Geography and major host evolutionary transitions shape the resource use of plant parasites

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The evolution of resource use in herbivores has been conceptualized as an analog of the theory of island biogeography, assuming that plant species are islands separated by phylogenetic distances. Despite its usefulness, this analogy has paradoxically led to neglecting real biogeographical processes in the study of macroevolutionary patterns of herbivore–plant interactions. Here we show that host use is mostly determined by the geographical cooccurrence of hosts and parasites in spider mites (Tetranychidae), a globally distributed group of plant parasites. Strikingly, geography accounts for most of the phylogenetic signal in host use by these parasites. Beyond geography, only evolutionary transitions among major plant lineages (i.e., gymnosperms, commelinids, and eudicots) shape resource use patterns in these herbivores. Still, even these barriers have been repeatedly overcome in evolutionary time, resulting in phylogenetically diverse parasite communities feeding on similar hosts. Therefore, our results imply that patterns of apparent evolutionary conservatism may largely be a byproduct of the geographic cooccurrence of hosts and parasites.

evolutionary conservatism | geographic signal | host use evolution | parasite–host interactions | spider mites

Ecological interactions are commonly thought to be evolutionarily conserved (1). This idea roots back to Darwin and is based on the assumption that traits regulating interactions are mainly an ancestor's legacy. Following this rationale, it is expected that phylogenetically related species will also interact with partners that are phylogenetically clustered. Plants and the herbivores that feed on them constitute a large amount of the Earth's terrestrial biodiversity. However, the processes behind the origin of such diversity remain controversial (2). Related plant hosts tend to harbor similar communities of both herbivores (3–5) and pathogens (6, 7). Still, host shifts may be favored when they involve distantly related plants producing similar chemical compounds as defense against parasites (8). In fact, macroevolutionary evidence shows that host shifts of parasites to unrelated plants are common (9–13), questioning the ubiquity of evolutionary conservatism.

These patterns of host use in parasites have led to the formulation of the "parasite paradox," which states that although parasites are generally specialized on a given (set of) host plant(s), host shifts to distantly related hosts occur frequently (14, 15). Further, the frequent shifts between evolutionarily distinct hosts observed in parasites have led to the analogy of considering plant species as resource islands separated by evolutionary distances (16–18). In this metaphor, related plants constitute resource archipelagos within which colonization of new resource islands entails few costs. Among such archipelagos, however, colonization processes may be costly, potentially leading to disruptive selection and hence to speciation via host shift (19, 20). Paradoxically, framing the evolution of plant host use as an analog of the theory of island biogeography has led to overlooking the potential importance of biogeography in this process. Recent evidence highlights the importance of spatial cooccurrence in determining host

attack (7). Going further, related parasite species often cooccur geographically and hence colonize similar plants, which can result in patterns of apparent niche conservatism at large scales (21–23). This implies that the existence of patterns of niche conservatism do not necessarily mean that interactions are phylogenetically constrained, as these patterns may simply result from the spatial cooccurrence of related species. Therefore, disentangling whether phylogenetic or geographical processes underlie patterns of host use requires addressing both types of processes in a joint analysis.

Here we study resource use by a group of parasitic herbivores in both phylogenetic and geographical space. Spider mites (Acari: Tetranychidae) are an ideal model system due to their large diversity, worldwide geographical distribution, different degrees of host specificity (from highly specialist to generalist species) and the wide phylogenetic range of their plant hosts (from ferns to angiosperms). We describe a comprehensive dataset of globally distributed information on 1,115 spider mite species feeding on 1,350 plant genera (24) through two different networks: one depicting the interactions between mite parasites and their host plants and another characterizing the global cooccurrence of mite species. Our results point to a major role of the geographical coincidence of hosts and parasites in determining host–parasite interactions. Further, the phylogenetic signal in plant host use disappears after accounting for the geographic distribution of mite species. However, we also found that major plant evolutionary transitions impose strong adaptive barriers, although spider mites have frequently overcome such barriers through evolutionary time.

