Arthropods in modern resins reveal if amber accurately recorded forest arthropod communities

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Amber is an organic multicompound derivative from the polymerization of resin of diverse higher plants. Compared with other modes of fossil preservation, amber records the anatomy of and ecological interactions between ancient soft-bodied organisms with exceptional fidelity. However, it is currently suggested that ambers do not accurately record the composition of arthropod forest paleocommunities, due to crucial taphonomic biases. We evaluated the effects of taphonomic processes on arthropod entrapment by resin from the plant *Hymenaea*, one of the most important resin-producing trees and a producer of tropical Cenozoic ambers and Anthropocene (or subfossil) resins. We statistically compared natural entrapment by *Hymenaea verrucosa* tree resin with the ensemble of arthropods trapped by standardized entomological traps around the same tree species. Our results demonstrate that assemblages in resin are more similar to those from sticky traps than from malaise traps, providing an accurate representation of the arthropod fauna living in or near the resiniferous tree, but not of entire arthropod forest communities. Particularly, arthropod groups such as Lepidoptera, Collembola, and some Diptera are underrepresented in resins. However, resin assemblages differed slightly from sticky traps, perhaps because chemical compounds in the resins attract or repel specific insect groups. Ground-dwelling or flying arthropods that use the tree-trunk habitat for feeding or reproduction are also well represented in the resin assemblages, implying that fossil inclusions in amber can reveal fundamental information about biology of the past. These biases have implications for the paleoecological interpretation of the fossil record, principally of Cenozoic amber with angiosperm origin.

amber | Anthropocene | fossil record | Madagascar | taphonomy

Reconstruction of ancient ecosystems and their organisms' relationships are key issues in paleobiology, and studies of modern analogs are fundamental for interpreting what happened in the past (1). Fossil assemblages record diverse information about ancient environments, but to reconstruct paleoenvironments it is essential to know the biological, physical, and chemical factors that may have influenced the transfer of paleoecological information to the fossil record. Amber, or fossil resin, of gymnosperms in the Mesozoic and both angiosperms and gymnosperms in the Cenozoic, exceptionally preserves soft-bodied organisms that otherwise are rarely preserved in the fossil record; thus, it is a key source of taxonomic, paleoecological, and paleoenvironmental data. Nevertheless, some authors have proposed that arthropod assemblages found in ambers, although very diverse, have significant taphonomic biases (2–7). Based on field observations, Martínez-Delclòs et al. (4) mentioned different factors that may influence the preservation of insects in amber, including: (*i*) behavior and habitat preferences, (*ii*) body size, (*iii*) resin chemistry, and (*iv*) resin viscosity. However, little is known about the relative importance of these factors. Body size for example was hypothesized to be an important control on arthropod fossilization in amber, presumably during the entrapment process, based on the observation that most arthropods in amber are small (4). Solórzano Kraemer et al. (7) concluded, however, that the size distribution of arthropods preserved in diverse ambers is similar to the general body size distribution of living insects in similar environments. Resins protect the trees from herbivores (8–10) with chemical components that can repel and therefore potentially reduce the abundance of certain insects and other animals. Resins also seal wounds as a natural antibacterial, antifungal, and antioxidant, preventing degradation of plant tissues (11–14). Insects that attack the plant, for example xylophagous beetles, may therefore be overrepresented if they are immobilized and killed by entrapment in the resin (15).

The limited research done on the topic has focused on comparing amber assemblages with arthropods collected from entomological traps, primarily using data from the literature, to determine the similarity of resin to the other traps, and therefore whether particular arthropod ecologies are preferentially preserved in amber. Henwood (3) argued that 20- to 15-My-old Dominican amber

Significance

It is not known whether the fossil content of amber accurately represents the arthropod biodiversity of past forests, and if and how those fossils can be compared with recent fauna for studies and predictions of biodiversity change through time. Our study of arthropods (mainly insects and spiders) living around the resinous angiosperm tree *Hymenaea verrucosa* Gaertner, 1791 in the lowland coastal forest of Madagascar, and arthropods trapped by the resin produced by this tree species, demonstrates that amber does not record the true past biodiversity of the entire forest. However, our results reveal how taphonomic processes, arthropod behaviors, and ecological relationships can influence arthropod death assemblages in resins and play a crucial role in controlling their taxonomic compositions.

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preferentially trapped arthropods from litter and shrub habitats; however, Penney (5) used the spider fauna to argue for a tree trunk source. Bickel and Tasker (16) demonstrated that sticky traps can also be useful for the analysis of the tree trunk arthropod diversity of a specific region. Sticky traps capture organisms upon contact with the surface, ranging in size from minute mites to small vertebrates and representing a wide range of behaviors and morphologies, including the fauna living in the litter. Thus, sticky trap assemblages captured after several days of activity can be considered a representative sample of the arboreal community, at least in terms of arthropods. Malaise traps act in a different manner and are not in contact with the trees, preferentially capturing arthropods less associated with the tree habitat. Solórzano Kraemer et al. (7) showed that both of these types of entomological traps record the largest amount of data and concluded that Mexican amber assemblages (approximately 22–15 My old) were most similar to modern assemblages trapped by sticky traps, but also by malaise traps after comparison with seven different entomological traps, proposing that some taxa appear overrepresented in amber because of their tree-dwelling habits. However, these previous studies used amber collections made by selective rather than unbiased sampling, compared ancient resins to entomological traps assuming that the modern forest is similar to the ancient resiniferous forest because of the presence of *Hymenaea* trees, or even compared ancient resins to entomological traps from other geographic regions and forest types. All of these previous studies have lacked the essential comparative data of arthropod assemblages from entomological traps and from resin collected today from the same tree genus/species in the same forest.

Here, as a crucial novelty we compare the arthropod diversity trapped in resins, produced by *Hymenaea verrucosa* Gaertner (Angiospermae: Fabales: Caesalpinioideae) in Madagascar, with the ensemble of arthropods collected with yellow sticky and malaise traps installed around the trunk (from 0 m to 2 m height) and close to, respectively, the same tree species. As a main goal of the present study, this direct comparison allows us to assess the role of specific taphonomic processes and to determine whether resins contain an accurate record of the forest arthropod community or they preferentially sample particular microenvironments, ecological behaviors, or taxa. The fidelity of resin trapping has implications for the robustness of paleoecological interpretations made from the fossil record of diverse ambers around the world.

Results and Discussion

Fauna Represented in the Resin and Sticky Traps. As an approximation, the combination of the two different samples from the two types of installed traps is a suitable, although not complete, representation of the arthropod fauna in the forest for comparison. Our results show that resin assemblages are similar to yellow sticky trap samples, both from *H. verrucosa* trees, and are a good representation of the arthropod fauna living in or near the resiniferous tree. In contrast, both differ from malaise trap samples collected nearby, indicating that habitat, especially litter, trunk, and branch habitats, and behavior influence entrapment in resin (Fig. 1).

At the arthropod order level, samples are best divided into two clusters by Dirichlet-multinomial mixture modeling (*SI Appendix*, Figs. S10*A* and S11*A*): one containing the malaise trap samples and the other containing the resin and yellow sticky trap samples (*SI Appendix*, Figs. S10 *B* and *D* and S11 *B* and *D*). The resin sample plots on the periphery of the yellow sticky trap samples in a 2D nonmetric multidimensional scaling (NMDS) ordination (Fig. 2 and *SI Appendix*, Figs. S10*C* and S11*C*), indicating that the arthropod order-level composition of resin differs in subtle ways from the composition of the yellow sticky traps. Although Diptera (flies) are more abundant in resin than in yellow sticky traps, and Hymenoptera (wasps, bees, and ants) and Collembola (springtails) are slightly less abundant in resin, random permutations of sample identities imply that those differences are not greater than might be expected by chance (Fig. 3*A*). Furthermore, the mixture modeling analysis consistently assigns resin and yellow sticky trap samples to a single cluster, suggesting that the difference in composition was small relative to the variability among sticky trap samples.

At family level, there are slight differences in the relative abundance of Diptera between resin and yellow sticky trap samples, but those differences do not exceed the confidence intervals obtained from random permutation (*SI Appendix*, Fig. S4), which are large, given the heterogeneity of the yellow sticky trap samples. For other groups [Coleoptera (beetles) and Araneae (spiders)], family-level data only come from yellow sticky traps and resin. However, as in the case of Diptera, the resin samples for both Coleoptera and Araneae plot near the periphery of the 2D NMDS solutions (*SI Appendix*, Figs. S1 and S3), but mixture modeling supports a single, heterogeneous group as the best solution. Ants in yellow sticky traps predominantly belong to small-bodied individuals of the subfamilies Formicinae and
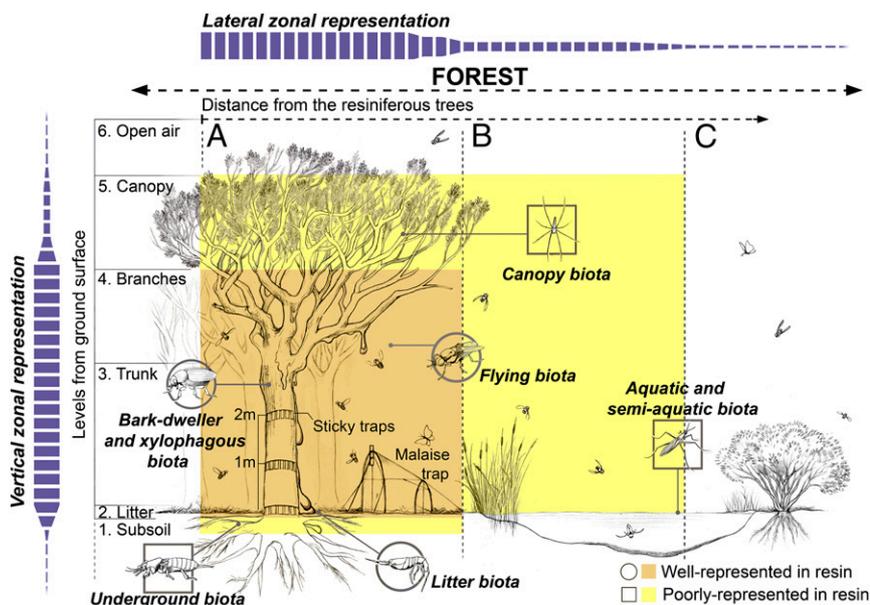
Fig. 1. Diagram of a resiniferous forest (*Hymenaea* model) with representation of biota trapped, mainly arthropods. Circles, main biota represented in resin; squares, scarcely represented; colored in dark orange, zones with a high representation in resin; colored in yellow, zones with a poor representation in resin. (*A*–*C*) Representation of the distance from the tree to the rest of the forest. Artificial malaise and sticky traps are also illustrated to indicate their location with respect to the trees (see *SI Appendix* for more information about methodology). Note: some species of arthropods would be found in several of the areas established here and their representation in resin will depend on several factors, including their abundance or scarcity in the areas best represented in resin.
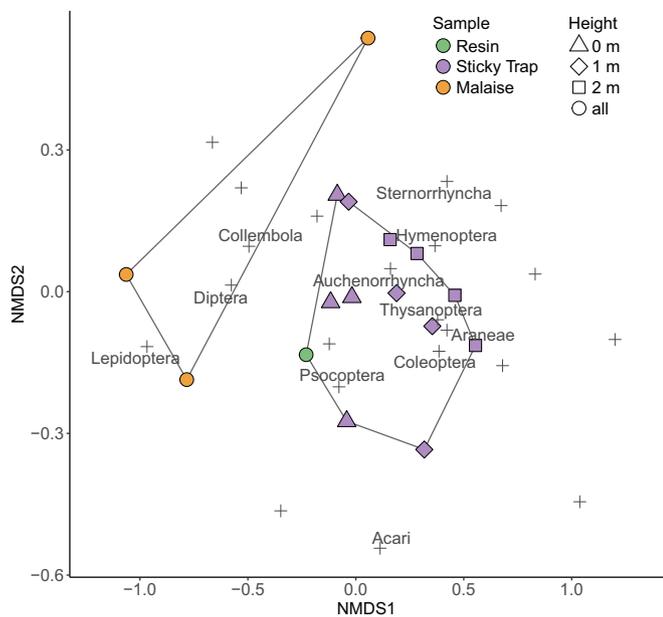
Fig. 2. Dirichlet-multinomial mixture modeling for orders collected in the resin and in the yellow sticky and malaise traps.

