

Research article

An experimental study of bamboo ants in western Amazonia

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Abstract. Numerous ant taxa naturally inhabit stems of live and dead *Guadua* bamboo (Bambusoidea, Poaceae) in western Amazonia. In an experiment at the onset of the wet season in Peru's Manu National Park, we augmented potential nest sites in stems of live bamboo, dead bamboo and dead caña brava (*Gynerium sagittatum*, another woody grass) at five stations within each of ten bamboo patches and ten control areas outside those patches. Each experimental stem possessed three vacant and available internodes, pre-drilled with, respectively, large, small and linear holes, mimicking the range of forms of surveyed natural entrances. After 24 days, approximately 13% of 798 available internodes had been colonized, the majority by fragments of existing colonies. Ignoring entrance type, which did not affect colonization for any species or species group, and censoring non-independent internodes of the same stem, we used individual stems as independent sample units in other tests. One specialist in live bamboo (*Camponotus longipilis*), and a likely specialist in dead bamboo (*Camponotus depressus*), were identified based on overrepresentation in bamboo habitat and disproportionate occurrence in live or dead bamboo stems. A third species, *Camponotus (Pseudocolobopsis)* sp.) was more abundant in bamboo areas but colonized both dead bamboo and dead caña. Relatively high abundance of standing dead stems in *Guadua* forests may account for the presence of a dead stem specialist. The experiment missed detecting specialization in one live culm specialist (*Camponotus mirabilis*), likely due to its failure to simulate conditions required for the species' unique modes of colony establishment and spread into new culms. Most opportunistic stem nesters colonized dead bamboo at significantly greater rates than dead caña, but were either equally well represented in bamboo and control areas, or underrepresented in bamboo habitat. Given low colonization rates overall, underrepresentation in bamboo cannot be attributed to competition from bamboo specialists for nesting space. Rather, it may be due to combined

effects of seasonal flooding of bamboo habitat, and greater importance of food limitation, relative to nest site limitation, in that habitat.

Keywords: Ants, bamboo, *Camponotus*, colonization, *Guadua*, Peru, plant-ant, stem nests, western Amazonia.

Introduction

Approximately 180,000 km² of *terra firme* habitat in southwestern Amazonia are covered in "bamboo-dominated forests" (Nelson, 1994). Both these, and some of the region's floodplain forests, consist of a mosaic of heterogeneous forests lacking bamboo, and monodominant stands of arborescent *Guadua* species (Bambusoidea: Poaceae) with just scattered trees. Within the latter, bamboo cover appears to be favored in zones where root growth is blocked seasonally by anoxic conditions in perched water tables, making trees unusually susceptible to windthrow (Griscom and Ashton, 2002). Once established, bamboo diverts normal forest succession to its advantage through a combination of root competition and mechanical bending, breaking and crushing of tree seedlings and saplings by relatively short-lived and structurally weak culms that are often water-filled and heavy (Griscom and Ashton, 2002).

Despite bamboo's prominence in this region, its associated biota remains poorly studied, due in part to the inaccessibility of a habitat where giant, recurved thorns of dense standing and fallen culms tear at clothing and flesh. Even in relatively well-known taxa, previously unrecognized cases of habitat specialization continue to be discovered (e.g., Kratter, 1997). Prominent among bamboo specialists in the Australasian tropics are various ant taxa (Hymenoptera, Formicidae) that reside in culms or woven leaf nests (Kohout, 1988, 1989; Dorrow and Maschwitz, 1990; Buschinger et al.,

1994; Dorrow, 1996; Schellerich-Kaaden et al., 1997; Maschwitz et al., 2000). Although ants are also listed among insects surveyed from western Amazonian *Guadua* (Louton et al., 1996), both their taxonomic affiliations and the degree of their specialization remain unexplored. Moreover, to the extent that these and other insects are specialized to *Guadua*, both the short life spans of individual culms (Smith, 2000) and the resultant high abundance of dead stems, are apt to have affected specialization in interesting ways.

