# *Ontogenetic succession in Amazonian ant trees*

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**In the tropical rain forest of the Central Amazon, a small guild of specialized plant-ants nest exclusively inside the leaf domatia of Tachigali (Caesalpinaceae). Since normally each plant houses a single ant colony, the number of unoccupied plants in the environment is quite low and the number of potential colonizer queens is high, the conditions for intense intra and interspecific competion for nesting site are set. This study describes an intriguing ecological pattern that explains how this ant guild can coexist using exclusively Tachigali plants as nesting site. We found that each of the eight different ant species occurs in plants of different heights (Kruskal-Wallis test statistics = 148.6, d.f. = 7, P < 0.001). This spatial pattern emerges due to interspecific ant colony replacements along the ontogeny of the tree. We discuss that this pattern can be seen as an ontogenetic succession since an organism's ontogeny is defining a non-seasonal, directional and continuous pattern of colonization and extinction of interacting populations. Ontogenetic succession can be classified at the same level of another class of succession that has been termed degradative succession. The ontogenetic succession view highlights chains of indirect interactions that are mediated by the focal organism and has the potential to produce unexpected outcomes in population interactions and community structure. We suggest that ontogenetic succession should be widespread in nature and that the concept can contribute to our understanding of the temporal and spatial organization of the world biodiversity.**

*Tachigali* are tropical trees that possess an odd life history. After escaping heavy post-dispersal seed predation, the wind-dispersed seeds of *Tachigali* germinate to remain in the seedling bank for many years (Kitagima and Augspurger 1989). The young shade-tolerant sapling, with long-lived leaves, grows very slowly waiting for a growth opportunity created by a canopy gap (Fonseca 1994). Given chance and enough time, the thin tree, with a modest crown, will reach the canopy to eventually become a magnificent emergent tree. After decades of reproductive inactivity, the tree will spend a few months producing a large number of bee and hummingbird-pollinated yellow flowers. After this single reproductive event, *Tachigali* plants will produce their single seed set to finally die (Foster 1977). The

theoretical basis for the evolution of semelparity in this singular canopy tree remains poorly understood (Young and Augspurger 1991).

Another aspect that makes *Tachigali* a fascinating system is that most species in the genus are ant-plants. Their leaves bear ant-domatia that are used by specialized ants as nesting sites (Wheeler 1921, 1942). Despite a century-old debate, this ant-plant association has proved to be mutualistic (Belt 1874, Bailey 1923, Wheeler 1942, Fonseca 1993, 1994). On the one hand, the plants receive protection against their herbivores, growing more vigorously in the presence of their ant partners (Fonseca 1994) and, on the other hand, the growth and reproduction of the ant colonies depend on the nesting space provided by the plant (Fonseca 1993, 1999).

In Central Amazon, *Tachigali* plants are used as nesting site by a small guild of specialized plant-ants (Fonseca and Ganade 1996). Because (i) each plant normally house a single ant colony, (ii) the number of unoccupied plants in the environment is quite low, and (iii) the potential number of colonizer queens in every reproductive season is high, the conditions for intense intra- and interspecific competition for nesting sites are set (Fonseca 1991, 1993, Fonseca and Ganade 1996). This study describes an intriguing ecological pattern that explains how this ant guild can coexist using exclusively *Tachigali* plants as nesting sites.

## Methods

This work was conducted on the tropical rainforest reserves Cabo Frio (2°24′S, 59°52′W) and Km 41 (2°24′S, 59°43′W) of the Biological Dynamics of Forest Fragments Project in Central Amazon (Lovejoy and Bierregaard 1991). The area has the richest ant-myrmecophyte community ever recorded with at least

16 myrmecophyte species and 25 ant species (Fonseca and Ganade 1996). The site has only two *Tachigali* species, *T. myrmecophila* Ducke and *T. polyphylla* Poepp. & Endl., that are associated with a small guild of specialized ant species which could not be found in other myrmecophytes of the region (Benson 1985, Fonseca and Ganade 1996, Fonseca 1999) or in ground-level bait collections (Benson and Harada 1988).

