated by Joshua Tewksbury.

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Introduction

The evolutionary persistence of mutualisms depends on the alignment of the reproductive interests of the interacting partners. If each partner gains from the association, the costs and benefits involved in maintaining the interaction can vary in both space and time. Such

variability is the primary source of conflicts of interest between the partners—especially if it is associated with a horizontal mode of transmission—and promotes cheating. Hence, the challenge is to identify the mechanisms that maintain evolutionarily stable, interspecific mutualisms in spite of the ubiquity of cheating (Bronstein et al. 2003; Herre et al. 1999; Sachs et al. 2004). Several factors, such as partner choice (i.e., filtering), partner fidelity or spatial structure (i.e., limited dispersal) have been identified as fostering the alignment of the mutualists' interests (Foster and Wenseleers 2006; Herre et al. 1999; Szilágyi et al. 2009). Consequently, both the spatial and temporal dynamics of the interactions are important features in understanding mutualistic associations between species.

Mutualistic ant–plant associations, which are widespread in tropical ecosystems, offer a suitable model for exploring this issue. Obligate ant–plants, or myrmecophytes, provide a nesting space, and, often, food to a limited number of plant–ant species. In exchange, plant–ants protect their host plants from phytophagous animals, competitors and pathogens, and can provide them with nutrients (Beattie and Hughes 2002; Heil and McKey 2003; Solano and Dejean 2004). Ant–plants and plant–ants share a common interest in growth, but not necessarily in reproduction. For both parties, the reproductive investments of the other are useless to the interaction. Winged sexuals are not involved in protecting the plant foliage and the energy invested by plants in producing flowers does not increase the nesting space for the ant colony. Consequently, natural selection should favor cheating to maximize each species' own benefits. Indeed castrating parasites have been identified in several ant–plant mutualisms (Edwards and Yu 2008; Gaume et al. 2005; Izzo and Vasconcelos 2002; Stanton et al. 1999; Yu and Pierce 1998). If castration can clearly reduce or even prevent plant reproductive success, it has, nevertheless, to be balanced against the overall reproductive activity of the plant throughout its lifetime.

In this study we concentrated on a one-to-one mutualism between the Neotropical understory myrmecophyte *Hirtella physophora* Martius & Zuccharini (Chrysobalanaceae) and its obligate and specific ant-partner *Allomerus decemarticulatus* Mayr (Myrmicinae). Due to the highly specialized nature of the *H. physophora*–*A. decemarticulatus* association, we focused on the temporal structuring and dynamics of this association by studying the life histories and growth rates of both partners. Through field inventories and using an experimental approach, we investigated the lifespan of both the plants and their associated ant colonies, and the beneficial or detrimental effects they can have on the reproductive growth of the other.

Materials and methods

Study site and model

This study was conducted between 2000 and 2009 in the pristine forest situated around the field station at Petit Saut, Sinnamary, French Guiana (05°03'30.0"N, 52°58'34.6"W).

Hirtella physophora grows strictly in the understory of pristine Amazonian forests and mostly in patches located on the upper slopes of hillsides (Solano et al. 2003). These treelets have long-lived leaves that bear extrafloral nectaries and a pair of pouches at the base of each lamina. The leaf pouches that shelter ant colonies, differ both morphologically and anatomically from the lamina (Leroy et al. 2008). Each *H. physophora* is almost always associated with *A. decemarticulatus* (99% of the inhabited plants, the remaining being inhabited by *Crematogaster* sp. aff. *crucis*), with a single colony per plant. Moreover, *A. decemarticulatus* has never been found in association with another myrmecophyte species in the study area (Solano et al. 2003). The *A. decemarticulatus* workers protect their host plants through their predatory behavior, including by building a gallery-shaped trap along the stems to capture prey (Dejean et al. 2005).

Peak flowering periods in *H. physophora* in French Guiana occur from December to February and June to August. Inflorescences arise at axillary fasciculate racemes and they comprise three to six flowers (Prance 1972).