Working in the Manu National Park of Madre de Dios, Peru, we used an experimental approach to assess both the degree and nature of ant specialization to bamboo. Like most ant-associated bamboos (Buschinger et al., 1994; Schellerich-Kaaden et al., 1997; and Maschwitz et al., 2000), *Guadua* spp. lack the ant-attractants typical of true myrmecophytes (e.g., Davidson and McKey, 1993). Therefore, any confirmed associations between ants and bamboo may reflect unidirectional specialization on the part of ants. Absence of ant attractants also complicates assessments of whether common bamboo inhabitants are true specialists versus just opportunistic stem nesters, taking advantage of suitable nest sites in any form. Even where exhaustive sampling turns up no colonies outside of bamboo habitat, it is difficult to rule out the presence of these same species elsewhere. This problem is exacerbated for residents of dead bamboo, where ant species richness may equal or exceed that in live bamboo (below). Our experiment constitutes an attempt to overcome such difficulties by investigating rates at which particular ant taxa colonize supplemental nests sites in live bamboo, dead bamboo, and another woody grass species. All supplemental stem-types were made available inside and outside of bamboo habitat, and both overrepresentation in bamboo habitat and selective use of bamboo stems were required for diagnosis of specialization. Queens of some bamboo-nesting ants have elongate, slender, rectangular heads (Dorow, 1996), which could possibly affect the sizes of holes they might block during the colony founding period (Schellerich-Kaaden et al., 1997). Our supplemental nest sites were provided with prefabricated entrance holes imitating naturally occurring entrances of three sizes and shapes.

Materials and methods

Study site, timing and plant species

Our study took place in tropical moist forest at the Estación Biológica Cocha Cashu in Madre de Dios, Peru (EBCC, 11°54'S 71°22'W). Mean annual precipitation here is ~2.2m, and is distinctly seasonal, falling mainly between October and April. Onset of the wet season coincides with release of many winged reproductive ants, and likely with rapid degradation of already decomposing stems. To increase the probability of observing colonization of newly available nests, we therefore timed our studies to coincide with the early wet season in late October and early November, 2001.

Most of EBCC's approximately 55 km of trails are situated in the floodplain of the Río Manu. Bamboo is patchily distributed within the trail system, with most stands located west of the oxbow lake (Cocha Cashu). Much more expansive and continuous bamboo forests occur on surrounding high terraces. Just a few kilometers from the trail system,

these upland forests likely serve as species source areas for bamboo specialists. The somewhat isolated patches in which we worked are therefore apt to house most or all of any bamboo ants in those greater expanses. Both *Guadua weberbaueri* and *G. sarcoarpa* occur at EBCC but were indistinguishable in the absence of reproductive structures (Londoño and Peterson, 1991). Recent and general masting of bamboo in the Río Manu floodplain occurred last in 1978. Masting in upland forests took place during a period encompassing our study (2001–2002), and many plants in those habitats still bore small numbers of reproductive spikes and were gradually dying back. However, a few small and isolated individuals failed to reproduce, and at least some live and dead bamboo culms are known to have been available continuously near EBCC during the past 30 years (J. Terborgh, pers. comm.).

Experimental study of nest site limitation

A preliminary survey of ants in lowland bamboo stands at EBCC suggested the presence of several bamboo specialists that had not been detected during prior intensive sampling of arboreal ants in other habitats (ten years of work represented in numerous publications by senior author). To determine the degree of bamboo specialization in these and other ant taxa, we initiated a field experiment in which potential nest sites were augmented in specific ways. We collected recently dead stems of both bamboo (*Guadua* sp. or spp.) and caña brava (*Gynerium sagittatum*, Poaceae), a second woody grass common along building river beaches, and returned them to the clearing grounds for processing. A total of 100 stems of each species were cut to ~1.3 m lengths and verified to have at least 3 vacant internodes, lacking obvious entrance holes or indications (upon shaking) of water or other material content. Then, in three such internodes, and alternating when possible with other unopened internodes, we used a hand drill to make entrances of three types (one hole per internode): small circular holes of 3 mm diameter, large circular holes 4.5 mm in diameter, and 12 mm x 4 mm linear slits, imitating the slit-like entrances occurring naturally in some culms (Davidson et al., in press). To make linear entrances, we used a narrow pocket knife saw to lengthen pre-drilled holes. Orders of entrance types were rotated systematically, so that each type was approximately equally represented in the center internode. All entrances were subsequently closed with small pieces of soft cardboard (egg carton). At least some "vacant" internodes in both caña and dead bamboo were confirmed during processing to house ant colonies or colony fragments that had entered these stem regions from other internodes through holes in internodal septa; such stems were rejected and replaced. Finally, to facilitate recognition and recovery of stems at the end of the experiment, the 200 lengths of stem were tagged with yellow string before placement in the field.