Significance

Patterns of host use by parasites are commonly thought to be limited by phylogenetic constraints, yet little is known about the role of the geographic distribution of hosts and parasites in such patterns. We show that evolutionary patterns in host use by a family of plant parasites are largely determined by the geographical distribution of hosts and parasites. Such phylogenetic lability in host use results in repeated colonizations of distantly related plant lineages, even across major plant evolutionary transitions. Still, these transitions constitute significant adaptive barriers in the evolution of host use. Our results thus show that host plant use by parasitic mites hinges more on where the plant and the mite are than on phylogenetic constraints.
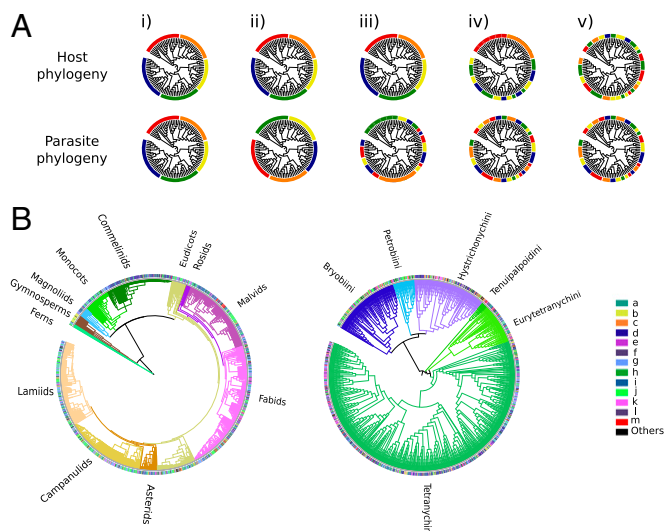
Fig. 1. Phylogenetic dissimilarities among spider mites parasitizing similar plants do not correlate with plant dissimilarities. (*A*) Five hypothetical scenarios representing different macroevolutionary patterns of host use. Colors represent plant and mite taxa forming each module. (*i*) Modules are formed by related plants that are used by related parasites. Here the phylogenetic dissimilarities between parasites associated with different plant modules are correlated with the dissimilarities of plants forming them. (*ii*) Both plants and parasites are phylogenetically related within modules but phylogenetic dissimilarities between plant and parasite modules are not correlated. (*iii*) Modules are formed by related plant taxa. Only some archipelagos are used by related parasites. (*iv*) Modules are formed by related or unrelated plants, whereas parasites using the same resources are unrelated. (*v*) Neither plant nor parasite species are related. (*B*) Module distribution in both plant (*Left*) and spider mite (*Right*) phylogenies as in *A*. Phylogenetic branch colors and their correspondent labels depict major taxonomic groups. Modules are identified by letter codes (*a–m*). Species not belonging to the 13 principal models are also shown.

Results

Network Characterization of Plant Use (i.e., the Interaction Network).
To characterize the patterns of plant use in spider mites, we used a community detection analysis borrowed from network theory. This analysis identifies groups (modules) of plant and mite species that tend to interact more among themselves than with others (25). The interaction network describing plant use by spider mites was significantly modular ($M = 0.48$, $P = 0.01$), being divided into 20 modules of which 13 were formed by more than 10 mite species and 10 plant genera (*SI Appendix*, Table S1). Sampling effort was largely similar for all modules, with little unevenness of no significant effect on our results (*SI Appendix, Appendix S1*). In total these 13 modules represent around 99% of both the mite species and plant genera analyzed. The remaining modules were mostly composed of fewer than three mite species and plant genera. Hence, although we also analyzed all modules having two or more taxa, we only focused on the 13 main modules.

Phylogenetic Structure of Spider Mite–Plant Interaction Modules.
If spider mite–plant interactions are evolutionary conserved, each module is expected to contain phylogenetically related taxa. To test this, we first described the evolutionary relationships between spider mite species from genetic and taxonomic information using phylogenetic uncertainty methods (26) and used the phylogenetic relationships among plant genera from the Angiosperm Phylogeny Group III classification (APG III, ref. 27). To take into account the topological uncertainties in the mite phylogeny, we developed four different algorithms to assign species based on taxonomy, which differ in the degree of credibility given to taxonomic information (*SI Appendix*, *Appendixes*

S1 and S2). Using an index of phylogenetic distinctiveness (*SI Appendix, Appendix S3*), we found that, out of 13 modules, plants were significantly phylogenetically clustered in 11 modules and mites in 10 (Figs. 1 and 2*A* and *SI Appendix*, Tables S2 and S3). This clustering shows that plant modules are formed by related plants, which are also used by phylogenetically related mites (Fig. 1*A*, scenarios *i* and *ii*). Results from the four algorithms were qualitatively and quantitatively consistent (*SI Appendix*, Table S3).