Life history and growth rate of *H. physophora*

A total of 1,320 *H. physophora* individuals were tagged, and their height and trunk diameters were measured. The measurements of trunk diameters were taken with calipers on the lowest part of the base of the trunk, closest to the ground.

The growth rate of *H. physophora* was estimated by recording changes in the trunk diameters of 36 tagged *Hirtella* trees over 6 years (2000–2006). We also monitored 257 individuals for 3 years (2003–2006), and recorded the number of trees that were heavily damaged by falling trees or branches plus those that had dried out after the formation of a tree-fall gap in their vicinity.

Radiocarbon dating the trees

Due to the lack of true annual growth rings in many tropical species, the estimation of the age of such plant individuals cannot be made dendrometrically. We therefore used radiocarbon (^{14}C) dating together with estimations of diametrical increments of the trunk to address this question. Four wood samples from *H. physophora* trees were analyzed along with samples taken from *Pinus caribaea* Morelet and

Table 1 Sample information, accelerator mass spectrometry ^{14}C measurements, and minimum AD age (relative to 2005) for the wood samples of *Hirtella physophora*, *Pinus Caribaea* and *Avicennia germinans*

Sample name	Laboratory code	Trunk diameter (cm)	Density	Sample weight (g)	$\delta^{13}\text{C}$ (‰)	Error $\delta^{13}\text{C}$	PMC	Error PMC	Minimum age	Age ^{14}C BP	Growth rate (cm/years)
<i>P. caribaea</i>	Poz 13575	14.9	0.69	0.65	-26.1	0.1	118.00	0.39	17	–	0.876
<i>A. germinans</i>	Poz 13574	14.3	0.66	0.26	-23.8	0.8	114.30	0.40	14	–	1.021
<i>H. physophora</i> sample A	Poz 13595	1.9	0.95	0.30	-37.7	0.1	103.05	0.36	48	–	0.040
<i>H. physophora</i> sample B	Poz 13594	2.2	0.95	0.40	-34.3	0.4	101.44	0.35	50	–	0.044
<i>H. physophora</i> sample C	Poz 13598	2.9	0.93	0.40	-36.7	1.4	98.12	0.35	–	150 $\pm$ 30	–
<i>H. physophora</i> sample D	Poz 13592	3.2	0.93	0.24	-32.8	0.5	98.67	0.34	–	110 $\pm$ 30	–

PMC percentage of modern C

Avicennia germinans (L.) L. of known ages growing in neighboring areas and that served as references (see Table 1 for details on trunk diameters, wood density and weight of samples). The pine sample was taken from a plantation whose age is known, while the mangrove tree is a natural pioneer species whose age was deduced from aerial photographs.

Plants assimilate ^{14}C during photosynthesis, and once trapped in the wood, the amount of ^{14}C decreases according to the exponential law of radioactive decay ($T_{1/2} = 5,730$ years), so that the ^{14}C content can permit us to date the age of the wood. However, concentrations of atmospheric ^{14}C doubled between 1950 and 1965 due to the aboveground explosions of atomic bombs; and then declined (Nydal and Lövseth 1983). Consequently, radiocarbon-dating wood formed before or after the detonation of the atomic bombs requires different methods of calculation. For trees formed after 1950, these changes in atmospheric ^{14}C are directly detectable by measuring radiocarbon. Dating older wood is complicated by the temporal variation in atmospheric ^{14}C resulting from massive emissions of CO_2 containing million-year-old ^{14}C that can trigger an overestimation of the age of the wood (Nydal and Lövseth 1983; Stuiver and Becker 1986). The age of wood samples is usually expressed after calibration as a percentage of modern C (PMC) for periods following the explosion of the bombs, or in the years before the present for trees that date from before the explosion of the bombs (BP years; where the present is arbitrarily defined as 1950).

We used the Calibomb program (<http://calib.qub.ac.uk/CALIBomb>) and the Wellington data set programmed for the Southern Hemisphere to estimate the age of the wood samples displaying a PMC value greater than 100, or wood formed after 1950. For the samples displaying a PMC value less than 100, or wood formed before 1950, we used the Calib 5.02 program (<http://calib.qub.ac.uk/calib/calib.html>) with the calibration curve shcal04.14c proposed by McCormac et al. (2004).

