

Fungi reduce preference and performance of insect herbivores on challenged plants

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Abstract. Although insect herbivores and fungal pathogens frequently share the same individual host plant, we lack general insights in how fungal infection affects insect preference and performance. We addressed this question in a meta-analysis of 1,113 case studies gathered from 101 primary papers that compared preference or performance of insect herbivores on control vs. fungus challenged plants. Generally, insects preferred, and performed better on, not challenged plants, regardless of experimental conditions. Insect response to fungus infection significantly differed according to fungus lifestyle, insect feeding guild, and the spatial scale of the interaction (local/distant). Insect performance was reduced on plants challenged by biotrophic pathogens or endophytes but not by necrotrophic pathogens. For both chewing and piercing-sucking insects, performance was reduced on challenged plants when interactions occurred locally but not distantly. In plants challenged by biotrophic pathogens, both preference and performance of herbivores were negatively impacted, whereas infection by necrotrophic pathogens reduced herbivore preference more than performance and endophyte infection reduced only herbivore performance. Our study demonstrates that fungi could be important but hitherto overlooked drivers of plant-herbivore interactions, suggesting both direct and plant-mediated effects of fungi on insect's behavior and development.

Key words: *biotrophic pathogens; endophytes; meta-analysis; necrotrophic pathogens; plant defense; plant-mediated indirect interactions; tripartite interactions.*

INTRODUCTION

Plant-associated fungi and herbivorous insects often co-occur on the same host plant. While most of the attention so far focused on their independent and additive effects on plant fitness (Hauser et al. 2013), direct and plant mediated effects of fungi on herbivorous insects are less well understood. Plant-associated fungi may modify plant functional traits and quality, and thus indirectly affect herbivorous insects (Friesen et al. 2011). Fungal infection can either increase (e.g., by releasing soluble sugars, Cardoza et al. 2003a) or decrease (e.g., through reduced nitrogen content, Hatcher et al. 1994a) the quantity and within-plant distribution of nutrients, thus affecting the performance of insects (Tinney et al. 1998, Cardoza et al. 2003a). Fungal infection can thus be detrimental (Hatcher et al. 1994a, Kruess 2002), beneficial (Friedli and Bacher 2001, Cardoza et al. 2002, 2003a) or neutral (Kok et al. 1996, Saikkonen et al. 2001) to herbivores. However, we still lack a quantitative estimate of the overall effect of fungal infection on insect preference and performance on challenged plants. Moreover, how these tripartite interactions depend on the feeding guild of the insect, lifestyle of the fungus and the

spatial scale of the interaction remains to be comprehensively explored (Hatcher 1995, Stout et al. 2006, Tack and Dicke 2013).

The way by which fungi obtain resources from their living host plants may have profound consequences for insect herbivores. Among the five main functional groups of plant-associated fungi (mycorrhizae, epiphytes, endophytes, biotrophic pathogens and necrotrophic pathogens, Porras-Alfaro and Bayman 2011), mycorrhizae is the group that received the greatest attention with respect to its effect on herbivores. Koricheva et al. (2009) showed that the impact of mycorrhizal-infected plants on insect performance depends on herbivore feeding specialization. Mycorrhizal infection generally increase the performance of mono- and oligophagous chewers and decrease the performance of polyphagous chewers. For sucking insects, mycorrhizal infection positively affects phloem feeders but has a negative impact on the performance of mesophyll feeders. Although they also received substantial interest over the past decades, the direct and indirect effects of plant infection by pathogenic fungi and endophytes on insect herbivores are far less well understood (Hatcher 1995, Stout et al. 2006, Raman et al. 2012, Tack and Dicke 2013). Our study focuses on biotrophic and necrotrophic pathogens and endophytes. Biotrophic pathogens develop and extract their nutrients from living plant tissues (Delaye et al. 2013, García-Guzmán and Heil 2014) while necrotrophic pathogens secrete enzymes and toxins that degrade and kill the host cells and then

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live and feed on the dead plant tissue (Spoel et al. 2007, Delaye et al. 2013, García-Guzmán and Heil 2014). Both biotrophic and necrotrophic pathogens may produce molecules that are deterrent or toxic to herbivores, but are also frequently consumed by the herbivore while feeding on the host plant. Endophytes correspond to another lifestyle and are defined as ‘microorganisms that live at least during a part of their life cycle inside living plant tissue without causing visible disease symptoms’ (Partida-Martínez and Heil 2011). Although their status along the continuum between parasitism and mutualism is evolutionarily and ecologically unstable (Arnold 2007, Delaye et al. 2013), some endophytes are known to strongly influence the outcome of plant-herbivore interactions (Clay 1996, Kuldau and Bacon 2008, Saikkonen et al. 2010). Although endophyte-free plants do not exist (Arnold and Lutzoni 2007, Partida-Martínez and Heil 2011, Peñuelas and Terradas 2014), the presence of particular endophyte species can have important consequences on plant functioning. Given the differences in the way that biotrophic pathogens, necrotrophic pathogens and endophytic fungi exploit plants, we predict that the direction and magnitude of fungal infection effects on insect herbivores depends on the fungus lifestyle.