We identified 10 bamboo patches ≥50 m distant from one another in the EBCC trail system. (Although this distance may not have ensured independence of plots relative to foundress sources, most actual colonists were colony fragments.) Patches were then matched with nearby (where possible) control areas with no or few (1–3) live bamboo culms (Fig. 1; see Discussion for justification of allowing some live culms in control patches). Sixty-eight percent of control patches lacked bamboo altogether. Within each patch, we flagged 5 stations, located haphazardly but not within 4 m of a trail, and we sought to impose a minimum distance of 15 m between stations (in one small patch, stations were necessarily closer but still a minimum of 10 m apart). One stem each of dead bamboo and dead caña was placed at each station in semi-erect position, lodged against other vegetation and with one end on the ground. At all stations in bamboo patches, we found healthy live bamboo culms with internodal diameters approximating those of the dead bamboo stems and caña (minimum ≈3 cm), and with at least three intact (unopened) internodes, 3-to-10 internodes from the culm base. We then made one entrance hole per internode, rotating the order of the three entrance types as above, and where possible, skipping alternate internodes. Procedures were identical for live bamboo culms present in control patches. Holes in live culms were sealed with soft cardboard immediately after drilling. Finally, we classified individual stations by their susceptibility to sea-

sonal flooding (low, intermediate and high), as indexed by the presence and density of *Heliconia marginata* (Heliconiaceae) (Foster et al., 1986). Due to small-scale undulations in terrain within this zone of successional former river beaches, stations within patches often fell into different inundation categories and were treated as independent.

On 18 October, we began the experiment by transporting dead stems to all stations and removing the cardboard plugs from each live and dead stem. This procedure took much of the day, but we alternated bamboo and control patches and recorded the order of patch visitation so as to harvest stems in the same order at the end of the experiment. On 11 November, we opened stems in situ and collected and identified their ant inhabitants.

For species or higher taxa sufficiently abundant among colonists of experimental stems, we used Likelihood Ratio Chi-square tests to assess whether colonization frequencies differed by habitat type, culm type, and flooding category. Analyses were repeated for 'opportunists,' including all species known or suspected (from rarity) not to be bamboo specialists. Expected frequencies for these tests were calculated from actual distributions of available internodes and focal stems across habitats, stem types, and flooding categories. We corrected α levels for multiple comparisons using the tablewise Bonferroni method of Rice (1989). Multiple comparisons reduce the power of individual tests. Therefore, and because greater stochasticity was expected for the effects of flooding than for those of habitat and culm type, we analyzed the relationship of colonization rates to flooding frequency only for the most abundant specialist and for lumped opportunists.

Results

In total, 798 newly opened internodes were available for colonization: 300 each in dead bamboo and dead caña, plus 198 in live culms, including 48 entrances in 16 culms scattered across control patches with rare live *Guadua* stems. After 24 days and three significant rainfall events (>2.0 cm), ants had colonized 15.2% of entrances in live bamboo, 19.7% of those in dead bamboo, and just 5% of those in caña. Of 102 colonizations by ants, 62.7% were by carpenter ants in the genus *Camponotus*. Rarer colonists included dolichoderines (*Dolichoderus* spp. *attelaboides* and *debilis*, and *Azteca* sp.), myrmicines (species of *Pheidole*, *Wasmannia*, *Solenopsis*, and *Crematogaster* [*brasiliensis* and *carinata*]), pseudomyrmecines (*Pseudomyrmex* sp.), and poneromorphs (*Pachycondyla* species *villosa* and *unidentata*, *Platythyrea* sp., and an *Ectatomma tuberculatum* alate). Just three individual ant species, and the combined species of three higher taxa (Tables 1 and 2), occupied enough internodes to permit further analysis of colonization patterns. Despite a prominent rainfall event (~ 6 cm) stimulating nuptial flights of at least one bamboo specialist (*Camponotus mirabilis* Emery, see Discussion), solitary foundresses comprised a significant fraction of colonists only in *Camponotus* (*Pseudocolobopsis*) sp. (hereafter *Ca.* [*Ps.*] sp., Table 3). Given the rarity of solitary foundresses, and the lack of evidence for a significant effect of entrance type on colonization frequencies ($P \gg 0.05$ for all common species and grouped taxa), the effects of entrance type were ignored in the remaining analyses. Moreover, replicate colonizations of individual stems by the same ant species were censored, under the assumption that they lacked statistical independence.