In 1989, a 9-ha permanent plot in the reserve Cabo Frio was intensively surveyed in order to investigate the patterns of ant species occurrence. All *Tachigali* plants were located, tagged, mapped and had their height measured. The occupancy status of understorey plants and mid-size trees were investigated either directly or with the aid of a 12 m pole. Canopy trees were climbed and had at least one sample from each major branch collected to verify its occupancy status and the identity of their ant partners. Each plant was classified as unoccupied (when the leaves showed no signs of domatia entrance in the leaf raquis and ants were absent) or occupied (when domatia entrance were present and ant activity was visible); in the latter case, we collected a representative sample of its ant colony to posterior identification. In 1991, we revisited the Cabo Frio site and repeated the same procedure in order to verify if ant species occurrence had changed through time.

Also in 1991, in order to verify if the patterns of ant species occurrence were consistent across space, we located, tagged and mapped all *Tachigali* plants in randomly located transects (200 × 5 m) in a 100 ha area in the Km 41 reserve (for details about the field site and methodology see Fonseca and Ganade 1996).

In 1994, we collected data on ant colony structure of the two most common *Tachigali* ant partners, the sister species *Pseudomyrmex concolor* and *P. nigrescens*. In the reserve Km 41, *T. myrmecophila* plants containing either *P. concolor* or *P. nigrescens* were located. Plants with different ant partners were paired based on the number of leaves and 10 pairs were randomly chosen for study. In a single week, all plants were collected. In the laboratory, all plants were dissected and ant colony size and structure were recorded.

## Results

In Central Amazon, *Tachigali* plants provided nesting sites to two *Pseudomyrmex* (Pseudomyrmecinae) and six *Azteca* species (Dolychoderinae). We found that different ant species occurred in plants of differing heights (Kruskal-Wallis test statistics = 148.6, d.f. = 7, P < 0.001, Fig. 1), suggesting an interesting mechanism of species coexistence.

*Pseudomyrmex concolor* F. Smith was the dominant ant in small understorey plants (0.5–4 m), occurring mostly up to 7 meters. *Pseudomyrmex nigrescens*, the
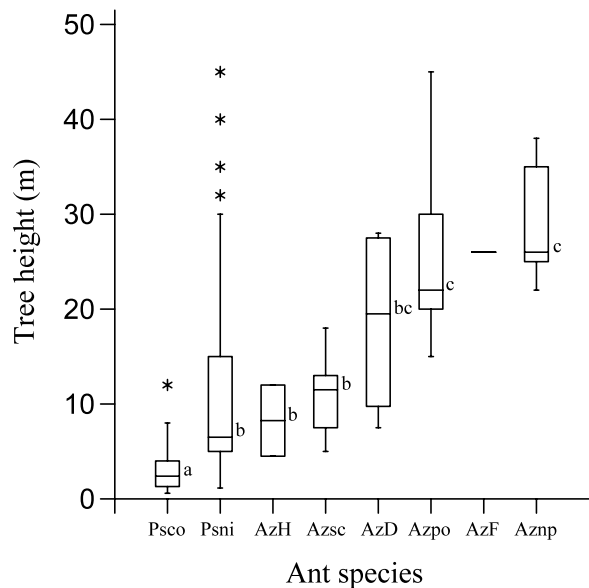


Fig. 1. Height of the trees occupied by each one of the eight ant species associated with *Tachigali* spp. in Central Amazon. In the box plot, the median tree height of each ant species is represented by the center vertical line; the box edges shows the first and third quartiles; whiskers indicate the 10th and 90th percentiles, while asterisks represent observations that fall beyond these limits. Medians marked with different letters are statistically different at least at the 5% level (Mann-Whitney). Species codes are: Psco – *Pseudomyrmex concolor* (n = 125); Psni – *Pseudomyrmex nigrescens* (n = 86); Azsc – *Azteca schummani* (n = 14); Azpo – *Azteca polymorpha* (n = 19); Aznp – *Azteca* nr. *polymorpha* (n = 5); AzD (n = 4), AzF (n = 1) and AzH (n = 2) – unidentified species of *Azteca*.

most height-generalist species, dominated the middle-size trees (5–15 m), followed in abundance by *Azteca schummani* Emery, and by the unidentified *Azteca* species D and H. Most canopy trees (20–30 m) were occupied by colonies of *Azteca polymorpha* Forel (*Azteca* F being recorded only once), while emergent trees, with fully exposed crowns, were occupied mostly by enormous colonies of the tiny *Azteca* nr. *polymorpha*. This pattern was quite consistent across plant species and between sites, except by minor differences. *Pseudomyrmex concolor* occurred in slightly taller *T. polyphylla* plants when compared to their occurrence in *T. myrmecophila* ones (Mann-Whitney U = 1093, d.f. = 1, P = 0.012) and plants occupied by *P. nigrescens* were taller in the Cabo Frio Reserve in comparison to plants that they occupied in the Km 41 reserve (Mann-Whitney U = 1364, d.f. = 1, P < 0.001).