Plants evolved common molecular mechanisms against aggression from both herbivores and fungal pathogens. Yet, not all mechanisms are elicited by, nor are effective against all aggressors. For instance, while the salicylic acid pathway is usually induced by and efficient against biotrophic pathogens and sucking herbivores, necrotrophic pathogens and chewing herbivores principally activate and respond to the jasmonic acid pathway (Spoel et al. 2007, Ali and Agrawal 2012, Thaler et al. 2012, Al-Naemi and Hatcher 2013). Given these specificities, we predict that the response of herbivores to plant infection by fungi will depend interactively on fungus lifestyle and herbivore feeding guild, with stronger negative effects of necrotrophic fungi on chewing than on sap feeding insects, but conversely more negative effects of biotrophic fungi on sap feeding insects. Mouttet et al. (2013) found partial support for this hypothesis. They showed a reciprocal negative effect of the sap-feeding whitefly *Bemisia tabaci* and the biotrophic pathogen *Oidium neolycopersici* in tomato plants, which is consistent with JA-SA crosstalk, but an asymmetrical positive effect of the leaf miner *Tuta absoluta* on tomato powdery mildew, which is inconsistent with JA-SA crosstalk.

Herbivores have often been reported to discriminate between “not challenged” (non-infected by a specific endophyte or pathogen) and “challenged” (by a specific endophyte or pathogen) plants, and thus exhibit preference. A likely reason is that fungal infection modifies the visual (Rizvi et al. 2015) or chemical cues (Rostás et al. 2015) that herbivores use to locate and select their host. However, there is no consensus about the consequences of such changes on herbivore behaviour: fungus challenged plants may be more (Cardoza et al. 2003b, Johnson et al. 2003, Jallow et al. 2008), less (Kruess 2002,

Laine 2004, Menjivar et al. 2012) or as attractive as not challenged plants (Jallow et al. 2004, Spafford Jacob et al. 2007). Although it is generally assumed that insect preference matches insect performance (Gripenberg et al. 2010), fungal infection may break down the preference-performance relationship by modifying only herbivore preference or performance, or, alternatively, affect preference and performance in opposite directions (for example, the fungus may increase insect preference but decrease insect performance). For instance, Kruess (2002) showed an increase in the preference and performance of the leaf beetle *Cassida rubiginosa* on creeping thistle *Cirsium arvense* challenged by the necrotrophic fungus *Phoma destructiva*. By contrast, Jallow et al. (2004) found reduced performance of the polyphagous moth *Helicoverpa armigera* on endophyte challenged tomato plants but no significant differences in foliage consumed on inoculated vs. control plants in choice tests. Given these discrepancies among studies, a general overview of patterns and mechanisms is needed.

At a within-plant scale, herbivores can discriminate between not challenged and challenged organs from the same host plant, and even between not challenged and challenged tissue of the same organ (e.g., the same leaf, Simon and Hilker 2003). But not all herbivores may be able to discriminate and avoid challenged organs or tissues. Notably, when the fungus and insect share the same plant organ, the effect of the fungus on the insect herbivore may be direct (through production of supplementary nutrients or toxins), indirect (i.e., fungal-induced changes in the host plant) or both. However, when a herbivorous insect feeds on not challenged organs of a fungal challenged plant, the effect of the fungus on insect performance is mainly indirect and mediated by changes in the host plant. As the impact of fungal infection on plant quality (direct and indirect) and fungal biomass may decrease with increasing distance from the site of infection, the effect of fungal infection on herbivore performance may then depend on the spatial scale of fungus-insect interactions (Simon and Hilker 2003, Mouttet et al. 2013, Tack and Dicke 2013). We thus hypothesize that the effect of fungal infection on herbivorous insects is stronger for local (i.e., when feeding on the same plant organ) than for distant (i.e., when feeding on the same plant) interactions.

Studies have tested how herbivore preference and/or performance are affected by fungal infection under both laboratory/greenhouse conditions (Friedli and Bacher 2001, Cardoza et al. 2003a) and in field experiments (Hatcher et al. 1994b, Kluth et al. 2001, Tack et al. 2012). Yet, field conditions are often more variable and the impact of fungal infection on the insect herbivore may therefore be obscured by confounding factors such as climatic conditions (e.g., water availability, Bultman and Bell 2003, Miranda et al. 2011) or local species pools of insects and fungi. We therefore hypothesize that the impact of fungal infection on insect herbivores is easier to detect, and has a stronger effect, under more

controlled experimental conditions, i.e., in laboratory or greenhouse experiments.

The main objectives of the present study were thus (1) to provide a quantitative estimate of the overall effect of fungal infection on the preference and performance of insect herbivores and (2) to explore the sources of variation in the magnitude of the fungus effect, by testing how insect feeding guild, fungus lifestyle, spatial scale of the interaction and experimental conditions impact on fungus-herbivore interactions. Detailed hypotheses and predictions are listed in Table 1.

MATERIALS AND METHODS

Data collection

We searched the published literature reporting fungal effects on herbivorous insects sharing the same host plant. A first set of studies was initially identified from

Tack and Dicke's review (2013) on plant-pathogen-herbivore interactions, which was used to define keywords to be searched in the Web of Science (ISI) electronic bibliographic database. We applied combinations of relevant terms such as: “(Plant or tree) and (insect) and (preference or performance or choice) and (fung* or oomyc*) not bacteri* not virus not *mycorrh*.” We retained only articles, book chapters, reviews, theses, dissertations and abstracts published in English. To further limit the search to relevant papers, we filtered outputs to retain only those matching with the following research areas: plant sciences, environmental sciences, ecology, pathology, agriculture, zoology, forestry, chemistry, physiology, behavioral sciences, microbiology, entomology, biochemistry, molecular biology, parasitology and mycology.

