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**Mutualism drives plant trait macroevolution beyond interaction-related traits**

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**Abstract [136 words//150 words MAX]:** Mutualisms have driven the evolution of some of the most conspicuous structures, yet, a growing body of theoretical and empirical work posit that it promotes slow evolution of interaction-related traits. How it affected the evolution of traits beyond those directly involved in the mutualism remains unclear. Here, we tested if and how mutualistic traits drive the evolution of non-mutualistic traits. We used a highly evolutionary replicated system –epiphytes forming symbioses with ants (Hydnophytinae, Rubiaceae)– and fit Ornstein–Uhlenbeck models that explicitly test the impact of discrete mutualistic traits on continuous non-mutualistic traits while controlling for climatic variables. We show that mutualistic traits shape the evolution of non-mutualistic traits, affecting both pace of morphological evolution, the strength of selection and the long-term meanof non-mutualistic traits. Mutualisms thus drive trait evolution beyond those that are directly involved in the interactions.

**Introduction:**

Mutualisms, the interactions of distinct species where all partner benefits, are thought to be important evolutionary forces (Sargent, 2004; Rezende et al., 2007; Gómez and Verdú, 2012; Van der Niet and Johnson, 2012; Chomicki et al., 2019, 2020; Zeng and Wiens, 2021a, 2021b). Concerning phenotypic evolution, several hypotheses have been put forward regarding the impact of mutualisms on traits that are directly involved in the interaction.

Theoretical work posited that mutualism should reduce the rate of phenological evolution in traits that are directly involved in the interaction – this should be especially true in highly specialized and obligate mutualisms in which trait matching phenotypes leads to strong reciprocal stabilizing selection (Thompson, 2005; Kopp and Gavrilet, 2006; Yoder and Nuismer, 2010; Raimundo et al., 2014). Another modelling effort identified the so-called ‘Red King effect’, a situation where the slowest evolving partner gain the largest share of the benefits (Bergstrom and Lachmann, 2003). Like in economic bargaining theory, the partner having its hand tied is less affected by threats from the other partner, and conversely can be more credible in the bargaining process (Bergstrom and Lachmann, 2003). This goes even further in suggesting that mutualism should foster species –not just interaction-related traits– to evolve slowly.

Models of mutualistic coevolution predicts that arms race or other dynamics whereby the trait value of reciprocally interacting traits increases should lead to breakdown (Week and Nuismer, 2021). Such models suggests that the few cases pollination mutualisms where there appear to be reciprocal trait exaggeration in pollinators and corolla length (Anderson and Johnson 2007, 2009; Pauw et al. 2009) may be outliers rather than the rule, or perhaps even represent mutualisms on the verge of breakdown (Week and Nuismer, 2021).

Empirical studies have found that highly specialized and dependent mutualisms promote evolutionary stasis of the traits involved in the interactions (Davis et al., 2014; Chomicki and Renner, 2017), but that changes in the partnership, such as the shift to a novel partner or the breakdown of the interaction can drive evolutionary change in mutualism-related traits (Whittall and Hodges, 2007; Bodbyl Roels and Kelly, 2011; Chomicki and Renner, 2017; Gervasi and Schiestl, 2017; Ramos and Schiestl, 2019). This is for instance the case of the size of entrance holes of ant-nesting structures (domatia) in the epiphytic Rubiaceae –a trait which limit which species can get access to the domatia– which entrance holes are highly constrained in size in specialized species (as this filter out potential unwanted partners) but enlarged substantially when the mutualism broke down (Chomicki and Renner, 2017). Similarly, plants excluded from pollinators independently evolved selfing – both at the micro and macroevolutionary scales (Bodbyl Roels and Kelly, 2011; Culley et al., 2012; Gervasi and Schiestl, 2017; Ramos and Schiestl, 2019).

