New
Phytologist

Research

Fungicide effects on wild plants: insights from a global meta-analysis

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Received: *23 April 2025*
Accepted: *12 August 2025*

New Phytologist (2025)
doi: 10.1111/nph.70530

Key words: biomass, biotic interaction, growth, non-native, pesticide, species diversity, survival.

Summary

- Many studies have investigated plant–pathogen interactions by testing whether fungicides affect plant survival, growth, biomass, and/or diversity.
- Here, we synthesize these studies using a global meta-analysis of 369 experiments from 62 papers that compared plants treated with fungicide to untreated controls.
- Overall, fungicide increased the survival of native plant species and community biomass but decreased diversity, mirroring the effects of fencing out vertebrate herbivores. There was no overall effect on plant growth. However, analyses of subsets of the data revealed a more varied and complex picture, with few consistent results. Strong geographical biases in sampling and small sample sizes for many combinations of variables make it difficult to distinguish between alternative explanations for this variation in fungicide effects.
- The results, overall, are largely consistent with a role for fungal pathogens in the maintenance of community diversity, but not with the latitudinal biotic interaction hypothesis. Future studies should aim to fill the gaps in the geographical spread of studies, standardize the methods as far as possible, and use molecular techniques to characterize the impacts of fungicide treatments on both target and nontarget organisms.

Introduction

The reciprocal interactions between fungi and plants are important drivers of plant performances, distributions, and abundances and thus contribute to plant community composition, diversity, and ecosystem processes (Kardol *et al.*, 2007; Pugnaire *et al.*, 2019; Jiang *et al.*, 2024). Fungal root symbionts can be crucial to nutrient acquisition and pathogen defense for many mycorrhizal species (Genre *et al.*, 2020; Tedersoo *et al.*, 2020; Liu *et al.*, 2024), and fungal endophytes may also protect against fungal pathogens above ground (Arnold *et al.*, 2003). Conversely, plant fungal pathogens as well as fungus-like pathogens in the Oomycota have been considered among the most important agents afflicting plant individuals and communities (Bagchi *et al.*, 2014; Chen *et al.*, 2019; Song & Corlett, 2021). The negative effects of fungal pathogens on plant individuals and species can suppress the community's productivity as a whole, often measured with aboveground biomass (Maron *et al.*, 2011; Liang *et al.*, 2019). Fungal pathogens are natural enemies that can drive key mechanisms supporting plant diversity by inducing negative density dependence (Bagchi *et al.*, 2014; Cheng & Yu, 2025; Milici *et al.*, 2024).

A key example of the role of fungal pathogens in shaping diversity is the Janzen–Connell hypothesis (Janzen, 1970; Connell, 1971). This hypothesis posits that adult plants are reservoirs of specialist enemies – including fungal pathogens – that cause nearby conspecific seeds and seedlings to suffer greater damage than offspring that are dispersed further from adults (Liu *et al.*, 2022; Milici *et al.*, 2024). This can result in negative density dependence, reducing the dominance of common species and giving an advantage to rare species, thereby promoting local plant diversity (Bagchi *et al.*, 2014). Variation among species in the existence and strength of Janzen–Connell effects may be related to plant resistance to fungal pathogens (Mangan *et al.*, 2010; Stump & Comita, 2018; Song *et al.*, 2021). For example, ectomycorrhizae sheath the fine roots of their host plants, possibly protecting against pathogens (van der Heijden *et al.*, 2015; Liang *et al.*, 2021), yet this remains largely untested (Tedersoo & Bahram, 2019; Jia *et al.*, 2020; Tedersoo *et al.*, 2020).

Plant pathogens could have different effects in low- and high-diversity plant communities (Rutten *et al.*, 2021) and on species that are native and introduced (Maron *et al.*, 2011; Schnitzer *et al.*, 2011). The dilution effect hypothesis (DEH) suggests that plant enemies will have less impact in which there is high plant diversity because abundant unpreferred hosts decrease the chances of an enemy encountering its preferred host (Keesing & Ostfeld, 2021). If this is generally true, the effect of fungal pathogens might decline as species diversity increases (Rottstock *et al.*, 2014). Simultaneously, the latitudinal biotic interaction hypothesis (LBIH) predicts that the strength of biotic interactions will increase toward lower latitudes (Pianka, 1966; Hargreaves, 2024). Tests of the LBIH on a range of biotic interactions have yielded conflicting results depending on the type of interaction, the organisms involved, and the methods used (Moles *et al.*, 2011; Lim *et al.*, 2015; Moles & Ollerton, 2016; Zvereva & Kozlov, 2021). There is inconsistent evidence supporting the predictions about the biogeography of fungal enemy effects, and the presence and generality of these hypotheses have yet to be settled.

Species with different life forms exhibit contrasting traits and respond differently along latitudinal and climatic gradients. A global meta-analysis suggested that species with different life forms also experience contrasting plant–soil microbe interactions (Jiang *et al.*, 2024). Compared with nonwoody species, woody species generally have thicker leaves and roots, lower specific root length and specific leaf area, and higher root and leaf tissue density (Diaz *et al.*, 2016; Freschet *et al.*, 2017). These trait differences may make woody plants less vulnerable to pathogens (Xi *et al.*, 2021; Jiang *et al.*, 2024), but this has not yet been tested for fungal pathogens on a global scale.