The search was limited to the period 1950–2015. Our initial search yielded 1,092 papers (the number of papers retained at each stage is reported in the PRISMA flow

TABLE 1. Effects of plant fungal infection on insect herbivores. For each hypothesis tested in the meta-analysis, the dataset used, main results and key references are given.

| | Hypotheses | Result | Key references |
|---|--|---|--|
| Full data set <i>k</i> = 1,113 (101) | | | |
| Overall response of insect to plant infection by fungi | H1: Fungal infection has a negative impact on insect herbivores associated with the same host plant | Insect preference and performance are negatively affected by fungal infection | Hatcher (1995), Rostas et al. (2003), Tack and Dicke (2013) |
| Experimental conditions | H2: The impact of fungal infection on insect herbivores is easier to detect and quantify under laboratory and greenhouse conditions than in the field | There are no statistical differences between experimental conditions (Table 2) | Kluth et al. (2001), Stout et al. (2006), Tack et al. (2012), Keathley and Potter (2012) |
| Laboratory and greenhouse studies on insect performance <i>k</i> = 678 (67) | | | |
| Fungus lifestyle | H3: The magnitude of herbivore response to fungal infection depends on the fungus lifestyle | Biotrophic pathogens and endophytes negatively impacted insect performance, but there was no effect of necrotrophic pathogens (Fig. 1a) | Clay (1996), Al-Naemi and Hatcher (2013), García-Guzmán and Heil (2014) |
| Cross-talk hypothesis | H4: Herbivore response to fungal infection is stronger for chewing herbivores when the plant is challenged by a necrotrophic fungus and for sucking herbivores when the plant is challenged by a biotrophic fungus | No significant interaction between insect feeding guild and fungus lifestyle on herbivore performance (Table 2) | Ali and Agrawal (2012), Thaler et al. (2012), Al-Naemi and Hatcher (2013), Mouttet et al. (2013), Lazebnik et al. (2014) |
| Spatial scale of the fungus-herbivore interaction | H5: The effect of fungal infection is larger at the local scale | The effect of fungal infection is, for chewing insects, larger at the local scale (Fig. 1b) | Hatcher et al. (1994b), Rostas and Hilker (2002), Mouttet et al. (2011, 2013) |
| Laboratory and greenhouse studies for chewing insects at the local scale <i>k</i> = 415 (45) | | | |
| Differences between insect preference and performance | H6: The impact of fungal infection differs between preference and performance | Insect preference and performance differ between plants challenged by different fungus lifestyles (Fig. 2) | Gripenberg et al. (2010), Crawford et al. (2010), Tack and Dicke (2013) |

Note: *k* = number of case studies, followed by the number of corresponding articles in parentheses.

TABLE 2. Summary of model values for the different moderators tested. Given are the moderator, hypothesis tested, number of case studies (k), model heterogeneity (Q_M) and associated P value.

| Moderators | Hypothesis tested | Q_M | k | P -value |
|--|-------------------|-------|-------|-------------------|
| Experimental conditions (Field vs. greenhouse/laboratory) | H2 | 0.34 | 1,113 | 0.560 |
| Fungus lifestyle (endophytes vs. necrotrophic pathogens vs. biotrophic pathogens) | H3 | 7.04 | 678 | 0.030 |
| Fungus lifestyle \times Insect feeding guild (endophytes vs. necrotrophic pathogens vs. biotrophic pathogens) \times (chewing vs. piercing-sucking herbivores) | H4 | 1.36 | 678 | 0.507 |
| Insect feeding guild \times Spatial scale (chewing vs. piercing-sucking herbivores) \times (local vs. distant) | H5 | 9.96 | 678 | 0.002 |
| Fungus lifestyle \times Response Type (endophytes vs. necrotrophic pathogens vs. biotrophic pathogens) \times (preference vs. performance) | H6 | 34.43 | 415 | <0.0001 |

Note: Bold values refer to significant effects.

diagram, Appendix S1: Fig. S1). To complete our dataset, we surveyed the cited references in the articles retained and in the main reviews about plant-fungus-arthropod interactions (Rostas et al. 2003, Stout et al. 2006, Tack and Dicke 2013) and additionally screened the articles that cited these three review papers.

To be retained in the meta-analysis, studies had to meet the following criteria: (1) report insect preference for, or performance on, plants infected by the studied fungus (hereafter referred to as challenged plants) vs. plants non infected by this specific fungus (hereafter referred to as not challenged plants), (2) report taxonomic information about plant, insect and fungus, at least at the genus level and (3) provide a measure of the mean and variability (i.e., variance, standard error or standard deviation) and the sample size in either the text, figures, tables or appendices. When needed, data were extracted from figures following digitalization using the open office extension *Oodigitizer* version 1.2.1 and *ImageJ*. We finally retained 1,113 study cases from 101 primary papers (see also Appendix S1). List of corresponding references are available in Appendix S2.

Moderators

For each study case, we extracted the following moderators (explanatory variables): plant, insect and fungus species identity (at least at the genus level); fungus lifestyle (*biotrophic pathogen*, *necrotrophic pathogen*, or *endophyte*); insect feeding guild (*chewing*, *piercing-sucking*, *phloem feeding* and *sucking*, *cell-content sucking*, *sap-feeding*, *stem-boring*, *root-boring*, *pollen-feeding*, *bud-feeding* and *seed-feeding*); experimental conditions (field and greenhouse or laboratory study); spatial scale of the interaction (*local*, when insects targeted organs challenged by the fungus, *distant* when insects targeted organs not challenged by the fungus, and missing data, *NA*, when organ infection was not explicitly indicated in primary papers); type of insect response (*abundance*, *acceptance*, *attraction*, *body size*, *resource consumption*, *density*, *development rate*, *development time*, *digestibility*, *egg hatching*, *emergence*, *fecundity*, *generation length*, *growth*, *longevity*, *mortality*, *oviposition*, *oviposition deterrence*, *population growth*, *population size*, *pupation*, *reproduction*, *survival*, *weight*). We

eventually grouped insect responses into two categories: *preference* and *performance*. In some cases, the distinction between preference and performance was not straightforward. We decided to code corresponding cases as missing data (*NA*) to avoid spurious classification.