The temporal processes related to this spatial pattern were carefully investigated by following the nature of interspecific ant colony replacements in permanently tagged plants, between 1989 and 1991, in 9 ha of the Cabo Frio Reserve. Out of the 338 marked plants in 1989, 253 were small saplings with no domatia. In agreement with the spatial pattern, these small plants

after producing their first domatia were mostly colonized by *P. concolor* (N = 4) and *P. nigrescens* (N = 3). Most of the 85 colonized plants in 1989 remained with the same ant species in 1991, showing no seasonal changes among years. Most of the observed interspecific ant colony replacements were in accordance with the spatial pattern. Understorey plants occupied by *P. concolor* colonies, after the two-yr time lag, were replaced by *P. nigrescens* (N = 5). Sub-canopy trees occupied by *P. nigrescens* were replaced by *A. polymorpha* (N = 4) and *A.* nr. *polymorpha* (N = 1). Canopy trees dominated by *A. polymorpha* were replaced by *A.* nr. *polymorpha* (N = 3). A few 'reversal' cases, however, were recorded but most of them between ant species that occur in plants of the same height class (e.g. *P. nigrescens* to *P. concolor*, *A.* nr. *polymorpha* to *Azteca* D). This temporal pattern suggests that the spatial pattern described above is indeed produced by a continuous and directional series of interspecific ant species replacements.

*Pseudomyrmex concolor* and *P. nigrescens* are two sister species that occurred in short and tall *Tachigali* trees, respectively,. The two species are very similar in size and shape but differ considerably in colony structure. While *P. concolor* colonies are facultatively poligynous, containing up to eight queens, *P. nigrescens* colonies always exhibit a single queen. Furthermore, the two species seem to have different patterns of resource allocation to reproduction. A covariance analysis on the number of winged reproductives as dependent variable showed a significant interaction between ant species, a categorical variable with two levels, and the number of workers in the colony as a covariant ($F_{[1,17]} = 4.4$, $P = 0.05$, $R^2 = 0.45$). The results indicate that comparing similar sized colonies, resource allocation is precociously diverted to the production of winged reproductives in *P. concolor*.

## Discussion

### The ontogenetic succession concept

Succession is defined as a non-seasonal, directional and continuous pattern of colonization and extinction of species populations (Begon et al. 1996). Our results suggest that the three proposed criteria for the recognition of a successional pattern – directionality, continuity and non-seasonality – were satisfied by the *Tachigali*-ant system. Therefore, we would like to propose that the intriguing ecological pattern described above can be seen as a case of ontogenetic succession. Here, we coin the term ontogenetic succession as a special kind of succession that is triggered by the birth and propelled by the ontogeny of a focal organism. In the ontogenetic succession, the birth of the focal organism will make available a new, unexplored substrate for species colonization. At the beginning, only some species are able to exploit it. During the ontogeny of the focal organism, however, the availability and quality of the resource can change dramatically, allowing new interactions to take place and forcing the termination of old ones.

Successional patterns have been classified following different criteria, depending on the history of the substrate (primary and secondary succession), the nature of the stimulus (autogenic and alogenic succession), the trophic level of the organisms involved (autotrophic and heterotrophic succession) and so on (Begon et al. 1996). Ontogenetic succession can be classified at the same level of a widespread type of succession that has been termed degradative succession (Begon et al. 1996). In this case, it is the death of the organism, animal or plant, that precipitates a successional pattern dominated by detritivores and microorganisms (Kendrick and Burges 1962, Doube 1987, Swift 1987). Indeed, in a sense, ontogenetic and degradative succession can be considered to be part of a single continuum process.