Two of the three most abundant *Camponotus* species colonized stems at greater rates inside than outside of bam-

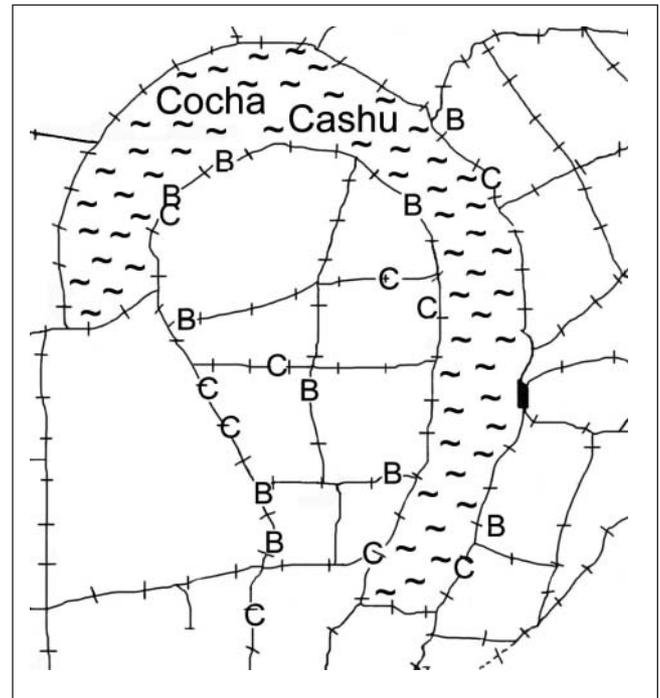


Figure 1. Map of intermingled bamboo patches (B) and control patches (C) within the EBCC trail system.

boo areas (Table 1). *Camponotus longipilis* Emery, a species known previously from just reproductive females (Emery, 1911), exhibited the greatest affiliation with bamboo habitat. Fully 14 of 16 colonization events, all but one involving fragments of established colonies, occurred within bamboo areas, and the two exceptional appearances were in control areas with a few live bamboo culms. Highly significantly (Table 2), all but two colonizations were of live bamboo. One dead bamboo culm was colonized in each habitat type, including a control site with limited live bamboo.

Ca. (*Ps.*) sp. was not significantly associated with bamboo habitat (Table 1), though six of eight foundresses and all three colony fragments appeared in bamboo areas. Both of the exceptional foundress colonizations occurred in control areas completely lacking bamboo. Unlike *Ca. longipilis*, *Ca.* (*Ps.*) sp. was found most frequently in dead stems (Table 2), mostly in dead bamboo, but association with type of dead stem was not statistically significant after tablewise Bonferroni correction (Table 2). Two of three colonizations in caña occurred in bamboo stands; one, by a solitary foundress, was in a control area with limited bamboo.

A third species, *Camponotus depressus*, ostensibly showed no tendency to associate with bamboo habitat (Table 1). However, each of three colonizations in control habitat occurred at stations with small numbers of live bamboo, despite just 34% of the control patches containing some live stems. When analyses were repeated with areas with limited bamboo reclassified as bamboo habitat (and expected colonization rates by habitat adjusted according-

Taxa	Habitat type Bamboo	Corrected Control	P	α
INDIVIDUAL SPECIES				
<i>Camponotus longipilis</i>	14(0.875)	2(0.125)	0.0070*	0.0167
<i>Ca. (Pseudocolobopsis) sp.</i>	9(0.82)	2(0.18)	0.0737	0.0250
<i>Camponotus depressus</i>	6(0.67)	3(0.33)	0.5292	0.0500
AGGREGATE OPPORTUNISTS				
All opportunists	13(0.31)	29(0.69)	0.0009*	0.0125
<i>Ca. (Myrmaphaenus)</i> , 3 spp.	2(0.18)	9(0.82)	0.0091*	0.0167
<i>Crematogaster</i> spp.	3(0.23)	10(0.77)	0.0144*	0.0250
Poneromorphs	3(0.33)	6(0.67)	0.1636	0.0500

* Significant after tablewise Bonferroni correction of alphas for multiple comparisons.

