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Review

The ontogeny of plant indirect defenses

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ABSTRACT

Plants frequently attract natural enemies of their herbivores, resulting in a reduction in tissue damage and often in enhanced plant fitness. While such indirect defenses can dramatically change as plants develop, only recently have ecologists begun to explore such changes and evaluate their role in mediating plant–herbivore–natural enemy interactions. Here we review the literature documenting ontogenetic patterns in plant rewards (i.e. extrafloral nectaries (EFNs), food bodies (FBs) and domatia) and volatile organic compounds (VOCs), and identify links between ontogenetic patterns in such traits and the attraction of natural enemies (ants). In the case of reward traits we concentrate in ant–plant studies, which are the most numerous. We report that all indirect defensive traits commonly vary with plant age but ontogenetic trajectories vary among them. Myrmecophytic species, which provide both food and shelter to their defenders, do not produce rewarding traits until a minimum size is reached. Then, a pronounced increase in the abundance of food rewards and domatia often occurs as plants develop, which explains the temporal succession or colony size increase of mutualistic ant species and, in some cases, leads to a reduction in herbivore damage and enhanced fitness as plants age. In contrast, ontogenetic patterns were less consistent in plant species that rely on VOC emissions to attract natural enemies or those that provide only food rewards (EFNs) but not nesting sites to their associated ants, showing an overall decline or lack of trend with plant development, respectively. Future research should focus on uncovering: (i) the costs and mechanisms underlying ontogenetic variation in indirect defenses, (ii) the relative importance of environmental and genetic components shaping these ontogenetic trajectories, and (iii) the consequences of these ontogenetic trajectories on plant fitness. Advances in this area will shed light on the context dependency of bottom-up and top-down controls of herbivore populations and on how natural selection actually shapes the ontogenetic trajectories of these traits.

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Introduction

Plant indirect defenses involve the expression of traits that promote the effectiveness of predators and parasitoids to locate their prey on plant tissues, resulting in decreased herbivore damage and, in the case of many tropical and perennial species, enhanced plant fitness (Kost and Heil, 2008; Rosumek et al., 2009; Trager et al., 2010). The association between plants and natural enemies of herbivores can range from loose facultative relationships such as those between plants and spiders, to the obligate mutualisms common in ant–plant interactions (Heil and McKey, 2003). However, the effectiveness of plant indirect defenses depends on the strength and stability of the association between plants and the enemies of their herbivores (Kessler and Heil, 2011). Because the expression of plant traits attracting and supporting predators and parasitoids can vary with resource availability, plant size and development-associated changes, there is a strong spatiotemporal aspect to plant–herbivore–natural enemy interactions that should be addressed when trying to understand the consequences of these associations for plants.

While numerous studies have examined the role of spatial variation (e.g. environmental gradients) in the direction and magnitude of these tritrophic interactions (e.g. Palmer, 2003; Rios et al., 2008; Shenoy and Borges, 2010), only recently have ecologists begun to explore the role of temporal changes (e.g. seasonal and ontogenetic variation) in the dynamics of such interactions (Boege and Marquis, 2005; Rico-Gray and Oliveira, 2007, and references therein). In the last decade, empirical studies demonstrating that ontogenetic variation in plant indirect defenses can have dramatic consequences for plant fitness have accumulated (e.g. Miller, 2007; Palmer et al., 2010). However, there is still a lack of knowledge regarding the generality of such ontogenetic changes, as well as their role in the temporal dynamics of plant–herbivore–natural enemy interactions.

Here we review the available literature documenting ontogenetic patterns in plant indirect defenses; specifically plant rewards (i.e. extrafloral nectaries (EFNs), food body (FB) structures, and domatia) and volatile organic compounds (VOCs) produced as plant cues for herbivore's natural enemies. Because previous reviews have described the variation in some indirect defenses associated with leaf development (Heil and McKey, 2003), here we limited our review to the ontogenetic trajectories of plant defense at the whole plant level, which none of the previous works explicitly and quantitatively addressed (but see Brouat and McKey, 2000 for the specific case of ontogenetic changes in domatia). We consider that resource allocation constraints shaping within-plant tissue development (e.g., source and sink relationships) are substantially different from those that regulate whole-plant ontogeny (e.g., changes in physiological priorities from growth to maintenance or reproduction, see Boege and Marquis, 2005) and thus should be treated as different processes.

Why are plant indirect defenses expected to change throughout plant ontogeny?

As is the case for ontogenetic trajectories in direct defenses (Boege and Marquis, 2005; Barton and Koricheva, 2010), ontogenetic shifts in indirect defenses should be shaped by a combination of internal constraints (e.g., allocation costs, architectural requirements, anatomical constraints, etc.) and external drivers (most notably temporal patterns in herbivore selection pressure, but also variation in the abundance and efficacy of natural enemies). Predictions about how internal and external factors should influence ontogenetic patterns in indirect defenses come from two prominent plant defense theories, the optimal defense theory