How mutualism affect the evolution of traits unrelated to the interaction is unclear. Mutualism could affect such traits in different ways. The origin of a new, mutualistic trait could impact other traits by shifting allometric relationships (Brouat and McKey, 2000; 2001; Chomicki and Renner, 2019a). Likewise, mutualisms could change the nutritional balances, in a way that metabolic allometric relationship shifts (Zhang et al., 2011). In this scenario, there is no need for the evolution of a new trait, but the redistribution of nutritional resources affects other traits as a result. In addition to these direct effects, mutualistic traits could affect the evolution of other traits through cascades of indirect effects. While a few studies have reported a possible link, the mode and tempo of how mutualism could have impacted organismal phenotypic evolution is unclear. Three main limitations have prevented progress in this direction. First, inferring the evolution of mutualism back in time relies on combinations of traits used as proxies. Some but not others of these traits could impact phenotypic evolution. Second, the effect of mutualism needs to be disentangled from that of important abiotic variables, for instance climate. And third, one needs a group with sufficient evolutionary replication in mutualism.

We here address this question using the Rubiaceae epiphytic ant-plants (Hydnophytinae). The Hydnophytinae are an ideal group to address these questions because they involve many evolutionary transitions in mutualistic strategies – four independent gains of highly specialized and dependent mutualisms and twelve losses of the mutualism (Chomicki et al., 2017). Yet they form a sizeable clade of ~105 species wherein the mutualistic traits are relatively well understood. The plant offers nesting sites (domatia) and sometimes food rewards to their ant partners, in return for nutrients, and in some species defence and seed dispersal (Chomicki et al., 2016, 2017, 2020; Chomicki and Renner, 2016a, b; 2017, 2019a, b). Recent work has shown that the domatia has affect other traits by shifting leaf/stem allometry (Chomicki and Renner, 2019a), but how the evolutionary dynamics of non-mutualistic traits were impacted is unclear, in particular when abiotic factors are accounted for.

We here develop an Specifically, we . SpeIt also paves the way to more phylogenetic comparative studies combining the analysis of discrete and continuous traits.

**Materials and Methods:**

**Taxon dataset**

We used the taxon sampling of Chomicki and Renner (2017), which provided a strongly supported phylogeny of the Hydnophytinae relying on a matrix of six markers (nuclear ITS and ETS and plastid ndhF, psbA-trnH, trnL intron, and trnL-trnF spacer). However, we expanded the sampling of 76 species out of ∼105 Hydnophytinae species. Here we expanded the dataset to 89 taxa, together with a broader outgroup sampling including 46 taxa, selected to include two important Rubiaceae fossils that were used for time-calibration (see below, section on *Molecular clock dating*). The total dataset consisted of 135 taxa (Table S1).

**Molecular clock dating**

Molecular dating analyses relied on BEAST v.1.8 (Drummond et al., 2012) and uncorrelated lognormal relaxed clock models. We used the GTR + G substitution model with four rate categories and a Yule tree prior. MCMCs were run for 100 million generations, with parameters and trees sampled every 10,000 generations. We used Tracer v1.7 (Rambaut et al., 2018) to check that the effective sample size (ESS) of all parameters was >200, indicated that runs had converged. After discarding 20% as burn-in, trees were summarized in TreeAnnotator v.1.8 (part of the BEAST package) using the options “maximum clade credibility tree” which is the tree with the highest product of the poster probability of all its notes “mean node height” and a posterior probability of 0.98. The final tree was visualised in FigTree v1.4 (Rambaut, 2012). To calibrate our tree, we used two secondary constraints, two minimum age fossil constraints and one maximum age geological constraint. First, we constrained the age of the root using a secondary constraint, following Chomicki and Renner (2017). To do so, we calibrated the split between the Pacific clade and the so-called *Psychotria* clade IV of Barrabé et al. (2014), to 22 ± 7 million years, based on the age of this node estimated by these authors, using a normal prior and a standard deviation of 4 corresponding to their 95% confidence interval. CHECK TWO FOSSIL CONSTRAINTS WITH LAURA. The obligate farmed *Squamellaria* clade, restricted to two Fijian islands (Vanua Levu and Taveuni) was constrained to maximally 4 million years, the age of the oldest of the two islands (Sarnat, 2009).