Finally, the enemy release hypothesis (ERH; Keane & Crawley, 2002) suggests that non-native species benefit by leaving their coevolved natural enemies – including fungal pathogens – behind when they are introduced outside of their native ranges (Mitchell & Power, 2003). Although there is evidence that native plant species support more herbivorous insects than non-natives, it is not clear whether this contributes to the success of non-natives (Liu & Stiling, 2006; Meijer *et al.*, 2016), and the few studies with fungal pathogens have been inconclusive (Levine *et al.*, 2004; Jiang *et al.*, 2024).

Plant–pathogen interactions are more difficult to study than those between plants and herbivores, since the damage is less obvious to researchers, especially for soil pathogens. As a result, many experiments have used selective pesticides to target pathogenic fungal groups ('fungicides' hereafter; Bell *et al.*, 2006; Zubrod *et al.*, 2019; Song & Corlett, 2021). Plant responses to fungicide treatments have been highly variable among sites and species (Fricke *et al.*, 2014; Gripenberg *et al.*, 2014; Cannon *et al.*, 2020). Here, we conduct a global literature review and meta-analysis of published manipulative experiments using fungicide treatments (including those targeting fungus-like pathogens in the Oomycota). We asked four questions about the effects of fungicide treatments: (Q1) What are the impacts on plant growth, survival, biomass, and diversity? (Q2) Do the effects vary between woody and nonwoody species? (Q3) Do the effects vary between native and non-native species? And (Q4) do the effects vary with latitude?

Based on site- and species-level work to date, we predicted that fungicide treatment: (P1) will increase plant survival, growth, and community biomass (Liang *et al.*, 2019), but reduce community diversity (Bagchi *et al.*, 2014); (P2) affect woody species less than nonwoody species (Jiang *et al.*, 2024); (P3) have stronger positive effects on native species than non-natives (Mitchell & Power, 2003); and (P4) have stronger effects at lower latitudes and in higher diversity communities consistent with the LBIH (Zvereva & Kozlov, 2021). Fungicide treatments may also have weaker effects at lower latitudes and in higher diversity communities due to the dilution of enemies encountering preferred hosts (DEH) (Keesing & Ostfeld, 2021).

Materials and Methods

Literature review and selection

We limited our synthesis to studies that used fungicide treatments with the intention of excluding fungi and oomycetes from natural or seminatural ecosystems. We did not distinguish between studies that focused on below- or aboveground pathogens since the methods used do not usually allow precise targeting on one or the other. A search was conducted using the following search string [TS = (fungicide*) AND (forest* OR grassland* OR savanna* OR old-field*) AND (diversity* OR abundance* OR richness* OR survival* OR growth* OR biomass*)] in the Web of Science (https://clarivate.com/webofsciencegroup/), Google Scholar (https://scholar.google.com), and CNKI (a Chinese database; https://www.cnki.net/) through 10 February 2025. We combined all records from the three literature databases and removed duplicates, yielding a total of 1505 papers (Supporting Information Fig. S1). From these papers, we first screened the titles and abstracts to select papers on the correct topic. We then examined each paper to determine whether it met the following criteria: (1) It included a control treatment and fungal exclusion treatments using fungicides, and we excluded studies in which fungicide effects were confounded by simultaneous application of other agrochemicals (e.g. insecticides or herbicide); (2) it reported the growth rate, survival rate, biomass, or species diversity indices, such as species richness, Shannon–Weiner index, or Simpson index, in the main text, tables, or figures (Table S1); and (3) if the study species were non-native plants, the experiment was conducted in the soil that had not been previously occupied by the non-native species in order to test the ERH.

Although all commercial fungicides claim some degree of specificity to pathogens, it is likely that all those currently available have nontarget impacts on mutualists and decomposers (Tables S2 and S3). These experiments thus measured the net effect of fungicide, *that is* the effects on fungal pathogens minus any effects on mutualists and decomposers (Baudy *et al.*, 2021; Gundale & Kardol, 2021; Lloyd *et al.*, 2021). In the analyses reported here, we follow the study authors in attributing the effects of fungicide treatments largely to their impact on fungal pathogens, but our discussion considers alternative interpretations.

Data extraction

For papers that contained multiple fungicide treatment experiments on multiple species or/and at multiple life stages, each species-by-experiment combination was considered separately, and for papers that tested multiple density levels of the same species, we considered each density level as an independent experiment. For each experiment, we extracted the mean, SD, and number of replicates of either the species diversity index (species richness was selected from four papers with more than two indices), biomass, growth rate, or survival rate from the control and fungicide treatments. We excluded experiments that did not present all three parameters. Information from studies in which results were only presented as graphs was extracted using Plot Digitizer (http://plotdigitizer.sourceforge.net/). Other key variables extracted were species, life-history stage (*i.e.* seed or seedling), and lifeform (woody or nonwoody). We categorized studies as addressing species diversity, community biomass (*i.e.* with more than one species), or growth or survival of a single species (consistent with Jia *et al.*, 2018 and Song *et al.*, 2021). We also recorded metadata and covariates including author, year, study site location, and, for the field studies, mean annual temperature and precipitation of the study site. We also recorded the type of fungicide used in each experiment.

