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ORIGINAL PAPER

The invasive pathogenic fungus *Hymenoscyphus fraxineus* alters predator–herbivore–ash food webs

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Abstract Plant pathogens have potential to change the relative importance of bottom-up and top-down regulation in forest ecosystems and may determine whether trophic cascades are present in local food chains. While evidence for such effects from field studies in forest ecosystems remains sparse, this would be valuable for the management of invasive plant pathogens. *Hymenoscyphus fraxineus* is an invasive pathogenic fungus that causes massive die-back across Europe, mainly of the common ash *Fraxinus excelsior*. Here, we investigated by a correlative approach how infestation by *H. fraxineus* affects the association between herbivory of ash leaves and densities of herbivores (herbivorous Hemiptera, Psocoptera, herbivorous Coleoptera, caterpillars and Symphyta) and predators (Araneae, Formicidae, and Dermaptera) in young ash plantations. Our results indicate that infestation with the pathogenic fungus changed community-wide regulatory mechanisms in arthropod food webs of young ash plantations. Bottom-up and top-down regulation was relatively balanced in plantations with low infestation levels, but with pronounced top-down control of herbivory by spiders in autumn. In highly infested plantations, by contrast, spiders were bottom-up limited as they aggregated in herbivore-rich patches and had no significant effect on herbivory. There was a top-down effect of herbivores on ash leaves in high infested plantations, but not in low infested plantations. These results suggest that the invasive fungus affects ecosystem functioning through a reduction of functional complementarity and intensification of negative intraguild interactions among predators. This consequently resulted in strong bottom-up limitation of predators and their reduced ability to suppress herbivores and herbivory.

Keywords Alien species · Ecosystem functioning · *Fraxinus* · Herbivory · Trophic cascade

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Introduction

Plant pathogens can alter the quality of plant resources for herbivores and consequently alter the type and strength of resource limitation in herbivores (Tack and Dicke 2013). Plant pathogens therefore have the potential to change the relative importance of bottom-up and top-down regulation and determine whether trophic cascades are present in local food chains (Burghardt and Schmitz 2015). Nevertheless, nothing is known about how plant pathogens affect the relative importance of regulatory mechanisms in predator–herbivore–plant food webs. This knowledge is essential for the management of invasive pathogens as it would facilitate predictions about the effect of pathogens on whole ecosystems (David et al. 2017).

There are multiple direct and indirect ways how plant pathogens can affect arthropod populations positively as well as negatively across trophic levels (Tack and Dicke 2013). For example, a plant pathogen can increase the vulnerability of plants (Kluth et al. 2001) and herbivores may consequently become limited by absolute rather than relative resource supply (Burghardt and Schmitz 2015). This switch from relative to absolute resource limitation would disrupt trophic cascades in the food chain, because herbivore mortality caused by a predator would be compensated by increased per capita herbivory of the remaining herbivore individuals (Burghardt and Schmitz 2015). However, a plant pathogen can also reduce plant quality for herbivores and consequently herbivore quality for their predators (Srisakrapikoop et al. 2020). This may potentially either increase bottom-up regulation of both herbivores and predators or change the ecosystem regulation from a top-down to a bottom-up mechanism.

Previous studies, limited to relatively simple tritrophic food chains, indicate that effects of plant pathogens may cascade upward from the plant to the herbivore and specialized parasitoid trophic level (e.g., Tack et al. 2012; Ngah et al. 2018). Most ecosystems are comprised of highly complex food webs and potential buffering mechanisms may prevent the effect of pathogens from going beyond certain food web modules and thereby eliciting changes in community-wide processes and regulations. Therefore, there is a need for field studies that complement the existing laboratory and seminatural studies to support the emerging pattern of plant pathogen effects on ecosystem functioning and regulation.

The pathogenic fungus *Hymenoscyphus fraxineus* (T. Kowalski) Baral, Queloz & Hosoya is highly invasive in Europe. The species has its native range in eastern Asia and was introduced to Europe in the early of 1990s (Enderle 2019). Infection by the fungus causes what is known as ash dieback, characterized by defoliation, branch loss, and ultimately leading to mortality of ash trees (Turczański et al. 2020). Ash dieback causes large-scale decline mostly of the common ash *Fraxinus excelsior* L, resulting in significant economic losses in forestry, and it may lead to the co-extinction of species that are closely associated with ash populations across trophic levels (Erfmeier et al. 2019; Hultberg et al. 2020).

A previous study has shown that ash dieback reduces complexity of the arthropod predator–prey network in ash plantations and suggested that the ash dieback reduces the capacity of web-building spiders and predatory beetles to suppress herbivores (Michalko et al. 2021). The observed reduced suppression of herbivores may result in increased herbivory in ash trees, which may then potentially accelerate the dieback in a self-amplifying cycle (Kluth et al. 2001). However, the impact of ash dieback on herbivore suppression by predators and the consequences for levels of herbivory on ash trees have not yet been investigated.