**Trait dataset**

We generated a large trait dataset for the Hydnophytinae ant-plants. To test the impact of mutualism on non-mutualistic trait evolution, we first coded the three evolutionary strategies found in the Hydnophytinae, following Chomicki and Renner (2017, 2019). We coded the strategies as follow: ‘0’ non-mutualist (no domatium, outgroups), ‘1’ generalist and facultative mutualism, ‘2’ specialized and obligate mutualism (these species are also farmed), and ‘3’ no mutualism with ants (but with domatium). More details about these evolutionary strategies are found in Chomicki and Renner (2017, 2019). Then, we broke down mutualism into four key mutualistic traits to ask how to have mutualistic traits driven non-mutualistic trait evolution. We focussed on the following key mutualistic traits, namely (1) inner domatium wall differentiation, inside the ant-nesting structures (domatia); (2) food reward presence or absence; (3) domatium entrance holes and (4) domatium growth type. In addition, we also coded mating systems, for a specific downstream analysis (see *Results* and *Discussion* sections). These traits were coded based on literature (Huxley, 1978; 1993; Huxley-Lambrick, 1981; Jebb, 1985, 1991a, 1991b; Huxley and Jebb, 1991a, 1991b, 1991c; 1993; Chomicki and Renner, 2016a, 2016b, 2017, 2019a, 2019b; Jebb and Huxley, 2019; Chomicki et al., 2016, 2017).

For the continuous, non-mutualistic traits, we focused on the following four traits, namely stem cross-section area, leaf area, corolla length, petiole length and they were either taken for references cited above or measured based on herbarium specimens, available from jstor Global Plants ([https://plants.jstor.org](https://plants.jstor.org")).

*Inner domatium tissue differentiation* with regard to warts (structures inside the domatium which are key in the ant-derived nutrients uptake; c.f. Huxley (1978), Chomicki and Renner (2019)) were coded as ‘0’ when they were lacking but the species lacked a domatium, ‘1’ when they were not fully differentiated, with interspersed areas being ‘warty-like’ (with the warts being unevenly spaced and sized) and others ‘smooth-like’ but without clear-cut full differentiation, ‘2’ when they were fully differentiated into warty and smooth areas, ‘3’ absent (but domatium present). *Food rewards*, consisting of post-anthetic sugar rewards, c.f. Chomicki et al. (2016), were coded ‘0’ when absent in species without domatium, ‘1’ when absent (but domatium present), and ‘2’ when present. *Domatium entrance holes* were coded as ‘0’ no domatium, ‘1’ several large holes at the base of the domatium and smaller holes on the side, ‘2’ one larger hole at the base connecting to the first cavity, and small holes on the side and ‘3’ large holes throughout. *Domatium growth* was coded as ‘0’ for species lacking domatium, ‘1’ domatium with diffuse growth, and ‘2’ domatium with apical growth. (5) Mating systems were coded ‘0’ for heterostylous, ‘1’ non-heterostylous and ‘2’ functionally unisexual. Two species (*Hydnophytum tetrapterum* and *H. trichomanes*) were inferred to have heterostylous flowers based on other trait correlates; their flowers are otherwise unknown (Jebb and Huxley, 2019). All raw data is provided in Table S2.

**Accounting for climatic variables**

Prior to fitting the models of trait evolution, we accounted for the potential non-independence of observations due to climatic similarities between the sampling areas. We first used a Principal Component Analysis (PCA) using climatic data from WorldClim (Fick and Hijmans, 2017). We used all 19 variables from WorldClim (Fick and Hijmans, 2017), and after the PCA we retained the first three Principal Components (PC1-3), as they explain more than 95% of the variance in the original data (Supp. Table XX). We tested for the correlation between each continuous trait (namely Stem Area, Leaf Area, Corolla Length, and Petiole Length) and the first three climatic PCs considering the phylogenetic structure of the errors using a Phylogenetic Generalized Least Squares (PGLS) approach. Ultimately, we used the residuals of all models as the climate-corrected variables in all downstream analyses.