(ODT; McKey, 1974, 1979) and the growth-differentiation balance hypothesis (GDBH; Herms and Mattson, 1992). Both models assume that defenses are costly and use adaptive explanations to predict patterns of variation in defensive traits as plants age, yet their predictions differ. The ODT predicts that plant parts and/or stages with high fitness value and higher risk of attack, such as young tissue, should be highly defended. Given that seedlings (e.g. Moles and Westoby, 2004; Clark et al., 2012) and reproductive stages (e.g. Noy-Meir and Briske, 2002) are particularly susceptible to damage and both stages also have high fitness value, the ODT would predict that plant investment in indirect defensive traits should be high early during seedling establishment, decrease during the vegetative stages and increase back again with reproductive maturity. In contrast, the GDBH predicts that defenses should be higher in tissue and/or stages in which growth demands for carbon and other nutrients have been met. In this case, the excess of carbon fixed through photosynthesis is then allocated to differentiation-related processes (i.e. processes that enhance the structure or function of existing cells such as maturation and specialization) (Stamp, 2003). Seedlings experience high inter- and intra-specific competition and are often carbon-limited due to relatively small photosynthetic surfaces, and indirect defenses (especially domatia, FBs and EFNs) require a sophisticated tissue differentiation process often constrained by plant architecture (e.g. Brouat and McKey, 2001). Thus, the GDBH would predict a low or almost complete lack of indirect defense traits until seedlings are able to accumulate resources for functions other than growth (i.e. differentiation-related process). Afterwards, a rather constant increase in the relative investment in defensive traits should be expected as plants continue to produce photosynthetic area, root:shoot ratio decreases, and plants are able to develop storage organs. The applicability of these two theories to indirect defenses has been previously exemplified in the context of within-plant tissue investment (i.e. between young and old leaves, vegetative and reproductive tissues, etc.) in EFN (Heil et al., 2000; Wackers and Bonifay, 2004; Radhika et al., 2008; Holland et al., 2009) and VOCs (Chou and Mullin, 1993; Radhika et al., 2008; Rostas and Eggert, 2008), but not in the context of the whole plant ontogeny.

Extrafloral nectaries, food body structures, and nesting space (domatia) are the three most common rewards offered by plants to attract mutualistic higher trophic levels (Heil and McKey, 2003; Chamberlain and Holland, 2009). Although natural enemies attracted by these plant rewards include multiple arthropod predators such as ants, wasps, lady-bird beetles, spider mites, and spiders, as well as parasitoids (reviewed by Heil, 2008), all studies documenting ontogenetic variation in plant rewards for tritrophic interactions are from ant–plant systems. Among these systems, the boundaries between obligate and facultative mutualisms can be hard to define, as often several intermediate associations occur, resulting in a continuum (Bronstein et al., 2006). Thus, for the purpose of this review, we divided this continuum into two subsections: examples where ants use host–plants as their nesting site versus those where ants do not nest on the plant but regularly visit them to forage on food rewards. Thus, in the first section we discuss some facultative (myrmecophiles) and all obligate (myrmecophytes) systems that involve ants nesting on their host–plants, including those cases where host–plants provide domatia to house mutualistic ants, as well as systems where the ants construct nesting sites themselves (see Appendix A for a list of genera). In the second section, we describe systems where ant–plant associations are only based on the provision of EFNs and ants do not permanently inhabit plant tissues, as well as the emission of volatile organic compounds used by various natural enemies to locate prey on host plants.

Combining a qualitative review with a meta-analytical approach, we assessed the following specific questions: (1) Are there generalizable and similar patterns in the ontogenetic trajectories of plant indirect defense traits? (2) Which of these two theories (ODT or GDBH) better explain the variation seen in indirect defenses over plant ontogeny? (3) Do ontogenetic trends in indirect defenses differ between plants that form mutualisms with nesting ants versus plants that have loose facultative interactions with non-nesting natural enemies? We then discuss the relevance of plant ontogeny in plant-herbivore-natural enemy interactions for our understanding of the evolution of plant defense, suggesting future venues of research.

Data collection and analysis

We performed a literature search using the ISI Web of Science online service to obtain all published studies reporting ontogenetic changes in indirect plant defense. The literature search was performed using all combinations of the following keywords: ontogeny or development with extrafloral nectaries, domatia, food bodies, volatile compounds, ants, natural enemies, tri-trophic interactions with active lemmatization for all available document types, languages and years (to January 2013). Literature cited in the retrieved studies was examined to detect additional published cases. Using all studies, we qualitatively describe the generality of ontogenetic patterns in plant indirect defense. In addition, for a subset of studies that assessed similar questions and provided appropriate data (n , mean, and standard deviation for different ontogenetic stages, or regression coefficients for the relationship between plant age and indirect defenses), we extracted data and conducted a meta-analysis using the MetaWin 2.1 statistical program (Rosenberg et al., 2002) to quantify ontogenetic patterns and test potentially important sources of variation. The final data set included 19 studies published between 1989 and 2013 conducted on 18 plant species from 10 plant families, giving a total sample size of $N = 31$ (Appendix B). Ontogenetic patterns were represented as the difference in defense of older ontogenetic stages – younger ontogenetic stages, and were calculated using the Hedge's d effect size.

The analyses were conducted using a mixed-effects model, and bias-corrected bootstrap 95% confidence intervals were generated from 4999 iterations; effect sizes were considered significant when confidence intervals did not overlap with zero. For significant mean effect sizes, we also calculated fail-safe numbers (n_{fs}) using the Rosenberg fail-safe number calculator, which represents the number of studies with null effects that would need to be added to the mean in order to reduce the significance level to 0.05. To examine whether ontogenetic patterns in indirect defense differed between plants that interact with nesting ants versus plants with non-nesting ants, we performed between-group heterogeneity tests using the χ^2 statistic Q_b (Gurevitch and Hedges, 2001). Additional between-group heterogeneity tests were conducted to examine variation in the ontogenetic patterns among different defense traits (food bodies, EFNs, VOCs, etc.). Because these traits were not distributed independently between nesting and non-nesting plants (for example, domatia are recorded only from nesting plant systems; Appendix B), heterogeneity tests were conducted separately within these two groups of plants. Finally, between-group heterogeneity was tested among plant families in order to assess whether the data reveal phylogenetic patterns in indirect defense.

