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Diacamma species Photo: Jochen Drescher

Ants in a Bornean rainforest: aggressive resource defence and a surprising case of tolerance

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In a tropical forest such as Danum Valley, ants are virtually everywhere. They are found in all microhabitats from the litter of the understorey up to the canopy of tallest trees, and are usually more abundant than any other animal (Hölldobler and Wilson 1990). Most ants are omnivores and use a broad spectrum of resources: they intensively collect nectar and honeydew, dead animals and faeces, but also heavily prey on other arthropods. Ants are so abundant that they detect most food items within minutes – every visitor to a rainforest will notice this immediately after dropping some food on the forest floor. Because of this extraordinary high density, ants regularly encounter other ants, and the most important enemies and competitors of ants are … ants. How do they cope with the high level of competition in such a situation?

Bornean rainforests are particularly diverse and densely populated by ants from a variety of lifestyles (Chung 1995). During our research in Danum, we were particularly interested in the structure of ant communities – how do different ants coexist and partition their resources on a small scale? Do they aggressively defend and effectively monopolize their resources, trails, and nests? Moreover, do the communities differ in complex rainforests in comparison to more simple environments altered by human activity?

Ants and plants

Many ant nests in the tropics are found above ground, on living plants or dead wood. They use various kinds of crevices and structures, nest in the roots of epiphytes, or construct their own shelters with collected material. Most ants are thus largely independent in their choice of tree species for their nests. However, some ants have evolved a tight relationship with plants. This is particularly pronounced on trees and shrubs of the genus *Macaranga* (Euphorbiaceae) and other so-called myrmecophytes. They are common in the forest at Danum and surrounding secondary vegetation. These ant-plants provide preformed structures (domatia) to continuously harbour ant nests, but also food bodies to nourish their colony (Fiala et al. 1999). In turn, the ants defend and protect their plants against enemies such as herbivores (Heil et al. 2001). Since both partners benefit from each other, this association represents a classic case of mutualism. Other kinds of mutualisms include flowers versus pollinators or fruits versus seed-dispersing animals, but the degree of specialisation in *Macaranga* – ant associations or other myrmecophytes is particularly high (Blüthgen et al. 2007). Often only one or two species of tiny *Crematogaster* ants inhabit a single *Macaranga* species (Fiala et al. 1999).

A large number of plant species in tropical forests regularly attracts ants with nectar glands (extrafloral nectaries) to their leaves. In contrast to myrmecophytes, associations between ants and extrafloral nectaries are much more loose and opportunistic (Blüthgen et al. 2007). The nectar is readily available on the surface, and a great number of ant species feeds on a single plant species and even on the same plant individual. It's more a come-and-go situation, not a long-term relationship as in myrmecophytes.

Like myrmecophytes, the plants bearing extrafloral nectaries also benefit from ants as bodyguards against leaf-feeding insects. However,

Carnivores: While most ants are omnivores and often consume nectar, this one disdains such vegetarian food: Danum 'fire ants' (*Leptogenys* sp.). Above: during a successful raid. (Photos: Nico Blüthgen, Arthur Chung)

Large: C*amponotus gigss* is one of the largest ants worldwide (up to 3cm body length) and common in the interior of Bornean rainforest. (Photo: Nico Blüthgen)

in both cases this protection is far from being perfect: several herbivores including some stick insects (phasmids) successfully attack leaves *Macaranga* and closely related *Mallotus* trees and seem to circumvent the ants' defences. *Mallotus floribundus* and *Mallotus miquelianus* are common small trees in the forest in Danum and actively secrete extrafloral nectar on their young, developing leaves to attract ants. These leaves are also particularly palatable and attacked by a common species of stick insects, *Asceles margaritatus*, among other species (Blüthgen et al. 2006a). This herbivore strongly prefers *Macaranga* and *Mallotus* and is stimulated by the chemistry of the young leaves that are more nutritious than the mature foliage (Blüthgen and Metzner 2007).