Evaluating the lifespan of *A. decemarticulatus* colonies

To evaluate the lifespan of *A. decemarticulatus* colonies, 193 *H. physophora* individuals were monitored twice each year between 2002 and 2005 (800 days). Each time, we recorded the presence or absence of an ant colony and its developmental status according to the quality of the galleries interconnecting the leaf pouches. Indeed the building of the gallery-shaped trap by *A. decemarticulatus* enables us to estimate the development of the colony and its death as the fungus they use in the galleries dies soon after the death of the ant colony. Consequently, the death of a given colony and the recolonization of the plant between two censuses can be easily determined as the trap is built after the colony develops (i.e., the length of the galleries is linked to the increase in the number of inhabited domatia on the plant). We hypothesized that all ages were represented in the ant colonies at the first census and that the death of the colonies was directly related to their age. This permitted us to establish a linear regression of the number of surviving colonies as a function of time, and the rate of colony extinction was used to estimate the half-life and maximum age of the colonies.

Ants' effect on plant growth and reproduction

To assess both the short- and long-term effects of the ants on the plants, each month for 16 months we monitored the vegetative and reproductive growth rates of individuals from which the ants were removed ($n = 25$) as well as control plants ($n = 22$). Both groups of plants were similar in size expressed as the number of leaves (mean $\pm$ SE = 17.04 ± 3.6 vs. 16.5 ± 5.3 for ant-excluded and control plants, respectively, two-sample t -test: $t = 0.335$, $df = 45$, $P = 0.74$). We eliminated the ants by injecting an aqueous solution (2%) of pyrethrum 25% inside all of the domatia. The rapid knockdown effect of the pyrethrum immediately killed all of the resident ants, and its photolability prevented

any residual effects on phytophagous insects. As founding queens re-colonized certain plants during the course of the experiment, we re-injected the pyrethrum solution into the domatia occupied by new queens 3 times over the 16 months. We recorded the total number of leaves, the number of new leaves as well as the number of floral buds, flowers and fruits on each plant individual monthly. Control and ant-excluded plants were compared according to either their total vegetative or reproductive investments during the 16-month period. We started the census 2 months after removing the ants because Grangier et al. (2008) demonstrated that excluding the ants has no effect on the rate of herbivory after 40 days.

To investigate the potential castrating virulence of *A. decemarticulatus*, 23 *H. physophora* bearing at least two early stage inflorescences were selected. Ant workers were removed from one inflorescence and their access to the floral buds was prevented using Tanglefoot; while the other inflorescence was used as a control. The numbers of flowers as well as the number of fruits produced were counted each week after treatment.

Size and structure of the ant colonies

We collected the ant colonies inhabiting 35 *H. physophora*, which ranged in size from having 7–96 domatia, and we investigated the relationship between colony size and the number of domatia on the host plant. All of the leaves and stems on each plant individual were cut off and placed into a plastic bag, and then preserved in 70% ethanol. Each domatium was then dissected and the number of workers, pupae, larvae, queens, and alate males and females was recorded. The number of workers that were in the galleries built under the stems of the plant was also recorded.

Results

Diameter and height distribution of *H. physophora* trees

The frequency distributions for height and stem diameter of the 1,320 plants measured were in both cases unimodal with a mean diameter of 1.6 ± 0.94 cm and a mean height of 1.31 ± 1.0 m (Fig. 1; data not shown for height distribution). The structure of the distributions showed that most of the trees were in the middle of the size range for both diameter and height, with a relatively small number of seedlings and a constant decrease toward the tallest individuals.