Each species was also assigned to a family and genus using the R package plantlist (Zhang, 2017), and we built the phylogeny using 'Scenario 3' of the R package V.phylomaker to add genera and species that are absent from the PhytoPhylo megaphylogeny (Jin & Qian, 2019). We then included the phylogenetic correlation matrix in the models as a random effect.

Data analysis

We calculated the effect sizes (*Hedges' d*) and the variance for each experiment from each paper using the escalc function in the METAFOR package in R v.3.6.0 (Viechtbauer, 2010) in R 4.1.0 (R Core Team, 2025). We tested for publication bias using Egger's regression test for asymmetry (Egger *et al.*, 1997; Sterne & Egger, 2001). We used the trim-and-fill method to account for missing data bias and reran analyses to determine whether the results were still statistically different (Table S4). We examined patterns in effect sizes using multilevel linear mixed-effects models (MLMEMs, which are a type of meta-regression), and we included a nested experiment-within-study random effect in all models. We also included a species-level random effect for noncommunity-level models.

To test how fungicide treatment impacted community productivity (biomass) and diversity, and species growth and survival (P1), we calculated mean effect sizes and confidence intervals. To test for variation between different life forms (P2), we assessed whether there was support for including the life form (a two-level categorical covariate: woody and nonwoody) using the Q_M test statistic for assessing the significance of categorical moderators in a meta-regression (Borenstein *et al.*, 2009). To test the species-level hypothesis that fungal pathogens have stronger effects on natives than non-natives (P3), we compared the effect sizes of fungicide on survival and growth for native and non-native species.

We also assessed whether the strength of the plant–pathogen interaction was influenced by shared evolutionary history by including a phylogeny into the MLMEMs as the phylogenetic correlation matrix (a random effect using *rma.mv* function). We compared the models with and without phylogenetic relatedness using Akaike Information Criterion (AIC) value (Bartoń, 2019). The inclusion of phylogeny improved the growth model (>2 AIC points lower) but not the survival model (Table S5) at the species level, so in the following analyses, we only include phylogeny in the growth models. To test the species-level hypothesis that fungal pathogens have stronger effects at lower latitudes and in higher diversity communities (P4), we included absolute latitude in the same models previously described and assessed whether the coefficient was significant ($P < 0.05$). Sample size limitations limited the latitudinal analyses to native species.

We also conducted MLMEMs to evaluate the effect of different study characteristics (glasshouse or field experiment), climatic zones (tropical or temperate), life stage (seed or seedling), lifeform (woody or nonwoody), and fungicide type on the effect sizes and assessed if their coefficients were significant ($P < 0.05$).

Results

There were 369 experimental treatment comparisons extracted from 62 papers that met our inclusion criteria. Of these, 86 experiments addressed community-level questions (*i.e.* fungal impacts on community performance and diversity), and 283 experiments addressed species-level questions (*i.e.* impacts on growth and survival). Among the species-level experiments, 268 focused on native species and 15 included non-native species. Most experiments were in the northern hemisphere (95%), particularly in North America, Europe, and East Asia (Fig. 1).

Fungicide impacts on the biomass, diversity, survival, and growth of native species

At the community level, fungicide treatments had a significant positive effect on community biomass (effect size = 0.6317; CI = 0.3508–0.9125; $P < 0.0001$) and a significant negative effect on species diversity (effect size = −0.3861; CI = −0.6205 to −0.1516; $P = 0.0012$; Fig. 2). At the species level, fungicide treatments had a significant positive effect on the survival of native species (effect size = 0.6449; CI = 0.3748–0.9151; $P < 0.0001$; Fig. 2), but there was no significant effect on growth (effect size = −0.1407; CI = −2.1533–2.4346; $P = 0.9043$).

Fungicide impacts for woody and nonwoody subsets of native species

For nonwoody plant communities in the temperate zone, fungicide treatments had a significant positive effect on the biomass (effect size = 0.7584; CI = 0.5201–0.9968; $P < 0.0001$; Fig. 3) and a significant negative effect on diversity (effect size = −0.7921; CI = −1.1815 to −0.4027; $P < 0.001$; Fig. 3). There were no