Here, we studied how infestation by *H. fraxineus* affects the association among herbivory on ash leaves, densities of herbivores, and densities of their predators in young ash plantations. We hypothesized that (1) natural enemies will suppress herbivores more effectively in low-infested than in high-infested plantations. This will lead to negative correlations between (2) predator and herbivore densities, and (3) predator densities and herbivory in low-infested plantations. Contrarily, (4) these relationships will be much weaker or absent in high-infested plantations. Moreover, we expected that the invasive fungus will increase the vulnerability of ash leaves to herbivores and that this effect will result in (5) a steeper positive association between densities of herbivores and herbivory.

Methods

The study area is located in a floodplain forest in vicinity of the Vranovice and Ivaň municipalities in Czechia (48° 57′ 57 N, 16° 36′ 23 E; Fig. S1; mean annual temperature 9 °C; mean annual perception 475 mm). The studied area is mainly covered by hardwood floodplain forest (Fraxino pannonicae-Ulmetum vegetation type). The studied plots (N = 8) were located in young ash forest plantations (10–15 years old) with low (29–39%; N = 4) and high infestation (55–85%; N = 4) by ash dieback (Fig. S1). The infestation degree of each plot was estimated according to the standardized methodology (Kučera et al. 2017). Firstly, four sub-plots were selected within each plot and within each sub-plot 20 random ash trees were selected. Then, the infestation within each sub-plot was estimated as the percentage proportion of infected trees scaled from low to high infestation ranks according to the presence of the main symptoms (e.g. defoliation, amount and position of secondary shoots, presence of necrotic lesions). The infestation level of each plot was then computed as the average across the four plots (Michalko et al. 2021).

We sampled the arthropods and herbivory at the turn of spring and summer (hereinafter termed spring/summer) in mid-end June 2019 and again in autumn at the start of October 2019. In each stand, 4–8 samples were collected during each sampling season (N = 96 samples). A sample constituted what was collected from the beating of branches of one tree for 10 s. The beating was performed above a sheet of standardized size (surface: 1 × 1 m) and we collected all arthropods falling upon the sheet. To estimate herbivory for each sample, we collected 10 random compound leaves from the beaten branches (N = 960). We let the collected leaves dry naturally for 2 months as herbarium items and preserved them in the laboratory before estimating herbivory.

We determined the collected arthropods to order or suborder level. We aggregated those taxonomic groups that could be classified as herbivores (i.e., herbivorous Hemiptera, Psocoptera, herbivorous Coleoptera, caterpillars, Symphyta). Only spiders, ants, and earwigs reached sufficiently high densities in our samples for further analyses of predaceous taxonomic groups. We treated the predator groups individually in all analyses (spiders, ants, and earwigs) because they differ in their degree of omnivory and we wanted to compare their relative contribution to top-down control in the ash plantations.

We estimated three indicators of herbivory that are related to the effects of different herbivore groups (e.g., sap feeders vs. leaf chewers), namely percentage damage, dry leaf biomass, and leaf mass area (LMA) (Zvereva et al. 2010). We used a standardized method to quantify the leaf damage by chewing herbivores (Johnson et al. 2016). In each compound leaf, we randomly selected three small leaflets (N = 2880 leaflets) and visually estimated the percentage damage in each leaflet. The mean percentage across the three leaflets then represented an estimate of herbivory per compound leaf. Moreover, a digital milligram scale was used to weigh leaf biomass (precision 0.1 mg). The biomass was measured by weighing the three small leaflets of ash per compound leaf. To determine LMA, we then cut a 1 × 1 cm sample from each leaflet and weighted it. The mean LMA across the three leaflets represents an estimate of mean LMA per 1 cm^2 for the whole leaf. To obtain a sample-level estimation of herbivory, we computed the mean for each herbivory indicator across the 10 leaves (30 leaflets) within each sample.