Myrmicinae with an extremely wide range of abundances; some samples contain nearly exclusively Formicinae, whereas others contain more than 95% Myrmicinae (*SI Appendix*, Fig. S5). Myrmicinae are the dominant group in the resin sample (comprising 85% of the ant individuals) and Formicinae are rare, but the abundances of both subfamilies fall within the range of yellow sticky trap samples. The median size and the overall shape of the size distribution are both strikingly similar between the resin sample and all three heights of yellow sticky trap samples (Fig. 3C).

Resin and yellow sticky trap samples seem to work in a similar way, representing the arthropod fauna living in or near the resiniferous tree. However, the arthropod fauna may vary with height (17) on the *H. verrucosa* tree, raising the possibility that some assemblages trapped by resin may be more representative of a certain height rather than of the entire tree fauna. In the NMDS ordination, the combined resin sample plots closest to the 0-m sticky trap samples (Fig. 2), with samples at 1 m and 2 m height progressively less similar. To further test the effects of height, we compared the dissimilarity of all sample pairs from yellow sticky traps from the same height (e.g., two samples at 0 m), all sample pairs from different heights (e.g., a sample at 0 m to a sample at 1 m), and all sample pairs between the arthropods trapped by resin collected from 0 m to about 4 m and those trapped by yellow sticky traps at different heights (e.g., the resin data to a sample at 0 m). Surprisingly, at order level (Fig. 3B) and among Coleoptera (*SI Appendix*, Fig. S6), Diptera (*SI Appendix*, Fig. S7), and Araneae (*SI Appendix*, Fig. S8), height does not significantly affect dissimilarity among samples. Pairs of samples from the same height (0 m–0 m, 1 m–1 m, or 2 m–2 m) are not more similar to each other than pairs of yellow sticky trap samples from different heights (1 m–0 m, 2 m–0 m, or 2 m–1 m), and the average dissimilarities of all pairs fall within 95% confidence intervals obtained from randomly permuting the samples. Only the within-height comparison of samples at 2 m, with order-level data, is more similar than expected from the random permutation (however, it is not surprising to observe one trial outside of the 95% confidence intervals when comparing 24 height pairs). Resin samples, which are a mixture of the arthropods present in resin pieces from diverse heights (*SI Appendix*, Table S1), do not exhibit any greater similarity to a certain height of yellow sticky traps. There are no consistent trends with height

and most pair averages fall within the confidence interval from randomly permuting the samples. Only the dissimilarity of Diptera abundances between resin and 0 m samples is greater than expected from random permutation, and Araneae are more similar between resin and 2 m than expected from random permutation.

Resin properties, such as the nonvolatile compounds that affect viscosity and polymerization to provide physical defenses, may also influence the trapping mechanism (3). According to our field observations the resin from *H. verrucosa* is thinly liquid and the surface remains sticky for a long time (days), enabling formation of long stalactite-shaped resin bodies. These resin bodies operate as hanging yellow sticky traps ideal for catching large amounts of flying or active runner insects, such as hymenopterans (much more common in resin and yellow sticky traps than in malaise traps) or active flying dipteran chironomids (the most common dipteran family in the resin samples and yellow sticky traps) (Fig. 4 *A* and *B*).

Fauna Poorly or Not Represented in the Resin. Resin and yellow sticky traps differ from the malaise traps that capture arthropods not as closely associated with the trees, even though malaise traps are installed next to the trunk. Malaise trap samples clearly have a higher proportional abundance of Collembola, Diptera, and Lepidoptera (moths and butterflies) (*SI Appendix*, Fig. S12). Diptera, Hymenoptera, Coleoptera, and Lepidoptera form the megadiverse orders of insects and are some of the most abundant insect orders in modern ecosystems (18, 19). Nevertheless,
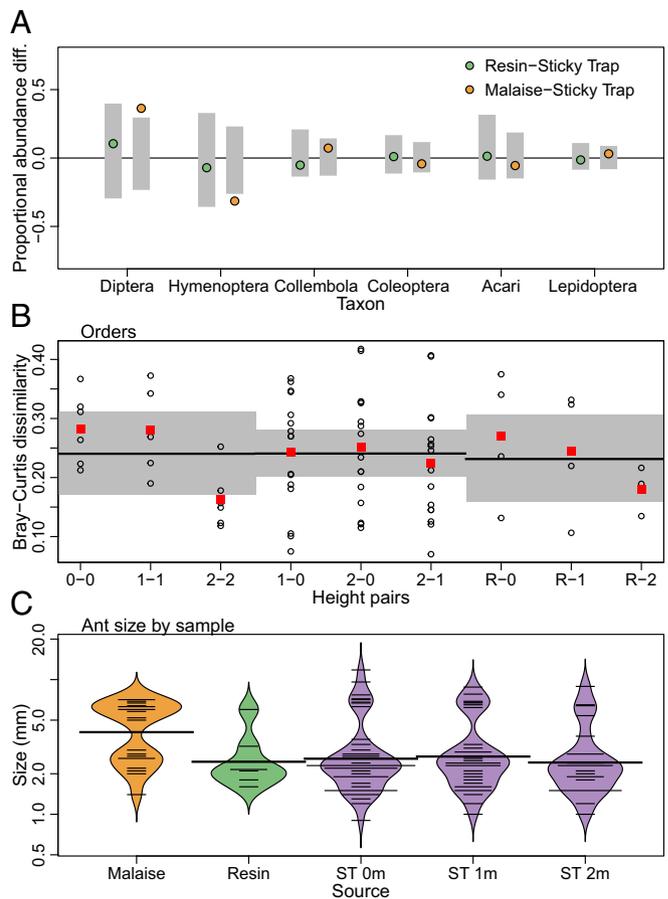
**Fig. 3.** Multiple random permutations for arthropod orders collected in the resin and yellow sticky and malaise traps (*A*). Monte Carlo analysis with random permutations of the three different heights (0 m, 1 m, and 2 m) for the sticky samples at arthropod order level (data from *SI Appendix*, Tables S1 and S2) (*B*). Body size distributions of Hymenoptera: Formicidae (ants) between collection methods (*C*).
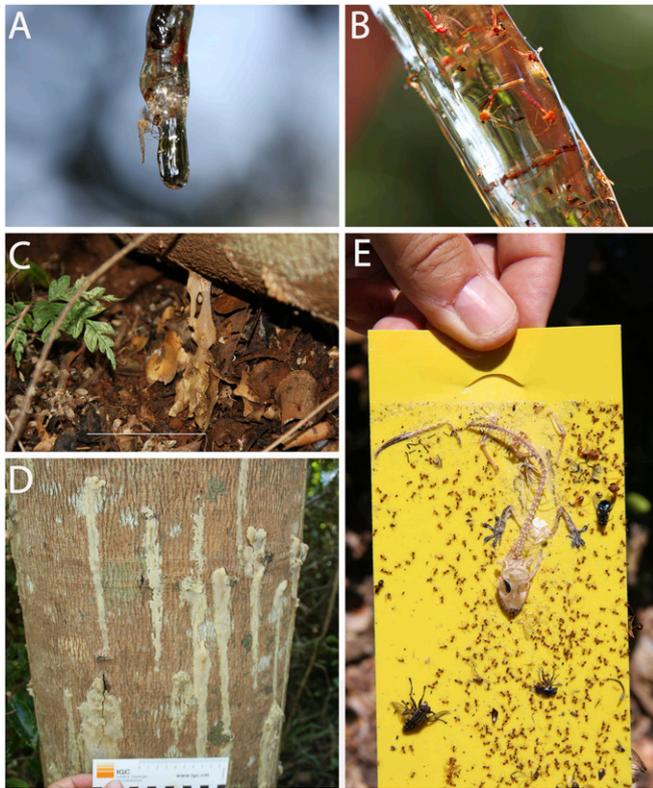
Fig. 4. Resin of *Hymenaea verrucosa* Gaertner (Madagascar) trapping biota and yellow sticky trap. Natural resin bodies operating like yellow sticky traps (chironomid body lengths approximately 5.5 mm) (*A* and *B*). Example of resin emission produced at the litter level (*C*). (Scale bar, 15 cm.) Example of trunk resin emissions due to attacks by ambrosia beetles (*D*). Example of yellow sticky trap showing insects attracted by a previously trapped comparatively large animal, all recorded in the same assemblage, as observed in some amber records (yellow sticky trap width 7.35 cm) (*E*).

Lepidoptera, principally the suborder Glossata, are rarely preserved in fossil resins (20, 21). According to our field observations, this is probably because the few butterflies that rest on the bark and become trapped by the sticky resin most likely are instead eaten by ants before being completely embedded, similar to the fate of large animals, such as lizards (Fig. 4*E*). At lower taxonomic levels, variability among samples is greater and mixture modeling suggests that dividing the samples into clusters is less likely than retaining a single, broad group (*SI Appendix*, Figs. S1–S3). Among Diptera, Chironomidae and Cecidomyiidae are overrepresented and Sciaridae are less common in malaise traps, relative to yellow sticky traps and resin. Subsoil [e.g., some Orthoptera (mole crickets) or some Acari families] and canopy (e.g., some Araneae, Orthoptera, Lepidoptera, or Coleoptera families) fauna, and fauna living far from the resiniferous tree (e.g., aquatic insects), are poorly represented in the resin (Fig. 1) and sticky traps.

The malaise trap samples differ in their abundance of large-bodied ants of the subfamily Ponerinae, comprising 30% of the individuals, in comparison with no more than 2.5% in any yellow sticky trap or resin samples. Furthermore, Ponerinae are absent from 11 of 12 resin samples. Due to the abundance of large Ponerinae in the malaise trap samples, that collection method also yields significantly larger ants (median size 5.2 mm; Fig. 3*D*) compared with either resin (median size 2.15 mm) or yellow sticky traps (median size 2.3 mm) (Kruskal–Wallis test, H = 9.7, df = 2, *P* = 0.008).

Resin and yellow sticky traps show subtle differences, however, potentially as a result of the production of volatile compounds as chemical defenses against herbivores (22, 23). In particular, the compound caryophyllene, found in African *Hymenaea* resin (24),

acts in different species of trees as a defense against herbivores, including some ants, some termites, and various other insect orders (25–27). Thus, the scarce presence of caterpillars in resin samples in comparison with the yellow sticky traps (over 30 specimens in the yellow sticky traps and none in the resin), and perhaps also the rarity of other herbivores such as hemipterans (true bugs) (*SI Appendix*, Table S2), can be explained through deterrence by caryophyllene or other chemical defenses.

Implications for Anthropocene Resins and Ambers. Our results imply that resins preserve an accurate record of the tree-associated arthropod fauna, mainly from the trunk but not from other zones of the forest ecosystem (Fig. 1). This is congruent with Bickel and Tasker (16) who studied tree trunk fauna using sticky traps. Resins collect organisms in a similar manner to the sticky traps, although with biases due to arthropod behaviors and resin properties. Our results contradict in part the results from Solórzano Kraemer et al. (7) who concluded that the fauna trapped in the malaise traps also resembled the fauna trapped in Miocene amber, possibly because the families of Diptera that are preferentially trapped with the malaise traps may also have been more abundant during the Miocene. Our findings provide a framework for interpreting the fossil assemblages from ancient angiosperm amber deposits.

Some arthropods abundant in the *H. verrucosa* forests are rare in the resin, because they do not come close to these trees, for example Lepidoptera. Within Diptera, families such as Cecidomyiidae, Corethrellidae, Culicidae, Keroplatidae, and Stratiomyidae have been extensively collected with the malaise traps, but seldom with yellow sticky traps and are rare in the resin. And within the Araneae, families such as Lycosidae or Mygalomorphae, which are collected with pitfall traps (7) and are common in coastal Malagasy forest, are neither collected in resin nor in sticky traps. Notably, aquatic insects such as Ephemeroptera (mayflies) or Odonata: Zygoptera (damselflies) are extremely rare in the resin, although a few are present in the yellow sticky traps from trees not directly related to water bodies. Usually adults of aquatic insects can fly some distance from their aquatic environments and could be entombed in resin (Fig. 1) when resting on the tree trunks.