The above results could be interpreted as evidence for evolutionary conservatism in the traits that regulate the interactions for both spider mites and plants. Under such a scenario, it may also be expected that host and parasite phylogenies are congruent (19). Note, however, that lack of congruence does not immediately rule out the possibility of evolutionary conservatism in host–parasite interactions (Fig. 1, scenario *ii*). If host and parasite phylogenies are congruent, we expect that the degree of phylogenetic relatedness among mites using different plant modules is correlated with relatedness among the plants forming them (e.g., two groups of distantly related mites should be affiliated with modules in which plants are also distantly related, Fig. 1*A*). However, using an index of phylogenetic β-diversity (28), we found that pairwise phylogenetic dissimilarities between mites from different modules were not significantly correlated with the dissimilarities of the plants grouped in those modules (mean Spearman's $\rho = 0.29$, SD = 0.045; in 99.36% of the spider mite phylogenetic hypotheses used, this correlation was not significant at 0.01; *SI Appendix*, Table S4).

In sum, the analysis of the interaction network reveals that (*i*) mites and plants are phylogenetically clustered inside modules and (*ii*) both phylogenies are not congruent among modules.

Spider Mite Geographic Network and Its Relation to the Interaction Network.
Related species tend to cooccur within the same regions (23). This cooccurrence may generate the observed pattern of module phylogenetic structure regardless of evolutionary conservatism in the traits regulating interactions. To test this possibility, we explored whether geographical cooccurrence among spider mites results in the use of similar plants. Using the same network approach as for resource use, we characterized the geographical occurrence of spider mite species. The structure of this geographical network was also significantly modular ($Q = 0.57$, $P = 0.01$), being formed by 10 modules (Fig. 2*B* and *SI Appendix*, Fig. S1).

Comparisons of the module affiliation of mite species in the interaction and the geographic networks revealed that mites were significantly geographically clustered in 11 of 13 interaction modules (Fig. 2*B* and *SI Appendix*, Fig. S1*C*). Moreover, spider mites from the same interaction modules were not more phylogenetically related among them than with cooccurring species from other modules (in 9 of 13 modules; Fig. 2*A* and *SI Appendix*, Table S5). This implies that species using similar plants tend to occur in the same geographical regions. Importantly, these findings also show that the phylogenetic signal in host use disappears when accounting for geography.

The Relative Weight of Phylogeny and Geography in Shaping Host Use in Spider Mites.
The results presented above show that geographic and phylogenetic effects may be intertwined. We evaluated the relative strength of each factor in effectively shaping the differences in host use across species. We did so using partial generalized matrix regressions (29) where host use dissimilarities were modeled as a function of geographic dissimilarities and phylogenetic distances (*Materials and Methods*). Results using the complete dataset showed that both geography and plant phylogeny significantly affected host use patterns. The independent association of host use with geography was considerably stronger than that with plant phylogeny, although the total deviance
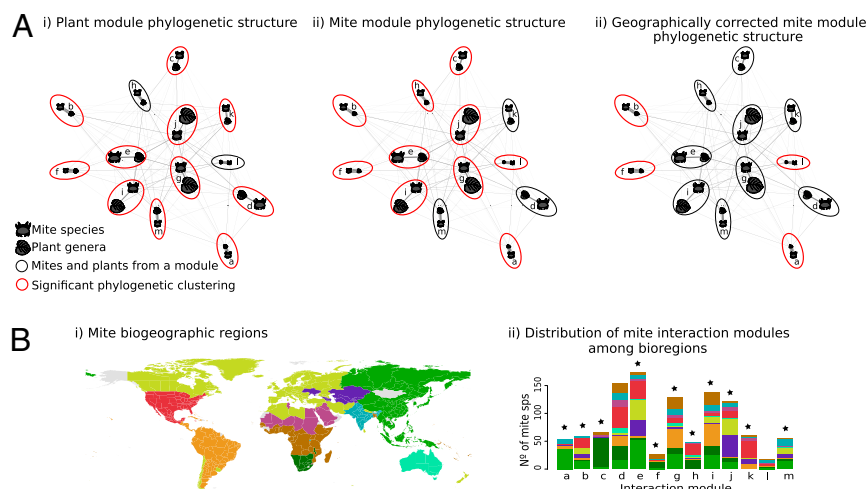
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Fig. 2. Phylogenetic signal in host use disappears after accounting for geography. (*A*) Module simplification of the clade-oriented spider mite–plant interaction network showing statistical significance in phylogenetic module structure. (*i*) Eleven of 13 modules were formed by phylogenetically clustered plant genera (red circles). (*ii*) Ten modules were formed by phylogenetically clustered mite species. (*iii*) After correcting for geography, only 4 modules show significantly phylogenetic clustering for mites. The size of mite and plant icons is proportional to the square root of the number of taxa belonging to each module, whereas link width is proportional to the number of links between taxa divided by the number of taxa. Module codes (*a–m*) are as in Fig 1. (*B*, *i*) Map showing the regions found through modularity analysis based on mite occurrences. Gray color corresponds to areas where no mites have been recorded. (*ii*) Mite species of 11 of 13 interaction modules also tended to be affiliated with the same geographic modules. Bars represent the number of mite species belonging to each interaction module. Bar colors correspond to the color of the bioregions to which mites belong. Stars above the bars indicate interaction modules showing significant geographical clustering at *P* < 0.01 (see also *SI Appendix*, Fig. S1*C*).