Patterns of indirect defenses across plant ontogeny

The overall ontogenetic pattern across all studies was positive ($E_+ = 0.372$), indicating a tendency for indirect defense traits

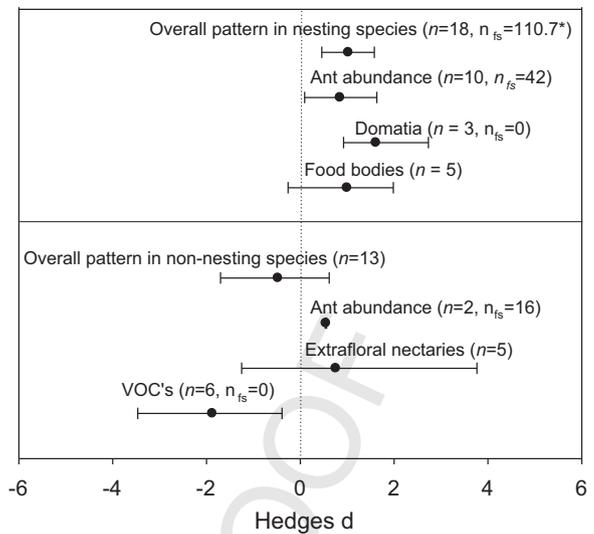


Fig. 1. Mean Hedge's d effect sizes (\pm 95% bias-corrected confidence intervals), sample sizes, and fail-safe numbers (n_{fs}) for studies comparing plant indirect defense traits in young versus old ontogenetic stages. Positive mean Hedge's d values indicate an ontogenetic increase in defense traits, while a negative Hedge's d indicates an ontogenetic decrease. Patterns are presented for plant species that interact with nesting ants in the top panel of the figure (i.e. plant providing both food rewards and shelter to mutualistic ants), and for non-nesting plants in the bottom panel (i.e. plant providing only food rewards to associated ants and plants emitting VOCs as signals to attract natural enemies). Significant patterns occur when the confidence intervals fail to include zero, which is marked with a dotted line. Asterisks indicate that the fail-safe number is robust ($>5n + 10$). "VOCs" represent volatile organic compound emission.

to increase across plant development, although this trend was not significant (bias-corrected 95% CI -0.294 – 0.982). There was no evidence for phylogenetic variation in the ontogenetic patterns ($Q_b = 1.73$, $df = 3$, $P = 0.6034$). This analysis however, suffered from low replication within plant families, rendering quite low power to detect differences among families. There was a significant difference in the ontogenetic trajectories of nesting versus non-nesting plants ($Q_b = 6.23$, $df = 1$, $P = 0.0334$; Fig. 1), with nesting species showing a significant increase in indirect defense across ontogeny ($E_+ = 1.023$, 95% CI 0.459 – 1.578 , $n = 18$, $n_{fs} = 111$) whereas non-nesting plants had no general pattern ($E_+ = -0.480$, 95% CI -1.702 – 0.616 , $n = 13$). Due to this difference between nesting versus non-nesting systems, we further consider them separately below.

The ontogeny of domatia and food rewards in nesting ant-plant interactions

Ontogenetic variation in indirect defenses in myrmecophytic species has been explored in a number of systems encompassing more than 17 genera, 13 families, and a variety of food rewards and domatia structures (Appendix A). In most cases, the first critical stage is determined by the time it takes for the host plant to reach a minimum size to produce enough rewards to sustain a colony of ants. This period, usually associated with the onset of domatia development, may vary from young seedlings reaching a height of 10–15 cm to saplings of 1–2.5 m in height (Appendix A). Once myrmecophytic plants surpass the critical uncolonized stage and a colony of ants is established, developmental variation in phenotypic expression of rewards occurs. The few studies available to date have reported that the quality and quantity of plant rewards increase as plants age and/or size increases, particularly in the total abundance of FBs (Heil et al., 1997; Itino et al., 2001), EFNs (Young

et al., 1997), and domatia (Fonseca, 1999; Brouat and McKey, 2001; Fonseca and Benson, 2003; Pringle et al., 2012).

For our meta-analysis, we had enough studies with suitable data to quantitatively assess ontogenetic trends for domatia and food bodies, and additionally considered how ant abundance changes during plant ontogeny. Among these three variables (domatia, FBs and ant abundance), there is no evidence for variation in their ontogenetic trajectories for myrmecophytic plants ($Q_b = 0.69$, $df = 2$, $P = 0.7188$; Fig. 1). Instead, we found that both ant abundance and domatia significantly increase across ontogeny, while food bodies show no general pattern (Fig. 1).

Changes in the absolute or relative investment of indirect defensive traits throughout plant age have been linked to constraints in plant resource allocation, morphology and physiology. For instance, Heil et al. (1997) showed that for *Macaranga triloba*, the relative FB production (per leaf mass) decreased with increasing plant size, whereas the absolute amount of FBs produced increased. This apparent discrepancy resulted mainly from the fact that the FBs are produced on all branches; and thus, larger plants with more branches have more FBs. Therefore, they concluded that while the relative cost of the defense decreases (FBs per unit leaf), the potential benefit does not. Similarly, ontogenetic trajectories in hollow-stemmed domatia may be linked to constraints in physical stability. For example, for a similarly sized cavity, seedlings would need to invest in additional tissues to reach a minimum thickness that covers a hollow structure without losing stability and/or resources to supply leaves and stems, whereas individuals further along in their development would have already invested in sufficient tissues to overcome this limitation (Brouat and McKey, 2000; Blatrix et al., 2012).