Although average dissimilarities between sample pairs at different heights do not show any effect, there is considerable variation among samples at a given height and aggregated data exhibit abundance trends with height that likely result from the habitat and biology of the arthropod groups. For example, soil surface arthropods, such as Acari (mites) and Collembola, are common organisms in resin, amber, and yellow sticky traps, frequently trapped at low heights (Fig. 4*C*) (*SI Appendix*, Table S2). Also, some ants, especially those that nest in litter, are frequent in yellow sticky traps at 0 m and 1 m height. For example, more than 700 specimens of the genus *Nylanderia* (Formicinae) occur at 0 m and 1 m in the sticky traps, likely attracted by dead animals (Fig. 4*E*) in the sticky glue, in contrast to the arboreal ants like *Crematogaster* (Myrmicinae) that dominate the resin samples. Only eight specimens of *Nylanderia* occur in resin, but seven of them were collected from a single piece together with other insects, suggesting that the ants were also attracted by already dead but not completely embedded arthropods. Ants in resin and amber are likely to be dominated by arboreal species. The arboreal *Crematogaster* is the dominant ant genus in tree canopies in Madagascar, where it builds carton nests and is also the most abundant ant in the resin samples. In Mexican and Dominican ambers the most abundant genus is *Azteca* (Dolichoderinae), also an arboreal ant (28, 29) that is not present in Madagascar.

The dipteran families Sciaridae and Phoridae are the two most abundant taxa in yellow sticky traps, also predominantly at 0 m height on the trees (*SI Appendix*, Table S3), as well as in resin and amber. In the case of Sciaridae, larvae and adults are abundant in soil with decaying roots, leaves, or rotten wood invaded by fungi (30). In the case of Phoridae, they share the habitat with Sciaridae but are also mostly predators that may

have been attracted by arthropod carcasses in the resin and yellow sticky traps. Other groups of dipterans such as Scatopsidae appear only in the resin and in the yellow sticky traps; their larvae can be found under bark, in mushrooms, under fallen leaves, or in deadwood. These traits increase the possibility of being trapped by resin; however, adults often do not live close to the tree trunks (17), so Scatopsidae tend to be less abundant in resin than Sciaridae, although they are present in similar habitats. Dolichopodidae also appear in the resin and in the yellow sticky traps, but are rare in the malaise traps. This family, including *Chrysotus* or *Medetera*, are also very abundant in Cenozoic Baltic, Dominican, and Mexican ambers, likely because they rest on tree trunks or the larvae live under bark (7, 31, 32) and because some of them are predators of Scolytinae bark beetles (33), which are also frequent in the resin and yellow sticky traps.

Although some ground-dwelling arthropods are common in the resin, our results do not support Henwood's hypothesis (3) that amber with inclusions reflects subterranean resin production (see also refs. 5 and 7). In some cases, the abundance of ground-dwelling arthropods can be explained by the development of favorable microenvironments at higher heights on the trees, for example, in *H. verrucosa* resin sample R9 (*SI Appendix*, Table S1) collected in a mite- and springtail-rich microenvironment at about 3–4 m high. *H. verrucosa* trees also produce large quantities of resin at low heights (close to the litter) (Fig. 4*C*), potentially trapping larger numbers of ground-associated flying insects such as sciarid and phorid dipterans.

Ground-dwelling beetles are common in resin and amber (Pselaphinae and Scydmaeninae, e.g., ref. 34, our resin samples) because of predatory behavior on small arthropods such as springtails and oribatid mites (35, 36). However, arboreal beetles are also well represented in recent and fossil resin and in the yellow sticky traps. Ptinidae and Chrysomelidae occur frequently in the yellow sticky traps and were also abundant at higher heights on the trees (*SI Appendix*, Table S4). Although Peris et al. (37) speculated that Ptinidae could have promoted resin production by damaging Upper Cretaceous trees, the jaws observed in amber specimens are not strong enough to damage wood and female genitalia are not cutinized for direct deposition into live wood. Thus, they more probably laid eggs on herbaceous plants, or dead or decaying wood (34). The abundance of Ptinidae in the Madagascar yellow sticky traps and in Cenozoic ambers can instead be explained by their high activity on tree trunks. However, some beetles likely were vectors triggering resin production through wood-boring activities and should be overrepresented within amber deposits. McKellar et al. (38) mentioned the possibility that Scolytinae were actively involved in the production of resin during the Turonian (90 My old), while Platypodinae may have played a similar role during the Miocene (15). In our study the genus *Mitosoma* (Platypodinae) is found in yellow sticky traps and in resin samples. In resin, it occurs in high abundance (91 specimens) (*SI Appendix*, Table S4), suggesting that it may have been involved in the production of resin (Fig. 4*D*).

Other arboreal groups of arthropods are similarly well represented in the resin and yellow sticky trap samples, and by extension in amber. Floren (39) found that spiders of the family Theridiidae were the most abundant arboreal spiders, followed by Salticidae (jumping spiders), in a dipterocarp lowland rain forest in Borneo. Those two families were also the most abundant in our resin and yellow sticky trap samples, along with other arboreal spiders such as *Hersilia madagascariensis* (Wunderlich) of the family Hersiliidae (*SI Appendix*, Table S5), a typical bark dweller. Some groups of insects are overrepresented; Psocoptera (barklices) were much more common in resin samples than in either yellow sticky traps or malaise traps, perhaps because of their greater activity on tree bark, where they feed principally upon lichens (40) or because they are attracted by the resin compounds; however, this is still uninvestigated. Isoptera (termites) may be common in resins, and ambers, depending on the presence of an active nest in the resin-producing tree. Worker and soldier castes are present in the yellow sticky trap assemblages from Madagascar, and few imagoes were also found, but only in the two trees with active termite nests (*SI Appendix*, Table S1). However, despite the abundant presence of termite coprolites, similar to their abundance in amber (41), termites were rare in the resins studied (*SI Appendix*, Table S1). The peak of synchronized flight coincides with the onset of the rainy season (ref. 42 and references therein); thus, winged individuals had a short-time window to be trapped in the sticky resin. The deterrence provided by the volatile compound caryophyllene in *Hymenaea* could further explain the reduced abundance of termites in resin samples (43).

Conclusions

Our results imply that the fauna recorded in amber or in Anthropocene resin is not a good representation of entire arthropod forest (paleo) communities, but instead is influenced by habitat and ecological biases. The modern resin in our samples mainly recorded biota living on, or having a close relation with, the resin-producing trees and the arthropods living there; thus important groups of arthropods abundant in the forests can be rare in resin assemblages. If the research focus is limited to the knowledge of the ancient resiniferous tree communities of arthropods, then amber contains a suitable fossil record. However, as trees are also protected from attacks by herbivores, those kinds of arthropods can be underrepresented. Nevertheless, the thanatocoenosis, or set of organisms that died together, constituted by faunal inclusions in resin, contains valuable data about the biology and ecology of the arthropods themselves, which is crucial for the reconstruction of paleohabitats and the study of the evolution of specific behaviors. Inclusions in amber and subfossil resin represent a relevant part of the forest biodiversity of the past. However, the entrapment is principally conditioned by some arthropod behaviors, especially scavenging, predation, microbivory, parasitism, and mating rituals that occur in the arboreal habitat, and herbivory. Although these results are specific to *Hymenaea* resin, an important source of Cenozoic amber, such as Ethiopian, Peruvian, Dominican, or Mexican, it is likely that the well representation of tree-dwelling arthropods is a robust pattern among all resins. Resins from other kinds of trees could have slightly different biases if the viscosity, polymerization rate, or presence of attractant or repellant compounds differed, a field still completely uninvestigated.

Our results allow more accurate paleoecological reconstructions and can explain some peculiar or unexpected aspects of previous reconstructions, for example the abundance of soil arthropods in some amber assemblages. The main implications of the results of the present study for the robustness of paleoecological interpretations made from the amber fossil record are: (*i*) tree-trunk habitats are well represented but there are important limitations for the interpretation of other habitats in the ancient forests, (*ii*) arthropod behavior may lead to over- or underrepresentation, and (*iii*) defensive strategies may also lead to further biases against herbivores.

Actualistic data obtained from faunal assemblages collected with yellow sticky traps are suitable in comparative studies with Anthropocene resin and amber. Also, an inverse approach could be very relevant, for example copal assemblages can be used to study loss of biodiversity in some terrestrial forested regions.

Materials and Methods

Collection Methods. Two different arthropod traps, yellow sticky and malaise traps, were located around and close, respectively, to four trees of *H. verrucosa*. The sticky traps were yellow, odorless, and with an insecticide-free sticky mixture (Fig. 4*E*). Traps were stable for 8 d (*SI Appendix*, Fig. S9) (see *SI Appendix* for separation method). All specimens trapped were preserved in 70% ethanol. Resin was collected from 12 different *H. verrucosa* tree trunks and from the litter (for locality data see *SI Appendix*, Table S6), without selection of those with apparent content of bioinclusions. Arthropods were sorted to order level; Diptera, Coleoptera, and Araneae were sorted to family level; Hymenoptera: Formicidae were sorted to subfamily level; and

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Coleoptera, Formicidae, and Araneae were also sorted by morphotypes and for some of them, the genus and species were identified. These orders were chosen because of their high abundance in modern and fossil resins.

Collection Area. The studied *H. verrucosa* trees are located in the lowland forest close to Pangalanes Channel, in the Ambahy community (Nosy Varika, Mananjary region), on the east coast of Madagascar (20°46′ S, 48°28′ W) (see *SI Appendix* for details). *H. verrucosa* Gaertner was chosen for our study because it is a tree that produces high amounts of resin and because it is considered the sister species of all other *Hymenaea* ssp. (44), today distributed in northern South America and the Caribbean. Sampling (permit no. 160/13) and exportation (no. 186 N.EA10/MG13) of samples were done with permits from the government of Madagascar.

Statistical Methods. We quantified the similarity among resin samples, yellow sticky trap samples (from 0 m, 1 m, and 2 m height), and malaise trap samples with NMDS ordination, using the vegan package in R (45). Samples were grouped into clusters on the basis of their taxonomic composition using Dirichlet-multinomial mixtures (46), a Bayesian approach that identifies whether the samples are best drawn from a single source pool (i.e., without habitat or taphonomic filters), or whether the samples are better clustered in multiple groups (see *SI Appendix* for details). We also used a Monte Carlo approach to evaluate difference in taxon abundance between sample categories, randomly permuting the identity of each sample to generate confidence intervals on the difference in abundance between taxonomic groups (see *SI Appendix* for details).