explained was low (*SI Appendix*, Tables S6–S9). In agreement with previous results, the effects of mite phylogeny partially overlapped with those of geography. Similarly, when we conducted this analysis independently for each module with more than 10 species ($n = 13$), we found that geography was the only significant factor in six modules, whereas mite phylogeny was significant in one module only (*SI Appendix*, Tables S6–S9). Further, in two of the three modules where both factors had significant effects, the geographic dissimilarities had stronger independent effects (*SI Appendix*, Tables S6–S9). In the remaining three modules, we found nonsignificant associations. These results suggest that host use by spider mites is largely phylogenetically unconstrained, entailing that they are potentially able to colonize any host within their distributional range.

Is Evolution in Host Use by Spider Mites Neutral, Relative to Plant Phylogeny? The question remains as to whether phylogenetic lability in mites is the consequence of the evolution in host use being neutral with respect to the plant phylogeny. To explore this question, we measured the relationships between the degree of mite phylogenetic specialism (30) and their intermodular participation (i.e., their inclusion into different modules, ref. 31) in the interaction and the geographic networks. That is, if plant modules are formed by phylogenetically related taxa due to trait inheritance, we should find that the levels of phylogenetic specialism in spider mites are correlated with their participation in different interaction modules. Alternatively, if the evolution of mite host use is neutral relative to plant phylogeny, the phylogenetic structure of plant modules should be mostly determined by the geographical distribution of plant lineages. Hence we should find that levels of mite phylogenetic specialism should be correlated with their participation into different geographical modules.

The degree of phylogenetic specialism of mite species was negatively correlated with their intermodular participation in the interaction network, but this was not the case in the geographic network (Fig. 3*A* and *SI Appendix*, Table S10). This finding shows that patterns of host plant use in spider mites are not neutral, relative to plant phylogeny. Accordingly, we found that the majority of mite species were phylogenetically specialist

(90% of mite species, 64.4% of them showing levels of specialism higher than random expectations). Note that this analysis requires the exclusion of mites specialized to one plant genus (*Materials and Methods*), so we are underestimating the actual proportion of phylogenetically specialist mites.

A closer look at the modular structure of the interaction network reveals that both phylogenetic specialism and intermodular participation vary greatly among modules. Participation is significantly lower and specialism significantly higher in modules *a*, *b*, and *d* (Fig. 3*B*). In addition, phylogenetic specialism is predicted better by mite species' intermodular participation in those modules ($R^2 = 0.26, 0.59$, and 0.42, respectively, vs. an average of 0.10 ± 0.08 SE in the other modules; *SI Appendix*, Table S11). Remarkably, most plants in these modules are either gymnosperms or commelinids (Fig. 3*C*), two evolutionarily distinct groups characterized by particular physical and chemical leaf features (32).