Nectar and honeydew

Ants are highly abundant on extrafloral nectaries and seem to consume nectar wherever available. Given their hunger for nectar, it is very surprising to observe only few ants on flowers. Many plants produce nectar in their flowers to attract pollinators, but ants are conspicuously missing on flowers from a number of species both in the forest and in the open vegetation. The nectar is clearly attractive: when it is removed from the flowers, the ants readily consume it. Recently, it became clear that ants are repelled from flowers, particularly by their sweet scent that both pollinators and humans find very attractive. Several flower species tested in Danum were repellent to ants, particularly from larger trees (Junker et al. 2007). This helps plants to prevent ants from stealing nectar. Moreover, too many ants on flowers may otherwise chase off the regular pollinators, particularly stingless bees that are the most common pollinators in the rainforest. Stingless bees themselves also use a chemical defence against ants (Lehmberg et al. 2008), possibly using similar substances like terpenes that are found in flower scents as well as on these bees.

Another type of association between ants and plants is mediated by a third partner: plant-sucking hemipterans. They secrete honeydew, which – like nectar – is composed on sugars and amino acids. Whereas the hemipterans are often quite specific in their choices of host plants, the ants are not: most ant species use a broad spectrum of honeydew-producing hemipterans. In a survey in the forest at Danum, we found 58 ant species that were associated with 62 hemipteran species in a relatively opportunistic way (Blüthgen et al. 2006b). The ant-tended hemipterans involve leaf hoppers, tree hoppers, scale insects, mealybugs and aphids among several other families. Ants even tend true bugs (Heteroptera: Coreidae) for honeydew on the climbing bamboos that are abundant in the forest. However, while ants are opportunistic in their choices of hemipteran partners, they are very possessive once they developed an intimate relationship with one of them. Particularly where larger aggregations of productive hemipterans are found on a twig, ants effectively monopolize these important food sources against their competitors, and maintain these associations over several weeks or months (Blüthgen et al. 2006b). For very productive and nutritious nectar and honeydew sources, competition between ants is severe and ants may aggressively defend their food sources – a common scenario in tropical forests (Blüthgen and Fiedler 2004).

