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**The nuanced impact of mutualism on trait macroevolution**

**Mutualism with ants drives plant trait macroevolution**

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**Abstract [136 words//150 words MAX]:** Mutualisms have driven the evolution of a wide range of specific structures linked to the interaction, especially in highly dependent interactions. How it affected the evolution of traits beyond those directly involved in the mutualism remains unclear. Here, we tested if and how mutualistic traits affect the evolution of non-mutualistic traits. We used a highly evolutionary replicated system –epiphytes forming symbioses with ants (Hydnophytinae, Rubiaceae)– and develop 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 optima of selection of non-mutualistic traits. Our work thus pinpoints a major role for mutualistic interactions by indirect effects on other traits as drivers of morphological evolution at the macroevolutionary scale.

**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). With regard to 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, perhaps even 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 were 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. 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 a sufficient number of evolutionary changes in mutualism. In addition to these direct effects, mutualistic traits could affect the evolution of other traits through cascades of indirect effects.

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 defense 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-mutualisitc traits were impacted is unclear, in particular when abiotic factors are accounted for.

We here develop approach to tackle this question using Ornstein–Uhlenbeck models that explicitly test the impact of discrete mutualistic traits on continuous non-mutualistic traits while controlling for climatic variables. Our work reveals that mutualism has generally affected the strength of selection, evolutionary rate and optimum of non-mutualistic traits, but in a patchwork way: the effects of the distinct mutualistic traits is highly uneven, and distinct mutualistic traits drove the evolution of different non-mutualistic traits. Our work shows how the important, but nuanced impact of mutualistic interactions on macroevolution. It also paves the way to more phylogenetic comparative studies combining the analysis of discrete and continuous traits.

**Materials and Methods:**

*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. We had seven discrete traits as well as five continuous, which we 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). The discrete trait dataset consisted of the following traits: (1) Inner domatium tissue differentiation, with regard to warts: structures inside the domatium which are key in the ant-derived nutrients uptake (i.e. 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 ‘wart-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). (2) 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. (3) Plant architecture was coded ‘0’ non-epiphytic shrub, ‘1’ multi-stemmed epiphyte, ‘2’ single-stem epiphyte. (4) 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). (6) Leaf structure was coded as ‘0’ for thick but non-succulent leaves, ‘1’ for variable, ‘2’ for thin papery leaves, and ‘3’ for fleshy, succulent leaves. (7) Domatium outgrowths were coded as ‘0’ for species lacking domatium, ‘1’ for no domatium outgrowth (when domatium is present), ‘2’ variable for species with both bald and hairy/spiny forms, or species where there is variable and often spare hairs or spines, and ‘3’ when spines are present (stiff or flexible). Additionally, we also coded the mutualistic strategy as ‘0’ non-mutualist (no domatium), ‘1’ generalist and facultative mutualism, ‘2’ specialized and obligate mutualism (these species are also farmed), and ‘3’ no mutualism with ants (but with domatium). The five continuous traits: stem area, leaf area, corolla length, petiole length and domatium entrance hole diameter were either taken for references cited above or measured based on herbarium specimens, available from jstor Global Plants (<https://plants.jstor.org>).

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 (REF). We used all 19 variables from WorldClim (REF), 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”, “Corola Length”, “Petiole Length”, and “Hole Diameter”) 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 MCC tree and in a set of 20 1,000 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. 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. 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 analyzed 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.

**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* forming the basalmost clade sister to the 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.

*Mutualism-dependent non-mutualistic trait comparative analyses*

The vast majority of pairwise combinations between discrete and continuous traits showed an OU model as the best model (Table 1). Moreover, it is possible to notice that the best models in most cases have distinct optima and alpha for each state of the discrete mutualistic trait, with the addition of distinct sigma² 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 the mutualism on the evolution of the trait and phylogenetic uncertainty will highlight/reinforce the observed differences.

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 were filtered to exclude parameter values that were larger than -10 (푒−10) and smaller than 10 (푒10), on the justification of representing bad fitting or unreasonable biological meaning.

**Domatium Growth**

Species with apical growth show higher θ values for corolla length, leaf and stem area and petiole length. For α values, species with apical growth show higher values for corolla length and stem area, whereas species with diffuse growth show higher values for hole diameter and petiole length. Regarding σ2, species with diffuse growth show higher values for all traits. Species with diffuse growth show higher values of both θ, α and σ2 for both PC1 and PC2.

**Reward**

Species that give rewards show higher θ values for all traits but hole diameter, for which the signal is mixed (both in PC1 and PC2). Also, these species show higher α values for all traits, and higher σ2 for all traits but hole diameter (both in PC1 and PC2).