Some studies have shown that during the uncolonized ontogenetic stage, levels of herbivore damage in myrmecophytic plants often exceed those of older and/or comparable life stages that house ants (e.g. Itino and Itioka, 2001; Del Val and Dirzo, 2003; Djieto-Lordon et al., 2004). This observation has raised the question of whether young stages of myrmecophytic plants should rely more on direct defenses, such as secondary metabolites and physical defenses, than older (colonized) plants (Nomura et al., 2001; Heil and McKey, 2003). However, evidence for this ontogenetic shift from direct to indirect defenses is scarce and ambiguous. Some studies have demonstrated higher unpalatability or lower herbivore damage/survival in younger pre-colonized plants as compared to older colonized stages (Nomura et al., 2001; Llandres et al., 2010). Nonetheless, the only study that explicitly measured direct defenses showed that in *Cecropia peltata* (Cecropiaceae), leaf phenolics, tannins and trichome density were lower in pre- than post-ant colonization (Del Val and Dirzo, 2003). Thus, contrary to expectations colonized *C. peltata* plants invested more in both direct and indirect defenses as compared with pre-colonized plants. Additional research is needed to assess whether ontogenetic switches from direct to indirect defenses are common in myrmecophytic plants.

Additional evidence of an increase in plant rewards as plants age may arise from studies looking at ant abundance and species replacement over time. Because ants are usually limited by space and resource abundance (Fonseca, 1999; Heil et al., 2001; Itino et al., 2001), temporal changes in colony size and species identity should correspond with changes in the abundance of different rewards produced over the plant's lifespan. Indeed, we found that for myrmecophytes, ant abundance significantly increases across ontogeny (Fig. 1). Temporal ant species replacement has been found early during the transition from facultative to obligate mutualistic ants (e.g. Longino, 1991; Djieto-Lordon et al., 2004, 2005; Dejean et al., 2008) or among obligate ant species that compete for nesting sites (e.g. Young et al., 1997; Feldhaar et al., 2003;

Fonseca and Benson, 2003) (see also Appendix A). Because mutualistic ant species vary in their competitive ability or nesting requirements, the temporal transition of associated ant species as plants develop can be very conservative, demonstrating a specific replacement of species across ontogeny (Fiala and Maschwitz, 1992; Fiala et al., 1994; Feldhaar et al., 2003; Fonseca and Benson, 2003; Djieto-Lordon et al., 2004; Dejean et al., 2008; Palmer et al., 2010). Hence, studies incorporating plant ontogenetic trajectories in reward traits and ant species turnover suggest that plant ontogeny is a key factor maintaining the coexistence of diverse ecological communities utilizing an apparently uniform resource. Furthermore, given that mutualistic ant species vary in life history traits, their dependency on plant rewards, as well as in their aggressiveness toward herbivores, turn-over in ant species during plant ontogeny can play a key role in determining the temporal patterns of herbivore damage (e.g. Djieto-Lordon et al., 2004). Even in the case of myrmecophytes associated with a single or few mutualistic ant species throughout their development, field studies have demonstrated that the magnitude of ant protection against herbivores generally increases as plants grow (Izzo and Vasconcelos, 2005; Trager and Bruna, 2006; but see Pringle et al., 2012). In these cases, differences in ant effectiveness throughout plant ontogeny have been related to reward quality or plant structure when larger plants are also capable of housing ant colonies larger (e.g. Fonseca, 1999; Frederickson and Gordon, 2009; Orivel et al., 2011) and more efficient at removing herbivores from foliage (Fonseca, 1993; Izzo and Vasconcelos, 2005; Palmer et al., 2010).

The ontogeny of plant volatile organic compounds and food rewards in non-nesting ant-plant interactions

In contrast with myrmecophytic systems, there are fewer studies examining the expression of indirect defense traits across ontogeny in non-myrmecophytic species or in plants that emit volatile organic compounds (VOCs) as signals to attract natural enemies. We found that whereas VOC emissions significantly decrease across ontogeny, EFN abundance or productivity shows a non-significant tendency to increase (Fig. 1). Furthermore, in non-myrmecophytic species, ant abundance significantly increases across ontogeny (Fig. 1). However, although patterns appear to be variable among these defense traits, low sample sizes and some variation within each measure of indirect defense, together with ant abundance, resulted in a non-significant heterogeneity test ($Q_b = 5.77$, $df = 2$, $P = 0.2218$).

Ontogenetic variation in the production of EFN could be related to changes in ant efficiency, in the trade-offs with other defenses or in their inducibility across ontogeny. For example, comparison of EFN frequency and density in trembling aspen (*Populus tremuloides*, Salicaceae) showed a dramatic decrease in EFN production as tree height or age increased (Doak et al., 2007; Wooley et al., 2007). This reduced investment in EFN production with plant age has been explained as a consequence of a decreased benefit of these rewards in tall trees, where ants do not confer sufficient protection against herbivores (Doak et al., 2007), or to shifts in plant defenses from indirect to direct defenses; however, no such trade-offs have been yet reported (Wooley et al., 2007; Young et al., 2010). In contrast, in other species, EFNs are more numerous or limited to mature reproductive stages (Veena et al., 1989; Falcao et al., 2003; Kobayashi et al., 2008; Holland et al., 2009; Villamil et al., 2013). EFN inducibility as plants age has been only explored in the annual legume *Vicia faba* (Fabaceae), showing that age-dependent induced responses are influenced by damage intensity (Kwok and Laird, 2012). In particular, Kwok and Laird (2012) found that induction of EFNs in damaged versus control plants did not vary across five developmental stages when damage was moderate, but under

a severe damage event only older stages, before the onset of flowering, were able to significantly increase EFN production as compared to younger juvenile stages.