In addition to moderators, each study case was attributed a single identifier (*Case ID*) and assigned to one original paper (*Study ID*) and one study system (*System ID*). A *Study ID* corresponded to a single published paper retained in our analysis. A *System ID* was the combination of plant, fungus and insect species. Within a paper, each combination of plant, fungus and insect species was thus assigned to a specific study system (*System ID*). Within each *Study ID*, we considered as a *Case ID* any response variable measured for each pair of challenged and control plants. In most studies, more than one insect response variable was measured for the same system. Although variables from the same study were not strictly independent (e.g., insect weight and survival), we used all variables to avoid possible bias due to a priori exclusion of some variables or losing valuable information. Non-independence among case studies was accounted for in the analyses using two independent and complementary approaches (see Statistical analyses).

Statistical analyses

For each study case, we calculated an effect size using the Hedges' d metric and its variance (Hedges 1981) as estimated with the 'metafor' package 1.9-8 version in R 3.2.3 (Viechtbauer 2010, R Core Team 2015). Refer to Appendix S3 for details of effect size calculation. First, we estimated the grand mean effect size using the complete data set. Second, we selected subsets of data for which there were enough observations for each level of moderators to enable testing their effects (Table 1). For instance, we excluded case studies on root-feeding ($k = 78$), seed feeding ($k = 2$), stem-boring ($k = 32$), pollen-feeding ($k = 5$) and bud-feeding insects ($k = 4$), and thereby only retained case studies on defoliators (chewing and mining insects) and piercing-sucking insects (including phloem feeders and suckers, cell-content suckers and sap-feeders).

To avoid confounding factors, moderators were tested using a hierarchical approach (Castagneryrol and Jactel

2012, Ferreira et al. 2015). Because results from field and laboratory/greenhouse studies may yield different results, we first tested the effect of experimental setting on effect sizes. Further analyses were restricted to laboratory/greenhouse studies for which it was possible to address the hierarchical effect of additional moderators (Appendix S1: Table S1).

In laboratory/greenhouse experiments, case studies were not evenly distributed among moderators (Appendix S1: Table S1). For instance, there were no case studies addressing the effect of plant infection by biotrophic pathogens on the preference of piercing-sucking insects. To avoid confounding the effects of fungus lifestyle and the type of insect response, we therefore used two independent models. We first tested how the effect size of fungal infection on insect performance was affected by fungus lifestyle (necrotrophic vs. biotrophic pathogen vs. endophytic fungi), insect feeding guild (chewers vs. piercing-sucking) and spatial scale of interaction (local vs. distant). Next, we compared the impact of fungal infection on insect preference vs. performance retaining only case studies where fungi and chewing insects interacted at the local scale, while accounting for fungus lifestyle (Appendix S1: Table S1).

For both models, all two- and three-ways interactions were included in the full model. We applied model simplification by sequentially removing non-significant interactions, starting with highest order interactions. For model comparison, parameters were estimated using Maximum Likelihood. Parameters of the final model were estimated using Restricted Maximum Likelihood (REML).

Most primary studies provided more than one single study case. Multiple outcomes from the same study are correlated, which is likely to increase the variance of model parameter estimates (Koricheva et al. 2013). We accounted for non-independence among effect sizes by conducting multi-level error meta-analyses, using two moderators as random factors. In particular, different measurements of insects (e.g., survival, body mass, number of eggs) were frequently taken in the same study for the same combination of plant, fungus and insect species. Because measurements taken from the same model species were likely correlated, we used *System ID* (i.e., the combination of plant, fungus and insect species corresponding to each effect size) as a random factor. We used *Case ID* nested within *Study ID* as an additional random factor to account for correlation among multiple case studies within the same primary study.

To ensure that our results were robust and unbiased by non-independence among effect sizes, we additionally conducted a sensitivity analysis. We randomly selected one study case per primary study, system and moderator level and re-ran models (those selected by simplification procedures). This procedure was repeated 1,000 times. We compared parameter estimates from the complete dataset to the distribution of 1,000 estimates obtained from random subsets of case studies.

We finally used four different approaches to verify that our results were not affected by publication bias (Koricheva et al. 2013): (1) inspection of funnel plots, (2) cumulative meta-analysis, (3) calculation of fail-safe number and (4) exploration of the relationship between effect-sizes and journal impact factor (Murtaugh 2002).

All analyses were conducted in *R* (R Core Team 2015). Model parameters were estimated using the *rma.mv* function from the *metafor* package (Viechtbauer 2010). Post-hoc comparisons were done using the *linearHypothesis* function from the *car* package (Fox and Weisberg 2011).

RESULTS

We identified a total of 1,113 case studies (*k*) obtained from 101 original (primary) papers that quantified the effects of plant infection by fungi on insect preference and/or performance. This included 63 different plant species (84% being herbaceous), 65 fungal species and 99 insect species for a total of 205 different plant-fungus-insect combinations (i.e., 205 *study systems*).

The grand mean effect size [\pm 95% CI] calculated with the full data set ($k = 1113$) was significantly negative and equaled $-0.42 \pm \text{CI}[-0.64; -0.20]$, indicating that, generally, insects avoid and perform worse on challenged plants than on control, not challenged plants (H1 in Table 1).

Studies performed in the field or under laboratory experimental conditions provided qualitatively similar results ($k = 137$, mean = $-0.36 \pm [-0.69; -0.02]$ and $k = 976$, mean = $-0.44 \pm [-0.68; -0.21]$, respectively; H2 in Table 2), but effect sizes were notably of higher magnitude and less variable in laboratory studies than in field studies.