We used piecewise structural equation models (SEMs) from the R package "piecewiseSEM" (Lefcheck 2016) to investigate the impact of ash dieback on the food web dynamics. We fitted four separate SEMs for the two infestation levels and two seasons because the top-down and bottom-up processes may interactively change, and that requires changing positions of terms in the models. We first preselected the potential direct and indirect trophic links based on the effect size using Spearman's rank correlation coefficient instead of *P*-values in order to avoid problems from multiple comparisons and an increasing probability of type II error (Nakagawa 2004). We selected only such correlations as were at least moderately strong (i.e., $\geq |0.30|$; Cohen 1992). The initial SEM models were then built based upon the preselected correlations, links that would violate the independence claim, and ecological theory (Lefcheck 2016). The component models in the SEMs were fitted with generalized linear mixed effect models (GLMM) from the R package "lme4" (Bates et al. 2015) with plantation ID as the random effect to reflect the sample design. If the response variables were abundances, we used negative binomial GLMMs (GLMM-nb) as there was overdispersion (Zuur et al. 2015). The continuous response variables were modeled with GLMMs with gamma error structure (GLMM-g) with either inverse or log link function depending upon which of these provided a better fit of the data (Zuur et al. 2015). The nonsignificant links in the SEM were removed by stepwise backward selection based upon critical values and the Akaike information criterion (AIC) and we present the most parsimonious model (Lefcheck 2016).

Results

Overall, we collected 1356 arthropods (579 spiders, 113 ants, 57 earwigs, and 607 herbivores) and 960 leaves. However, only spiders and earwigs as generalist predators showed moderately strong association with herbivores and herbivory (Fig. 1).

In spring/summer, the SEM models had good fits for low-infested (Fisher's C = 5.2, *df* = 6, *P* = 0.515, AIC = 21.2; Fig. 1) as well as high-infested ash plantations (Fisher's C = 12.8, *df* = 12, *P* = 0.384, AIC = 36.8; Fig. 1). There was only a marginally positive relationship between earwigs and LMA in low-infested ash plantations (*P* = 0.080; Fig. 1A, Fig. S2A). By contrast, there was a significant negative relationship between earwigs and LMA in the high-infested ash plantations (*P* = 0.022; Fig. 1B, Fig. S2B). In the high-infested ash plantations, there was indication of a top-down effect of herbivores on ash trees as increasing densities of herbivores decreased the dry leaf biomass (*P* < 0.001, Fig. 1B, Fig. S2C).