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Do fossil resins accurately record forest arthropod paleocommunities?: An actualistic approach on amber-archived arthropods

SUPPORTING INFORMATION

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Extended results

I.   GRAPHICS OF THE RESULTS AT LOWER TAXONOMIC LEVELS
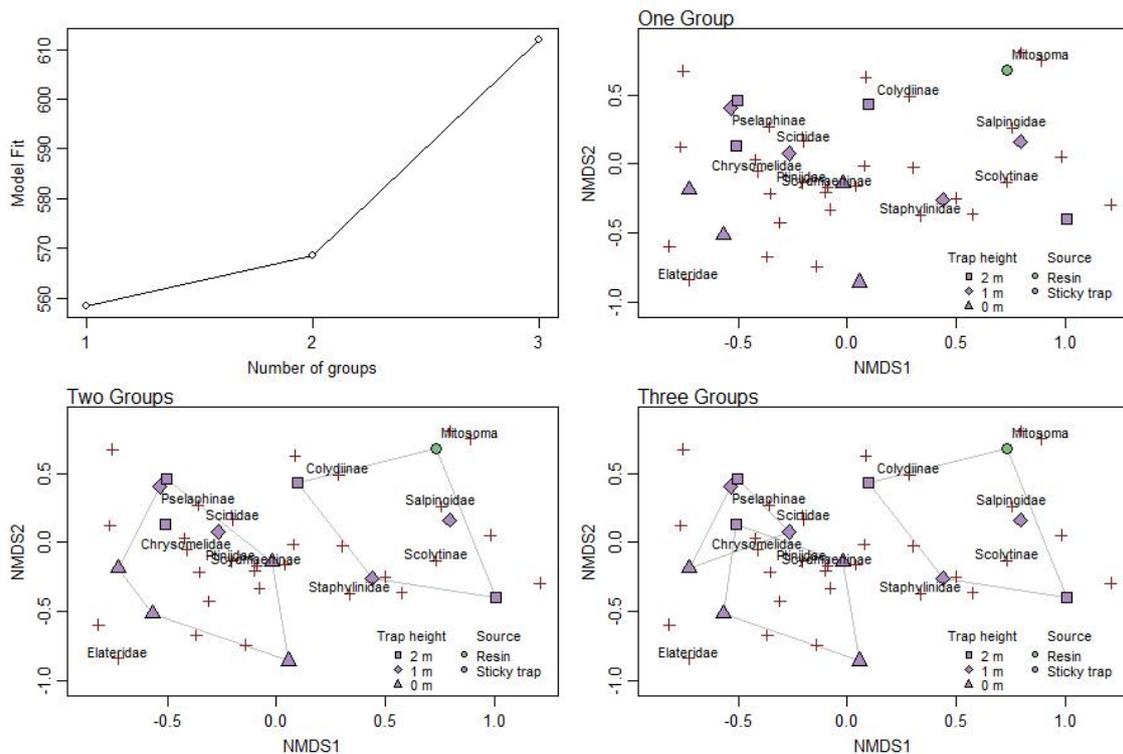
Fig. S1. Dirichlet-multinomial mixture modeling with three-cluster model for the Coleoptera families collected in the resin and yellow sticky trap (divided by the three heights with symbols). The single-group model is best supported. A two-group model has slightly worse model fit, but the resin sample (green circle) still groups with the majority of sticky trap samples. Height also does not explain group membership within the sticky trap samples. Only the eleven most common taxonomic groups are labeled.
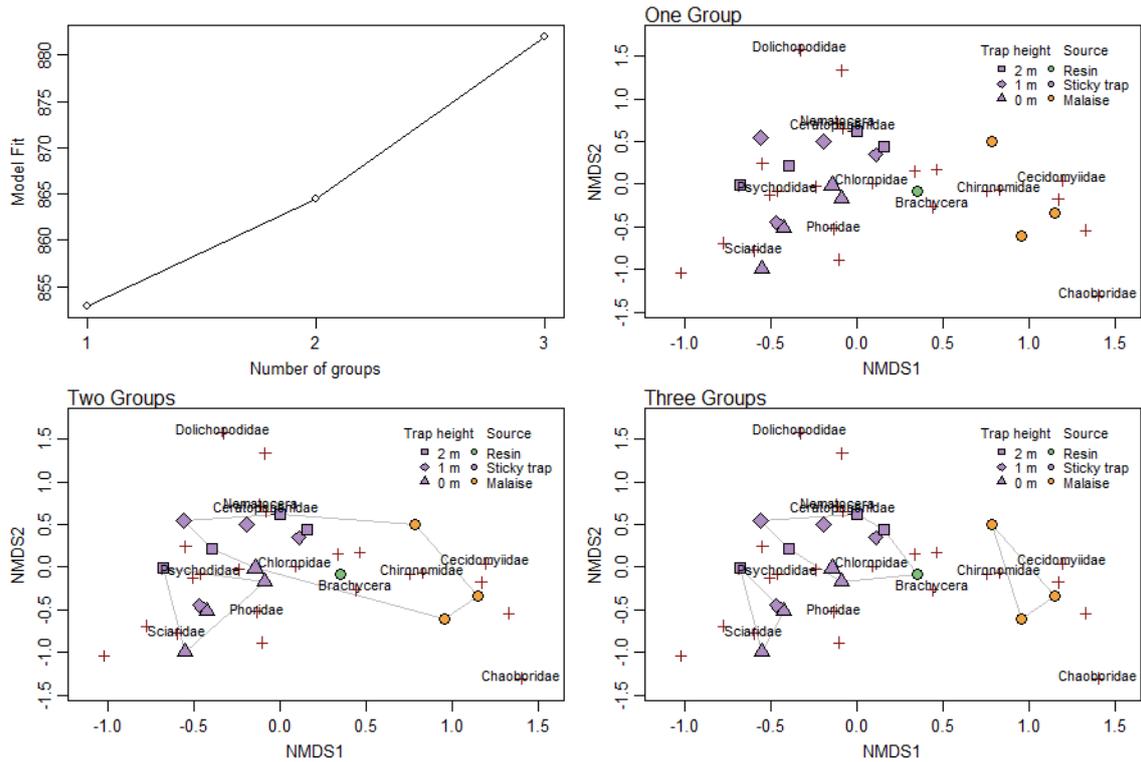
Fig. S2. Dirichlet-multinomial mixture modeling with three-cluster model for the Diptera families collected in the resin and Malaise and yellow sticky traps (divided by the three heights with symbols). The single-group model is best supported. Height does not explain group membership within the sticky trap samples. Only the eleven most common taxonomic groups are labeled.
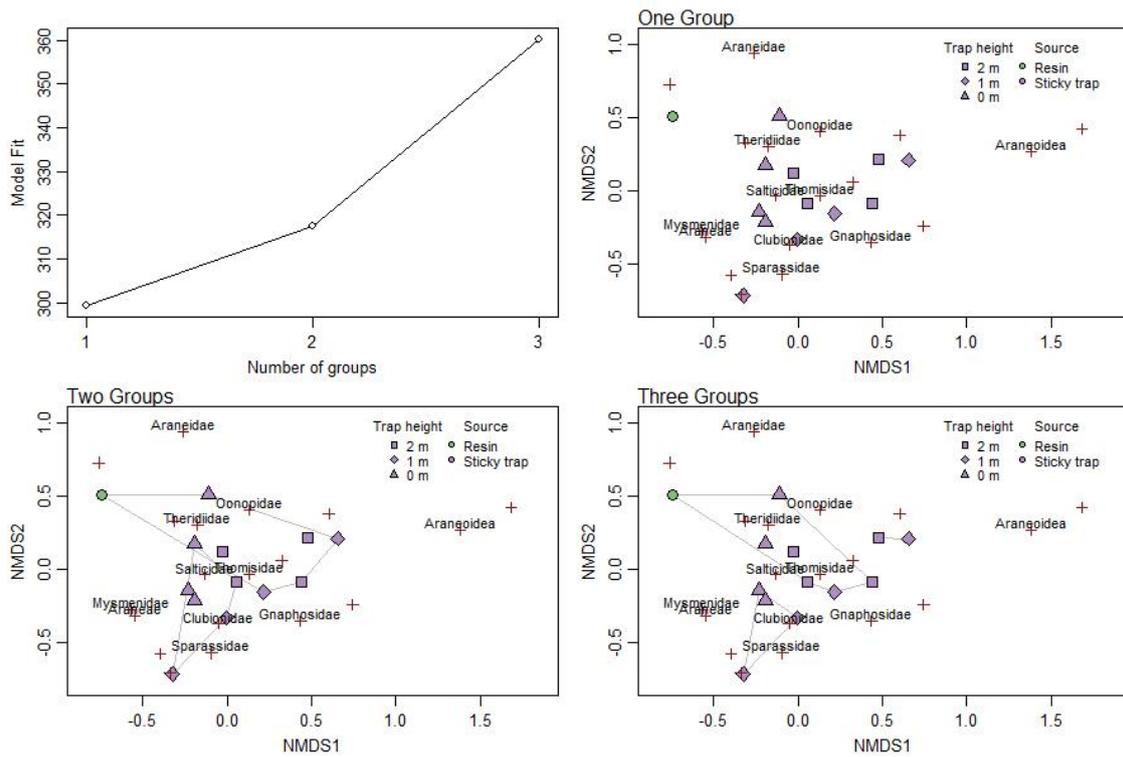
Fig. S3. Dirichlet-multinomial mixture modeling with three-cluster model for Arachnida collected in the resin and yellow sticky traps (divided by the three heights with symbols). The single-group model is best supported. Height also does not explain group membership within the sticky trap samples. Only the eleven most common taxonomic groups are labeled.