Studies on chewing and piercing-sucking insects in laboratory studies represented 75% of the case studies ($k = 839$). For these insects, the grand mean effect sizes were consistently negative and significantly different from zero, even when only including case studies using laboratory and greenhouse conditions ($-0.38 \pm [-0.63; -0.12]$). In the analysis on overall effect size, there was a large amount of residual heterogeneity ($Q_E = 8137.26$, $P < 0.0001$) that could be further accounted for by moderators. From this point on, all results will refer to studies conducted on leaf chewing and piercing-sucking insects under laboratory conditions because data on other insect types and under field conditions were too few to allow for robust tests of moderators (see Methods).

Effect of fungal infection on insect performance

The impact of fungal infection on insect performance was dependent on the lifestyle of the fungus (H3, Table 2): insect performance was significantly reduced on plants challenged by biotrophic pathogens and endophytes, whereas insect performance was unaffected by infection with necrotrophic pathogens (Fig. 1a). Contrary to our prediction, we detected no interaction

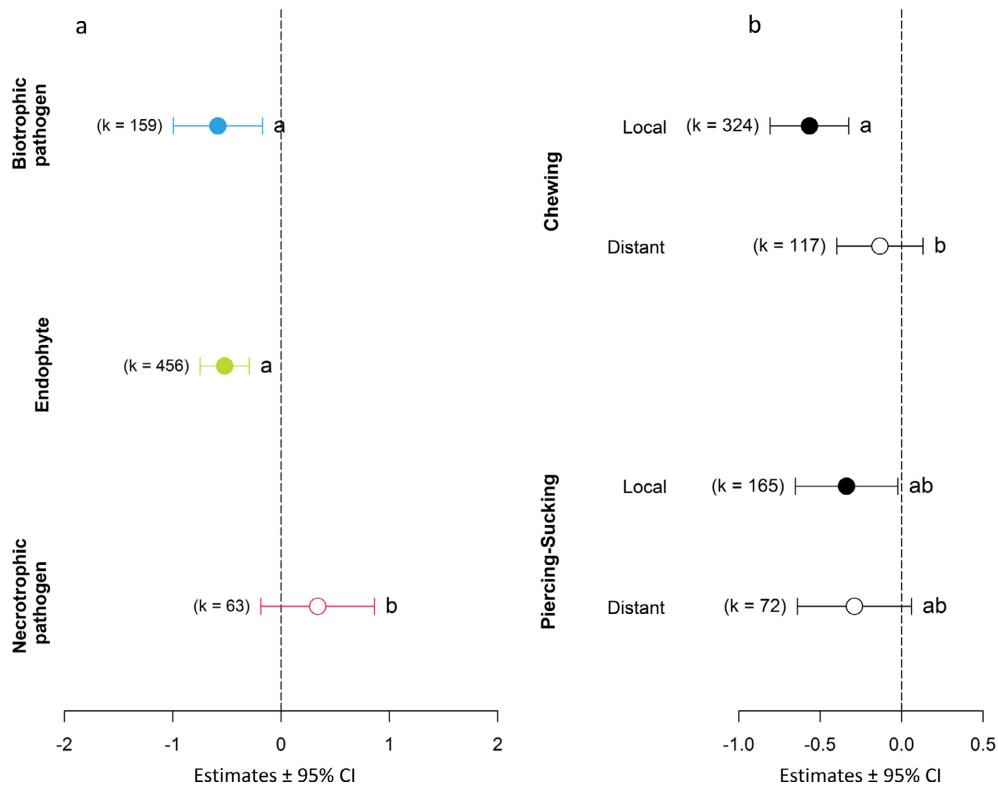


FIG. 1. Response of insect performance to plant infection by fungal pathogens as a function of (a) fungus lifestyle and (b) insect feeding guild and spatial scale of interaction. Circles and error bars represent model parameter estimates and corresponding 95% CI. k is the number of case studies. The vertical dashed line centered on zero represents the null hypothesis (i.e., no difference between insect response to not challenged vs. challenged plants). Filled and empty circles represent significant and non-significant effect sizes, respectively. Different letters indicate significant differences between moderator levels.

between fungal lifestyle and insect feeding guild (H4, Table 2). However, we detected a two-way interaction between insect feeding guild and the spatial scale of the interaction between insects and fungi (H5, Table 2). In particular, fungal infection strongly reduced the performance of chewing insects at a local scale (but not at a distant scale), whereas the piercing sucking insects responded in similarly to both local and distant interactions (Fig. 1b). Finally, we did not detect a three-way interaction between fungal lifestyle, insect feeding guild and spatial scale on the response of insects to plant infection ($Q_M = 3.34$, $k = 678$, $P = 0.188$).

Effect of fungal infection on preference vs. performance in chewing insects

Generally, both preference and performance of chewing insects were reduced in challenged plants as compared to not challenged plants (Fig. 2). However, the magnitude of the insect response depended on fungus lifestyle (H6, significant *Fungus lifestyle* \times *Response type* interaction, see Table 2, Fig. 2). Plant infection by biotrophic fungi reduced both insect preference and performance to a similar degree, whereas plant infection by

endophytes had a stronger negative effect on insect performance than on insect preference (Fig. 2). Plant infection by necrotrophic fungi did not significantly affect either preference or performance of chewing insects (Fig. 2).