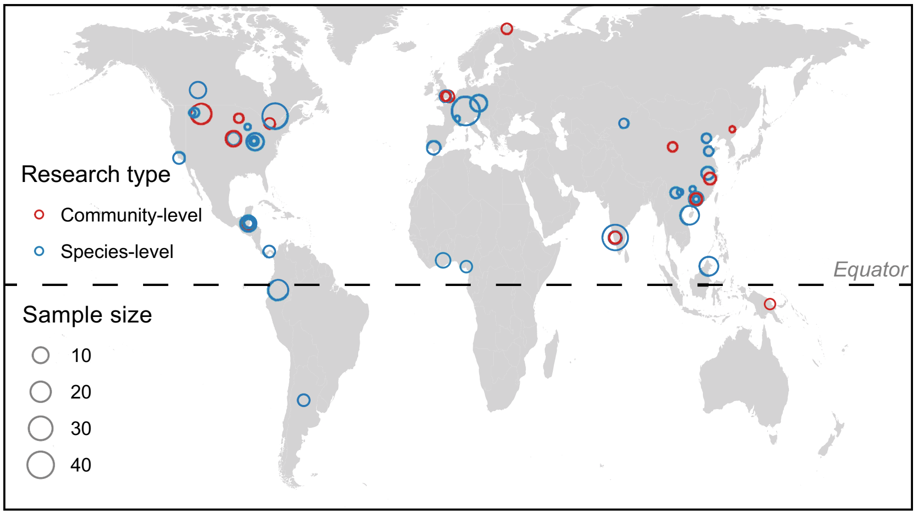

Fig. 1 Geographic distribution of the 369 fungicide treatment experiments included in this meta-analysis. Circle sizes reflect the number of experiments at each site; red indicates experiments at the community level (biomass and diversity) and blue at the species level (growth and survival).

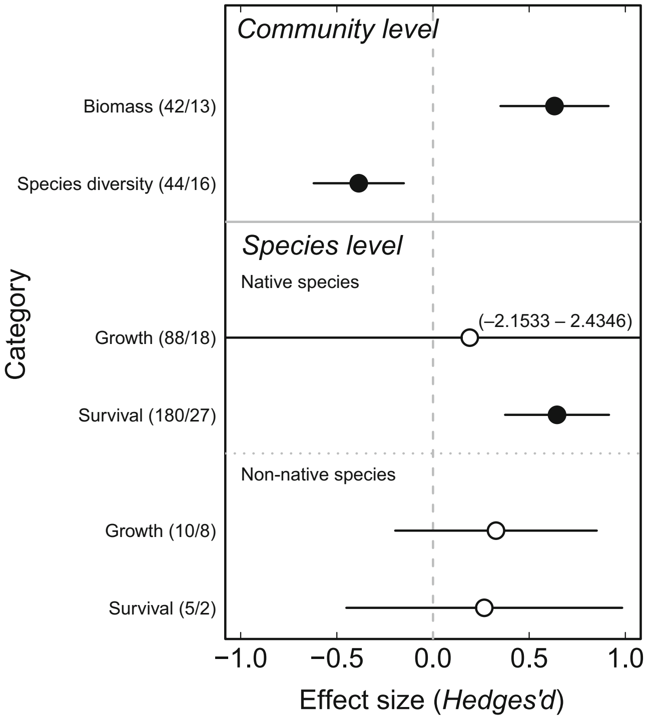

Fig. 2 Effect sizes and 95% confidence intervals for fungicide treatment experiments (negative values denote fungicide treatment reduced the measure). Filled circles are significantly different from zero ($P < 0.05$), and empty circles are not. Parentheses show the number of experiments/number of papers. The confidence interval for native plant growth is truncated by the panel, so the range is given above.

data for nonwoody communities in the tropics, and there were no significant effects on woody biomass or diversity.

Fungicide treatments had a significant positive effect on the survival of native woody species in both tropical and temperate zones (tropical effect size = 0.4302; CI = 0.1446–0.7159; $P = 0.0032$; temperate: effect size = 0.7608; CI = 0.4582 to −1.0634; $P < 0.0001$). They also had a significant negative effect on woody species growth in the tropics (effect size = −0.8639; CI = −1.3526 to −0.3751; $P = 0.0005$), but a significant positive effect in the temperate zone (effect size = 0.2040; CI = 0.0495 to 0.3585; $P = 0.0097$; Fig. 3). The effects on the growth and survival of native nonwoody species were not significant (Fig. 3).

Fungicide impacts on non-native species

Fungicide treatments had no significant effect on growth (effect size = 0.3071; CI = −0.2546 to 0.8688; $P = 0.2839$) or survival (effect size = 0.2666; CI = −0.4504 to 0.9835; $P = 0.4662$; Fig. 2) of non-native species. For the single experiment conducted on non-native woody species in the temperate zone, the effect size was significantly positive (Fig. 3).

Variation with latitude

There was no latitudinal trend in the effect of fungicide treatment on biomass for either woody or nonwoody species (Fig. 4a) and a marginally significant negative trend for diversity (coefficient = −0.0111 ± 0.0065; $P = 0.0872$; Fig. 4b). There was a significant positive latitudinal trend in the effect of fungicide treatment on native species growth, driven mainly by nonwoody species growth within the temperate zone (Fig. 4c). There were significant latitudinal trends with more positive effects at lower latitudes for the survival of nonwoody species (Fig. 4d). There were no significant latitudinal trends for woody species, for either growth or survival (Fig. 4c,d).