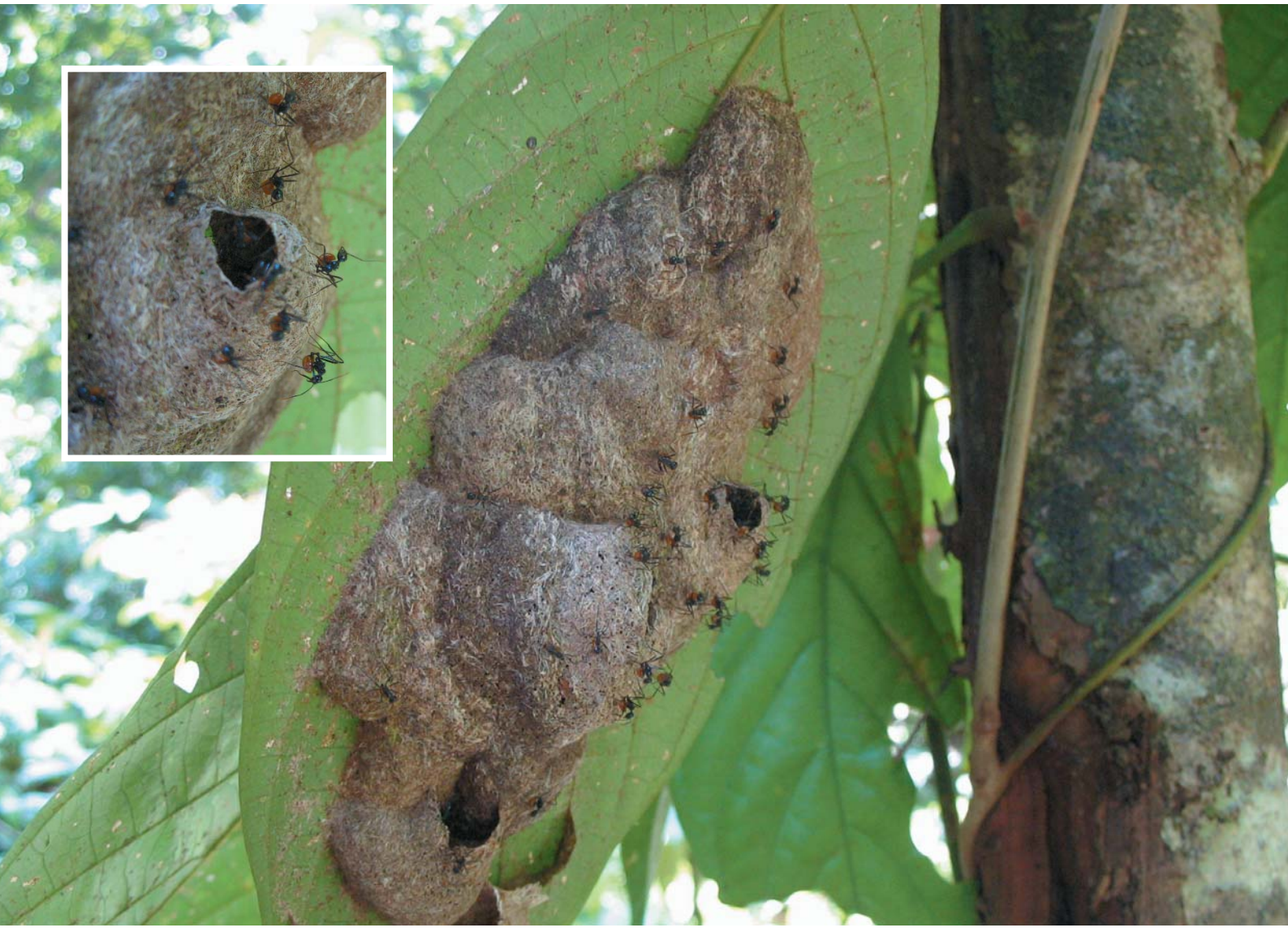
Nectar and honeydew are rich in carbohydrates, but also contain nitrogen in the form of amino acids, albeit in a much lower proportion than in a carnivorous diet. Nevertheless, many ant species depend on this source of amino acids from their plants, and the growing body mass of larvae in their nests is mainly composed of nitrogen

obtained from nectar, honeydew or other plant sap. This has been confirmed by isotope analysis in different rainforests in Borneo, South America and Australia (Blüthgen et al. 2003, Davidson et al. 2003). Most of these ants occasionally feed on other insects as well, but nectar and honeydew seem to provide a more abundant and continuous nutrient supply. Nutrient-rich honeydew and nectar sources are thus worth being defended. Most surprisingly, some ants deviate from this rule: *Crematogaster modiglianii* and *Camponotus rufifemur* farm their hemipterans together, and do not show any aggressive interactions (Blüthgen et al. 2006b). Such a peaceful interaction between two ant species is exceptional among ants, and will come back to these two ant species below.

Aggression and tolerance

There is a widely accepted law for ants and other social insects: ants from one colony are very defensive against other colonies of their own species or any other ant species. Their ability to distinguish nestmates from non-nestmates, a friend from an enemy, is crucial in the life of a colony and a central force in the evolution of chemical signals and their perception. Aggression against non-nestmates is particularly strong at the entrance and surrounding of their nests.