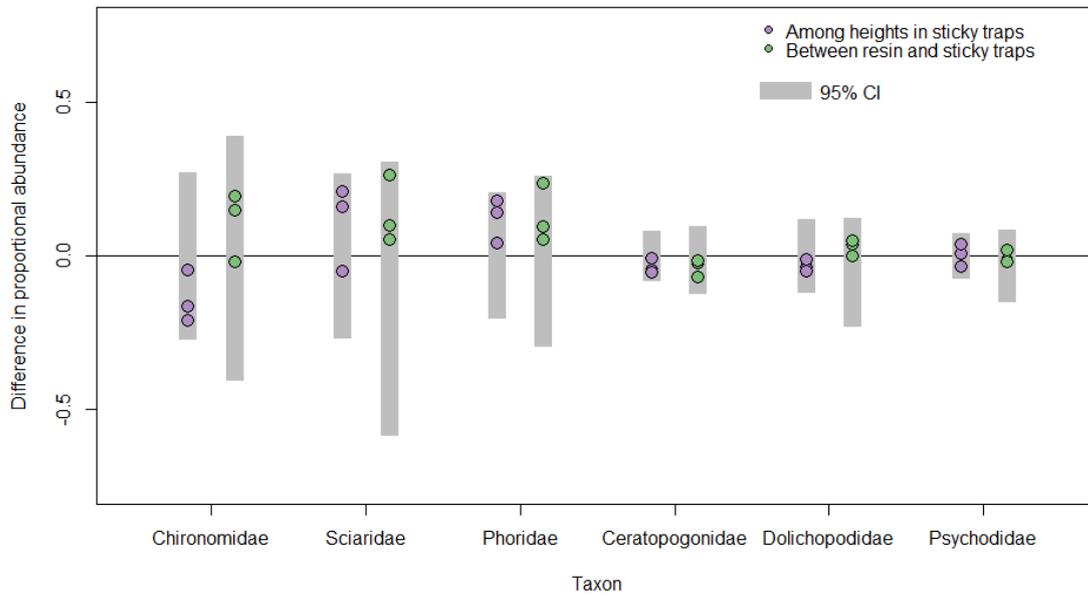
Fig. S4. Multiple random permutations, comparing proportional abundance of Diptera families among the three heights in sticky traps and between the resin sample and the three sticky traps heights.
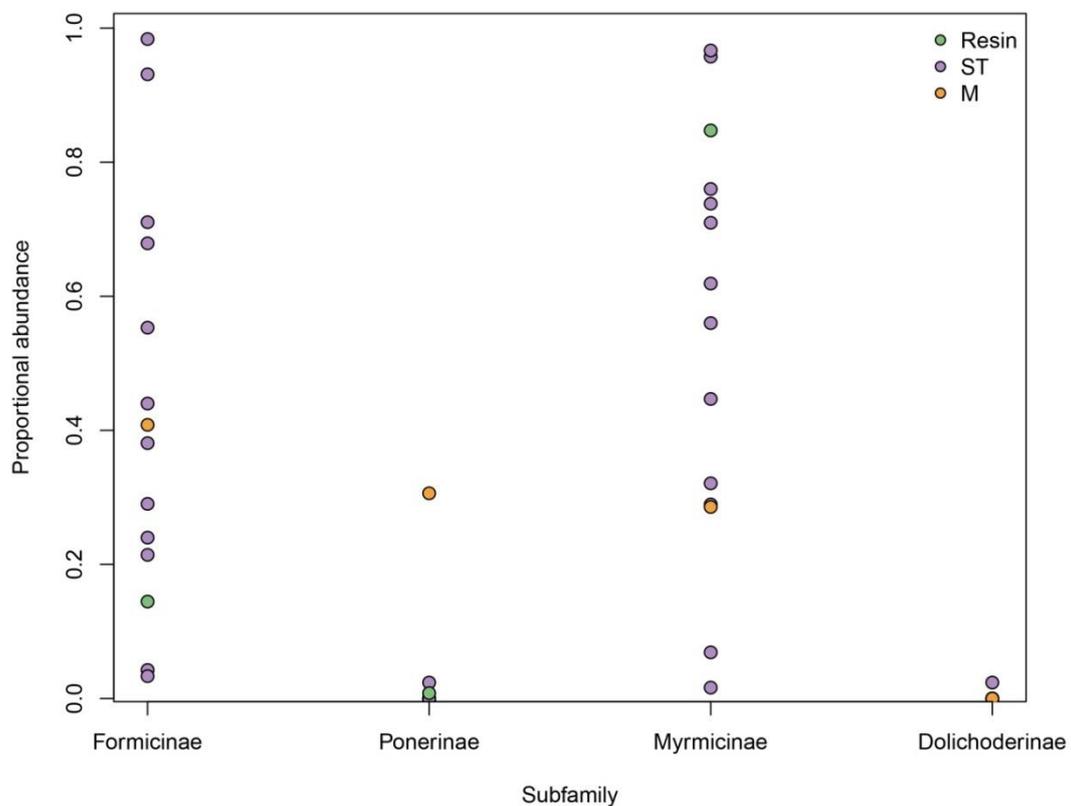
Fig. S5. Proportional abundance of Formicidae subfamilies collected in the resin and in the sticky and Malaise traps. M = Malaise trap; ST = sticky trap.
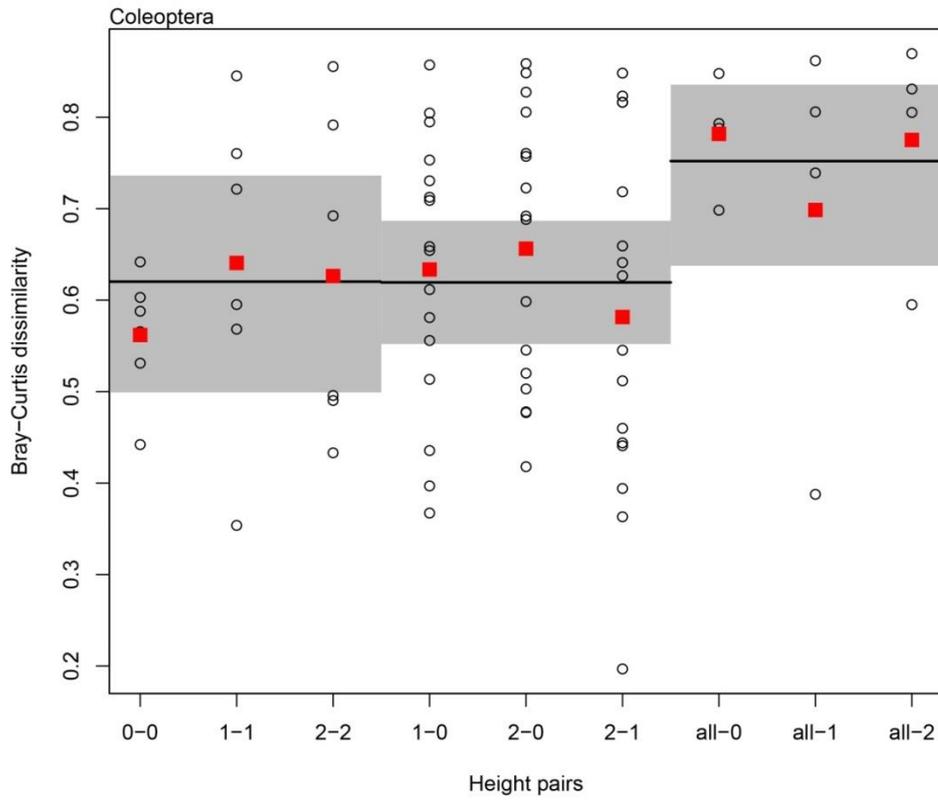
Fig. S6. Monte Carlo analysis with random permutations of the three different heights of the yellow sticky traps (0 m, 1 m and 2 m) for the Coleoptera families. Open circles are the dissimilarity between two individual samples and red squares are the mean dissimilarity between all samples in the pair. Pairs compare samples from height levels (0 m to 0 m, 1 m to 1 m, 2 m to 2 m, 1 m to 0 m, 2 m to 0 m, and 2 m to 1 m) and between resin ("all") and each height. The solid lines and shaded gray rectangles indicate the mean and 95% confidence interval when height labels are randomly permuted.
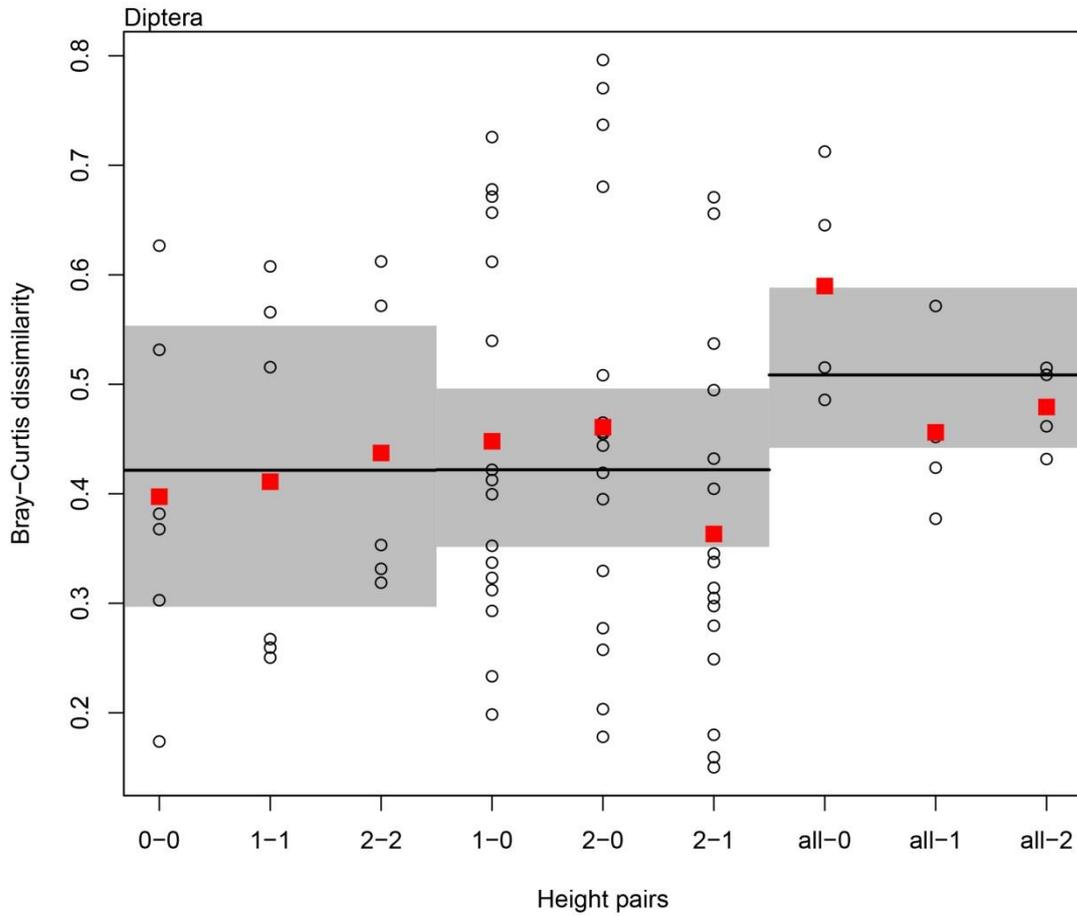
Fig. S7. Monte Carlo analysis with random permutations of the three different heights of the yellow sticky traps (0 m, 1 m and 2 m) for the Diptera families. Symbols as in figure S6.
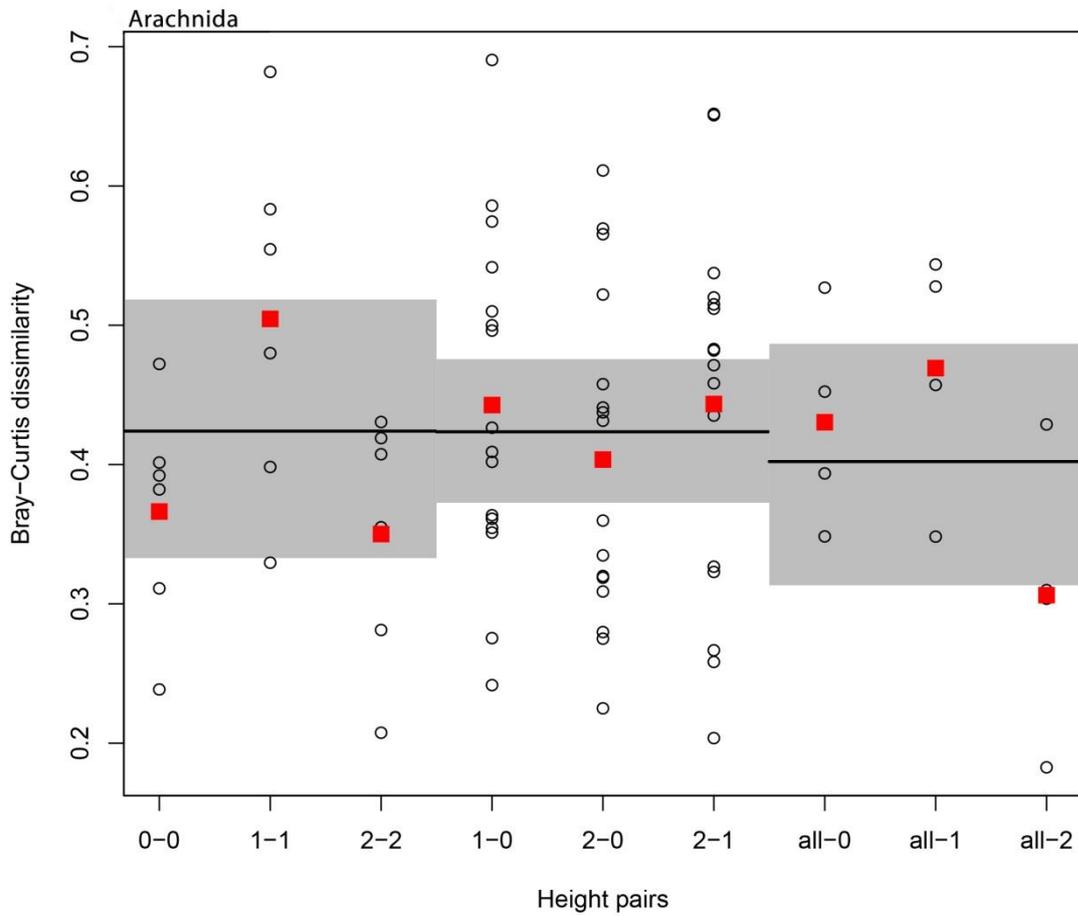
Fig. S8. Monte Carlo analysis with random permutations of the three different heights of the yellow sticky traps (0 m, 1 m and 2 m) for the Arachnida (spiders and mites) groups. Symbols as in figure S6.