Variation with other covariates

Fungicide treatments had significant positive effects on both biomass and diversity in nonwoody communities but no significant effects on either in woody communities (Tables S6 and S7). Note that all studies of nonwoody communities came from the temperate zone. Fungicide treatments had significant positive impacts on native species survival in both field and glasshouse experiments, with both seeds and seedlings, and in both temperate and

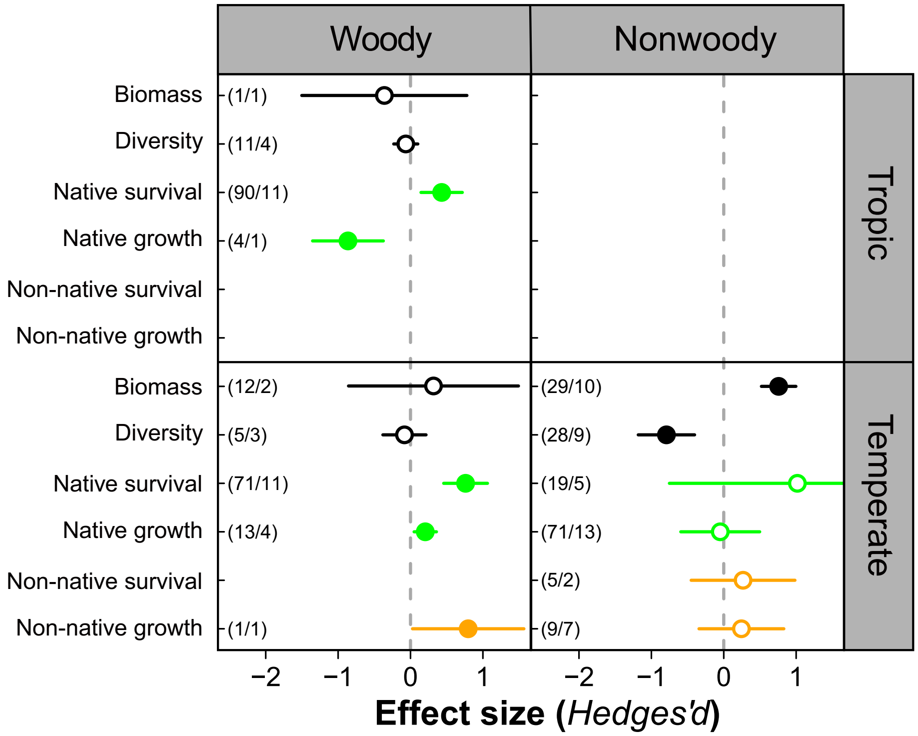

Fig. 3 Effect sizes and 95% confidence intervals for fungicide treatment experiments, separated for woody and nonwoody species by latitudinal zone (temperate and tropic). Interpretation follows Fig. 2. Community metrics (biomass and diversity) are shown in black, native species results are shown in green, and non-native results are shown in orange.