**Ancestral state estimations**

We performed all the analyses in both the Maximum Clade Credibility (MCC) tree and in a set of 20 trees randomly sampled from the posterior distribution of trees. We used stochastic character mapping (Huelsenbeck et al., 2003; Revell, 2012) to reconstruct evolutionary histories of each discrete trait for the Hydnophytinae. For the mcc tree, we assumed a model where all transition rates are empirically estimated and independent from each other since it was selected as the best model for this topology, and set the root state to be sampled from the conditional scaled-likelihood distribution. For the trees sampled from the posterior distribution, we used the best model selected for each of the trees. We generated 1000 maps for the MCC tree and 100 for each of the sampled topologies from the posterior distribution, and used all to summarize the states at each node to account for the many possible evolutionary histories of each trait. We thus analysed the proportion of each state at the main nodes to assess the ancestral state of each discrete trait.

**Linking rates of continuous trait evolution to transitions in discrete traits’ states**

To assess the evolutionary dynamics of the continuous traits for each of the discrete traits’ state, we sampled 100 of the 1000 maps in the MCC tree (and 10 for each of the sampled trees from the posterior distribution) and used them to fit seven different models of evolution for each continuous trait: (i) Single-rate Brownian Motion (BM1); (ii) Multiple-rate Brownian Motion (BMS); (iii) Single-rate OU (OU1); (iv) OU with multiple optima but same alpha and sigma (OUM); (v) OU with multiple optima and alpha but same sigma (OUMA); (vi) OU with multiple optima and sigma but same alpha (OUMV); (vii) OU with multiple optima, alpha, and sigma (OUMVA). The total number of parameters varied with the discrete trait and the model used, with the simplest model having always a single parameter (BM1 - one sigma² for all states) and the most complex model having up to 12 (OUMVA - one sigma², one alpha and one optimum for each of the 4 states of the discrete trait).

To avoid any arbitrary threshold to select the best model (such as a deltaAIC value smaller than 2) within all pairwise combinations of discrete and continuous traits, we used the Akaike weights of each model to calculate averaged parameter values for each stochastic map. Lastly, we generated pseudo-posterior distributions of averaged parameter values to assess how different continuous traits’ states evolved under distinct states of the discrete trait. All scripts are available at www.github.com/gburin/hydnoants.

**Results**

**Phylogenetics and molecular clock dating of the Hydnophytinae**

Maximum likelihood and Bayesian analyses yielded a tree topology similar to Chomicki and Renner (2017), with *Squamellaria* being sister to all remaining Hydnophytinae taxa. The next clade is the genus *Anthorrhiza*, as in Chomicki and Renner (2017), but the newly sampled species *Hydnophytum orichalcum* is placed as sister to *Anthorrhiza*, albeit with low support (but geographically consistent with *Anthorrhiza*). The molecular clock dating analysis yielded similar ages to Chomicki and Renner (2017), with the Hydnophytinae being 18.8 ± 3 Myrs.

**Ancestral state estimations of discrete mutualistic traits**

To test the impact of discrete mutualistic traits on non-mutualistic, continuous traits, we first inferred ancestral state estimations for all discrete mutualistic traits using stochastic mapping (*Materials and Methods*). Rather than constraining transition rates to standard models (e.g. Equal rates, all rate different models), we assumed a model where all transition rates are empirically estimated and independent from each other, and set the root state to be sampled from the conditional scaled-likelihood distribution. All ancestral state estimations are shown in Figs. S1-SX.

**Mutualism-dependent non-mutualistic trait comparative analyses**

Our analyses did not show significant associations between the climatic PCs and the continuous traits for the majority of the cases (Supp. Table XX). This indicates that microclimatic conditions do not appear to be a major driver for the evolution of our continuous traits of interest . Nevertheless, we ran all downstream analyses using the residuals from these models to directly control for minor effects of climatic variables..