However, every law has its exceptions. There are cases where two ants live together: they share food sources and trails. One of the most spectacular and mysterious cases is found in Danum Valley and elsewhere in Borneo: *Crematogaster modiglianii* and *Camponotus rufifemur* inhabit the same nest. They use the same entrance holes and disappear into the interior of hollow tree trunks, where they keep their brood. *Crematogaster* is active day and night, while the larger *Camponotus* often remains inside the nest during daytime, occasionally seen at the entrance hole in an aggressive pose if disturbed. Both ants tolerate each other, but are very aggressive against other species even from the same genus. At least *Crematogaster* also discriminates between its partner colony and other colonies of the same species (Menzel et al. 2007). Why they tolerate each other, is currently still unknown. *Crematogaster* can do very well without its partner, they inhabit tree hollows and also actively enlarge their tree nests inside the trunk. *Camponotus rufifemur* may be



Independence: Many ant species (here: *Myrmicaria*) build their own nests on trees using carton-like material and are thus independent in their choice of plant species they inhabit, like other ants that use crevices or holes in trees. (Photos: Florian Menzel)

more dependent on *Crematogaster* than vice versa, and we never found a colony without *Crematogaster*. They peacefully share food sources as well.

The association is relatively common in may trees of the forest interior. While the ants often prefer to live in small trees of the genus *Syzygium*, they use other tree species as well. However, they maintain a very close relationship to another plant, the hemi-epiphyte *Poikilospermum cordifolium*. Most entrances of these ants on tree trunks have some seedlings of this *Poikilospermum*, obviously planted by the ants that act like gardeners. Some of the plants grew very large and sent roots down the trunk into the soil. As the ant colonies around those large hemi-epiphytes are currently still active, this suggests that such colonies may live for many years at the same spot, and that the association between *Crematogaster* and *Camponotus* is a very stable one. This relationship between the two ants in a common nest is termed parabiosis, and other species of the same two genera maintain parabioses in South America and Europe as well. In South America, they are also known as gardening ants and integrate epiphytes into their nests – a striking case of parallel evolution from different continents.

Parabioses in Borneo are only found in mature rainforests. Several other complex associations between insects and plants are confined to the forest interior. The ant fauna in secondary forests or small forest fragments is a largely different one (Floren et al. 2001, Brühl et al. 2003, Widodo et al. 2004), and the ant community of the open vegetation around settlements is strongly impoverished. Invasive ants from outside Borneo play a dominant role in the secondary vegetation, e.g. the crazy ant *Anoplolepis gracilipes* that recently arrived at the field station in Danum, and may provide additional negative impacts on the diversity. Several colonies of this species may fuse into powerful 'supercolonies' (Drescher et al. 2007), which may even accelerate their impact. However, intact rainforests seem to be largely resistant against these invaders. Forest reserves such as Danum Valley are important to preserve the original fauna as well as the richness of spectacular interactions among plants and animals.

References

Blüthgen, N., and K. Fiedler. 2004. Competition for composition: lessons from nectar-feeding ant communities. Ecology **85**:1479-1485.

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

Blüthgen, N., F. Menzel, T. Hovestadt, B. Fiala, and N. Blüthgen. 2007. Specialization, constraints, and conflicting interests in mutualistic networks. Current Biology **17**:341-346.

Blüthgen, N., and A. Metzner. 2007. Contrasting leaf age preferences of specialist and generalist phasmids. Oikos **116**:1853-1862.

Blüthgen, N., A. Metzner, and D. Ruf. 2006a. Food plant selection by stick insects (Phasmida) in a Bornean rain forest. Journal of Tropical Ecology **22**:35-40.

Blüthgen, N., D. Mezger, and K. E. Linsenmair. 2006b. Ant-hemipteran trophobioses in a Bornean rainforest – diversity, specificity and monopolisation. Insectes Sociaux **53**:194-203.

Brühl, C. A., T. Eltz, and K. E. Linsenmair. 2003. Size does matter – effects of tropical rainforest fragmentation on the leaf litter ant community in Sabah, Malaysia. Biodiversity and Conservation **12**:1371-1389.

Chung, A. Y. C. 1995. Common lowland rainforest ants of Sabah. The Borneo Nature Series, Kota Kinabalu.

Davidson, D. W., S. C. Cook, R. R. Snelling, and T. H. Chua. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. Science **300**:969-972.

Drescher, J., N. Blüthgen, and H. Feldhaar. 2007. Population structure and intraspecific aggression in the invasive ant species *Anoplolepis gracilipes* in Malaysian Borneo. Molecular Ecology **16**:1453-1465.