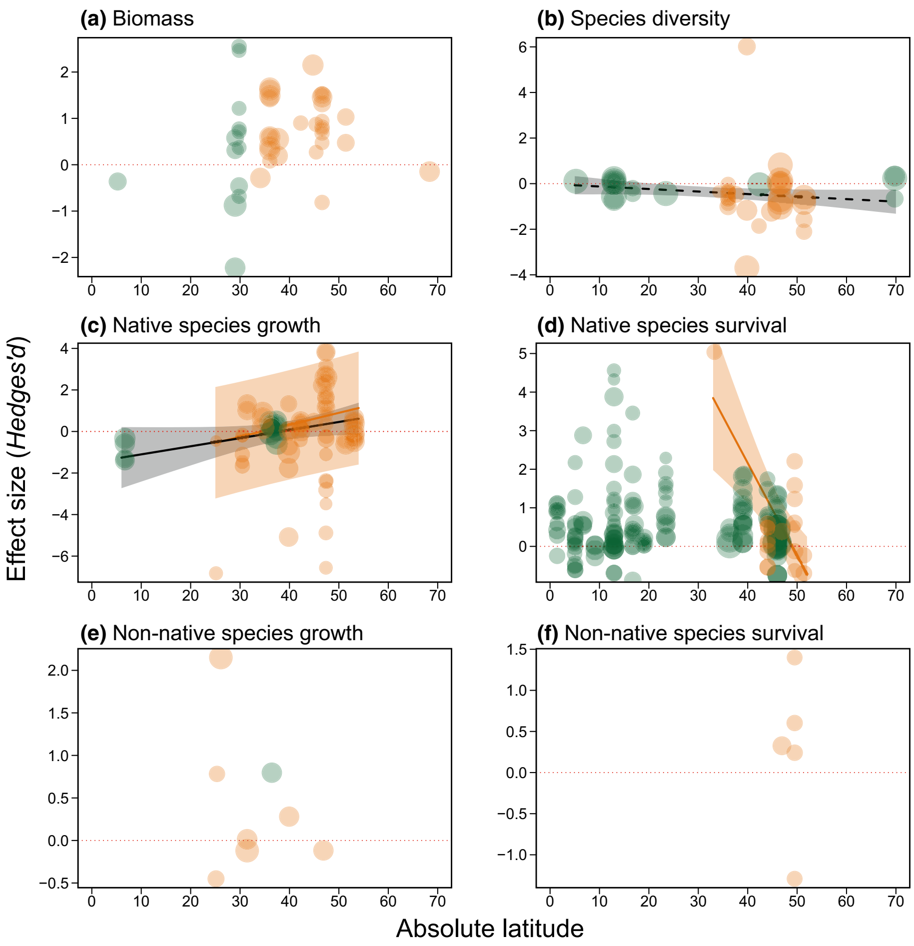

Fig. 4 Effect of fungicide treatment across latitudinal gradients for woody (green) and nonwoody species (orange) for biomass (a), species diversity (b), native species growth (c), native species survival (d), invasive species growth (e), and survival (f). Circle sizes are proportional to the inverse of the variance (larger is more meaningful). Significant trends ($P < 0.05$) are shown with solid regression lines, with black colors showing overall trends (woody and nonwoody grouped), orange trends showing nonwoody species, and the absence of trend lines indicating a lack of significant relationships (e.g. there were no significant latitudinal trends for woody species). The dashed black line in panel b denotes marginal significance ($0.05 < P < 0.1$). The grey and orange shaded areas in panels b, c and d are the 95% confidence intervals of overall and nonwoody species, respectively.

tropical zones (Table S8). Impacts were also positive for both woody and nonwoody species, but only marginally significant for woody species (Table S8). By contrast, there were no significant impacts of fungicide treatments on native species growth in either field or glasshouse experiments, with either woody or nonwoody species, and in either temperate or tropical zones (Table S9).

Temperature did not influence the impact of fungicides on biomass ($\text{coefficient} = -0.0022 \pm 0.0247$; $P = 0.9289$) or diversity ($\text{coefficient} = 0.0105 \pm 0.0141$; $P = 0.4565$), or on growth (native: $\text{coefficient} = -0.0555 \pm 0.0393$; $P = 0.1579$; non-native: $\text{coefficient} = -0.0027 \pm 0.0962$; $P = 0.9772$) or survival (native: $\text{coefficient} = 0.0065 \pm 0.0199$; $P = 0.7438$; non-native $\text{coefficient} = -0.0426 \pm 0.5796$; $P = 0.9414$). Precipitation also did not influence the impact of fungicides on biomass ($\text{coefficient} = -0.0004 \pm 0.0003$; $P = 0.1149$), or on growth (native: $\text{coefficient} = -0.0008 \pm 0.0006$; $P = 0.2157$; non-native: $\text{coefficient} = 0.0011 \pm 0.0008$; $P = 0.1649$) or survival (native: $\text{coefficient} = -0.0001 \pm 0.0001$; $P = 0.6773$; non-native: $\text{coefficient} = -0.0003 \pm 0.0046$; $P = 0.9414$). However, increasing precipitation weakened the negative effect of fungicides on species diversity, although the effect size was small ($\text{coefficient} = 0.0002 \pm 0.0001$; $P = 0.0233$).

Variation with fungicide active ingredients

Different fungicide-active ingredients did not have significantly different effects on biomass, while for diversity, the differences were significant if all fungicides were included in the analysis but not when only those used in at least five experiments were included (Table S10). At the species level, there were no significant differences in the effects on the growth of native species, and the differences were significant for survival only when all fungicides were included (Table S10). Among the 16 fungicide-active ingredient groups, eight had significant positive effects on native species survival (four of which were tested on ≥5 experiments; Fig. 5), and none had significant negative effects (Fig. S2). There was also a significant difference in the effects on the growth of non-native species (Table S10).

Variation with measurement types

Fungicide effects on biomass were significant when biomass was measured directly and not when measured indirectly via basal area, and effects on diversity were significant only when species richness was measured and not when the Shannon or Simpson indices were used (Table S11). In both these cases, the measurements with significant effect sizes (direct biomass measurements and species richness) were the most common. At the species level, measurement type had no influence on whether significant effects were found (Table S11).

Test for publication bias

The regression test found that the funnel plots for studies of community biomass ($z = -0.0123$; $P = 0.9902$), native species growth ($z = -1.4219$; $P = 0.1551$), non-native species growth ($z = 1.5391$; $P = 0.1238$), and non-native species survival ($z = -0.1057$; $P = 0.9158$) were symmetrical, suggesting that there was no systematic publication bias (Fig. S3). However, the plots for studies of community diversity ($z = -2.9648$; $P = 0.0030$) and native species survival ($z = 7.4591$; $P < 0.0001$) were asymmetrical. We then used the trim-and-fill approach to explore potential publication bias for the diversity and survival of native species (Table S4). Treatment with fungicides still increased native species survival (effect size = 0.1590; CI = 0.0295–0.2885; $P = 0.0161$), but the effect size was smaller than with the original data. Treatment with fungicides had no significant effect on the diversity when all diversity metrics were included (species richness, Shannon and Simpson index; effect size = −0.1412; CI = −0.3567–0.0742; $P = 0.1989$) but had a significant negative effect if only studies using species richness were included (effect size = −0.4820; CI = −0.6420–0.3220; $P < 0.0001$).