Publication bias and sensitivity analyses

Visual assessment of funnel plots confirmed a symmetrical distribution of effect sizes (Appendix S1: Fig. S2), which makes publication bias unlikely. The Rosenberg's fail safe number was 292,725, which was much greater than the critical conservative value of $5 \times k + 10 = 5,575$. This result does not prove the lack of publication bias but indicates that, if present, publication bias can safely be ignored (Rosenberg 2005). There was no temporal tendency in combined effect sizes; sequentially aggregating case studies across years only contributed to increase in the accuracy around the grand mean in the cumulative meta-analysis (Appendix S1: Fig. S3). Finally, the Pearson's coefficient of correlation between effect sizes and impact factors of journals from which they were retrieved was weakly positive ($r = 0.061$, $P = 0.043$). Altogether, these analyses indicate that our

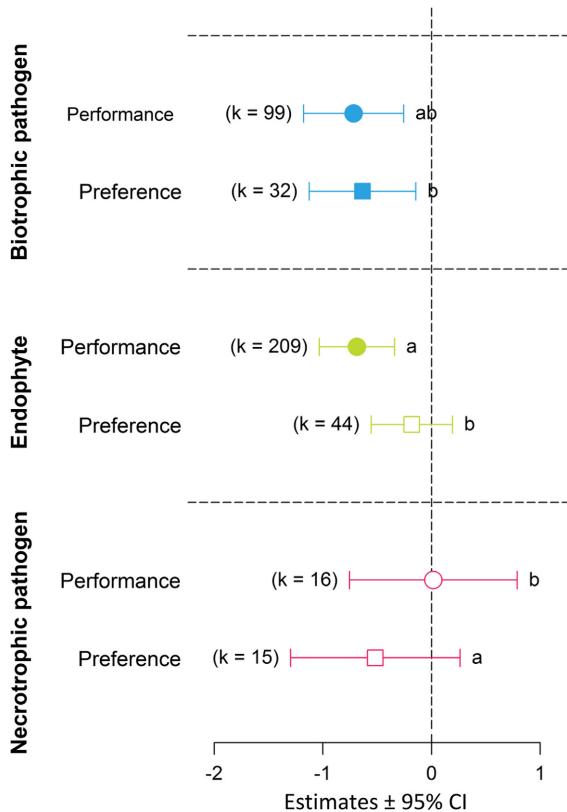


FIG. 2. Effects of fungal infection on preference and performance of chewing insects on fungus-challenged plants. Dots and error bars represent model parameter estimates and corresponding 95% CI. k is the number of case studies. The vertical dashed line centered on zero represents the null hypothesis (i.e., no difference between insect response to not challenged vs. challenged plants). Filled and empty dots represent significant and non-significant effect sizes, respectively. Different letters indicate significant differences between moderator levels.

findings were robust to selective reporting and dissemination bias.

Model parameters estimated with the original dataset (i.e., with multiple outcomes taken from the same primary study) were within the range of the 95% distribution of the 1,000 parameters estimated after random drawing of only one case per combination of study, system and moderator level (Appendix S1: Fig. S4). Our initial predictions were therefore robust and unlikely biased by multiple measurements on the same individuals.

DISCUSSION

Our meta-analysis, based on several hundreds of case-studies, unequivocally demonstrates that plant infection by pathogenic and endophytic fungi, on average, reduces preference and performance of insect herbivores. Even though some primary studies reported a positive effect of fungal infection on insect preference and performance (e.g., by reducing phenolic content and increasing soluble

sugar content, Cardoza et al. 2003a), the overall effect size is pervasively negative and consistent across a large set of plants, herbivores, fungi and methodological approaches. And, although most of the studies used do not necessarily reflect the whole complexity of these interactions (i.e., with plants being infected by several fungi and insects at the same time), they do imply overall strong effects of the fungi on insects. Importantly, and as discussed in detail herein, we detected several sources of variation in the magnitude of plant-fungus-insect interactions providing new insights on underlying mechanisms (i.e., spatial scale of interactions, insect feeding guild and fungus lifestyle).

Insect performance on fungus-challenged plants are dependent of fungus lifestyle

Biotrophic pathogens and endophytes reduced herbivore performance more than necrotrophic pathogens did. The way endophytes exploit their resources is more similar to biotrophic pathogens as they both develop in living plant tissues (Partida-Martínez and Heil 2011, García-Guzmán and Heil 2014). Such a similarity may therefore be the likely explanation of their similar negative effect on insect performance. On the contrary, necrotrophic pathogens produce cell-wall degrading enzymes which may contribute to the release of plant carbohydrates. A rapid increase of soluble sugars and others plant nutrients can have a positive effect on insect performance which could explain the tendency of necrotrophic fungi to increase insect performance (Cardoza et al. 2003a, Johnson et al. 2003). For example, Johnson et al. (2003) showed a positive effect of the necrotrophic pathogen *Marssonina betulae* on performance of the aphid *Euceraphis betulae* when co-occurring in silver birch trees, which was correlated with a higher concentration of free-amino acids following the degradation of leaf mesophyll cells by fungus enzymes.

A strong negative impact of endophytes on insect performance was expected, given that some of them are considered potential biocontrol agents (Gurulingappa et al. 2010, Akello and Sikora 2012, Castillo Lopez et al. 2014, Lopez and Sword 2015). Endophytes are a very diverse group (Rodríguez et al. 2009) which are present in virtually all plants (Partida-Martínez and Heil 2011). Here we show that the proven presence in plants of some particular endophyte species may have a negative impact on insect performance. Additionally, some variability in endophyte effect may be explained by their division in two major groups: clavicipitaceous and non-clavicipitaceous endophytes (Partida-Martínez and Heil 2011), the former being known to have a negative impact on insect herbivores in some grass systems (Clay 1996, Kuldau and Bacon 2008). However, we found no evidence for a stronger negative effect of clavicipitaceous endophytes than non-clavicipitaceous endophytes on herbivores, which makes unlikely that our result is blurred by a lack of taxonomic resolution in this particular group (Appendix S4). Little is known about the effect of the whole community

of endophytes on insect performance in challenged plants (Peñuelas and Terradas 2014) and we cannot exclude that some plants defined as not challenged and used as control in primary studies were actually colonized by one or several endophytic fungi. In addition, many fungi can act as endophytes and pathogens depending on the host plant, environment, and biotic interactions (Arnold 2007). We classified them following information provided in the primary studies we used. However, we acknowledge that taking environmental context into account in further studies will deeply improve our understanding of how fungal pathogens influence herbivorous insects on shared hosts. Moreover, plants are infected by a wide community of microorganisms that may play an important role in their extended phenotype (Partida-Martínez and Heil 2011). However, little is known about the effect of the whole microbiome on insect preferences and performances. This question will require further attention, which will surely benefit from the rapid development of new generation sequencing methods (Lindahl et al. 2013).