II. EXTENDED MATERIALS AND METHODS

Area of study. The studied *Hymenaea verrucosa* Gaertner trees are located in a lowland forest close to Pangalanes Channel, in the Ambahy community (Nosy Varika, Mananjary region), on the east coast of Madagascar (20º46'S, 48º28'E). Ambahy is located 5–10 m above sea level. The Pangalanes Channel runs parallel to the Indian Ocean coast. The study was conducted in October 2013; during this month Mananjary has its annual maximum average of sunshine, a monthly temperature mean of 25ºC (day between 20º–26ºC, however temperatures sometimes can arrise the 31 ºC), and a mean humidity of 80% with 15 rainy days/month (beginning of the wet season). However, during the time that the traps worked it did not rain. The east coast has a subequatorial climate and, being most directly exposed to the trade winds, has the heaviest rainfall, averaging as much as 3.5 meters annually during the rainy season. The *H. verrucosa* trees where traps were placed (abbreviated henceforth as H.v.1 to H.v.4) and *H. verrucosa* trees from which the resin was collected (abbreviated henceforth as R0 to R9) are located in a primary forest, without an associated vanilla plantation.

Collection and studied methods of specimens included in the resin from *H. verrucosa*. Resins pieces from twelve *H. verrucosa* trees were collected at random with and without inclusions. The study of the arthropods included inside the resins was carried out as usual for the study of inclusions in amber. The pieces of resin were polished in order to open "windows" to observe individuals when visibility was difficult or incomplete. In some cases, the resin bodies were also cut and then polished to isolate the bioinclusions in separate preparations. For a better visualization of the inclusions under the microscope, a sugar-water solution with a cover glass was used. Each inclusion received a code number and a coordinate system to facilitate its subsequent location in the resin piece. Some pieces, in which bioinclusions were very abundant, required mapping done using a camera lucida to count and to well-record all the individuals. The total of arthropods collected in the resin per tree is presented herein in Table S4. The abbreviation R refers to a tree with resin exudations. The abbreviation R-SN refers to trees with resin exudations, without coordinates but sampled in the same area for us. Resin from the tree R1 were collected from the litter and from the branches. Resins from R0 and R2 were collected from the litter and from the trunk. Resins from trees R2–R9 were collected from their respective trunks. R-SN-1 and R-SN-2 are resin from the branches. Resins were collected from 0 m to at an approximate height of 4 m. Fresh resin remained sticky some days after exposure; however, the resin masses on the trees can remain sticky if the trees are producing resin and new flows cover again the masses.

Collection methods of Recent specimens with artificial traps. Two different arthropod traps, sticky and Malaise traps, were located around and close to four different trees of *H. verrucosa*: Three of them were located inside the forest (H.v.1– H.v.3) and one close to a water body (H.v.4); more information about the place of each tree can be found in Table S6. The sticky traps were yellow from Neudorff Gelbtafeln®, odorless and with an insecticide-free sticky mixture. The same yellow sticky trap has been used by Solórzano Kraemer et al. (1) who also tested transparent ones and corroborated that they are not statistically different. The size of each sheet was 20 cm in length and 7.35 cm in width. Fifteen were placed homogenously at three different heights: at the base or zero meters, at one meter and at two meter high in each tree (0 m, 1 m, 2 m). We used a total of 45 sticky trap sheets for each tree. Traps were stable for

eight days and required a special method for the isolation of the arthropods from the sheets, explained below. The time-framework of eight days was chosen to preserve the sampled organism in good conditions, because after eight days the arthropods begin to rot.

Standard Malaise traps were acquired from Bioform® (Germany); they were located very close to the *H. verrucosa* trees having sticky traps (Fig. S9*A*), two in the forest (H.v.1 and H.v.2) and one close to Pangalanes Channel (H.v.4), during the same days as the sticky traps. All specimens trapped were preserved in 70% ethanol separated in the different samples and heights.

Sticky and Malaise traps were chosen because they were used by Solórzano Kraemer et al. (1) with satisfactory results, who argued the convenience of using them for this kind of actualistic research, thus our data can be suitably compared.

Sorting. Arthropods were sorted to order level, whereas Diptera, Coleoptera and Araneae were also sorted to family level. Formicidae were sorted to subfamily level. Coleoptera, Formicidae and Araneae were also sorted by morphotypes and, when possible, the genus and species were also identified to obtain more ecological information. Order Hemiptera has been divided in the suborders Auchenorrhyncha, Sternorrhyncha and Heteroptera due to their different biology. Acari is only represented by individuals of the order Acariformes. Sizes of specimens were measured using a Nikon Microscope SMZ25 and an Olympus SZX9.

Number of specimens. To count the specimens in resin, and in sticky and Malaise traps according to the minimum number of individuals, an individual was accounted when the thorax/prosoma was present; this was done for all orders except for the termites in yellow sticky trap samples and ants in resin. In the case of termites, the minimum number of individuals was the number of wings of the same taxon in a sample divided by 4 and the number of heads in the case of the ants. Adults and immatures of Orthoptera and Hemiptera have been taken into account; larvae or caterpillars were accounted separately and not included in the statistics because of low identification accuracy.

Separation of arthropods from the yellow sticky traps. Fifteen sticky sheets were placed homogenously at the base, at one meter, and at two meters high in each tree (0 m, 1 m, 2 m) in the trees H.v.1 to H.v.3 (Fig. S9*A*). In the tree H.v.4 only ten sticky sheets were located at each height because of its small trunk diameter. Traps were stable, in place, for eight days, with daily supervision.

Glue of the yellow sticky traps were first dissolved during 4 to 5 hours in gasoline to obtain the arthropods avoiding disarticulation, and then transferred to alcohol 70%. The traps were submerged in gasoline in commercial plastic recipients (Tupperware®) with suitable lock for a secure transportation (Fig. S9*B)* and then cleaned carefully when glue dissolved (after 4 to 5 hours). For the hand protection we used disposable nitrile gloves (Fig. S9*C*).

The transfer to the alcohol was done using a nylon strainer cloth (0.05 mm) as a sieve that allowed retaining of the smallest arthropods like mites, collembolans or other minute insects (Fig. S9*D*). After sieving the bottles of 30 and 50 ml were filled with 70% ethanol and all the suitable information was annotated in the labels inside and outside the bottles for the transport (Fig. S9*E*).
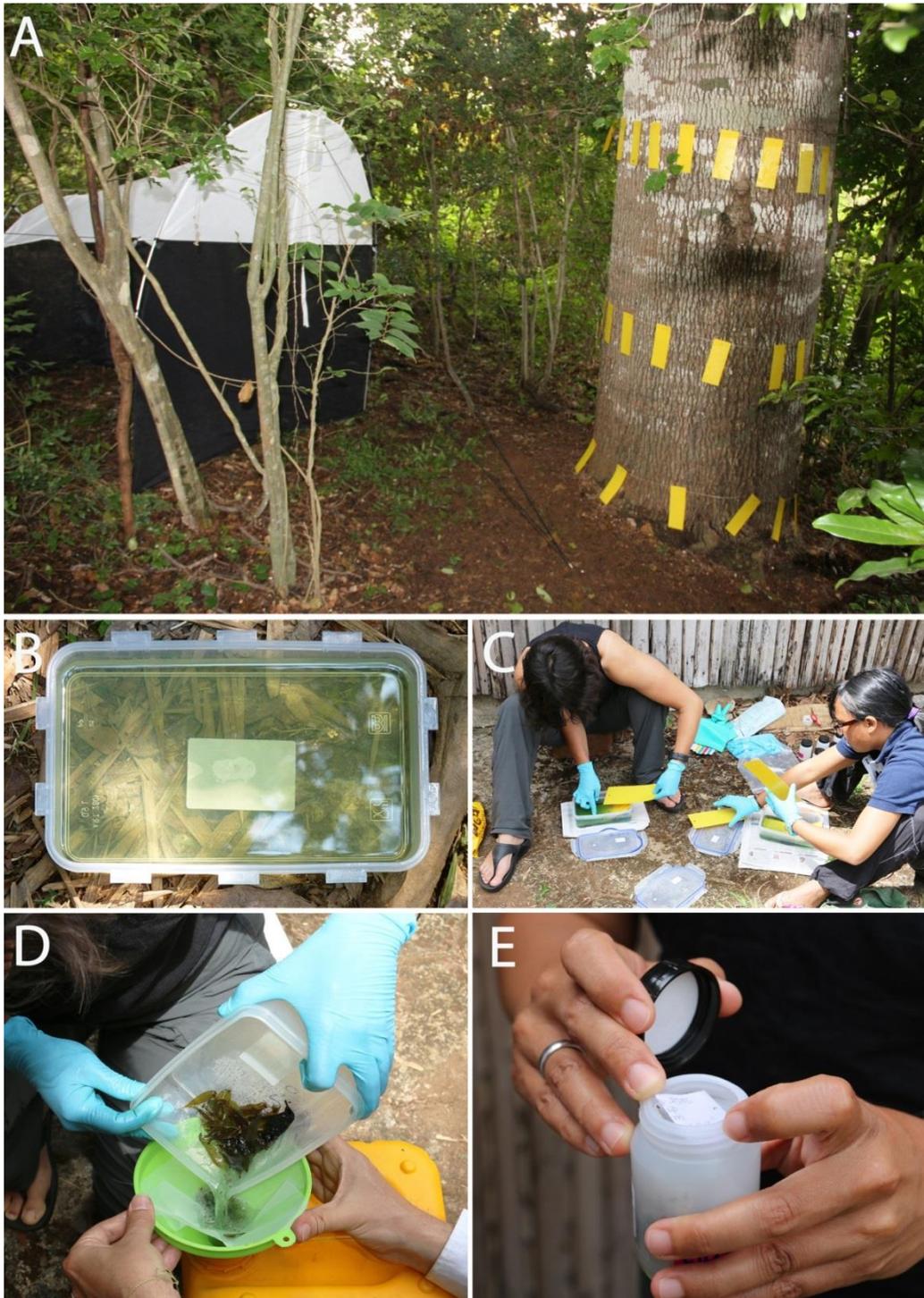
Fig. S9. General view of the entomological traps (Malaise and yellow sticky traps close to and at a *H. verrucosa* tree respectively, in Madagascar) (*A*). Tupperware® with suitable lock and infill with gasoline (*B*). Yellow sticky traps cleaning process to isolate the biotic remains, mainly arthropods (*C*). Yellow sticky trap content after cleaning and transfer to alcohol for preservation and transportation (*D–E*).