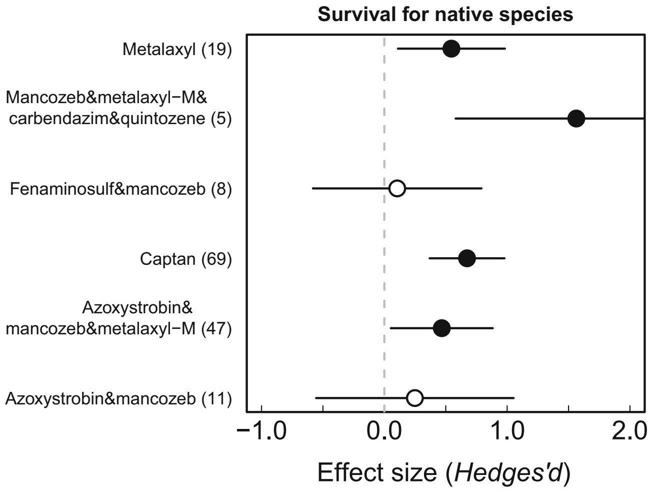

Fig. 5 Effect sizes and 95% confidence intervals for different fungicides (active ingredient) with ≥ 5 experiments (QM = 29.4661; df = 6; *P*-val < 0.0001). Filled circles are significantly different from zero ($P < 0.05$), and empty circles are not. Parentheses show the number of experiments. Results for rarer fungicides are presented in Supporting Information Fig. S3.

Discussion

Our global synthesis of fungicide impacts on wild plants and vegetation confirmed the expected positive impacts on plant species survival and community biomass, as well as the expected negative impact on community diversity. Surprisingly, however, there was no significant overall impact on plant species growth, a result that is difficult to reconcile with either the strong impact on species survival or the increase in biomass at the community level. The results also show the muted impacts on non-native species as predicted, albeit with small sample sizes. Our predictions were based on the assumption that the negative impacts of fungal pathogens on plants are, on average, greater than any positive impacts from mutualists and decomposers, and the results are, in general, consistent with this assumption.

Although the total number of studies and experiments included in the meta-analysis is large, the available studies are highly heterogeneous in terms of study systems, locations, and methods, with strong geographical biases. Analyses of subsets of the data reveal a much more varied and complex picture (Figs S4–S7). This variability in the impacts of fungicides could have multiple, nonexclusive explanations, including variation in the susceptibility of plant species to fungal pathogens (Mangan *et al*., 2010; Bruijning *et al*., 2024; Cheng & Yu, 2025) and variation in the effects of the wide range of different fungicides and fungicide combinations used in the included studies. There may also be variations in the relative importance of fungal pathogens, mutualists, and decomposers in different environments and in different types of plant communities (Pan *et al*., 2024) and in the importance of fungi in comparison with other natural enemies (Fricke *et al*., 2014; Gripenberg *et al*., 2014). Unfortunately, small sample sizes and inadequate spatial and environmental replication make it impossible to distinguish between these alternative explanations using the available data.

The positive impact of fungicide treatment on native species survival is the most consistent result, robust to almost all variations in the experimental setups. By contrast, when data subsets are examined, the overall positive impact on biomass and negative impact on diversity are both shown to be driven largely by studies on temperate grasslands. Both are also sensitive to the choice of measurement type, but this may reflect low sample sizes for the less common types.

The impact of fungicides on growth shows a particularly interesting pattern, with an overall positive effect on woody species and a negative effect on nonwoody species. It is possible that this suggests woody plants such as trees have comparatively more beneficial fungal associations (e.g. mycorrhizal fungi) while nonwoody plants have more negative associations (i.e. pathogens).

Do pathogens contribute to species diversity?

The robust positive effect of fungicide treatment on species survival adds mechanistic support to the evidence for the role of fungal pathogens in negative density dependence, Janzen–Connell effects, and the resulting positive effects on local diversity (Milici *et al*., 2020; Song *et al*., 2021; Fig. 2). Indeed, in the temperate zone, we found support for a positive role of fungal pathogens in diversity maintenance as measured by species richness and, thus, a negative impact of fungicide application. We note that there were no effects on species evenness, a finding that differs from studies excluding herbivores, in which effects on evenness were greater than for richness (Jia *et al*., 2018; Luskin *et al*., 2021). There are no equivalent fungicide data for the diversity of tropical woody communities.

Fungal pathogens and the enemy release hypothesis

While the non-native sample size was small, the absence of significant positive impacts of fungicide treatments on non-native plant species is consistent with the idea that recent invaders have left their species-specific natural enemies behind (Liu & Stiling, 2006).

Latitudinal variation in the impact of fungal pathogens

The results of this meta-analysis show stronger positive effects of fungicide application at higher latitudes, suggesting that the effect of fungal pathogens – or, at least, the net effect of fungi – is reduced at lower latitudes. This pattern does not support the LBIH and indicates that we should focus more on the mechanisms behind the geographic gradients (Hargreaves, 2024). The results may be explained by the DEH, which suggests that plant enemies are less likely to locate their preferred hosts in species-rich communities at low latitude. Our result is also consistent with other studies, suggesting that negative plant–soil feedbacks are stronger at higher latitudes (Jiang *et al*., 2024).