Fiala, B., K. E. Jakob, U. Maschwitz, and K. E. Linsenmair. 1999. Diversity, evolutionary specialization and geographic distribution of a mutualistic ant-plant complex *Macaranga* and *Crematogaster* in South East Asia. Biological Journal of the Linnean Society **66**:305-331.

Floren, A., A. Freking, M. Biehl, and K. E. Linsenmair. 2001. Anthropogenic disturbance changes the structure of arboreal tropical ant communities. Ecography **24**:547-554.

Heil, M., B. Fiala, U. Maschwitz, and K. E. Linsenmair. 2001. On benefits of indirect defence: short- and long-term studies of antiherbivore protection via mutualistic ants. Oecologia **126**:395-403.

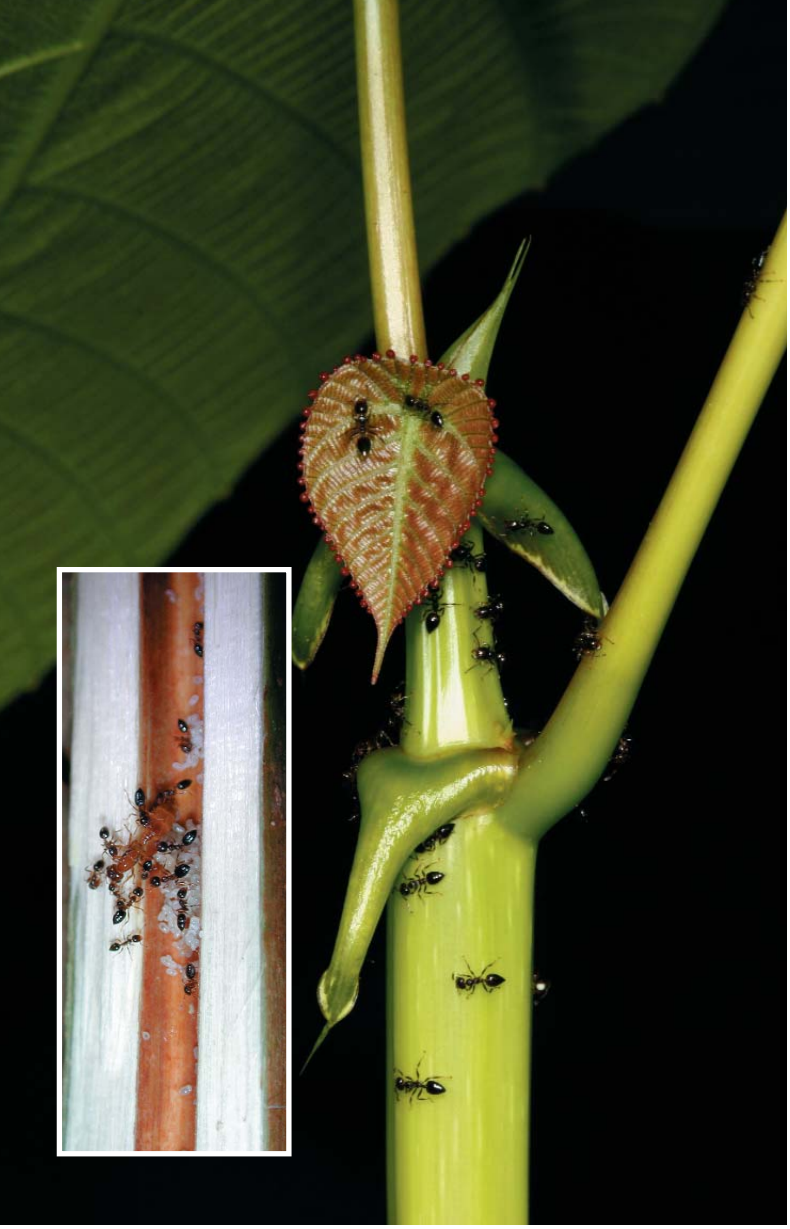
Hölldobler, B., and E. O. Wilson. 1990. The ants. Harvard University Press, Cambridge, Mass.