Discussion

Using a comprehensive dataset on the geographical distribution and parasitic interactions between spider mites and the plants they colonize, we show that patterns of phylogenetic signal in plant host use can be the result of geographic cooccurrence of spider mite species. Indeed, the simultaneous analysis of the phylogenetic and geographic effects on the interactions among plants and the parasitic spider mites that colonize them highlight the importance of historical biogeographical processes (23) as determinants of patterns of host use. As related species tend to inhabit the same regions, they mostly interact with species that also cooccur in those regions. On a large scale, this process may result in patterns of evolutionary niche conservatism regardless of the actual existence of evolutionary constraints in host use, as we show here for the evolution of host use in spider mites. Hence, it seems that spider mite adaptation to novel plant lineages is more restricted by geographical than by evolutionary processes. This finding suggests that spider mites are evolutionarily labile, being able to colonize new host plants in the course of time, provided they have geographical access to them.
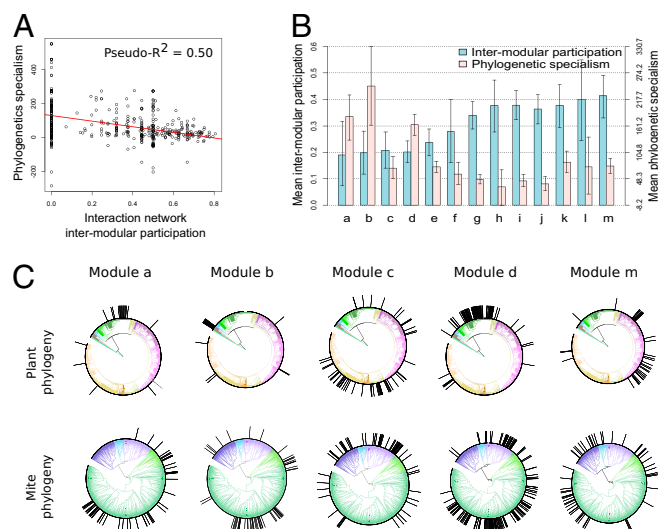
Fig. 3. Major evolutionary plant transitions shape host use in spider mites. (*A*) Intermodular participation in the interaction network is negatively correlated with levels of phylogenetic specialism. Pseudo-R^2 corresponds to the conditional pseudo-R^2 found in linear mixed models with module as a random term. (*B*) Mite species belonging to modules *a*, *b*, and *d* show higher levels of phylogenetic specialism (pink) and lower levels of intermodular participation (blue). Bars are average values with bootstrap confidence intervals at 95%. Module codes (*a*–*m*) are as in Fig 1. (*C*) Modules *a* and *d* are mainly formed by commelinids (depicted by black lines on the phylogenies), module *b* by gymnosperms, and module *c* by mite species mainly occurring in southern Africa, which includes the Cape floristic realm and hosts a large number of endemic plant genera and families (see also Fig. 2*B*). Module *m* is shown for comparative purposes.

The geographic signal in the evolution of plant host use entails that ecological interactions may be labile, which questions the extent to which patterns of evolutionary conservatism are the consequence of an ancestral inheritance of traits regulating interactions (1). Based on previous evidence, conservatism of ecological interactions was proposed to shape the organization of ecological communities (1). However, as shown here, such patterns of conservatism can be mostly shaped by geographic processes. This finding obscures the supposed implications of evolutionary conservatism in ecological systems. In fact, it may simply be that the density of dispersing parasites near infected plants increases the probability that spatially cooccurring plants host the same parasites (see ref. 7). Additionally, parasite evolutionary history has been found to be of little relevance in shaping parasite–host communities (e.g., ref. 33). Our results further suggest that geographical attributes should also be considered in the study of ecological communities. Communities whose species differ in their geographic distribution, islands with different geologic histories (34) or the impact of recent biological invasions (35), might be useful to disentangle the effects of historical geographic processes on the structure of ecological networks.