The vast majority of pairwise combinations between discrete and continuous traits showed an OU model as the best model (Table 1). Moreover, in most cases the best models have distinct long-term mean values (θ) and strength of selection (α) for each state of the discrete mutualistic trait, with the addition of distinct evolutionary rates (σ2) values for a subset of the stochastic maps. Thus, we can expect that despite model uncertainty, these two parameters are strongly affected by the evolutionary history of the discrete traits, indicating important effects of mutualistic traits on the evolution of the non-mutualistic trait.

Due to the elevated number of variables and models, we opted to use a model averaging approach by calculating the weighted average of parameter values. The final value of each parameter was calculated by multiplying the estimated value for a given parameter in a given model by the Akaike weight of the given model. Thus, we need not resort to any arbitrary criterium (such as δAIC > 2) and can evaluate the dynamics solely based on the parameter values. All plots below only show the results from simmaps for which parameter values were larger than -10 (푒−10) and smaller than 10 (푒10), on the justification of values outside this range represent likely poor fitting or unreasonable biological meaning.

The type of domatium growth (**Fig. 1X**) had the greatest impact on non-mutualistic traits. Apical domatium growth (**Fig. 1X**) was associated with higher strength of selection (α) on corolla length and stem area (**Fig. 2X**). However, diffuse domatium growth correlated with higher strength of selection (α) for petiole length. The long-term mean values (θ) for corolla length, leaf area, petiole length and stem area were always higher in specie with apical domatium growth (**Fig. 2X**). Conversely, the evolutionary rate (σ2) of all four continuous non-mutualistic traits was always higher in species with diffuse domatium growth (**Fig. 2X, Table X**).

The presence of food rewards (post-anthetic nectaries; Fig. 1X; Chomicki et al., 2016) was associated with higher long-term mean values (θ) for all four continuous non-mutualistic traits. However, the opposite situation occurred for the evolutionary rate (σ2), which was higher for all four traits in species lacking food rewards (Fig. 2X, Table X).

The presence of differentiated warts in domatium (Fig. 1; Chomicki and Renner, 2019) was associated with greater long-term mean values (θ) in leaf area, petiole length and stem area. Again, the opposite situation occurred with the evolutionary rate (σ2), which was greater in species with without warts in the case of leaf area or in species with variable warts for stem area (Fig. 2X, Table X).

For domatium entrance holes (Fig. 1; Chomicki and Renner, 2017), species with one large hole at the base had higher long-term mean values (θ) in leaf area, petiole length and stem area (Fig. 2X, Table X). Species with several large entrance holes had higher evolutionary rate (σ2) for stem area.

All these results were consistent across climatic PCs (Figs. SX-SY).

**Sensitivity analyses**

Comment on impact of phylogenetic uncertainty You said earlier that it reinforced/highlighted the observed differences found? Can you expand a bit?

**Discussion**

Many traits associated with specialized mutualisms favour higher long-term means (θ) in non-mutualistic traits, indicating directional selection. By contrasts, others are associated with increased evolutionary rate (σ2). Our data reveals a consistent pattern with specialized and obligate mutualistic trait states associated with higher long-term means of non-mutualistic traits, suggesting that the directional effect of mutualisms goes beyond traits directly involved in the interaction (REF TABLE + SUPP). Conversely, we found that traits states of facultative and generalist mutualisms or non-mutualists were associated with higher evolutionary rates in non-mutualistic traits. Our results thus suggests that the stabilizing impact of mutualisms on trait evolution goes beyond the traits directly involved in the interaction. This is line with the Red king effect model (Bergstrom and Lachmann, 2003), which suggests that species, not simply mutualistic traits, should evolved slower when involved in mutualisms.

This further reinforces the idea that major transitions in mutualistic interactions, such as shifts between mutualistic strategies, are major drivers of trait evolution. While this has been widely documented, so far the traits studied were those directly involved in the interaction, such as floral traits in pollination mutualisms (Whittall and Hodges, 2007; Bodbyl Roels and Kelly, 2011; Davis et al., 2014; Gervasi and Schiestl, 2017). Our works shows that this effect goes beyond the traits that are directly involved in the interaction. Much like coevolutionary effects spread through indirect effects in mutualistic networks (Guimarães et al. 2017), the stabilizing effects of mutualisms, in particular of obligate and specialized mutualisms spread beyond the traits involved directly in the interaction.