Taxa	Type of supplemental stem		Corrected Dead caña	P	α
	Live bamboo	Dead bamboo			
INDIVIDUAL SPECIES					
<i>Camponotus longipilis</i>	14(0.875)	2(0.125)	0(0.000)	0.0070*	0.0167
<i>Camponotus depressus</i>	0(0.000)	8(0.89)	1(0.11)	0.0128*	0.0250
<i>Ca. (Pseudocolobopsis) sp.</i>	1(0.09)	7(0.64)	3(0.27)	0.1797	0.0500
AGGREGATE OPPORTUNISTS					
All opportunists	4(0.10)	30(0.71)	8(0.19)	<0.0001*	0.0125
<i>Ca. (Myrmaphaenus)</i> , 3 spp.	1(0.09)	9(0.82)	1(0.09)	0.0103*	0.0167
Poneromorphs	1(0.11)	7(0.78)	1(0.11)	0.0466	0.0250
<i>Crematogaster</i> spp.	1(0.08)	8(0.62)	4(0.31)	0.1396	0.0500

* Significant after tablewise Bonferroni correction of alphas for multiple comparisons.

Table 3. By ant taxon, frequencies of colonization of supplemental stems by female foundresses versus colony fragments at EBCC, over 24 days in October–November, 2001; sample sizes in Tables 1 and 2, and $N = 1$ for *mirabilis*.

Taxon	Colonization frequency	
	Founding queens	Colony fragments
<i>Ca. depressus</i>	0.000	1.000
<i>Ca. longipilis</i>	0.125	0.875
<i>Ca. mirabilis</i>	1.000	0.000
<i>Ca. (Ps.) sp.</i>	0.545	0.455
<i>Ca. (Myrmaphaenus)</i> , 3 spp.	0.000	1.000
<i>Crematogaster</i> spp.	0.077	0.923
Poneromorphs	0.222	0.778
All opportunists	0.071	0.929

ly), *Ca. depressus* was significantly overrepresented in bamboo habitat ($\chi^2 = 4.33$, $df = 1$, $P < 0.05$). [Reclassification did not affect conclusions for either *Ca. longipilis* or *Ca. (Ps.) sp.*] Moreover, all occurrences of this species were in dead stems, and dead bamboo was significantly overrep-

Table 1. By ant taxon and habitat type, colonist numbers (and colonization frequencies), compared by Likelihood Ratio χ^2 to frequencies of available stems in bamboo (0.564) and control (0.436) patches.

Table 2. By ant taxon and stem type, colonist numbers (and colonization frequencies), compared by Likelihood Ratio χ^2 to frequencies of available stems: live bamboo (0.248), dead bamboo (0.376) and dead *Gynerium sagittatum* (0.376).

resented in relation to dead caña ($LR\chi^2 = 6.20$, $df = 1$, $P = 0.01$, Table 2).

In contrast to these three species, all four groups of opportunists occurred mainly in control areas. Of the three significant results for opportunists in Table 1, only that for all opportunists together was non-significant after reclassification of limited bamboo areas as bamboo habitat. Opportunists as a whole, but not in individual categories thereof, were underrepresented in live stems, relative to dead stems of bamboo plus caña ($LR\chi^2 = 6.40$, $df = 21$, $P = 0.0114$, Table 2). When live stems were omitted from data sets, all categories of opportunists except *Crematogaster* were overrepresented in dead bamboo culms relative to dead caña [all opportunists: $LR\chi^2 = 13.6$, $df = 1$, $P = 0.0002$; CA(MP): $LR\chi^2 = 7.36$, $df = 1$, $P = 0.0067$; poneromorphs: $LR\chi^2 = 4.50$, $df = 1$, $P = 0.0245$].

Consistent with the occurrence of bamboo at sites with perched water tables (Griscom and Ashton, 2002), bamboo stands were significantly more likely than were control areas to have experienced moderate-to-high frequency of seasonal inundation (Fig. 2, $\chi^2 = 14.60$, $df = 2$, $P = 0.0007$, comparing the two distributions). Not surprisingly then, the live bamboo specialist, *Ca. longipilis*, colonized selectively in flooded