Even if tree height and diameter showed a positive correlation, the variance between groups of individuals was not homogeneous [14 groups from 0.1 to 0.3 cm in diameter to >4 cm; Fig. 1; Levene test $F_{(13,1306)} = 61.24$, $P < 0.01$], highlighting the large variation observed in tree height as

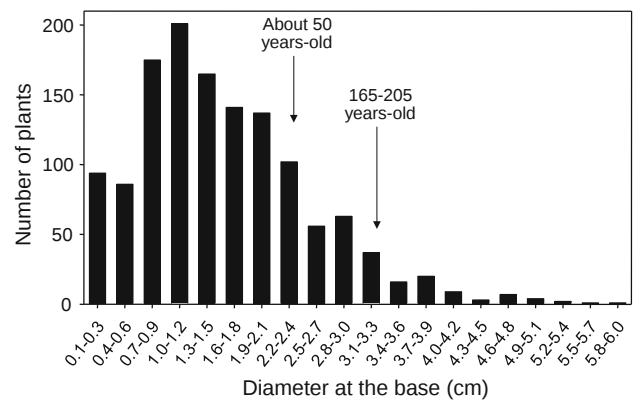


Fig. 1 Distribution of the trunk base diameters of a population of 1,320 *Hirtella physophora*. The age of the plants is indicated based on radiocarbon dating

the trees age and, consequently, the amount of damage they can sustain during their lifetime. Indeed, during the 3-year-long monitoring period, a total of 29 trees out of 257 were affected in some way, resulting in 4% of the trees affected each year.

Determining the age of the trees

The ^{14}C analyses conducted using the Calibomb program for wood with PMC values greater than 100 generally resulted in one single date (Table 1). The Calibomb program estimated the ages of two trees of known ages (*P. caribaea* and *A. germinans*) to within 1–2 years of their real ages. The evaluation of the ages of the two of *H. physophora* tree samples with 1.9- and 2.2-cm-wide trunks corresponded to 48 and 50 years, respectively (Table 1). Thus, the corresponding mean growth rate from seedlings of such trees was about 0.042 cm/year [0.040 (1.9/48) and 0.044 (2.2/50) for the 1.9- and the 2.2-cm-wide trees, respectively]. Note that the differences in age and trunk diameter reflect possible variations in environmental conditions for these two individuals, but their growth rate was quite similar.

The ^{14}C analyses concerning the two largest *H. physophora* trees (2.9- and 3.2-cm-wide trunks) resulted in PMC values lower than 100, and thus had to be recalibrated using the Calib 5.02 program. This recalibration resulted in three theoretically possible dendro-ages for each sample (*H. physophora* sample C, 73 ± 75 BP, 150 ± 30 BP and 244 ± 25 BP; *H. physophora* sample D, 36 ± 30 BP, 110 ± 30 BP and 240 ± 20 BP). This multi-age result originates from the very low rate of decrease in atmospheric ^{14}C and from the fact that this logarithmic curve is not smooth: it has many small peaks, which can be matched with the measured PMC value. To select the right age, we used the growth rate of adult trees determined in the field by measuring the increase in trunk diameters between

2000 and 2006: (mean $\pm$ SE) 2.078 ± 0.755 to 2.181 ± 0.776 cm. The mean difference (0.103 ± 0.070 cm) corresponds to a mean growth of 0.0171 cm/year over this period for *H. physophora* trees whose trunk diameters were already about 2 cm, so about half from early growth, knowing that these 2-cm-wide trees are around 50 years old. Consequently, a tree with a 3-cm-wide trunk is theoretically approximately 108 years old [$50 + (1/0.0171)$], permitting us to estimate that *H. physophora* samples C and D were 150 and 110 BP-years old, respectively (Table 1). These BP values correspond to real ages of about 205 and 165 years, respectively.

To evaluate the age of the individual in our dataset with the widest trunk (6 cm), we based our calculations on the ages of the ^{14}C -dated trees with trunk diameters of about 3 cm (see above). We thus estimated that this tree was between approximately 340 [$165 + (2.8/0.0171)$] and 385 [$205 + (3.1/0.0171)$] years old.