Beyond geography, the generalized phylogenetic lability in host use identified here may be the consequence of the mites' evolutionary lability. Experimental evolution studies reveal that spider mites adapt to novel host plants within few generations (36–38), indicating weak intrinsic limits to adapt to new host plants on a microevolutionary timescale. Here we found that colonization of novel hosts can happen despite the strong adaptive barriers imposed by major plant evolutionary transitions. These barriers appear to be associated with the particular characteristics of gymnosperms and commelinids, because these plant lineages also shape the interaction network structure. Gymnosperms, monocots, and eudicots are known to represent major transitions for herbivore host use in other arthropods (39, 40). Gymnosperm leaves

are rich in lignin, and commelinids—which include palms, water hyacints, *Poa* grasses, or bromeliads among others—are characterized by the presence of ferulic and coumaric acids in their cell walls and silicic acids in their leaves. Spider mites feed by sucking cell content, so they have to pierce the cell wall to acquire nutrients (41). Hence, our results suggest that these fundamental differences in plant leaves, associated with major evolutionary transitions, constitute significant adaptive barriers in the evolution of spider mite host use. However, spider mites have been able to overcome these barriers repeatedly throughout their evolutionary history (Fig. 3*C*).

These results may fuel the ongoing discussion over the macroevolutionary patterns in the diet of herbivores. Some studies suggest that host plant use by herbivores is mainly constrained by plant defenses (8). However, the ability to overcome such defenses has repeatedly evolved in different insect orders, revealing parallel evolution even at the molecular level (42). Our results reconcile these apparently contradictory observations, providing solid evidence that colonization of distantly related hosts may be frequent over evolutionary history.

The ability of specialist parasites to colonize distantly related plants while retaining a high phylogenetic host specificity is termed the parasite paradox (14, 15). Our results are consistent with such a paradox, because spider mites simultaneously show high phylogenetic host specificity and repeated successful colonizations of distantly related plant clades that constitute isolated archipelagos within the resource space. Pushing further the analogy with island biogeography may shed some light on the origin of this paradox. Extremely isolated archipelagos—such as Hawaii or Azores—have been repeatedly colonized by many unrelated lineages through long-distance dispersal processes. Despite being extremely rare, the integration of such events over time results in a highly phylogenetically diverse biota in such islands (43). In the same way, many parasite groups, such as spider mites, may be able to colonize disparate host lineages—such as gymnosperms or commelinids—through long phylogenetic distance dispersal processes. Despite being rarely successful, these colonization events can result in phylogenetically similar parasite communities using distantly related resource archipelagos, given enough evolutionary time.

Whether colonizations of isolated resource archipelagos promote the diversification of parasite lineages remains an open question. It could be expected that tradeoffs in the adaptation to distantly related plants would enable speciation via host shift (17). However, recent experimental studies question the existence of such tradeoffs in the evolution of both parasites (38) and hosts (44). In fact, the evolution of new parasite species by host shifts has been found to be overestimated (13) or predominantly allopatric (20). Future studies combining fully resolved phylogenies, geographic information, and experimental evolution approaches are required to unravel these questions.

Overall, the high phylogenetic lability shown by our results indicates that resource use in spider mites is evolutionarily labile. Such lability in host use could be general, at least for arthropod herbivores (39, 40, 42). This questions the role of evolutionary constraints as the sole process underlying patterns of niche conservatism on a macroevolutionary scale, for they can be mostly determined by the geographical distribution of clades and species. Similar results were found for other dimensions of the niche, such as climatic tolerances (22, 45). This accumulated evidence highlights the importance of geographic historical processes as determinants of current niches, which calls for conducting empirical and experimental studies that evaluate alternative hypotheses for the origin of niche conservatism patterns. Based on current evidence, resource use by plant parasites is shaped mostly by biogeographical processes, rather than by evolutionary conservatism.

Materials and Methods

Data on Host–Parasite Interactions and Species Distributions. Data on the geographical distribution of spider mites and their interactions with host plants

were obtained from the spider mite website (ref. 24; freely available at www1.montpellier.inra.fr/CBGP/spmweb/, accessed May 2014). Spider mite species lacking information on their host use were excluded. Information on the plant hosts was provided at different taxonomic levels so we used data at the genus level. The final dataset consisted of 1,350 plant genera and 1,115 mite species occurring in 184 regions and countries (SI Appendix, Appendix S4).