## Ontogenetic succession in *Tachigali*

Field observations allowed us to understand some of the behavioral processes behind the ontogenetic succession pattern. *Pseudomyrmex concolor* queens are responsible for the majority of the colonization trials in small unoccupied saplings (N = 13 observations against one of *P. nigrescens*), being the main pioneer species in this succession. Once the queen gets in, it seals itself inside the domatium to produce its first brood. After three to four months from the colonization event, the first workers of *P. concolor* will start patrolling the plant's surface. Then, the colony will grow and occupy any domatium subsequently produced (Fonseca 1993). *Pseudomyrmex concolor* colonies during several years will protect their hosts against their specialized and generalist herbivores, clean the leaf surface of microepiphytes, fungi and debris, and cut down eventual encroaching lianas (Fonseca 1994). All together, these activities will stimulate plant growth that eventually will set the conditions for their own replacement by the mid-successional *P. nigrescens*.

The transitional period, when both ant species coexist in a single host, is temporally short and starts when a solitary *P. nigrescens* queen is able to successfully colonize the apical domatium of a 3–5 m height, unbranched *Tachigali* tree. Based on field observations (N = 10 plants), it seems that colony replacement is assured by two different mechanisms: a) direct competition for nesting space (domatia), involving overt aggression at the territory frontiers with behavioral dominance of *P. nigrescens*; b) loss of nesting space for *P. concolor* due to higher rates of leaf loss at the bottom of crown, together with continuous gain of

nesting space for *P. nigrescens* due to the production of new, apical leaves. The latter mechanism is crucial, since it has been demonstrated that nesting space is the main limiting factor controlling ant colony size in *P. concolor* (Fonseca 1993). The behavioral process involved in the substitution of ant species occurring in higher trees is much more difficult to study, however a few observations suggest that invading species initially establish and dominate lateral, isolated branches to eventually expand to the whole crown.

The comparative data on ant colony structure of *Pseudomyrmex concolor* and *P. nigrescens* suggest that ant succession can affect the evolution of ant colony life history traits. A comparison of the reproductive allocation pattern between the sister species *Pseudomyrmex concolor* and *P. nigrescens* suggests that resource allocation is precociously diverted to the production of winged reproductives in the pioneer species *P. concolor*. Colonies of *P. concolor* with less than a hundred workers can be found to be reproductively active, a weird strategy considering the possibility of staying in the tree until it reaches the canopy, but in fine accordance with its pioneer life history. In contrast, during the colonization process the mid-successional *Pseudomyrmex nigrescens* allocates its resources primarily to the production of more workers, postponing the investment into reproductives to a later phase when the tree and the colony have reached a larger size. Another important divergence is also worth noticing. While *P. nigrescens* colonies have a single queen, the colonies of *P. concolor* are facultative polygynous with up to eight queens contributing to colony growth (Fonseca 1993).

The processes behind the spatial and temporal patterns in *Tachigali* are not yet fully understood, however, part of the answer seems to be related to the connection between the architecture of the host and the life history of the ants (Davidson and Fisher 1991, Fonseca 1999). Along its ontogeny, *Tachigali* grows from a small, architecturally simple, understorey sapling with a few domatia, to a huge, highly complex emergent tree containing hundreds to thousands domatia. Also, domatia size changes considerably along the plant ontogeny; domatia are relatively small in samplings, reach their maximum size in trees that are 5–10 m high, and are also small in emergent trees (Fonseca 1991). Concomitantly, along the plant ontogeny, the ant partners seem to change from low energy demanding species with specialist and solitary feeding habits, large body, small colony size, low growth rates, and early reproductive investment (e.g. *Pseudomyrmex concolor*) to high energy demanding species with generalist feeding habits, group foraging behaviour, small body size, large colony size, high growth rates, and with late reproductive investment (e.g. *Azteca* spp.). Independent of which factor is driving the ant partitioning of *Tachigali* resources along its ontogeny, it seems to be allowing ant species coexistence.
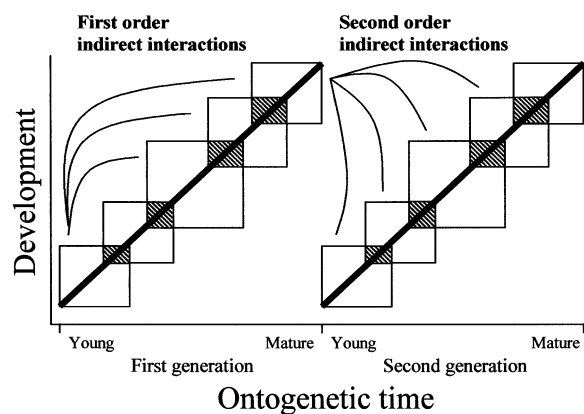