III. EXTENDED STATISTICAL METHODS

Visualizing sample similarity with non-metric multidimensional scaling. We examined the similarity among samples using non-metric multidimensional scaling (NMDS) using the vegan package in R (1) (Fig. 2, S1 to S4 and S10). We performed ordination on the raw counts, rather than transforming counts to proportional abundances, to maintain consistent data with the Dirichlet modeling described below, but this choice does not alter the interpretations. We also pooled counts from individual resin pieces to make their sampling more comparable to the yellow sticky traps, which are also contain insects averaged over time and space. Pooling resin counts also does not affect the conclusions from MDS results or subsequent analyses (Fig. S11). The NMDS technique first quantifies pairwise dissimilarity in samples using the Bray-Curtis coefficient. It then arranges the samples in *n*-dimensional space (we specified a two-dimensional ordination space) to maximize the rank-order agreement between pairwise distances in the ordination solution and Bray-Curtis dissimilarities in the original multidimensional dataset. NMDS produces ordination scores for samples and taxa, allowing visualization of associations between taxa and groups of samples that potentially represent different types of habitats or taphonomic biases.
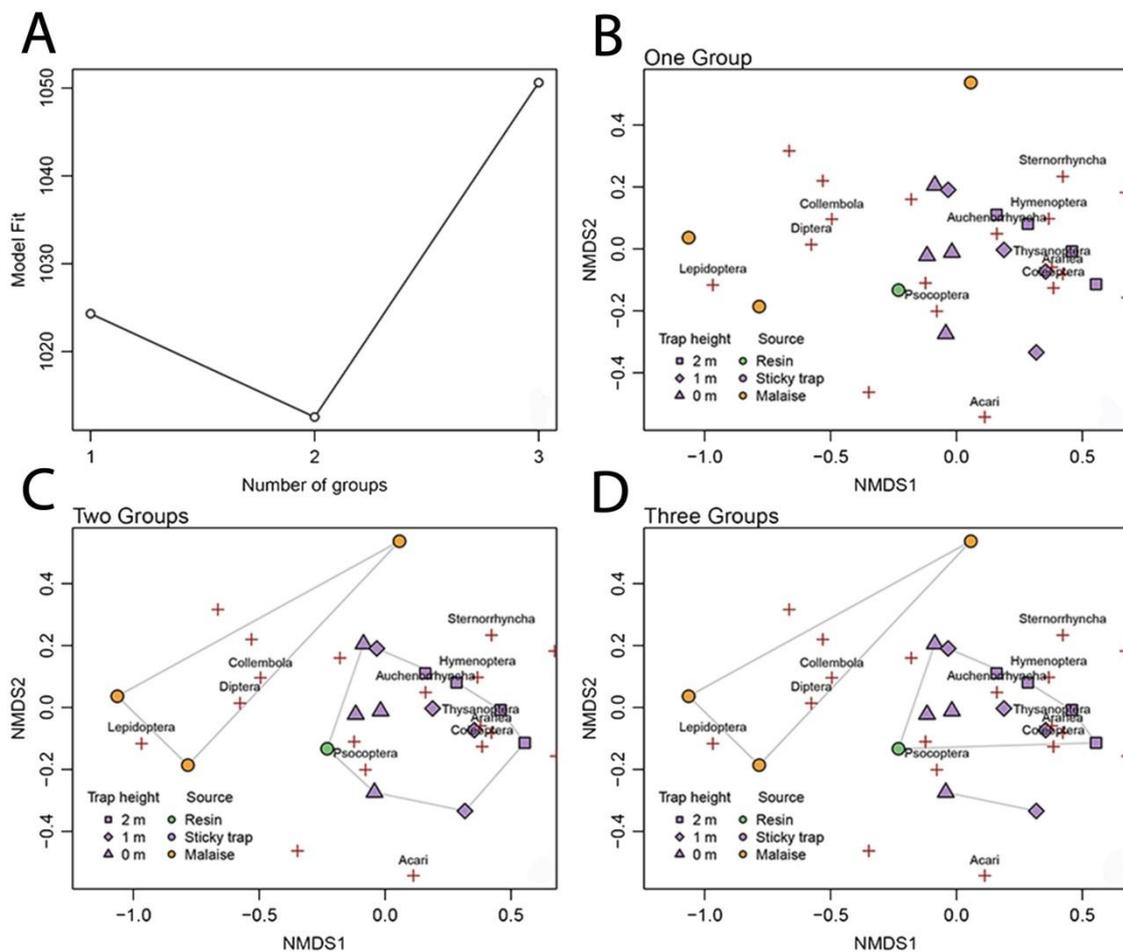
Fig. S10. Dirichlet-multinomial mixture modeling with three-cluster model (*A*) for orders collected in the resin and in the yellow sticky and Malaise traps (*B*, *C*, and *D*).
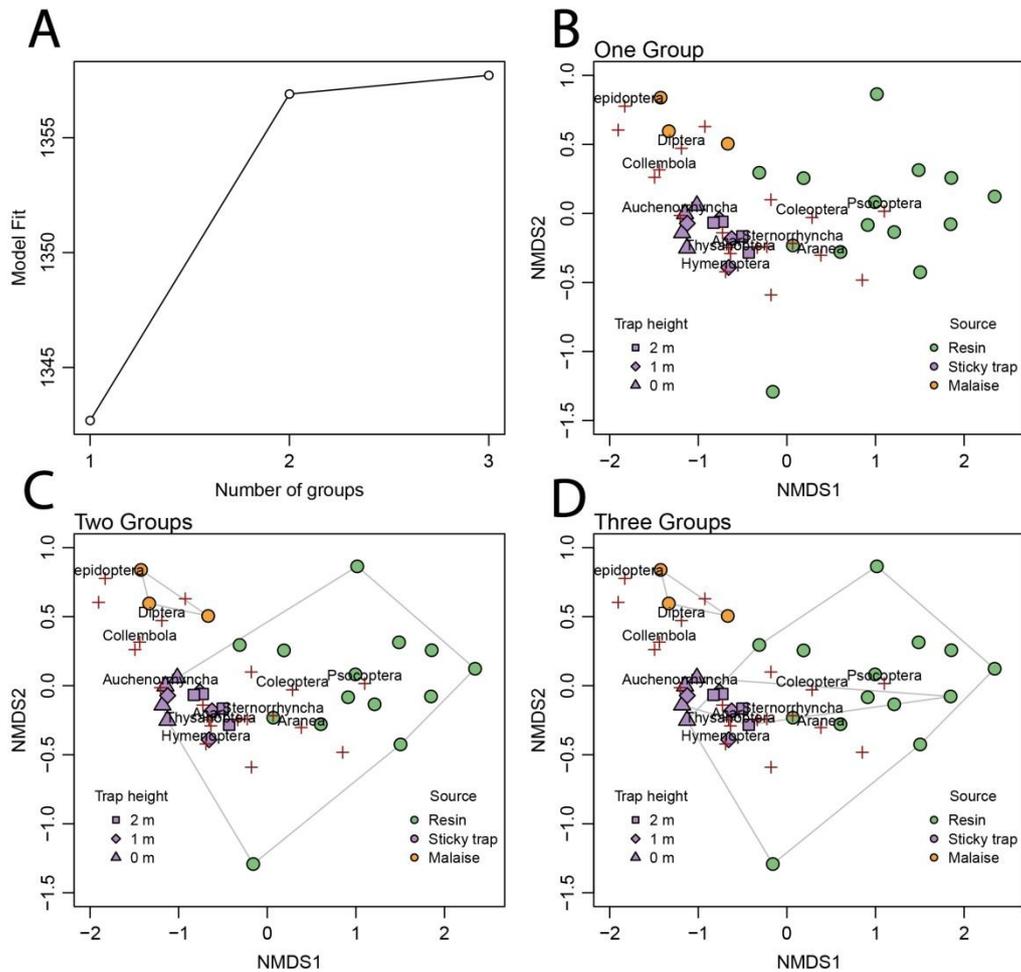
Fig. S11. Dirichlet-multinomial mixture modeling with three-cluster model showing the main results when treating each resin piece as a separate sample (*A*) for orders collected in the resin and in the yellow sticky and Malaise traps (*B, C*, and *D*).

Comparing sample compositions with Dirichlet multinomial mixture modeling. We used Dirichlet multinomial mixtures (2) to group samples into clusters on the basis of their taxonomic composition. Each sample (resin, yellow sticky trap, or Malaise trap) is derived from a broader pool of individuals, referred to as the metacommunity. Because samples are tiny relative to the size of the metacommunity, the taxonomic composition of a sample reflects a process of sampling with replacement – the metacommunity is effectively unchanged when an individual is trapped and removed from it. The probability that a taxon will be trapped is proportional to its abundance in the metacommunity; however, the true composition of the metacommunity is unknown. As there are many taxa with enormous variations in abundance, we would like to estimate the best value for the probability of sampling each taxon from the metacommunity, as well as the uncertainty in that value. A Dirichlet distribution can provide such estimates – in effect, each axis in multidimensional space is the probability of sampling a taxon from the metacommunity, and the Dirichlet distribution is the probability distribution over those probability axes.

We would expect the taxon abundances to follow a single Dirichlet distribution if all samples were derived from a single metacommunity. However, insect abundances may change because of habitat specificity (tree-associated arthropods may differ in abundance from other habitats) or because of other entrapment biases (resins may have

chemicals that attract or repel particular arthropods). If these effects are important, the samples may instead appear to derive from multiple metacommunities and, in that case, would be best modeled as a mixture of Dirichlet distributions.

The modeled Dirichlet distribution, or mixture of distributions, provides prior expectations for the taxonomic composition of the samples. We can then calculate the likelihood of observing the actual taxon counts in each sample, using a multinomial distribution to reflect the process of sampling with replacement. The method determines the best model by a Bayesian approach, combining the Dirichlet distribution prior with the multinomial likelihood to estimate the evidence, the probability that the observed counts were obtained from a particular mixture of metacommunities. This Bayesian approach enables comparison of models to determine the best number of metacommunities in the mixture of Dirichlet distributions. This is achieved by estimating the evidence of each complete model (with one metacommunity, a mixture of two metacommunities, a mixture of three, and so forth) while penalizing more complex models that include more mixtures. Specifically, the method uses the Laplace approximation to obtain negative log model evidence, with smaller values indicating the best model.

After the number of clusters has been determined, it is possible to calculate the probability that a given sample belongs to each cluster. Each sample is assigned to the cluster with the highest Bayesian posterior probability. If sampling method (resin, yellow sticky trap, or Malaise trap) biases the taxonomic composition, the best model should contain multiple clusters that divide the samples by sampling method.

Comparing taxonomic abundances with random permutation. To determine the effects of taphonomic biases on taxonomic composition, we evaluated whether particular taxonomic groups were over- or under-represented in resin, yellow sticky trap, or Malaise trap samples (Fig. 3 and S4 to S8). Barplots showing the abundances of different orders has been also done (Fig. S 11). For each taxonomic group, we compared the observed mean difference in its proportional abundance between resin and yellow sticky trap samples or between Malaise and yellow sticky trap samples. We permuted sample identity by randomly assigning one sample to be from resin, three from Malaise traps, and the remaining 12 from yellow sticky traps. Resampling was done without replacement, so all 16 samples were included in the randomly permuted dataset and each sample was only represented once. By repeating that random assignment 1000 times we generated 95% confidence intervals for the expected differences in mean abundances if samples were drawn randomly from a single pool. We compared the observed difference to the 95% confidence interval to identify taxonomic groups that were over- or under-represented.

We performed a similar procedure to investigate whether taxon abundances varied with the sample height on the tree trunk. Because only yellow sticky trap samples were collected from multiple heights (0 m, 1 m, and 2 m), we randomly permuted sample height among yellow sticky trap samples (again using sampling without replacement), assigning four samples at random to come from 0 m, four samples from 1 m, and four samples from 2 m. We repeated the random permutation 1000 times to generate 95% confidence intervals for the expected differences in taxon abundance if there was no difference with height.

We also assessed whether the resin sample was more similar to yellow sticky trap samples from a particular height. To do that, we randomly permuted the sample identities and heights among the 12 yellow sticky trap samples and one resin sample, again using sampling without replacement so that each original sample was represented

only once in the randomly permuted dataset. Like before, the random resampling process was repeated 1000 times to generate 95% confidence intervals.
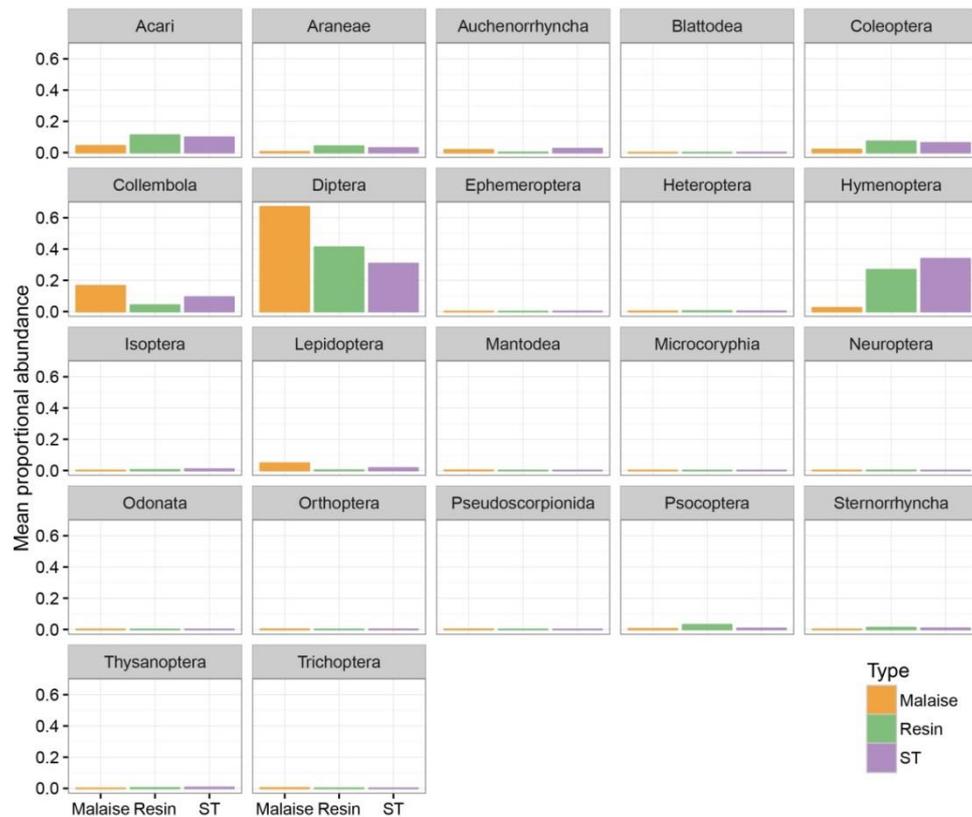
Fig. S12. Barplots showing the abundances of 22 orders collected in Malaise and sticky traps and in resin. Order Hemiptera has been divided in the suborders Auchenorrhyncha, Sternorrhyncha and Heteroptera due to their different biology. ST = sticky traps.