Phylogenetic Hypotheses. To reconstruct the phylogeny of spider mites, we first reconstructed a molecular phylogeny based on the cytochrome C oxidase subunit 1 (COI) of 68 spider mite species for which we found available sequences in GenBank (accessed June 2014) (SI Appendix, Appendix S2). Subsequently, we used phylogenetic uncertainty methods (26) to create 40,000 different phylogenetic hypotheses using both molecular and taxonomic information (SI Appendix, Appendixes S1 and S2). For the plants, a phylogenetic tree including all 1,350 genera was created using Phylomatic v3 (46) based on data from Bremer et al. (27). We fixed the age of 176 internal nodes based on Wikstrom et al. (47) and spaced all remaining nodes evenly among the dated nodes using BLADJ in Phylocom v.4.2 (48). Finally, a genus within Selaginelaceae was included at the phylogenetic root at the age of 410 million y, based on Willis et al. (32).

Network Characterization of Plant Use (the Interaction Network) and Geographic Occurrence (the Geographic Network). To map plant use by spider mites, we took advantage of community detection analysis—borrowed from network theory—to study network topological communities or modules (49). First, a bipartite interaction network was created based on the known interactions between mite parasites and their plant hosts regardless of whether they cooccur in the same localities (i.e., a so-called clade-oriented network, ref. 1). Community detection approaches have also been applied to explore the compartmentalization of occurrence networks (50–52). We created a spatial cooccurrence network, that also had a bipartite structure, so that mite species constitute one subset of nodes and the countries and regions where they occur the other, establishing a link based on the presence of a given species in a given site.

When applied to a bipartite network community detection analysis informs which groups of nodes from both levels are more densely connected (i.e., groups of plants and their associated mites, in the interaction network, and groups of mites occurring in same regions, in the geographic network). To analyze the modular structure of both networks, we used the modularity index proposed by Barber (53) for bipartite networks. This index was optimized using the Louvain algorithm [as implemented in the Matlab function genlouvain (refs. 25 and 54), available at netwiki.amath.unc.edu] and significance was assessed through randomizations of observed networks (SI Appendix, Appendixes S1 and S4).

Phylogenetic Structure of Spider Mite–Plant Modules. To investigate the phylogenetic structure within modules we calculated to what extent taxa belonging to a given module were, on average, more closely related within them than with taxa from other modules. In other words, we calculated the phylogenetic mean pairwise distances (MPD) between the $taxon_i$ and all other taxa belonging to its module (i.e., $MPD_{i\ intracommunity}$) minus the mean pairwise distances of $taxon_i$ and all other taxa from different modules ($MPD_{i\ intercommunity}$). Finally, we computed relative phylogenetic distinctiveness (RPD) as the inverse of the average between all taxa in a module, to obtain higher values when the phylogenetic distinctiveness was higher

$$RPD = -1 * \frac{\sum_{i=1}^{N} MPD_{i\ intracommunity} - MPD_{i\ intercommunity}}{N},$$

where N is the number of species in a given module. We preferred this index of distinctiveness rather than other indices of phylogenetic clustering that are more commonly used [such as net relatedness index (NRI) or phylogenetic species variability (PSV); refs. 55 and 56, respectively] because, although highly correlated, we found it more robust against assumptions of Brownian modes of evolution (SI Appendix, Appendix S3). To assess significance for the levels of phylogenetic clustering in each module, we followed a randomization procedure where either the mite phylogeny or the tip labels of the plant phylogeny were randomized (SI Appendix, Appendix S4).

Next, we explored the relationship between the phylogenetic dissimilarity among the spider mites from each interaction module and that of the plants grouped in the same module. We first used an index of phylogenetic β-diversity (28) to quantify the phylogenetic dissimilarities between mite and plant taxa belonging to pairs of modules. This index takes into account the differences due to gradients in phylogenetic diversity (57) and it is implemented in the R (58) package betapart (59). Secondly, to explore the correlation between mite- and plant-module pairwise phylogenetic dissimilarities, we used the Spearman rank correlation coefficient, assessing significance by comparing the observed values against those of 999 null models created by randomizing the spider mite phylogeny.

