



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

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Edited by Paul A. Selden, University of Kansas, Lawrence, KS, and accepted by Editorial Board Member David Jablonski April 17, 2018 (received for review February 12, 2018)

Amber is an organic multicomponent 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.

Author contributions: M.M.S.K., X.D., and E.P. designed research; M.M.S.K., X.D., M.E.C., and E.P. performed research; M.M.S.K., X.D., M.E.C., A.A., D.P., P.J., F.S., and E.P. contributed new reagents/analytic tools; M.M.S.K., X.D., M.E.C., and E.P. analyzed data; M.M.S.K., X.D., M.E.C., and E.P. wrote the paper; M.M.S.K., X.D., A.A., F.S., and E.P. classified arthropods; D.P. classified beetles; and P.J. classified spiders.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. P.A.S. is a guest editor invited by the Editorial Board.

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See Commentary on page 6525.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1802138115/-DCSupplemental.

Published online May 7, 2018.

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 micro-environments, 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. S10A and S11A*): one containing the malaise trap samples and the other containing the resin and yellow sticky trap samples (*SI Appendix, Figs. S10B and D and S11B 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. S10C and S11C*), 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. 3A). 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

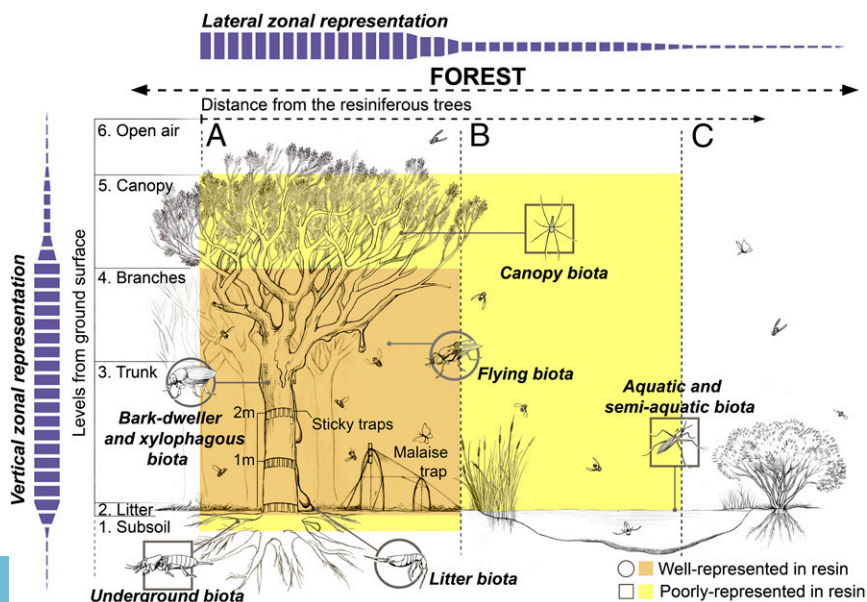


Fig. 1. Diagram of a resiniferous forest (*Hymenaea* model) with representation of biota trapped, mainly arthropods. Circles, main biota represented in resin; squares, scarcely represented; colored in dark orange, zones with a high representation in resin; colored in yellow, zones with a poor representation 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.

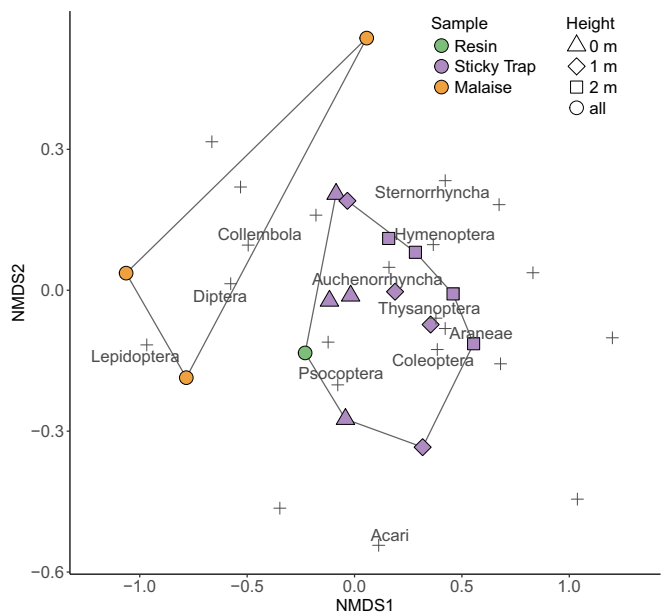


Fig. 2. Dirichlet-multinomial mixture modeling for orders collected in the resin and in the yellow sticky and malaise traps.