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IV. TABLES OF ALL ARTHROPODS COLLECTED AND COLLECTION PLACES

Table S1. Total of arthropods collected in the resin from *H. verrucosa* separated by trees. Arthropods mainly herein considered at order level; Order Hemiptera has been divided in the suborders Auchenorrhyncha, Sternorrhyncha and Heteroptera due to their different biology **and Acari is only represented by individuals of the order Acariformes. The abbreviations R0 to R9 refer to trees with resin with coordinate information. R-SN refers to trees with resin without coordinates, but from the same area.**

Resin *H. verrucosa*	R0-trunk	R0-litter	R1-branch	R1-litter	R2-trunk	R2-litter	R3	R4	R5	R6	R7	R8	R9	R-SN-1	R-SN-2	Total
Acari	3	6	14	9	12	5	2	1	0	4	0	6	132	0	0	194
Araneae	10	1	7	2	9	1	2	0	4	10	0	3	9	9	4	71
Auchenorrhyncha	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2
Coleoptera	14	1	4	0	3	0	2	56	0	9	0	1	32	4	0	126
Collembola	8	18	2	4	9	4	0	1	0	2	0	9	14	0	0	71
Diplopoda	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Diplura	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Diptera	129	10	306	66	21	6	10	13	8	32	4	19	64	17	13	718
Heteroptera	1	0	0	0	0	0	0	0	1	0	0	0	2	1	0	5
Hymenoptera	84	5	45	36	18	2	7	9	0	22	177	16	38	4	3	466
Insecta indet.	6	5	1	14	1	0	0	1	1	0	1	0	11	0	0	41
Isoptera	1	0	0	1	1	0	0	1	0	0	0	2	0	0	0	6
Lepidoptera	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	3
Neuroptera	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1
Odonata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Psocoptera	12	0	2	5	2	0	0	0	0	3	0	3	17	6	2	52
Sternorrhyncha	4	0	1	0	0	0	0	0	0	0	0	0	12	2	1	20
Thysanoptera	2	0	0	0	1	0	0	0	0	0	0	0	1	1	1	6
Trichoptera	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2

Table S2. Total arthropods collected in four _H. verrucosa_ trees in Ambahy (Madagascar) with yellow sticky traps (ST) (divided in the three heights), resin, and Malaise (M) traps. All collected at the beginning of the rainy season (October 2013). H.v.= _Hymenaea verrucosa_.

Ambahy, Madagascar	Total ST H.v. 0 m	Total ST H.v. 1 m	Total ST H.v. 2 m	Total Resin H.v.	Total M H.v.
Acari	845	394	116	194	239
Araneae	160	106	94	71	16
Auchenorrhyncha	173	68	92	2	73
Blattodea	2	0	2	0	0
Coleoptera	162	272	246	126	110
Collembola	650	435	182	71	805
Diptera	1751	1125	965	718	3428
Ephemeroptera	1	3	4	0	1
Heteroptera	9	8	4	5	8
Hymenoptera	2151	1436	1003	466	135
Isoptera	8	11	57	6	0
Lepidoptera	45	56	68	3	274
Mantodea	2	0	0	0	3
Microcoriphia	0	1	0	0	0
Neuroptera	0	0	0	1	0
Odonata	1	0	1	0	0
Orthoptera	6	1	2	0	4
Pseudoscorpiones	0	0	0	0	3
Psocoptera	39	15	26	52	21
Sternorrhyncha	14	23	58	20	0
Thysanoptera	49	16	20	6	2
Trichoptera	3	2	4	2	11

Table S3. Total of families of Diptera collected in four *H. verrucosa* trees in Ambahy (Madagascar) with yellow sticky traps (ST) (divided in the three heights), resin, and Malaise (M) traps. All collected at the beginning of the rainy season (October, 2013). H.v.= *Hymenaea verrucosa*.

Ambahy, Madagascar	Total ST H.v. 0 m	Total ST H.v. 1 m	Total ST H.v. 2 m	Total Resin H.v	Total M H.v.
Anisopodidae	0	0	0	1	0
Asilidae	0	0	0	1	0
Cecidomyiidae	9	32	40	57	526
Ceratopogonidae	21	49	71	57	28
Corethrelidae	0	0	0	0	1
Culicidae	1	2	1	0	19
Chaoboridae	0	0	0	0	133
Chironomidae	310	354	412	151	2159
Chloropidae	8	10	7	113	0
Dolichopodidae	17	48	72	7	6
Drosophilidae	0	0	0	2	0
Empididae	20	6	9	0	0
Keroplatidae	1	1	0	0	67
Limoniidae	0	1	2	8	4
Lonchopteridae	0	0	0	1	0
Lygistorrhinidae	2	0	0	0	1
Muscidae	5	5	0	2	0
Mycetophilidae	0	0	0	36	17
Phoridae	487	176	92	48	326
Psychodidae	47	76	22	29	11
Scatopsidae	3	4	2	3	0
Sciaridae	716	195	178	82	154
Simuliidae	3	0	0	1	0
Syrphidae	1	0	0	0	0
Tabanidae	0	5	0	0	0
Tachinidae	0	0	0	2	0
other Brachycera	54	33	15	67	103
other Nematocera	27	39	12	16	16
indet.	0	0	0	34	0

Table S4. Total of families of Coleoptera collected in four *H. verrucosa* trees in Ambahy (Madagascar) with yellow sticky traps (ST) (divided in the three heights), and resin. All collected at the beginning of the rainy season (October, 2013). H.v.= *Hymenaea verrucosa*.

Ambahy, Madagascar	Total H.v. 0 m	Total H.v. 1 m	Total H.v. 2 m	Total Resin H.v
Aderidae	4	5	1	1
Anthicidae	2	0	1	0
Anthribidae	0	0	0	1
Carabidae	1	0	0	5
Cerambycidae	1	0	0	0
Chrysomelidae	21	13	21	4
Ciidae	0	1	0	0
Clambidae	2	1	0	0
Cleridae	0	0	1	0
Coccinellidae	2	1	5	0
Corylophidae	0	5	3	4
Cryptophagidae	1	1	1	0
Curculionidae: Platypodinae: *Mitosoma*	3	32	14	91
Curculionidae: Scolytinae	10	33	37	12
Curculionidae: other groups	1	2	2	0
Dermestidae	0	0	0	1
Elateridae	31	3	0	0
Erotylidae	0	0	0	1
Eucnemidae	0	0	1	0
Laemophloeidae	0	1	0	0
Melandryidae	0	1	1	0
Melyridae	0	0	2	0
Mordellidae	3	1	0	0
Nitidulidae	0	3	3	0
Phalacridae	0	1	1	0
Ptiniidae	8	20	10	1
Salpingidae	0	9	6	0
Scarabaeidae	1	0	0	1
Scirtidae	3	3	25	3
Sphindidae	0	0	1	0
Staphylinidae: Pselaphinae	30	71	78	11
Staphylinidae: Scydmaeninae	17	8	9	3
Staphylinidae: other subfamilies	4	7	3	0
Tenebrionidae	0	1	0	0
Throscidae	1	1	0	0
Zopheridae: Colydiinae	0	5	11	0
indet.	0	0	0	3

Table S5. Total of specimens of arachnids, mainly Araneae and except mites, collected in four *H. verrucosa* trees in Ambahy (Madagascar) with yellow sticky traps (divided in the three heights), and resin. All collected at the beginning of the rainy season (October, 2013). H.v. = *Hymenaea verrucosa*.

Ambahy, Madagascar	Total H.v. 0 m	Total H.v. 1 m	Total H.v. 2 m	Total Resin H.v.
Araneae indet.	16	20	9	14
Araneidae	1	1	3	5
Araneoidea indet. (superfamily)	0	10	6	0
Clubionidae	11	6	5	0
Gnaphosidae	1	1	5	0
Hersiliidae: *Hersilia madagascariensis*	0	1	0	0
Liocranidae	3	0	0	0
Mysmenidae	1	3	1	2
Nesticidae: *Nesticella* sp.	1	0	0	0
Oonopidae	4	1	1	0
Pholcidae	0	0	1	1
Pisauridae	1	1	1	0
Salticidae	29	8	7	4
Sparassidae	4	1	1	0
Tetragnathidae	2	0	0	0
Theridiidae	62	32	54	45
Thomisidae	14	5	6	0
Uloboridae	2	1	0	0
Pseudoscorpiones	0	1	0	0

Table S6. *Hymenaea verrucosa* trees location and field data. The abbreviations H.v.1–H.v.4 refer to trees where two different arthropod traps, yellow sticky and Malaise traps, were located. R0–R9 refer to trees with resin with coordinate information. R-SN refers to trees with resin without coordinates. The abbreviation m.a.s.l. refers to meters above sea level.

Tree	Coordinates	Altitude (m.a.s.l.)	Temperature	Atmospheric pressure	Humidity in the tree cutting at 1.5 m	Humidity in the bark	Trunk perimeter at 0 m / 1 m / 2 m	Presence of a termite nest	Resin collected from
H.v.1	S 20º 47.283'/E 48º 28.526'	20	29.7º C (at 11:38 AM)	1016.5 hPa	50%	26.0%	4.08 m / 1.67 m / 1.65 m	Yes	No collection of resin
H.v.2	S 20º 47.343'/E 48º 28.510'	15	30.3º C (at 12:23 AM)	1016.0 hPa	50%	27.5%	3.79 m / 1.68 m / 1.10 m and 1.0 m (2 series of yellow sticky traps at 2 m)	Yes	No collection of resin
H.v.3	S 20º 47.315'/E 48º 28.530'	11	32.2º C (at 1:32 PM)	1015.4 hPa	50%	27.5%	1.47 m / 0.96 m and 0.84 m / 1.80 m (2 series of yellow sticky traps at 1 m) in two branches	No	No collection of resin
H.v.4	S 20º 46.780'/E 48º 28.752'	10 On a canal	27.9º C (at 2:26 PM)	1017.7 hPa	50%	30.0%	0.93 m / 0.90 m / 0.90 m (in all only 10 yellow sticky traps)	No	No collection of resin
R0	S 20º 43.385'/E 48º 28.888'	23	Lack inf.	Lack inf.	Lack inf.	Lack inf.	No entomological trap	No	Litter
R1	S 20º 43.385'/E 48º 28.888'	23	38.8º C (at 10:25 AM)	1018.9 hPa	50%	40.0%	No entomological trap	Yes	Litter and trunk at different heights
R2	S 20º 43.407'/E 48º 28.896'	23	32.1º C (at 11:25 AM)	1017.9 hPa	50%	17.5%	No entomological trap	Yes	Litter and trunk at different heights
R3	S 20º 43.255'/E 48º 28.805'	22	30.4º C (at 11:41 AM)	1018.1 hPa	50%	43.0%	No entomological trap	No	Trunk at low heights
R4	S 20º 43.106'/E 48º 28.821'	12	30.5º C (at 11:51 AM)	1017.7 hPa	50%	40.0%	No entomological trap	Yes	Trunk and branch at high heights
R5	S 20º 43.215'/E 48º 28.726'	6	30.1º C (at 14:26 AM)	1016.1 hPa	50%	40.0%	No entomological trap	No	A wound at about 2 m height

R6	S 20º 43.237'/E 48º 28.745'	3	26.6º C (at 14:42 AM)	1016.0 hPa	50%	35.0%	No entomological trap	No	Trunk at different heights
R7	S 20º 43.251'/E 48º 28.753'	0	29.1º C (at 14:59 AM)	1016.1 hPa	50%	35.0%	No entomological trap	No	Trunk at different heights
R8	S 20º 43.258'/E 48º 28.757'	16	29.0º C (at 15:08 AM)	1016.0 hPa	50%	48.0%	No entomological trap	No	Trunk at different heights
R9	S 20º 41.499'/E 48º 28.183'	16	Lack inf.	Lack inf.	Lack inf.	Lack inf.	No entomological trap	No	About 4 m height with a microenvironment of dry leafs, at about 3 m and close to a river
R-SN-1	From the Ambahy region	Lack inf.	Lack inf.	Lack inf.	Lack inf.	Lack inf.	No entomological trap	Lack inf.	A local inhabitant by acquisition
R-SN-2	From the Ambahy region	Lack inf.	Lack inf.	Lack inf.	Lack inf.	Lack inf.	No entomological trap	Lack inf.	A local inhabitant by acquisition