Whether ontogenetic changes in the presence and abundance of EFNs and/or ants translate into shifts in herbivore damage affecting plant fitness has been little explored in facultatively mutualistic associations. To our knowledge, only one study to date has considered enough stages of plant development to explore ontogenetic changes in the production of plant reward, herbivore attack, identity and effectiveness of associated bodyguards, and the combined effect of all these patterns on overall plant fitness (Miller, 2007). In this study, tree cholla cacti (*Opuntia imbricata*, Cactaceae) provide EFNs at all plant ages, but in greater abundance and/or quality following the onset of reproduction (Miller, 2007; see also Villamil et al., 2013). As a consequence, ant occupation rate increases and species identity changes as plants mature. Whereas younger plant stages have equal probability of being occupied by either of the two associated ant species, older plant stages are almost exclusively occupied by the more effective of the two ant partners (Miller, 2007). Because herbivore pressure also increases with plant age, temporal variation in ant partners has a positive effect on lifetime fitness (Miller, 2007). In other systems however, the evidence for EFN-mediated ontogenetic changes in predator effectiveness has been inconclusive (e.g. Wooley et al., 2007; Chamberlain et al., 2010).

In turn, the emission of volatile organic compounds appears to consistently decline across ontogeny among the species studied to date (Fig. 1). However, these measures can obscure more important qualitative changes in VOC emissions across ontogeny due to shifts in the composition of compound blends. For example, Kollner et al. (2004) showed that volatile blend complexity increased in leaves but decreased in roots as maize plants (*Zea mays*, Poaceae) developed from seedling to mature individuals (Kollner et al., 2004). In other cases, changes in VOC emissions were associated with their presence in specific plant tissues, such as the case of several cultivated crucifers, where overall concentrations of volatile hydrolysis products show a rapid decrease during the first weeks of development after sowing, followed by a steady increase as plants reached reproductive maturity and produced seeds with high contents of glucosinolates (Cole, 1980).

In addition to ontogenetic patterns in the constitutive expression of VOCs, there is recent but scarce evidence that the induction of VOCs also changes during plant ontogeny. In general, most studies have reported high VOC induction early in ontogeny (Shiojiri and Karban, 2006; Rostas and Eggert, 2008; Hare, 2010; Hare and Sun, 2011; Shiojiri et al., 2011), although there are also examples where VOC induction increase as plants age (Mattiacci et al., 2001; Zhu and Park, 2005). Furthermore, there is also evidence that the composition of induced VOCs changes during ontogeny (Zhu and Park, 2005; Hare, 2010). For example, in soybeans, aphid damage increased levels of *p*-Limonene in younger plants, whereas levels of (*E,E*)- α -farnesene were induced in older plants (Zhu and Park, 2005).

The evolution of ontogenetic trajectories in indirect defenses

Although indirect defenses have been shown, in some cases, to positively impact plant fitness, we know very little about the action of natural selection on such traits (Rudgers, 2004), and no studies have investigated their evolvability. To properly assess this, we need evidence that genetic variation in the ontogenetic patterns of indirect defense traits is associated with variation in overall plant fitness. This imposes important logistic challenges because it is

difficult, particularly in long-lived plants, to measure entire ontogenetic trajectories and lifetime reproductive success with enough replicates to determine their genetic variation. Hence, it should be most fruitful to initially investigate the evolution of the ontogeny of indirect defense in short-lived plants. Moreover, for plants interacting with multiple species of natural enemies, it is imperative to consider the specific timing and effectiveness of each species across ontogeny (e.g. Feldhaar et al., 2003; Fonseca and Benson, 2003; Palmer et al., 2010).

A revealing example of the role of ontogeny in the evolution of plant indirect defenses is the case of *Acacia drepanolobium* trees (Fabaceae). These trees interact with four different species of ants throughout their development. The ant species vary in their effectiveness as defenders and in their consumption of plant rewards and reproductive tissues, directly and indirectly altering plant performance (Palmer et al., 2010). One of the associated ant species, *Crematogaster nigriceps*, might even be viewed as parasitic, as the ants sterilize the plants by destroying all of the floral meristems in the canopy (Stanton et al., 1999). However, because *C. nigriceps* ants tend to inhabit juvenile plants and because they are very active defenders against herbivores, their residence has an overall positive effect on plant performance via survival and growth during early ontogenetic stages (Palmer et al., 2010). Plant ontogeny also determines the outcome of interactions with the ant species *C. sjostedti* and *Tetraponera penzigi*. Ants of these two species enhance plant performance in mature trees, not because they are effective defenders, but due to several other factors: high temporal reliability, low dependency on plant rewards allowing the trees to allocate resources into reproduction (Young et al., 1997; Palmer et al., 2010), and/or due to a higher tolerance response by plants subject to enhanced herbivory. In contrast, when *C. sjostedti* ants inhabit juvenile plants, they reduce survival, having a negative impact on fitness. Hence, *Acacia* fitness appears to be higher when plants partner with all four ant species over their lifetime due to synergistic effects of timing and duration of ant inhabitants couple with their contrasting benefits and costs (Palmer et al., 2010). The details and temporal dynamics of these interactions took over a decade of field investigations and yearly demographic sampling of nearly 1800 *Acacia* trees (Palmer et al., 2010), shedding light on why our knowledge about the evolution of ontogenetic trajectories is so limited.

Conclusions and future directions

We provide clear evidence that indirect defenses markedly change across plant ontogeny. However, using meta-analysis and a qualitative review of the literature, we have shown that there is no single ontogenetic trajectory of these traits. Instead, significant differences occur between plants that closely interact with nesting ants compared to plants that interact more loosely with their herbivores' natural enemies, highlighting interesting variation between mutualistic versus non-mutualistic interactions. While plants providing food and shelter to nesting ants consistently demonstrate ontogenetic increases in domatia and ant abundances, consistent with ontogenetic delays in architecture and allocation to indirect defense, plants that rely on VOC signals and/or provide just food rewards to non-nesting ant-plant systems are much more variable.