Evaluating the lifespan of *A. decemarticulatus* colonies

The linear regression of the number of surviving ant colonies as a function of time resulted in $r^2 = 0.97$, permitting us to estimate a colony half-life (i.e., the point in time at which 50% of the initial number of colonies would have survived) at 10.13 years. As it takes about 1 year for a colony to reach maturity (J.O., personal observation), a better estimate of the half-life of the colonies would be closer, therefore, to 11 years. The estimated maximum age of the colonies is 20.36 years (a minimum of 21 years starting from foundation), and, thus, by far shorter than that of the host *H. physophora* individuals.

Ants' effect on plant growth and reproduction

Removing the ants over a long period of time affected the vegetative growth of the plants, and the *H. physophora* leaves produced after the ants were removed suffered from herbivory (Fig. 2). Indeed, the plants devoid of ants produced a significantly lower number of new leaves than the control plants (mean number per plant $\pm$ SE = 17.4 ± 7.4 vs. 24.9 ± 6.7 for ant-excluded and control plants, respectively; Mann–Whitney U test: $U = 134.5$, $P < 0.01$), which resulted in a lower vegetative growth rate over the course of the experiment for plants devoid of ants (Fig. 2; Table 2). However, no significant differences in reproductive growth rates could be discerned. Reproductive investment occurred in most of the plants (21/25 vs. 19/22 for ant-excluded and control plants, respectively; Fisher's exact test $P = 0.57$) and the reproductive effort of those plants did not differ between the two groups (floral buds, mean number per plant $\pm$ SE = 21.4 ± 13.0 vs. 22.9 ± 12.9 for ant-excluded and control plants, respectively; Mann–Whitney U test,

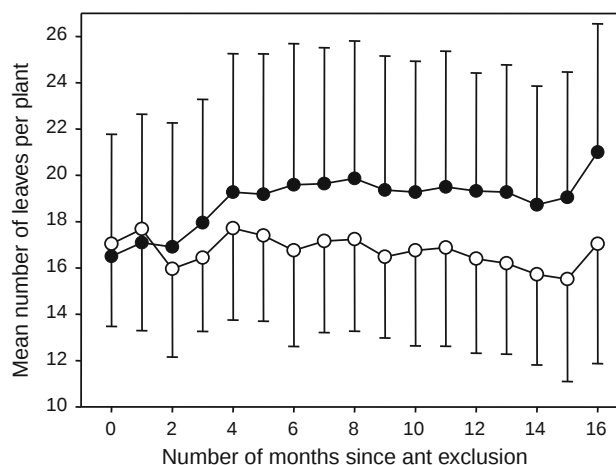


Fig. 2 Vegetative growth expressed as the mean number $\pm$ SE of leaves in ant-removed (empty circles) and control (filled circles) *H. physophora* plants during a 16-month field experiment

Table 2 Repeated-measures ANOVA examining the impact of ant removal from the plant on the number of *H. physophora* leaves over time

	<i>df</i>	MS	<i>F</i>	<i>P</i> value	G–G ^a
Treatment	1	947.47	1.531	0.222	
Error	45	618.98			
Time	16	22.10	5.530	<0.001	<0.001
Time $\times$ treatment	16	19.08	4.775	<0.001	0.001
Error	720	3.99			

MS mean square

^a Probabilities corrected for sphericity are provided using the Greenhouse–Geisser correction (G–G)

$U = 40.5$, $P = 0.29$; flowers, 4.6 ± 2.8 vs. 5.6 ± 3.1 , $U = 51.5$, $P = 0.64$). The percentage of plants that produced fruits did not differ between both groups (5/25 vs. 7/22 for ant-excluded and control plants, respectively; Fisher's exact test $P = 0.28$). Moreover, and as usually observed in *H. physophora*, fruit production was very low and the difference between plants that produced fruits was not significant between the two groups (mean number per plant $\pm$ SE = 1.4 ± 0.5 vs. 2.3 ± 1.3 for ant-excluded and control plants, respectively, Mann–Whitney U test: $U = 12.5$, $P = 0.42$).