**Strategy**

Species that are obligate mutualists show higher values of θ for all traits but hole diameter, for which species that lost this interaction have higher hole diameters than other species for PC1, and the facultative ones for PC2. On the other hand, species that are facultatively mutualistic show higher α values for corolla length, and petiole length, whereas for leaf area the higher α values are from species who lost this interaction, and for stem area the higher are obligate mutualists. For σ2, facultative species show higher values for all traits but leaf area, for which species that lost the interaction show higher values.

**Warts**

Species with differentiated warts have higher θ and σ2 values for all traits, for which higher values belong to species that lost this structure (whereas for PC2 higher values are for species with variable warts). For α, species with variable warts show higher values for hole diameter and petiole length, whereas species who lost these structures show higher values for leaf and stem area.

**Entrance holes**

Species only one large entrance hole at the base have higher θ values for stem area, petiole length, and leaf area, while species with large entrance holes had lower θ values for these traits. The strength of selection (α) was similar across traits, except for species with several large entrance holes at the base for which α was greater than other groups for corolla length. There was no major variation of σ2 values for all traits.

**Sensitivity analyses**

Comment on impact of phylogenetic uncertainty

**Discussion**

|  | **Corolla length** | | | **Leaf area** | | | **Petiole length** | | | **Stem area** | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Parameters** | **α** | **θ** | **σ2** | **α** | **θ** | **σ2** | **α** | **θ** | **σ2** | **α** | **θ** | **σ2** |
| **Domatium growth** | **Apical higher** | **Apical higher** | **Diffuse higher** | **-** | **Apical higher** | **Diffuse higher** | **Diffuse higher** | **Apical higher** | **Diffuse higher** | **Apical higher** | **Apical higher** | **Diffuse higher** |
| **Reward** | **-** | **Reward higher** | **No reward higher** | **-** | **Reward higher** | **No Reward higher** | **-** | **Reward higher** | **No Reward higher** | **-** | **Reward higher** | **No Reward higher** |
| **Strategy** | **-** | **-** | **-** | **-** | **Obligate higher** | **Lost higher** | **-** | **Obligate higher** |  | **-** | **Obligate higher** | **Facult higher** |
| **Warts** | **-** | **-** | **-** | **-** | **Differentiated higher** | **Lost slightly higher** | **-** | **Differentiated higher** | **-** | **-** | **Differentiated higher** | **Variable higher** |
| **Entrance holes** | **-** | **-** | **-** | **-** | oneLbase higher | **-** | **-** | oneLbase higher | **-** | **-** | oneLbase higher | **Several large base slightly higher** |

*Mutualism impact non-mutualistic traits in nuanced ways* **[GC to do]**

Our analyses reveal that mutualism affect traits in diverse ways, shifting the strength of selection, rate of morphological evolution and selection optimum. Interestingly, the mutualistic interaction itself has an indirect role: it is the traits related to the mutualism which effect other traits. BUT NOT IN THE CASE OF THE ANT-POLLINATOR CONFLICT

* Examples will likely include the indirect effect of the evolution of specialized mutualism on pollination systems  ant/pollinator conflicts  evolution of selfing

| **Log flower corolla max length [cm]** | | |
| --- | --- | --- |
|  |  |  |
| 0 | -0.2905344 | 0.7478638 |
| 1 | -0.1082294 | 0.89742174 |
| 2 | 0.38304026 | 1.46673708 |

**Correlation btw corolla length and mating system!**

Allometry

Direct effect of mutualism

*Comparative analysis of discrete/continuous traits controlling for climatic variables [method discussion section –* ***Gustavo****]*

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 influence the evolution of most traits. Even though we still run all downstream analyses using the residuals from these models, for practical purposes the results for the OUwie analyses represent the parameters estimated using the raw continuous variables.

**Conclusion**

Theory of phenotypic evolution at the macroevolutionary scale – expand on that.

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 the impact of mutualism on traits not involved in the interaction is more nuanced and varied. We found that evolutionary change in mutualistic traits affect the strength of selection, the optimum of selection as well as the evolutionary rate of traits, but every mutualistic affect the phenotypic evolution of distinct traits, and in distinct ways.

Mutualistic interactions have led to the evolution of a wide range of specific structures linked to the partnerships. But how it affected the evolution of traits beyond those directly involved in the mutualism remains unclear. Our aim was to test whether mutualistic traits affect the evolution of non-mutualistic traits. To do so, we developed a series of OU models in which we tested the impact of

LINK TO the debate on BIOTIC VS ABIOTIC DRIVERS OF MACROEVOLUTION

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