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. 4A 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,

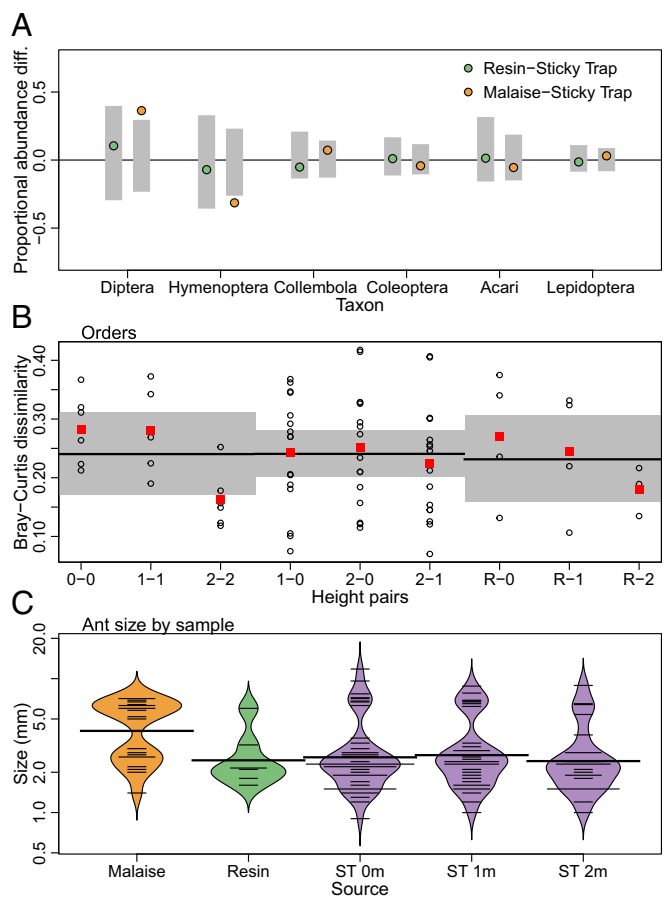


Fig. 3. Multiple random permutations for arthropod orders collected in the resin and yellow sticky and malaise traps (*A*). Monte Carlo analysis with random permutations of the three different heights (0 m, 1 m, and 2 m) for the sticky samples at arthropod order level (data from *SI Appendix, Tables S1 and S2*) (*B*). Body size distributions of Hymenoptera: Formicinae (ants) between collection methods (*C*).

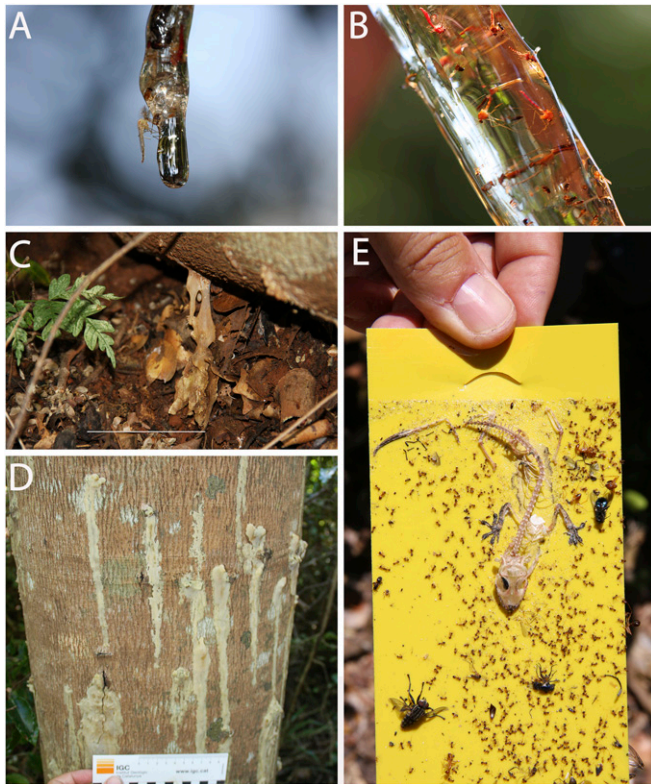


Fig. 4. Resin of *Hymenaea verrucosa* Gaertner (Madagascar) trapping biota and yellow sticky trap. Natural resin bodies operating like yellow sticky traps (chironomid body lengths approximately 5.5 mm) (A and B). Example of resin emission produced at the litter level (C). (Scale bar, 15 cm.) Example 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. 4E). 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. 3D) 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. 4C) (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* (Formicidae) occur at 0 m and 1 m in the sticky traps, likely attracted by dead animals (Fig. 4E) 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. 4C), 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. 4D).

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 (barklice) 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 repellent 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. 4E). 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

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).

ACKNOWLEDGMENTS. The authors thank R. Ravelomanana, M. Asensi, S. Rahanitriaina, and T. Rakotondranaivo for their assistance and help during the scientific fieldwork; B. Razafindrahama and W. Nandroinjafihita (Commune Rurale d'Ambahy, Madagascar) and the Ministère de L'Environnement de L'Ecologie et de Forêts for granting permits and offering assistance during the fieldwork stage in the Réserve Naturelle Ambahy, Forêt d'Analalava; Dr. E. Randrianarisoa (Université d'Antananarivo) for his help during the administrative issues and for advice; Malagasy Institute for the Conservation of Tropical Environments (ICTE/MICET) and Dr. B. Andriamihaja of this institution, and his team, for their assistance in aspects of the administrative development of our work in Madagascar; J. Altmann and R. Kunz (Senckenberg Research Institute) for their great support by sorting specimens; A. Solórzano K. (Universidad Autónoma Nacional de México) for discussions; José Antonio Peñas Artero for drawing Fig. 1; and anonymous referees for valuable comments that improved the manuscript. This work was supported by National Geographic Global Exploration Fund Northern Europe Grant GEFNE 127-14; Spanish MINECO/FEDERUE Grants CGL2014-52163 and CGL2017-84419; and VolkswagenStiftung, Germany Grant 90946.

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