Junker, R., A. Y. C. Chung, and N. Blüthgen. 2007. Interaction between flowers, ants and pollinators: additional evidence for floral repellence against ants. Ecological Research **22**:665-670.

Lehmberg, L., K. Dworschak, and N. Blüthgen. 2008. Defensive behavior and chemical deterrence against ants in the stingless bee genus *Trigona* (Apidae, Meliponini). Journal of Apicultural Research:in press.

Menzel, F., K. E. Linsenmair, and N. Blüthgen. 2007. Selective interspecific tolerance in tropical *Crematogaster-Camponotus* associations. Animal Behaviour:doi:10.1016/j.anbehav.2007.1007.1005.

Widodo, E. S., T. Naito, M. Mohamed, and Y. Hashimoto. 2004. Effects of selective logging on the arboreal ants of a Bornean rainforest. Entomological Science **7**:341-349.



Spiny (above): *Polyrhachis* ants are unable to sting, but the spines of their body may protect them against some large enemies.
(Photo: Arthur Chung)

Specialised: *Macaranga hosei* trees provide pre-formed apartments for *Crematogaster* ants. Myrmecophytic plants like these also nourish their ant colony with nutritious excretions. The associations are often relatively specific: each *Crematogaster* is only found on one of few *Macaranga* species. Inset: Stem interior of *Macaranga glandibracteolata* with ant workers, brood and queen.
(Photos: Brigitte Fiala and Eduard Linsenmair)

Handcraft: Weaver ants (*Oecophylla smaragdina*) use the silk of their larvae to construct nests. Above: a founding queen with silk. Below: the nest of a mature colony woven from tree leaves.
(Photos: Arthur Chung)

Top left: **Aggressive posture:** When disturbed or when encountering non-nestmates, ants are often highly aggressive (*Oecophylla smaragdina*). (Photo: Arthur Chung)

Top right: **Up and down:** These two ants share the same trail on a tree trunk and do not show any mutual aggression (*Camponotus* is running up and *Polyrhachis ypsiloni* down). (Photo: Nico Blüthgen)

Middle: **Group housing.** The small *Crematogaster modiglianii* and the larger *Camponotus rufifemur* inhabit the same tree trunk nest (parabiosis). From the entrance holes grow seedings of the hemi-epiphyte *Poikilospermum cordifolium*. (Photo: Nico Blüthgen)

Bottom: **Group farming:** *Crematogaster modiglianii* and *Camponotus rufifemur* attend honeydew-producing leaf-hoppers together on the underside of a leaf. Sharing of such trophobioses is uncommon among other ants. (Photo: Florian Menzel)

Monopoly: Ants attend hemipterans for honeydew (trophobiosos) and often monoplize such farms against competitors. But in this case, a mosquito manages to participate in the meal. (Photo: Nico Blüthgen)

When others are asleep: Some ants like this *Camponotus* only attend their hemipterans during the night. (Photo: Nico Blüthgen)

Invader: The yellow-crazy ant *Anoplolepis graciplies* is invasive to Borneo. Here, two workers exchange their liquid food (trophallaxis). (Photo: Jochen Drescher)

Pollinator disturbance: Ants (*Dolichoderus thoracicus*) disturb pollinators during their flower visits, e.g. the stingless bee *Trigona binghami* flying towards *Diospyros durionoides* flowers (lower right corner). In the absence of ants, these bees calmly harvest large amounts of pollen (upper left). (Photos: Nico Blüthgen)

Imperfect protection: Various ants regularly use extrafloral nectaries on young leaves of *Mallotus miquelianus* (Euphorbiaceae), here represented by a species of *Gnamptogenys*. However, such young leaves are often attacked by specialised herbivores, particularly the stick insect *Asceles margaritatus*. (Photos: Nico Blüthgen)