Fungus-insect interactions are scale dependent and insect guild-specific

The magnitude of negative effects of plant pathogens on insect herbivores varies with insect feeding guild and spatial scale of fungus-insect interactions. Performance of both chewing and piercing-sucking herbivores were more reduced when they fed on fungus challenged organs (i.e., local interaction) than when they fed on not challenged organs of challenged plants (i.e., distant interaction). However, this difference was significant only for chewing insects. When interacting locally, chewing herbivores may consume both the plant and the fungal material (Moran 1998, Rostas et al. 2003, Mondy and Corio-Costet 2004). Yet, fungi may produce mycotoxins that are toxic to insects and thus directly contribute to a reduction of insect performance (Dowd 1989, Bultman and Bell 2003). This may be mainly harmful to chewing herbivores that indiscriminately consume plant and fungus tissue, but less to piercing-sucking herbivores that only consume sap.

When insects and pathogens feed on different plant organs, the insect-fungus interaction is usually presumed to be plant mediated. Plant-mediated indirect interactions may then result from the fungus reducing plant growth (e.g., Al-Naemi and Hatcher 2013) or nutritional quality to herbivores (Tinney et al. 1998). Fungal infection may also trigger systemic defense responses against both fungi and herbivores (Simon and Hilker 2003, Stout et al. 2006). Although only few studies clearly distinguished between direct and plant mediated effects of fungi on insect herbivores (e.g., by infecting a part of the leaf and subsequently allowing the insect to only feed on the not challenged part of the same leaf, Simon and Hilker 2003), the additive contribution of direct and plant mediated effects may explain the stronger negative impact of fungal infection observed on chewing and piercing-sucking herbivores in local interactions.

Guild specific response to fungus infection does not depend on fungus lifestyle

How plants respond to multiple aggressors has been widely debated (reviewed by Thaler et al. 2012) and our results contribute to this debate. Current thinking often states that while the pathway involving salicylic acid (SA) is usually induced by and effective against biotrophic pathogens and sucking herbivores (Ali and Agrawal 2012, Thaler et al. 2012, Al-Naemi and Hatcher 2013), necrotrophic pathogens and chewing herbivores principally activate and negatively respond to the jasmonic acid (JA) pathway (Ali and Agrawal 2012, Thaler et al. 2012). Empirical evidence shows reciprocal antagonism between the SA and JA signaling pathways (reviewed by Thaler et al. 2012). If such cross-talk between these two defense-related hormonal pathways (Stout et al. 2006) is a general pattern, then piercing-sucking herbivores should perform worse on plants challenged by biotrophic pathogens than by necrotrophic pathogens, whereas chewing herbivores should have lower performance on plants challenged by necrotrophic fungi. This hypothesis received some experimental support (Mouttet et al. 2013). For instance, Al-Naemi and Hatcher (2013) showed inhibitory effect of the necrotrophic pathogen *Botrytis cinerea* on individual aphid *Aphis fabae* performances while the biotrophic rust *Uromyces viciae-fabae* infection enhanced aphid performance. In addition, when both fungi were applied simultaneously to the same organ they generally cancelled out each other's effect, resulting in comparable performance of aphids on dually challenged plants and challenged, control plants. Our meta-analysis did not find support for the trade-off between JA and SA. In our study, differences in performance of chewing and piercing-sucking insects on not challenged vs. challenged plants were comparable in both direction and magnitude, irrespective of fungus lifestyle. The lack of interaction between insect feeding guild and fungus lifestyle on insect performance to pathogen infection suggests that JA or SA pleiotropic effects may not be universal (Thaler et al. 2012), that they can act together, or that mechanisms other than changes in plant defenses explain the observed differences in plant-mediated effect of fungal infections.

Fungal infection differentially affects herbivore preference and performance

There is a general agreement that insect preference should match their performance (Gripengberg et al. 2010). Consistently, we show that plant infection by fungal pathogens reduces (or has no effect on) both the preference and performance of chewing herbivores. However, the difference between herbivore preference for and performance on not challenged vs. challenged plants did vary with the lifestyle of fungi. Such a difference may result from different fungus lifestyles differentially affecting plant traits involved in plant selection (preference) or plant quality for herbivores (performance).

While insect performance is mainly affected by a change in nutritional quality and defense of host plants (Hatcher 1995, Tack and Dicke 2013), preference is frequently affected by host selection cues, like attractive colors or odors (Schoonhoven et al. 2005, Tasin et al. 2012, Rizvi et al. 2015). In plants challenged by biotrophic fungi, the negative impact of the fungus was as strong for insect preference as for performance. However, the effect of endophyte infection was stronger for insect performance than insect preference. Plant infection by endophytes is, in contrast to biotrophic pathogens, basically symptomless (Partida-Martínez and Heil 2011) and thus the endophyte is unlikely to modify host plant visual cues for insect location. We therefore suggest that reduced insect preference may be mainly driven by endophyte mediated changes in host chemical cues (e.g., volatile emissions, Rostás et al. 2015).