Returning to the predictions based on the ODT and GDBH, the patterns reported here offer partial support for both. In particular, the production of domatia in nesting ant-plant systems and ant abundance on both nesting and non-nesting ant-plant systems support an increase in indirect defense, consistent with the GDBH predictions. In contrast, ontogenetic declines in VOCs support the ODT. Patterns of food body production and extrafloral nectaries are ambiguous,

offering support for neither model. Nonetheless, given the current limited number of studies on this subject, overall conclusions should be interpreted with caution for several reasons. First, we often lack complete trajectories that span the entire ontogeny of plants, particularly for long-lived plants, preventing us from properly assessing the ODT and GDBH. Second, a greater breadth of systems needs to be investigated. For example, few plant families have more than one species represented (Appendix B), and there is non-independence between trait type and plant life history. In particular, most of the research done on ontogenetic trajectories of plant reward traits (FBs, EFNs and domatia) has been conducted on perennial species whereas herbaceous plants dominated the studies looking at ontogenetic trajectories in VOC emissions.

Notwithstanding the increasing interest in describing these ontogenetic trajectories and their ecological implications, much remains to be assessed. In particular, we identify the following areas to be especially fruitful for future research: (i) *defense syndromes and costs* – detailed studies are needed to simultaneously examine multiple direct and indirect defense traits and estimate changes in the metabolic costs of all defense traits across plant development, in order to assess the potential trade-off between direct (chemical, physical, and tolerance traits) and indirect defenses as plants grow (e.g. Nomura et al., 2001; Del Val and Dirzo, 2003; Llandres et al., 2010); (ii) *induction of indirect defense traits* – despite the plastic and inducible nature of these defenses, few studies have explored the role of plant age on the induction of VOCs and reward traits (e.g. Zhu and Park, 2005; Rostas and Eggert, 2008; Hare, 2010; Kwok and Laird, 2012), which could shed new light on the relationship between plasticity and plant ontogeny; (iii) *natural enemies* – it is essential that we broaden our knowledge to include associations other than ant-plant mutualisms in the case of plant rewards and multiple natural enemies in the case of VOCs, such as parasitoids and other generalist predators (e.g., mites, beetles) in order to generalize about ontogenetic patterns in top-down control of herbivores; (iv) *heritability* – measures of additive genetic variation in the ontogenetic trajectories of indirect defense traits are needed in order to assess the evolvability of these patterns; and (v) *plant diversity* – more species need to be examined with respect to the ontogeny of indirect defense in order to develop more robust patterns and more precise examinations of phylogenetic patterns. Particular emphasis should be paid to herbs, which have been largely neglected in this topic. Finally, the

consequences of ontogenetic trajectories in plant indirect defenses on natural enemy attraction, herbivore abundance and damage, and plant fitness need to be quantified. Although the evidence is strongly suggestive that temporal patterns in herbivory are at least partly driven by ontogenetic patterns in indirect defense, this has only been experimentally tested in a few systems.

In sum, ontogenetic changes in plant defense offer a challenging opportunity to study the evolution of complex phenotypes, shaped by the action of natural selection on the variation of multiple traits across plant development. Understanding the ontogenetic variation of indirect defenses can shed light on why bottom-up and top-down controls of herbivore populations are context dependent (temporally variable in direction and strength) or even hard to find. Thus, the evolutionary ecology of ontogenetic trajectories in plant indirect defenses offers an exciting and fertile field for future research.

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Appendix A.

Plant families, genera and species associated with ants nesting on/within host-plant tissues, and known to show ontogenetic trajectories in plant rewards (i.e. onset of domatia formation). Food type: EFN = extrafloral nectaries, FB = food bodies, H = homopteran trophobionts, F = fungi, W = lipid-rich or protein-rich wound calus; size at first domatium indicates tree size (usually height in meters) when the first swollen internode/stem (caulinary domatia), swollen thorn or leaf pouches (foliar domatia) has been reported to develop and thus, initiation of myrmecophytic interaction occurs. Ant species turnover refers to the replacement of ant species identity throughout plant development, and has been classified as L: low, M: moderate, H: high, or ? : unknown.

Family	Genus	Species	Symbiotic ant species	Geographic region	Food type	Domatia type	Size at first domatium	Turnover	Reference
Boraginaceae	<i>Cordia</i>	<i>C. nodosa</i>	<i>Allomerus</i> cf. <i>demerarae</i> /Azteca spp.	Neotropics	H	Caulinary	>0.5 m	M	Brouat and McKey (2000)*, Solano et al. (2003)
		<i>C. alliodora</i>	Multiple	Neotropics	H	Caulinary	<1 year old	H	Brouat and McKey (2000)*, Trager and Bruna (2006)
Cecropiaceae	<i>Cecropia</i>	<i>C. obtusifolia</i>	Azteca sp.	Neotropics	FB	Caulinary	?	H	Longino (1991)
		<i>C. membranacea</i>	Multiple	Neotropics	FB	Caulinary	0.5 m	?	Brouat and McKey (2000)*
		<i>C. pachystachya</i>	Azteca sp.	Neotropics	FB	Caulinary	>ca. 2 cm trunk diameter	?	Nishi and Romero (2008)
		<i>C. peltata</i>	Azteca sp.	Neotropics	FB	Caulinary	>1 m	?	Del Val and Dirzo (2003)
		<i>C. prov. tessmannii</i>	<i>Pachycondyla luteola</i>	Neotropics	FB	Caulinary	0.1 m	?	Brouat and McKey (2000)*
Crypterionaceae	<i>Crypterionia</i>	<i>C. griffithii</i>	<i>Cladomyrma maschwitzii</i>	SE Asia		Caulinary	0.5 m	?	Brouat and McKey (2000)*