Fig. 2. Indirect interactions mediated by the ontogeny of a focal host species can occur within a given generation (first order indirect interactions) and between generations (second order indirect interactions). The diagonal line represents the ontogeny of the host species. Interacting species, represented by rectangles, can be restricted to ontogenetic phases and time. Direct interactions, represented by the hatched areas, are only possible when the species co-occur in ontogenetic time. A few, first and second order, indirect interactions are indicated by the curved lines.

## Corollaries of the concept

The ontogenetic succession concept highlights chains of indirect interactions that are mediated by the focal organism (Fig. 2). Those indirect interactions have the potential to produce unexpected outcomes in population interactions and alter community structure. In *Tachigali*, an analysis of the direct interactions alone suggests that competition is the single force driving the ant community structure, since the ants are obliged to compete for the limiting nesting sites offered by the same host species. However, early successional ants guarantee plant growth and survival for their replacements (Fonseca 1994), and late successional ants possibly increase seed and sapling production beneficial to early successional ants, therefore, generating indirect, mutually positive interactions among ant species.

The cross-generation nature of the ontogenetic process determines asymmetric relationships between earlier and later species involved in the ontogenetic succession. While the effect of earlier populations on later populations are verified within a given generation of the focal species (first order indirect interactions, Fig. 2), the impact of the later on earlier populations is expressed only across generations of the focal species (second order indirect interactions, Fig. 2). We believe that this special case of indirect interactions have been frequently neglected because the interacting populations are separated in ontogenetic time. In extreme cases, interacting populations can be separated by centuries through ontogeny, as can be the case for leaf herbivores and seed predators of monocarpic bamboos (Janzen 1976).

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## Where can ontogenetic succession be found?

In principle, the birth of any organism has the potential to create a new substrate for species colonization in the same way that volcanic eruption, glacial retreat and treefalls do. We expect, however, that ontogenetic succession will be more evident in systems offering resources that change significantly in quantity or quality along its ontogeny. If changes in resource quantity and quality along the ontogeny are marginal, species will overlap widely and ontogenetic patterns will fade. Therefore, ontogenetic succession patterns should be widespread both in higher plants and large, complex animals.

Natural historians have long known that particular species of phytophagous insects are associated with plants of a certain age or size (Lawton 1983). The activities of pollinators, nectar-robbers and florivores are all associated with the reproductive age of their hosts (Barth 1991). In other myrmecophytes, size-specific ant associations involving different ant partners have been recorded in some ant-myrmecophyte systems (Davidson et al. 1989, Longino 1991, Young et al. 1997, Vasconcelos and Davidson 2000). Lichens, lianas and many epiphytes are known to prefer trees of different heights (Sillet and Rambo 2000). In insects, parasitoid and hyperparasitoids, are known to attack victims of certain size (Price 1980). The complex symbiotic gut flora of most animals, especially the ruminant mammals, is continuously assembled during their infancy, changing considerably along the organism's ontogeny (Hungate 1975). Also, many important diseases in humans are known to be age dependent (Nokes 1992).

Among the several systems where ontogenetic succession can be expected to occur, one seems to us particularly noteworthy. In tropical rainforests, a single old canopy tree can support thousands of individuals from a myriad of arthropod species and an additional number of lianas, epiphytes and pathogens (Erwin 1982). This complex species assemblage was produced by a continuous historical process that was initiated by the dispersal, germination and establishment of a relatively species-free seed. We know very little about the building-up of this ontogenetic succession pattern. How do species numbers change through time? What is the rate of species turnover during the process? Does the colonization by some species facilitate or inhibit the colonization of later species? Can ontogenetic succession allow species coexistence? Is it leading to evolutionary responses in life history and host use? Considering the unquestionable contribution of the tropical tree arthropod fauna to the world biodiversity (Erwin 1982, Wilson 1988), and the pace that ecosystem degradation is occurring throughout the tropics, it seems to us that the ontogenetic succession concept can help us structure our understanding of the temporal and spatial organization of such a complex and diverse community.

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