Limitations of current fungal pathogen exclusion methods

Commercial fungicides claim various degrees of specificity but, as with other pesticides, nontarget impacts on nonpathogenic fungi, other microbes, plants, and animals have been widely reported (Wan *et al*., 2025). Moreover, commercial claims of specificity are based on agricultural monocultures with simplified biotas, not necessarily applicable to natural systems. A common feature of most fungicide experiments is that, while the identities of the plants involved are known in full, the fungi are incompletely known, and the changes in fungal composition before and after the treatment are largely unknown. Differences between fungicide formulations, concentrations, and methods of application could, therefore, underlie much of the unexplained variation in impacts. However, as long as studies are limited to identifying the net effects of all on- and off-target impacts on plants and plant communities, the interpretation of fungicide treatment experiments will continue to be difficult. Resolving this will require studies that examine changes in fungal community composition with fungicide treatments under natural conditions. High-throughput sequencing has been widely used in economically valuable plants and agricultural fields to examine the changes in the bacterial and fungal community after fungicide application (Knorr *et al*., 2019; Ma *et al*., 2021; Wu *et al*., 2024) but has not yet been used in studies of wild plants and vegetation.

Future research priorities

In addition to the use of molecular techniques to characterize the impacts of fungicide applications on target and nontarget organisms, it is important that the geographical biases that limit the usefulness of the existing dataset are reduced. In particular, there is a need for studies in tropical nonwoody plant communities, and in both woody and nonwoody communities in the boreal region and the southern hemisphere. It would also be useful to standardize measurements, as far as possible, and to use novel fungicides or combinations only if they have a clear advantage. For plant communities, more species diversity metrics, including evenness, should be reported.

Conclusions

The results of this global meta-analysis of studies that applied fungicides to wild plant species or communities confirm the importance of fungal pathogens in the ecology of plants. Overall, pesticide treatments increased the biomass of plant communities and decreased their diversity while, at the species level, they increased plant survival but only increased the growth of woody species (they had a negative effect on nonwoody species' growth). Analyses of subsets of the data, however, revealed a more varied and complex picture, with few consistent results and a lot of unexplained variation. This variation can probably be explained by the diversity of study species and communities, of locations, and of methods, but strong geographical biases in sampling and small sample sizes for many combinations of variables make it impossible to distinguish between these alternative explanations. The results are largely consistent with a role for fungal pathogens in community diversity maintenance, but not with the LBIH. Future studies should aim to fill the gaps in the geographical spread of studies, standardize the methods as far as possible, and use molecular techniques to characterize the impacts of fungicide treatments on both target and nontarget organisms.

Acknowledgements

This research was supported by the National Natural Science Foundation of China (32171531, 31800353), the Youth Innovation Promotion Association CAS (2021396), the Applied Fundamental Research Foundation of Yunnan Province (202205 AC160028), the NSFC China-US Dimensions of Biodiversity Grant (DEB: 32061123003), the Yunnan Xingdian Talents Yunling Scholars, Western Light Foundation of Regional Development Fund, the 14th Five-Year Plan of the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (XTBG-1450101 and XTBG-1450102), and the Australian Research Council Discovery Early Career Researcher Awards (DECRA DE210101440 to MSL).

Competing interests

None declared.

Author contributions

XS and JY designed the study and collected the data. XS and MSL analyzed the data. XS, RTC and MSL wrote the manuscript.

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Data availability

The dataset and statistics code are available on ScienceDB (https://www.scidb.cn) at https://doi.org/10.57760/sciencedb.06869.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 PRISMA flow diagram of selection of studies included in the meta-analysis.

Fig. S2 Effect size of each fungicide on native species survival.

Fig. S3 Funnel plots to check publication bias for community productivity, community species diversity, native species survival and growth, non-native species survival, and growth. Lowercase indicates the funnel plots used the trim-and-fill method to account for missing data and balance the SE.

Fig. S4 Forest plot of all experimental studies investigating biomass included in the meta-analysis.

Fig. S5 Forest plot of all experimental studies investigating species diversity included in the meta-analysis.

Fig. S6 Forest plot of all experimental studies investigating plant survival included in the meta-analysis.

Fig. S7 Forest plot of all experimental studies investigating plant growth included in the meta-analysis.

Table S1 Details of how similar variables were grouped for meta-analysis.

Table S2 Active ingredient of each fungicide and its specificity.

Table S3 Diseases treated by various fungicide active ingredients, data from PESTICIDE MING NETWORK http://www.nyfzx.com/.

Table S4 Testing for publication bias.

Table S5 Meta-analysis Akaike Information Criterion model selection with and without the inclusion of phylogenetic random effects.

Table S6 Meta-analysis model summaries testing the effect of fungal pathogens on biomass for different subsets of data.

Table S7 Meta-analysis model summaries testing the effect of fungal pathogens on species diversity for different subsets of data.

Table S8 Meta-analysis model summaries testing the effect of fungal pathogens on plant survival for different subsets of data, grouping woody and nonwoody species.

Table S9 Meta-analysis model summaries testing the effect of fungal pathogens on native species growth for different subsets of data.

Table S10 Testing for the effect of fungicide active ingredient (Table S3) on the effect size at the community and species levels.

Table S11 Effect size of different measurements for all data.