Appendix A Continued

Family	Genus	Species	Symbiotic ant species	Geographic region	Food type	Domatia type	Size at first domatium	Turnover	Reference		
Chrysobalanaceae	<i>Hirtella</i>	<i>H. myrmecophila</i>	<i>Allomerus octoarticulatus</i>	Neotropics	–	Pholiar	?	?	Izzo and Vasconcelos (2002), Izzo and Vasconcelos (2005)		
		<i>H. physophora</i>	<i>Allomerus decemarticulatus</i>	Neotropics	EFN	Pholiar	>22 leaves	L to none	Solano et al. (2003), Leroy et al. (2010), Orivel et al. (2011)		
Euphorbiaceae	<i>Macaranga</i>	<i>M. hosei</i>	Multiple to <i>Crematogaster</i> sp. 4	SE Asia	FB, EFN, H	Caulinary	0.7 m	H	Brouat and McKey (2000)*, Itino and Itioka (2001)		
		<i>M. pruinosa</i>	<i>Crematogaster</i> sp. to diverse	SE Asia	FB, EFN, H	Caulinary	0.7 m	?	Brouat and McKey (2000)*		
		<i>M. punctulata</i>	<i>Camponotus (Colobopsis)</i> sp.	SE Asia	FB, EFN	Caulinary	0.15 m	?	Brouat and McKey (2000)*		
		<i>M. beccariana (M. triloba)</i>	<i>Crematogaster decamera</i>	SE Asia	FB, EFN, H	Caulinary	0.05–0.02 m	L?	Brouat and McKey (2000)*, Itino and Itioka (2001), Handa et al. (2013)		
		<i>M. bancana (M. triloba)</i>	<i>Crematogaster borneensis</i>	SE Asia	FB, EFN, H	Caulinary	0.05–0.01 m	L?	Brouat and McKey (2000)*, Itino and Itioka (2001), Feldhaar et al. (2003)		
		<i>M. trachyphylla</i>	<i>Crematogaster borneensis</i>	SE Asia	FB, EFN/H?	Caulinary	<0.5 m	?	Itino and Itioka (2001), Itino et al. (2001)		
		<i>M. winkleri</i>	<i>Crematogaster</i> sp. 2	SE Asia	FB, EFN, H	Caulinary	0.05–0.01 m	?	Brouat and McKey (2000)*, Itino and Itioka (2001)		
Fabaceae	<i>Acacia</i>	<i>A. cornigera</i>	<i>Pseudomyrmex</i> spp.	Neotropics	FB, EFN	Swollen thorns	?	?	Heil et al. (2009)		
		<i>A. hindsii</i>	<i>Pseudomyrmex</i> spp.	Neotropics	FB, EFN	Swollen thorns	?	?	Heil et al. (2009)		
		<i>A. collinsii</i>	<i>Pseudomyrmex</i> spp.	Neotropics	FB, EFN	Swollen thorns	?	?	Heil et al. (2009)		
		<i>A. chiapensis</i>	<i>Pseudomyrmex</i> spp.	Neotropics	FB, EFN	Swollen thorns	?	?	Heil et al. (2009)		
		<i>A. drepanolobium</i>	<i>Crematogaster</i> spp., <i>Tetraponera penzigi</i>	Africa	EFN	Swollen thorns	>0.5 m or less	H	Stanton et al. (2002), Palmer et al. (2010)		
		<i>Leonardoxa</i>	<i>L. africana rumpiensis</i>	Multiple	Africa	EFN, H	Caulinary	0.5 m	?	Brouat and McKey (2000)*	
			<i>L. africana letouzei</i>	<i>Aphomomyrmex afer</i>	Africa	EFN, H	Caulinary	0.6 m	?	Brouat and McKey (2000)*	
			<i>L. africana africana</i>	<i>Petalomyrmex phylax</i>	Africa	EFN	Caulinary	0.1 m	M	Mckey (1984), Brouat and McKey (2000)*	
			<i>Humboldtia</i>	<i>H. brunonis</i>	Multiple to <i>Technomyrmex albipes</i>	SE Asia	EFN	Caulinary	0.7–1 m	M?	Brouat and McKey (2000)*, Gaume et al. (2005)
				<i>H. laurifolia</i>	Multiple	SE Asia	EFN	Caulinary	?	?	Brouat and McKey (2000)*
	<i>Tachigali</i>	<i>T. paniculata</i>	Multiple	Neotropics	H	Caulinary	?	?	Brouat and McKey (2000)*		
		<i>T. myrmecophila</i>	<i>Pseudomyrmex concolor</i>	Neotropics	H?	Caulinary	?	?	Brouat and McKey (2000)*		
		<i>T. spp.</i>	<i>Pseudomyrmex</i> sp./ <i>Azteca</i> sp.	Neotropics	–	Pholiar	>0.5 m	H	Fonseca and Benson (2003)		
Gentianaceae	<i>Anthocleista</i>	<i>A. vogelii</i>	Multiple	Africa	EFN	–	–	H	Dejean et al. (2008)		
Lamiaceae	<i>Vitex</i>	<i>V. thyrsoiflora</i>	<i>Tetraponera tessmannii</i>	Africa	F, W	Caulinary	<0.3 m	H	Brouat and McKey (2000)*, Djieto-Lordon et al. (2005)		
Melastomataceae	<i>Maieta</i>	<i>M. guianensis</i>	<i>Pheidole minuta/Crematogaster</i> sp.	Neotropics	H	Pholiar	>13 leaves	M	Solano et al. (2003), Lapola et al. (2005), Leroy et al. (2010)		
		<i>Tococa</i>	<i>T. bullifera</i>	<i>Crematogaster laevis/Azteca</i> sp.	Neotropics	H	Pholiar	?	?	Lapola et al. (2005)	
		<i>T. guianensis</i>	Multiple	Neotropics	–	Pholiar	>16 leaves	M	Michelangeli (2003), Solano et al. (2003), Leroy et al. (2010)		
Ochnaceae	<i>Lophira</i>	<i>L. alata</i>	Multiple	Africa	–	–	–	L	Dejean et al. (2008)		
Passifloraceae	<i>Barteria</i>	<i>B. dewevrei</i>	Multiple	Africa	EFN, H	Caulinary	?	?	Brouat and McKey (2000)*		
		<i>B. fistulosa</i>	<i>Tetraponera aethiops</i> to multiple	Africa	EFN, H	Caulinary	1 m	L to none	Brouat and McKey (2000)*, Dejean et al. (2008)		
		<i>B. nigritana</i>	Multiple	Africa	EFN, H	Caulinary	>1–1.5 m	H	Brouat and McKey (2000)*, Djieto-Lordon et al. (2004)		
Rutaceae	<i>Zanthoxylum</i>	<i>Z. myriacanthum</i>	Multiple	SE Asia	EFN, H	Caulinary	>4 m	H	Moog et al. (2002)		
Sapindaceae	<i>Pometia</i>	<i>P. pinnata forma glabra</i>	Multiple	SE Asia	EFN, H	Pholiar	>2 m	H?	Moog et al. (2008)		