Nevertheless, the presence of the ants had a negative effect on the reproduction of their host plants that was demonstrated when the ants were selectively removed from the inflorescences of their host (Fig. 3). The inflorescences to which the ants had access indeed produced significantly fewer flowers than the ant-excluded ones (mean percentage of flowers per inflorescence compared to the initial number of buds $\pm$ SE = 24.5 ± 32.3 vs. 76.9 ± 24.8 for control and ant-excluded inflorescences, respectively; Wilcoxon test: $W = 193$, $P < 0.0001$). This negative effect was also reflected

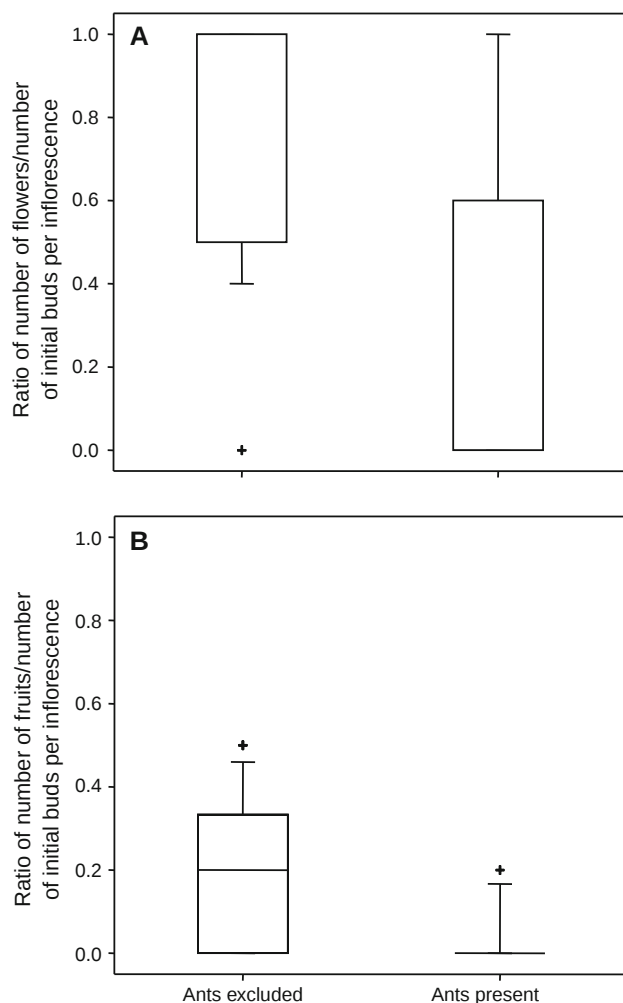


Fig. 3 *Allomerus decemarticulatus*' impact on the reproduction of *H. physophora* expressed as the number of flowers (a) or fruits (b) produced according to the initial number of buds per inflorescences in ant-excluded or control inflorescences. Error bars above and below the boxes indicate the 90th and 10th percentiles, the ends of the boxes indicate the 25th and 75th percentiles and crosses indicate outliers

in the number of plants that produced fruits (12/23 vs. 3/23 for control and ant-excluded inflorescences, respectively; Fisher's exact test $P = 0.005$) and in the number of fruits produced (mean percentage of fruits per inflorescence compared to the initial number of buds $\pm$ SE = 2.3 ± 1.3 vs. 17.1 ± 3.8 for control and ant-excluded inflorescences, respectively; Wilcoxon test: $W = 78$, $P < 0.0025$).

Size and structure of the ant colonies

There was a positive and linear relationship between the size of the ant colony and the number of domatia on the host plant (Fig. 4; $r^2 = 0.8356$). This relationship accounts for most of the variation in colony size and strongly suggests that for all plant sizes, the amount of available nesting space is an important limiting factor for colony growth. The