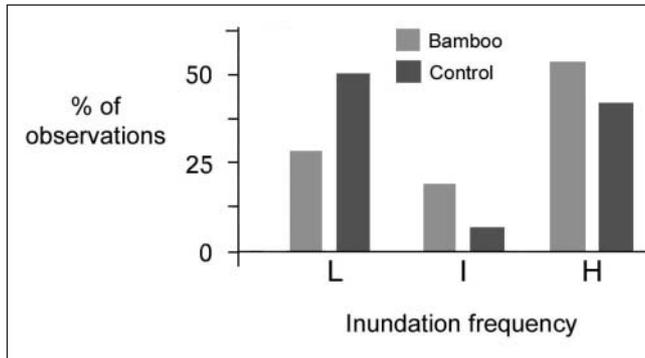


Figure 2. Percentages of (50) bamboo stations and (50) control stations by category of inundation frequency: L = low, I = intermediate, and H = high frequency.

areas, though the species was overrepresented only in areas of intermediate flooding frequency (Fig. 3, $LR\chi^2 = 6.91$, $df = 2$, $P = 0.03$). In contrast, opportunists colonized disproportionately in areas with low inundation frequency (Fig. 3, $LR\chi^2 = 6.04$, $df = 2$, $P = 0.05$).

Discussion

Bamboo specialization

Our experiment identified unambiguously just one live bamboo specialist, *Ca. longipilis*, which was overrepresented in both bamboo areas and live bamboo culms and appears to be nutritionally dependent on coccids (*Cryptostigma guadua*, Kondo and Gullan, 2004; authors' unpubl. data). *Ca. depressus* was detected only in areas with limited-to-much bamboo (opposite the pattern for opportunists), in addition to colonizing dead *Guadua* stems selectively. During 10 field seasons studying arboreal ants at Cocha Cashu, the senior author has frequently observed this diurnal and conspicuous species in bamboo habitat but never in intervening forest, and workers followed to nest sites invariably nested in bamboo. *Ca. depressus* may be tied to dead bamboo because it provides superior nest sites, or by nutritional dependency on prodigious wound exudates produced at sites of insect damage to growing culm tips (authors' unpubl. data). Such strict reliance on nests in dead bamboo currently appears to be restricted to neotropical bamboo ants. Its detection could be due to the power of an experimental approach, rather than to intercontinental differences in ant faunas, but we doubt that dead bamboo specialists would have eluded colleagues working in Asia. More likely, it reflects a real disparity in standing proportions of dead versus live bamboo culms. Compared to many Asian bamboos, *Guadua* culms are weak and impermanent, and their stands full of recently downed stems (Smith, 2000; Griscom and Ashton, 2002, Davidson et al., in press).

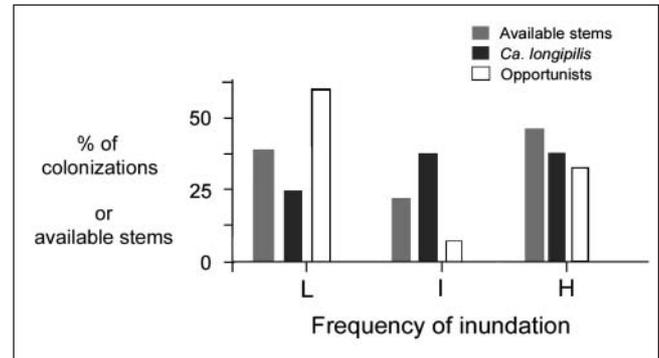


Figure 3. Percentages of total colonization events by estimated flooding frequency for *Ca. longipilis* and lumped opportunists; for comparison, percentages of 100 experimental and control stations in those same flooding categories.

Like *Ca. depressus*, *Ca. (Ps.)* sp., also occurs principally in dead stems, but it is not a bamboo specialist. This species both colonized two experimental stems in areas totally lacking in bamboo, and failed to discriminate between dead caña (>1/4 of colonized stems) and dead bamboo (Tables 1 and 2). Although it and *Ca. longipilis* (which is occasionally found in dead stems), are placed in different informal subgenera of *Camponotus* (*Pseudocolobopsis* and *Myrmostenus*, respectively), the two species are sufficiently alike morphologically to be classified together in subgenus *Pseudocolobopsis* (R. Snelling, pers. comm.). This similarity raises the conjecture that the two taxa could have shared a common ancestor nesting in dead stems generally but somewhat more successful in bamboo habitat.

Confounding our ability to detect specialization was our allowance for a few live bamboo culms in 34% of control areas. We designed the experiment this way intentionally, initially anticipating higher colonization rates of foundresses and the possibility of identifying colonization/competition tradeoffs among various bamboo-specialized ants (sensu Yu et al., 2001). However, foundress colonizations were few, and isolated stems just rarely occupied by live bamboo specialists. Rapid occupation of experimental stems by colony fragments suggests that established colonies search constantly for new nests, perhaps because nest quality declines relatively quickly (authors' unpubl. data). Exceptionally high representation of foundresses among colonizing *Ca. (Ps.)* sp. (Table 3) suggests either conditions uniquely favorable to their nuptial flights, or relatively high reproductive investment and widespread searching by queens of this nonspecialist.