Brouat and McKey (2000)* indicates references therein.

Appendix B.

Meta-data extracted from publications and used in the meta-analyses of ontogenetic patterns in indirect defense traits. Studies needed to have reported key data in order to be included in the meta-analysis, including sample size mean (\pm S.D.) values for young and old ontogenetic stages; or sample size and regression coefficients. Heterogeneity analyses were conducted to examine potential sources of variation in ontogenetic patterns, including

phylogeny (plant family), whether or not the species associate with ants nesting on/within host-plant tissues, the indirect defense trait type (domatia, food body abundance (FB), extrafloral nectary abundance or production (EFNs), volatile organic compound emissions (VOCs)). As an indirect measure of the effectiveness of these traits, ontogenetic patterns in ant abundance on host plants were also analyzed. Hedge's *d* values and sample sizes are reported for each entry; multiple entries exist for publications that examined more than one plant species or defense trait.

Family	Species	Associate with nesting ants?	Defense trait	N	Hedge's <i>d</i>	Reference	
Asteraceae	<i>Artemisia tridentata</i>	NO	VOC	60	0.650	Shiojiri and Karban (2006)	
Boraginaceae	<i>Cordia alliodora</i>	YES	Ant abundance	16	0.445	Trager and Bruna (2006)	
	<i>Cordia alliodora</i>	YES	Ant abundance	11	-1.661	Pringle et al. (2012)	
	<i>Cordia alliodora</i>	YES	Domatia	13	2.730	Pringle et al. (2012)	
Cactaceae	<i>Opuntia imbricata</i>	NO	Ant abundance	120	0.560	Miller (2007)	
Chrysobalanaceae	<i>Hirtella physophora</i>	YES	Ant abundance	35	0.914	Orivel et al. (2011)	
Euphorbiaceae	<i>Croton bonplandianum</i>	NO	EFN	10	24.325	Veena et al. (1989)	
	<i>Macaranga bancana</i>	YES	Ant abundance	8	0.952	Itino et al. (2001)	
	<i>Macaranga bancana</i>	YES	FB	7	1.523	Itino et al. (2001)	
	<i>Macaranga beccariana</i>	YES	Ant abundance	26	3.490	Handa et al. (2013)	
	<i>Macaranga beccariana</i>	YES	Ant abundance	10	0.969	Itino et al. (2001)	
	<i>Macaranga beccariana</i>	YES	FB	8	1.265	Itino et al. (2001)	
	<i>Macaranga triloba</i>	YES	FB	25	-1.152	Heil et al. (1997)	
	<i>Macaranga trachyphylla</i>	YES	Ant abundance	6	0.901	Itino et al. (2001)	
	<i>Macaranga trachyphylla</i>	YES	FB	8	2.441	Itino et al. (2001)	
	<i>Macaranga winkleri</i>	YES	Ant abundance	8	0.967	Itino et al. (2001)	
	<i>Macaranga winkleri</i>	YES	FB	8	1.784	Itino et al. (2001)	
	Fabaceae	<i>Glycine max</i>	NO	VOC	12	-4.926	Zhu and Park (2005)
		<i>Glycine max</i>	NO	VOC	12	-3.668	Rostas and Eggert (2008)
<i>Tachigali myrmecophila</i>		YES	Ant abundance	8	0.949	Fonseca (1993)	
<i>Tachigali myrmecophila</i>		YES	Domatia	8	0.923	Fonseca (1993)	
<i>Tachigali polyphylla</i>		YES	Ant abundance	8	0.590	Fonseca (1993)	
<i>Tachigali polyphylla</i>		YES	Domatia	8	0.983	Fonseca (1993)	
<i>Vicia faba</i>		NO	EFN	210	2.444	Kwok and Laird (2012)	
Passifloraceae	<i>Turnera velutina</i>	NO	Ant abundance	110	0.532	Villamil et al. (2013)	
	<i>Turnera velutina</i>	NO	EFN	110	1.360	Villamil et al. (2013)	
Poaceae	<i>Zea mays</i>	NO	VOC	9	-3.707	Kollner et al. (2004)	
Salicaceae	<i>Populus tremuloides</i>	NO	EFN	80	-0.805	Doak et al. (2007)	
	<i>Populus tremuloides</i>	NO	EFN	128	-2.272	Wooley et al. (2007)	
Solanaeae	<i>Datura wrightii</i>	NO	VOC	170	-0.494	Hare (2010)	
	<i>Datura wrightii</i>	NO	VOC	32	-0.792	Hare and Sun (2011)	

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