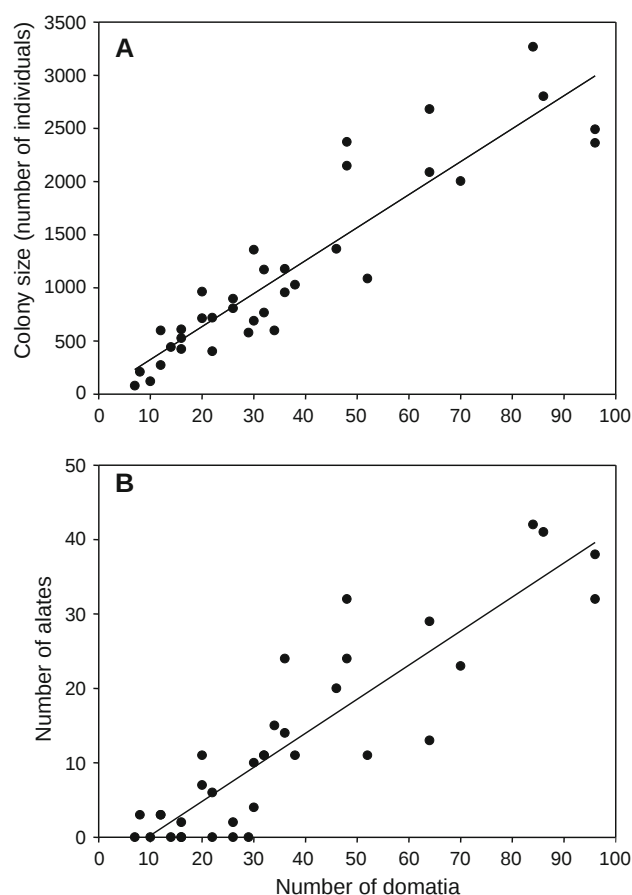


Fig. 4 Linear regression of the number of domatia on *H. physophora* by a the size of the colony expressed as the total number of individuals ($r^2 = 0.8356$, $P < 0.001$) and b the number of alates among the resident ants, *A. decemarticulatus* ($r^2 = 0.7984$, $P < 0.001$)

lack of curvilinearity in the relationship (test of significance for domatia²: $F = 0.109$, $P = 0.80$) also showed that the amount of available nesting space is probably one of the most important limiting factors in colony development.

The onset of alate production begins early in colony development (e.g., when there are fewer than 300 workers), but most of the alate individuals are produced in colonies containing more than 600 workers. Moreover, the number of alates (brood and adult males and females), and thus the rate of alate production is also strongly correlated with the amount of nesting space offered by the host plant (Fig. 4; $r^2 = 0.7984$). The same relationship exists when colony size rather than the number of domatia is taken into account. Then, the amount of available nesting space not only limits colony size, but also its rate of reproduction.

Discussion

Altogether our results highlight some important features that can deeply influence the evolutionary dynamics of

ant–plant symbioses. As in most ant–plant mutualisms, the myrmecophytism in *H. physophora* clearly enhances the growth of individuals, but *A. decemarticulatus* also negatively affects its host’s reproduction by reducing by two-thirds the number of flowers and thus the number of fruits. However, such a negative effect has to be balanced over the entire lifetime of the plant individuals and it appears that the overall effect of the ants on their host plant is clearly positive. Indeed, even if the reproductive effort does not differ between ant-inhabited plants and plants devoid of ants, the latter nevertheless suffer from herbivory. Thus, over the long term, this can be detrimental to their growth and survival.

Functioning and importance of myrmecophytism

Through their predatory behavior, which includes the constant patrolling of their host tree foliage and their induced response to foliar wounds (Grangier et al. 2008), resident ants protect the foliage of their host plant. This also benefits the ants as the production of new leaves is the only means by which their nesting space can increase. The limitation in colony growth and reproduction induced by the amount of available nesting space highlights the importance of this limiting factor for the ants (Fonseca 1993, 1999). According to these results, it is in *A. decemarticulatus*’ best interest to favor the vegetative growth of their host plant, like in any protective ant–plant symbioses, not only in terms of the production of more food rewards or domatia, but also to maximize their own reproductive success.