Finally, we did not detect any significant effect of plant infection by necrotrophic pathogens on insect preference or performance, although there was a notable tendency for preference to be more reduced than performance. Necrotrophic fungi can change visual and chemical cues used by herbivores to locate and select their host plant (Rizvi et al. 2015) which can explain the stronger negative effect of necrotrophic pathogens on insect preference than on insect performance. Moreover, there is a greater variability of insect response to necrotrophic plant infection. This is due to the fact that several papers reported a positive effect of necrotrophic fungus infection on associated insects, which was explained by the release of soluble sugars (Cardoza et al. 2003a), amino acids (Johnson et al. 2003) or volatile compounds that could enhance insect oviposition and feeding behaviors (Cardoza et al. 2002). Alternatively, variability in the magnitude of necrotrophic pathogen effects on herbivores could result from differences in the severity of induced symptoms, which may vary with the quantity and quality of infective fungal propagules. The time lag between infection by a pathogen and the expression of symptoms by the plant may also depend on the specific plant–fungus interaction. In general, larger and older necrotic lesions may produce more modified plant tissues and necrotic tissue, resulting in a stronger negative impact on herbivores. However, this possibility remains poorly addressed in the literature (Jaber and Vidal 2009, Mouttet et al. 2011, Akello and Sikora 2012).

Conclusion and future research directions

Meta-analyses enable testing hypotheses that cannot be addressed in a single primary study. Here, we could unequivocally show that plant infection by fungal pathogens is generally detrimental to insect herbivores, reducing both their preference and performance. Importantly, we unravel some biological mechanisms behind the variability among published studies. In particular, we show that the magnitude of insect negative response to plant infection by fungi varies with insect feeding guild, fungus

life history traits and the spatial scale of insect–fungus interactions. However, some aspects remain unclear. We identified particular gaps in knowledge that would require more experimental studies in order to better explain and predict the outcomes of such complex, tripartite interactions. An important future avenue will be to compare the relative importance of fungi on tripartite interactions, as compared to other abiotic and biotic drivers of plant–herbivore interactions and herbivore demographics.

1. *What are the molecular mechanisms at work?* Only few studies (Cardoza et al. 2002, 2003a) reported solid evidence for fungus-induced change in metabolites content of plant organs. In particular, the pivotal and pleiotropic role that phytohormones play in these interactions remains unclear as most studies did not measure their levels (but see Cardoza et al. 2003a). In this respect, we believe that developments in transcriptomic analyses will pave the way for a better understanding of plant physiological responses to single and multiple biotic stresses (Lazebnik et al. 2014).
2. *Does timing and disease progression matter?* Insect response to fungal infection was shown to vary with the time elapsed since the first fungal infection (Mouttet et al. 2013) and the phase of fungal disease. Yet, there are only few studies to date that explicitly took time, disease phase or infection severity into account (Jaber and Vidal 2009, Mouttet et al. 2011, Akello and Sikora 2012). More studies controlling the timing of interactions between herbivores and fungi are required to better understand how insect response to fungal infection varies along a time gradient.
3. *How are plant–fungus–insect interactions modified by other biotic factors?* Most of our current knowledge is based on highly controlled laboratory or greenhouse studies (ca 87% of our dataset). Such studies are definitely useful to isolate the effects of different treatments, but they fail to address the real complexity of interactions at play. For instance, natural enemies of herbivores may respond directly or indirectly to plant fungal infection. For example, Tack et al. (2012) showed higher parasitism rates in the leaf miner *Tischeria ekebladella* on mildew-infected oak leaves. Fungal infection can change attraction of insect predators and parasitoids by modifying volatile emissions (Cardoza et al. 2003b, Hare 2011) or prey resource quality (Omacini et al. 2001). Fungi can also modify host plant protection provided to insect herbivores against natural enemies by altering refuge structures such as fruits and galls (Biere et al. 2002). This needs to be further evaluated (but see Bultman et al. 2003, 2012, Härrri et al. 2009, Miranda et al. 2011, Bixby-Brosi and Potter 2012, Tack and Dicke 2013).
4. *How do plant–fungus–insect interactions scale up to the community level?* Herbivores sharing the same host plant interact with each other, either directly or indirectly (e.g., via resource depletion) (Crawford et al. 2007, Kaplan and Denno 2007, Wielgoss et al. 2012).

Plant interactions with fungi may thus indirectly affect the whole insect community structure (Tack et al. 2012), triggering changes in herbivory through competitive or facilitative processes.

5. *Are tripartite interactions symmetrical?* So far, most studies addressed the additive and interactive effects of herbivores and pathogens on plants (Hauser et al. 2013). The present meta-analysis expands our understanding to the effects of fungi on herbivores within the same plant (Koricheva et al. 2009). Yet, very little is known about the reciprocal effects, i.e., the plant-mediated effects of insect herbivores on fungus infection (Rostas and Hilker 2002, Simon and Hilker 2003, Rayamaghi et al. 2006, Eyles et al. 2007, Tack and Dicke 2013) or on plant susceptibility to other pathogens such as bacteria and viruses.

In natural and agricultural ecosystems, plants have to deal with a large variability of antagonistic organisms, including pathogens and insects. A better understanding of plant-fungus-insect tripartite interactions is therefore crucial to improve management and control strategies of pests and diseases in these ecosystems. While our quantitative synthesis provides new insights into plant-fungus-insect interactions, a complete understanding of tripartite interactions will require expanding the results of our meta-analysis (1) with current knowledge on additive and interactive effects of herbivores and pathogens on plants (Hauser et al. 2013) and (2) with a review of the reciprocal effect of insect herbivores on fungi (Rostas and Hilker 2002, Simon and Hilker 2003, Rayamaghi et al. 2006, Eyles et al. 2007, Tack and Dicke 2013) and other pathogens like bacteria and viruses.

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