Effects of Geographical Cooccurrence on Host Use Phylogenetic Patterns. If mites using similar resources also tend to cooccur, we should find that the species affiliated with the same interaction modules should also cluster together into similar geographical modules. Thus, to investigate the geographical clustering of mites belonging to the same interaction modules, we first recorded the geographical module where each species of an interaction module was grouped. Then, we measured the entropy of the information in each module using the Shannon's diversity index (H). To assess significance, we compared the observed H values against 999 null values obtained from randomly selecting the geographic modules of the same number of species of each interaction module, with a probability based on the number of species present in each geographic module. A module was considered to be significantly geographically clustered if the observed H value fell below the 99% of null values. Finally, we also calculated a standardized effect size for H by subtracting the average of the null values of H and dividing by their SD.

We further explored to what extent the geographic distribution of mite lineages accounts for the phylogenetic structure of interaction modules. To do so, we calculated the degree to which mite species belonging to the same plant module were, on average, more closely related among themselves than with the species occurring in the same geographical module. Modifying the RPD index, we calculated $MPD_{intracommunity}$ for each mite species of a given interaction module in the same way as previously explained. However, when calculating the $MPD_{intercommunity}$, we only took into account the mite species that cooccur in the same geographical module. The remaining calculations were done as explained above for the RPD index. Finally, significance was assessed following the above-explained randomization procedure.

The Relative Weight of Phylogeny and Geography in Shaping Host Use in Spider Mites. To measure both host use and geographic dissimilarities we used the Simpson dissimilarity index (60) as implemented in the R package betapart (59). We chose this index because it does not take into account dissimilarities due to differences in generalism levels (60). We then fitted a generalized matrix regression (see ref. 29 for a similar approach) to host use dissimilarities as a function of geographical dissimilarities and phylogenetic distances using a binomial family and the following link function (SI Appendix, Appendix S4, ref. 29):

$$\mu = 1 - e^{-\eta}.$$

Further, to assess significant relationships, we randomized the interaction matrix 500 times using the independent swap algorithm as implemented in picante (61) and recalculating each time null host use dissimilarities. Factors explaining more deviance than 95% of the null cases were interpreted as being significant. We followed a forward stepwise selection procedure to test the significance of each variable independently. In cases where both phylogeny and geography were significant, we conducted a deviance partitioning analysis (62). We firstly used this procedure for the complete dataset to explore general patterns. Then, we applied this analysis to modules having more than 10 mite species to explore intramodule phylogenetic and geographic relationships.

Is Evolution in Host Use in Spider Mites Neutral, Relative to Plant Phylogeny? To calculate mite phylogenetic specialism, we used the RPD index (see above and SI Appendix, Appendix S3). Here we only used mite species known to interact with more than one plant genera ($n = 510$) because this was a requisite to compute this index. As previously explained, the RPD index will give positive values for high levels of phylogenetic specialism and negative values otherwise. We explore the statistical significance of levels of phylogenetic specialism by comparing observed levels against null values where the tip labels of the plant phylogeny were randomized. We further used an index of intermodular participation to calculate the participation in both the interaction and the geographical networks. The index is based on the density of intermodular connections (31), taking values of 0 when all connections are within a module and tending to 1 when connections are evenly distributed across all modules.

To investigate the relationships between levels of phylogenetic specialism and the intermodular participation in the interaction (IMPI) and geographic networks (IMPG), we fitted linear mixed effects models to phylogenetic specialism as a function of IMPI and IMPG. Further, to account for the potential effects of unevenness in sampling effort, the number of publications recording an interaction for each mite species was included as a covariable (SI Appendix, Appendix S1). Given that differences in the factors underpinning the species composition of modules may exist, we included the modules of the interaction network as a random term, testing different hypotheses on its effects on the intercept and/or explanatory variables (SI Appendix, Appendix S4). Model selection was based on the Akaike information criterion corrected (AICc) for small sample sizes (63). We assumed a difference of two AICc units to consider that two

models are significantly different. All models were run using the lme4 package (64) and AICc was calculated with package AICcmodavg (65) in the R environment. Once the best supported model was identified, we assessed a pseudo-R^2 following Nakagawa and Schielzeth (66), using the MuMIn package (67).

In case we found among-module differences in the relationships between phylogenetic specialism and either IMPI, IMPG, or both, we explored these relationships independently for each module using linear models.

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