Moreover, castration also enables host-plant resources to be reallocated from reproduction to vegetative growth (Frederickson 2009; Yu 2001). Castrating parasites have been identified in several systems and especially in all of those involving the *Allomerus* ant species studied so far (Izzo and Vasconcelos 2002; Yu and Pierce 1998). *Allomerus decemarticulatus* is no different in this matter than the other *Allomerus* species. But, *A. decemarticulatus* destroy about two-thirds of the floral buds whereas the other *Allomerus* species generally destroy 100% of the floral buds, reducing their host reproduction to zero (but see Edwards and Yu 2008). In the present case, the combination of both the positive effect of the *Allomerus* on the vegetative growth of *H. physophora* and the much longer longevity of the host plants than their specific plant–ants are important factors favoring the persistence of the interaction. The loss of ant inhabitation by the plant can be considered as a fitness valley as the loss of biotic protection would affect the survival of the plants. In absence of alternative solution for *H. physophora*, this system could be thus considered as an example of a local adaptive peak.

Beside its myrmecophytism, *H. physophora* also shares several biological traits with many plant species from the

understory that enables its survival in this environment, such as shade tolerance and slow growth, mortality, and recruitment rates (Easdale et al. 2007; Gourlet-Fleury et al. 2005; Nascimento et al. 2005; Vieira et al. 2005). Moreover, like for any plant species in the understory, the impact and consequences of the physical damage caused by debris falling from the canopy are of importance. The frequency of the damage suffered by *H. physophora* is of the same magnitude as that recorded in other studies, with around 4% of the trees affected per year (Clark and Clark 1989, 1991; Gartner 1989). However, the ability of this plant species to develop reiterations from its lower part reflects its adaptation to these frequent disturbances.

Evolutionary consequences of the asymmetry in the partners’ lifespan

Because the plants are colonized early in their development, they will host several successive ant colonies during their lifetime. Neither the ontogenetic successions of different partners nor the secondary polygyny of *A. decemarticulatus* colonies have been noted in *H. physophora*, thus requiring the de novo colonization of the plant by founding queens (Djiéto-Lordon et al. 2005; Feldhaar et al. 2000, 2003; Young et al. 1997). The temporal succession of colonies induces periods of time during which the plants are not protected by their associated plant–ants and, thus these periods are unfavorable to their growth and survival. However, given that the re-colonization process is rapid and continuous throughout the year, these unfavorable periods of time are generally kept to a minimum. Moreover, the evolutionary persistence of this association is favored by the highly specialized nature of the interaction that ensures the constant re-colonization of the plants by *A. decemarticulatus* queens (Grangier et al. 2009).

Altogether these results demonstrate that the specialized interaction between long-lived plants and ants with a shorter lifespan produces an asymmetry in the generational turnover and the evolutionary rates of the two partners. On the one hand, such an asymmetry could be seen as a destabilizing factor for the association because the populations of the long-lived mutualist can only respond slowly to increases in densities among the shorter-lived partner. Thus, when members of this shorter-lived guild of mutualists compete for access to their host, asymmetries in the generational turnover may increase the intensity of this competition (Stanton 2003). However, in the present case interspecific competition for the occupancy of *H. physophora* individuals is extremely weak (Grangier et al. 2009). Thus, the evolutionary persistence of the *H. physophora*–*A. decemarticulatus* association seems possible due to the absence of an alternative partner for the plant combined with the dynamics of the interaction

which enables *H. physophora* to still produce offspring during their lifetime.

Acknowledgments We are grateful to T. Goslar from the Poznan Radiocarbon Laboratory, Poland and M. Paterne from the LSCE CNRS-CEA, France, for their help in the determination of the ^{14}C age, to C. Trontin for her valuable assistance in the lab and to Andrea Dejean for proofreading the manuscript. We would like to thank V. Rico-Gray and two anonymous reviewers for their valuable comments on the manuscript. We would also like to thank the Laboratoire Environnement de Petit Saut for furnishing logistical assistance. Financial support for this study was provided by the Programme Amazonie II (project 2ID) of the French Centre National de la Recherche Scientifique (CNRS), by the Programme Convergence 2007–2013 Région Guyane (project DEGA) from the European Community, by a research program of the French Agence Nationale de la Recherche (research agreement no. ANR-06-JCJC-0109-01), and by the ESF-EUROCORES/TECT/BIOCONTRACT program. The experiments comply with the current laws of France.

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