The predominance of colonization by colony fragments over solitary foundresses likely traces to two causes. First, compared to ants associated with myrmecophytes, those living in clonal bamboo have relatively short-lived nests and an abundance of new nest sites developing nearby. Second, solitary foundresses may have specialized modes of colony founding that assure access to nutritionally important coccids but prevent them from colonizing experimental stems (Davidson et al., in press, and below). For example, our experiment

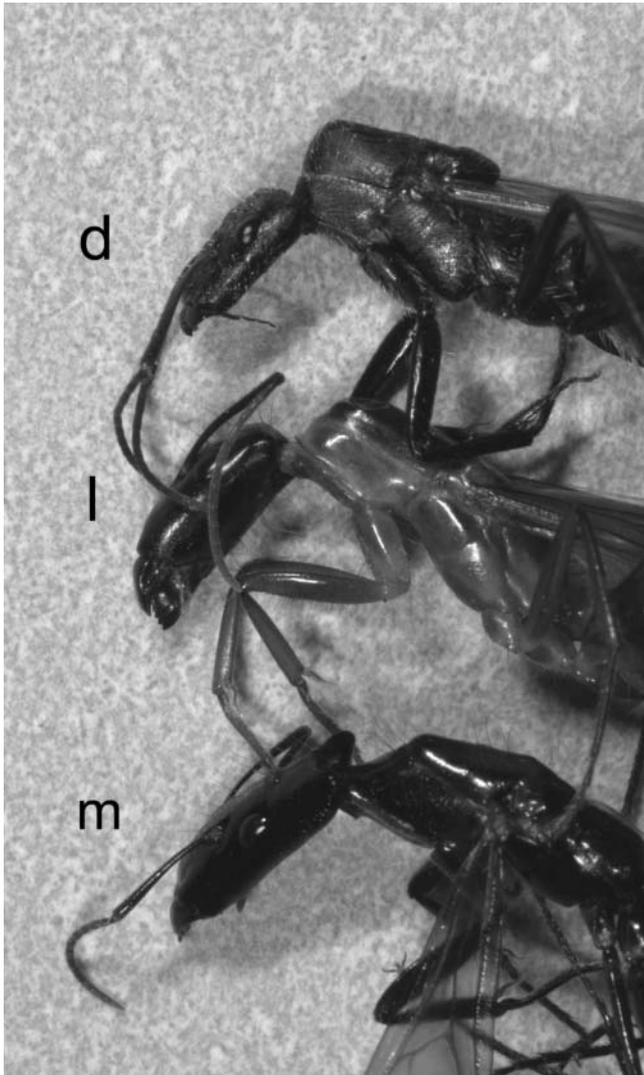


Figure 4. Foundresses, illustrating long, flattened, nearly rectangular head shapes, of *Camponotus* species: *depressus* (d), *longipilis* (l) and *mirabilis* (m).

detected just a single occurrence of one highly specialized bamboo ant (*Camponotus mirabilis* Emery), unique among recognized bamboo ants in modes of colony foundation and expansion (Davidson et al., in press). Established colonies grow and occupy multiple culms after workers open entrances in young *Guadua* stems prior to lignification. Furthermore, *Ca. mirabilis* foundresses appear to initiate their colonies by invading *Ca. longipilis* nests and taking over established coccid populations, a primary source of food (honeydew). Like *Ca. mirabilis* foundresses, those of *Ca. longipilis* do not appear to transport coccids with them on nuptial flights (authors' obs.), and the source of their coccids is unknown. However, after frequent damage to nest stems by *Cebus* monkeys, *Ca. mirabilis* colonies regularly abandon their stems and live coccids (Davidson et al., in press). If *longipilis* foundresses can take advantage of abandoned coccids, they too may have evolved specialized modes of colony initiation. Fi-

nally, nests of *Ca. (Ps.)* sp. can contain *Cryptostigma*, as well as relicts of the shelves that *Ca. mirabilis* builds inside its stems (Davidson et al., in review). These observations suggest that it also may inhabit abandoned *mirabilis* nests and perhaps tend remaining coccids. However, absence of coccids from some *Ca. (Ps.)* sp. nests in live bamboo suggests that the species does not propagate its own coccids.