This implies that mutualisms are important mediators of trait evolution and act through different direct and indirect pathways. A single trait model showed that coevolutionary effects radiate through non-interacting species through complex mutualistic networks (Guimarães et al. 2017). Here, we focused on a clade approach, where the type of mutualistic interactions has repeatedly is highly evolutionary replicated (Chomicki and Renner, 2017). Our study thus expands our understanding of the role of mutualism in trait evolution by showing that mutualisms drive the evolution of non-mutualistic traits, through interaction with distinct mutualistic traits. Importantly, it showed that less intimate, facultative and generalist mutualistic interactions have greater impact on non-mutualistic trait evolution. Because such mutualisms are most common that highly specialized and obligate mutualisms (Chomicki et al., 2020, REFS), this implies that mutualisms may have a more important role in shaping trait evolution than is currently acknowledged. A second implication is that mutualism may alter a species’ environmental selective pressures, by driving evolutionary change in non-mutualistic trait. In our case, the evolution of leaf area was strongly affected by mutualistic traits (Fig. XX). Because leaf area is under strong environmental constraints (Wright et al., 2017), our results suggest that mutualism may alter the outcome of environmental sorting. Third, because mutualistic interactions are mediated by species traits, the evolutionary effects on non-mutualistic traits likely generate eco-evolutionary feedbacks, thus affecting the mutualistic interactions directly.

This raises the question of what mediates these indirect effects? One possibility is that in many specialized and obligate mutualisms, notably in macro-mutualisms such as insect/plant mutualisms, the specialized mutualisms is mediated by specific traits. Because the traits, such as a long corolla, a domatium, etc, are costly investment, they weight very much on the allometric balance of the species’s traits. If these specific traits are maintained tightly through stabilizing selection, then they reduce the leverage for other traits to change.

These results further suggests that specialized and obligate mutualisms places allometric barriers so that reversion could be more difficult. Thus, the much higher propensity of facultative and generalist mutualisms to break down as opposed to specialized and obligate ones which are much more stable (Chomicki and Renner, 2017; Chomicki et al, 2020) may not only be linked to the importance of the partnership. It may thus also relate to allometric metabolic constraints. Hence such mutualistic interactions may constrain the evolution of other traits. This idea is consistent with the fact that the different mutualistic traits that we studied have differential impact on non-mutualistic trait evolution. Thus, domatium growth has a major effect on all non-mutualistic traits, while the small warts inside domatia have smaller effects overall.

Interestingly, mutualistic strategies, while showing the overall the same relationships, do not fully allow to unveil this pattern. Because mutualistic strategies are combination of mutualistic traits, they likely hinder some relationship. This further suggests that the impact of mutualisms on non-mutualistic traits is largely mediated by mutualistic traits, rather than by the mutualisms itself. This is consistent with the idea that allometric relationships mediate these relationships.

Method discussion:

Methods available to combine discrete and continuous traits (+ climatic variables?). Review current methods quickly + show what this adds. And what might be needed in further developments.

Maybe a more general discussion going back to models of trait evolution – your Cetacean manuscript was very inspiring! And I wondered whether we could pull out some though in that conceptual direction (?)







**Conclusion**

Partner shifts morphological change are concentrated at speciation events (Whittall and Hodges, 2007). Mutualism appears to have a stabilizing effect on traits that are directly involved in the interaction, but it also generates phenotypic diversity through partner switching and loss of the interactions. Our study has revealed that mutualism drive non-mutualistic trait evolution through indirect effects likely involving allometric relationships. We found that facultative multi-species mutualisms have the strongest effect on non-mutualistic trait evolution. Because they are the most widespread partnerships, this suggest that mutualism have a large, hidden role in driving trait evolution.

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