After culm walls have lignified, no bamboo specialist appears able to open entryways to unbreached internodes (Davidson et al., in review), and both live and dead bamboo specialists apparently depend either on entrances cut by other arthropods, or on cracks and fissures in fractured stems. In retrospect, bamboo specialization by *Ca. longipilis*, *Ca. mirabilis* and *Ca. depressus* might have been suspected from the long, narrow or flattened head shapes referenced in the initial descriptions of females (the only castes yet described in the former two species, Fig. 4 and Emery, 1903, 1911) and also occurring in foundresses of known Asian bamboo ants (e.g., Dorow, 1996). The morphology of *Ca. (Ps.)* sp. queens is not unusual for subgenus *Pseudocolobopsis*.

Opportunistic stem nesters in relation to stem type and habitat

Opportunists as a whole rarely colonized live bamboo stems, and those invading dead stems were significantly overrepresented in bamboo relative to caña. The question of why opportunists so rarely colonize live bamboo, or indeed, live stems generally (D. Davidson, pers. obs.), is an interesting but poorly explored aspect of the biology of tropical arboreal ants. Although we expected bamboo specialists to colonize at greater rates within than outside of bamboo patches, we had not anticipated the more than two-fold higher representation of opportunistic *Crematogaster* in control areas. Low occupancy of experimental stems overall suggests that competition from bamboo specialists for nests in bamboo areas cannot account for this result. Instead, our findings may reflect habitat differences in one or both of two factors. First, seasonal inundation may be particularly detrimental to opportunists, which nest overwhelmingly in dead stems that can continue to afford acceptable nest space even after falling (see also Majer and Delabie, 1994, for reductions in litter and shrub-associated ant faunas in seasonally flooded habitats). Disproportionate seasonal flooding of bamboo areas (Fig. 2) might then strongly favor taxa with the capacity to colonize live stems. Supporting this hypothesis, *Crematogaster* species were the most common (and nearly the only) residents of *Guadua* stems in higher-ground areas immediately north of the research station on the east side of Cashu Cocha. Although specializing in live culms, *Ca. longipilis* was overrepresented only in areas estimated to flood at intermediate frequencies. It is possible that this highly timid species finds a refuge from opportunists in intermittently and moderately flooded areas but is disadvantaged by deep flooding due to its occasional dependence on terrestrial nests (above) or the difficulty of commuting among stems in search of new nests (Davidson et al., in press). Deeply

flooded bamboo areas tend to be dominated by *Ca. mirabilis* (Davidson et al., in press).

Alternatively, or in addition, bamboo and control areas may differ on average in the relative availabilities of food versus nest sites. As evidenced by a high frequency of vacant stems (authors' observations, see also Maschwitz et al., 2000), favorable nest sites are likely so plentiful in bamboo stands that, except for coccid-tending *mirabilis* and *longipilis*, carrying capacity is generally set by availability of food resources. Plant biomass in such areas is approximately two-thirds that in surrounding forest (Nelson et al., 2001), and *Guadua* has not evolved to produce ant rewards. Opportunistic stem-nesters of bamboo stands included species of *Ec-tatomma*, *Wasmannia* and *Solenopsis*, all omnivores that, like *Ca. depressus*, feed avidly on wound exudates at culm tips. Insect herbivores, a potential protein source, occur principally on the growing tips of young shoots, representing just a tiny fraction of standing biomass (authors' observations). Greater depth of accumulated leaf litter in bamboo stands (authors' observations) suggests slower decomposition rates, likely correlated with low densities of decomposers, including leaf litter arthropods on which many ants feed. Seasonal flooding of bamboo stands on perched water tables (Griscom and Ashton, 2002, and above) may also reduce arthropod abundance. Lending support to these hypotheses, prior to reductions in litter arthropod biomass by removal trapping at a nearby site in Madre de Dios, Pearson (1986) found lower biomass in bamboo habitat than in both floodplain and *terra firme* forests. In contrast to the high balance of nest sites to food supply in bamboo stands, limitation of stem nests in surrounding forests may regularly hold ant populations below the carrying capacity set by relatively abundant food resources, and/or stimulate individual colonies to investigate and occupy new nest sites at greater frequency.

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