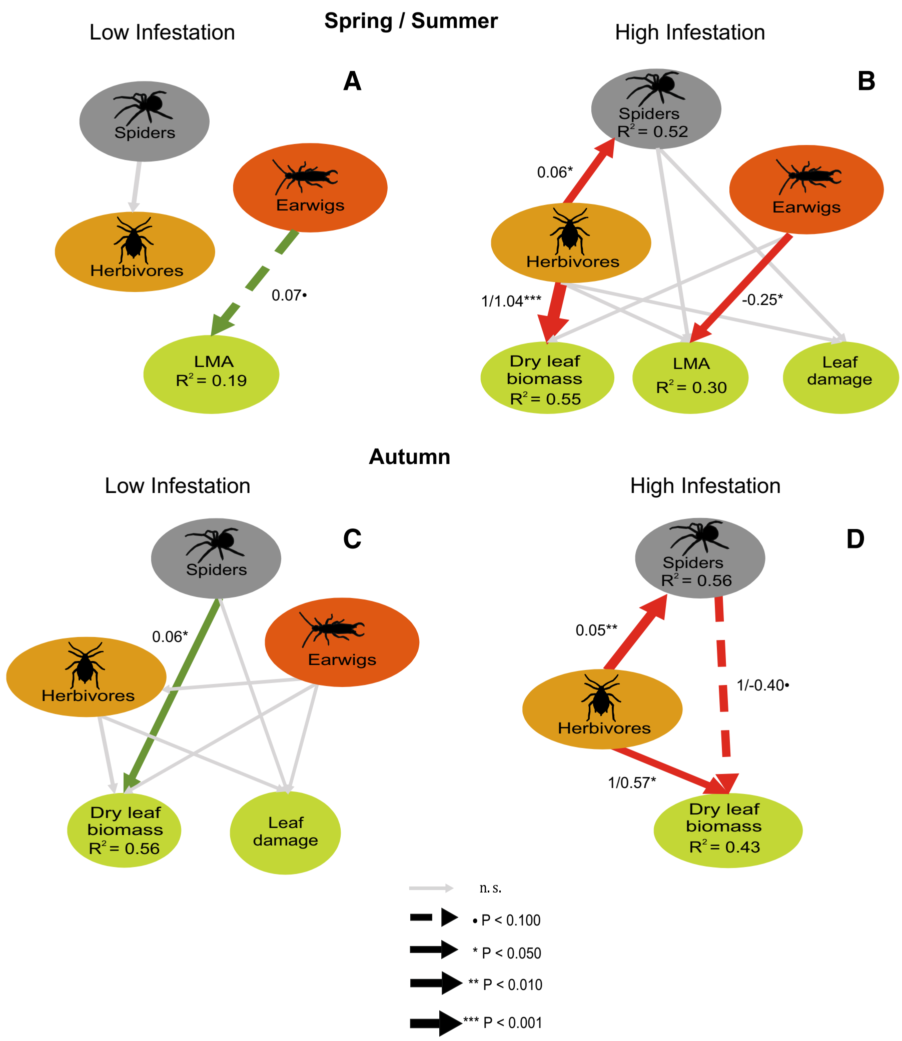

Fig. 1 Structural equation models investigating relationships between ash leaves, herbivores, spiders, and earwigs in ash stands with low (**A**, **C**) and high (**B**, **D**) levels of infestation by the invasive pathogenic fungus *Hymenoscyphus fraxineus* at the turn of spring and summer (**A**, **B**) and in early autumn (**C**, **D**). Arrows point from explanatory to response variable. Size and type of arrow shows level of statistical significance. Estimated slope parameters are shown next to arrows. Note: Because the parameters containing a fraction come from GLMMs with gamma error and inverse link function, the positive sign means a negative relationship while the negative sign means a positive relationship between the variables (see Fig. S2 for the individual component models). The conditional R^2 values for the internal variables are displayed

Bottom-up control from herbivores to spiders was also indicated as spiders aggregated in patches with high abundances of herbivores ($P = 0.028$; Fig. 1B, Fig. S2D). No such clear relationships were found in the low-infested ash plantations (Fig. 1 A).

In autumn, the SEM models for low-infested (Fisher's C = 0, df = 0, $P = 1.0$, AIC = 8.0; Fig. 1C) and for high-infested (Fisher's C = 0, *df* = 0, $P = 1.0$, AIC = 18.0; Fig. 1D) ash plantations were just identified models (saturated SEMs with zero degrees of freedom). There was a positive association between abundances of spiders and dry leaf biomass ($P = 0.020$; Fig. 1C, Fig. S2E) in ash stands with the low infestation, potentially indicating either top-down or bottom-up control. In highly infested ash stands, there was only a marginally positive relationship between spider abundances and dry leaf weight ($P = 0.069$; Fig. 1D, Fig. S2F). In the highly infested ash plantations, dry leaf biomass was negatively associated with herbivore abundance ($P = 0.015$; Fig. 1D, Fig. S2G), potentially indicating top-down effects of herbivores on ash leaves. In highly infested plantations, spiders also positively responded to densities of herbivores ($P = 0.004$; Fig. 1D, Fig. S2H), which indicates bottom-up control from herbivores to spiders. No such clear relationship was observed in the low-infested ash plantations (Fig. 1C).

Discussion

The infestation by ash dieback established a negative relationship between abundance of herbivores and dry leaf biomass in high-infested plantations while there was no significant relationship in low-infested stands. Although leaf damage and LMA were not significantly affected, the impact on the overall dry leaf biomass may be explained by a joint effect from leaf chewers and sap feeders. Leaf chewers remove leaf biomass directly, but this damage can be compensated by regenerative growth (Zvereva et al. 2010). By contrast, sap feeders suck nutrients and thereby reduce photosynthesis and the capacity for regenerative growth (Zvereva et al. 2010). The additional stress induced by *H. fraxineus* infection might therefore reduce the capacity of ash to cope with high densities of herbivores (Kluth et al. 2001). Another non-exclusive explanation is that the pathogenic fungus might reduce the nutritional quality of ash leaves for herbivores (Tack et al. 2012). To achieve their nutritional targets, herbivores might compensate for the reduced quality by increasing their per capita feeding rates (Raubenheimer et al. 2009).

We measured infestation level at plantation scale and not directly at tree scale. Therefore, the observed pattern may arise from changes in the spatial distribution of resources and spatial structure of biotic interactions. In highly infested plantations, individual trees differ in the degrees of their infestation and healthy, low-, and high-infested trees co-occur. In the low-infested plantations, by contrast, mostly healthy trees co-occurred (authors, pers. obs.). As the pathogenic fungus might increase or decrease the nutritional quality of ash leaves for herbivores, the mosaic of variously infested trees may increase the resource patchiness and induce source-sink dynamics. Herbivores might aggregate in high-quality patches and increase herbivory there while emigrating from low-quality patches. Another possible nonexclusive explanation is that the pathogenic fungus reduced the efficacy of natural enemies to suppress herbivores (Michalko et al. 2021; see below), which might increase the impact of herbivores on ash leaves.

A high level of infestation by the invasive pathogenic fungus increased bottom-up regulation of spiders by herbivores as spiders aggregated in prey-rich patches while no such association was observed in the low-infested plantations. The increased importance of bottom-up limitation in high-infested plantations may be caused, for example, by reducing the quality of herbivores as prey for spiders (Toft and Wise 1999; Tack and Dicke 2013). To meet their nutritional requirements spiders may compensate the suboptimal nutritional composition of prey in high-infested stands by increased feeding rate (Toft 2013). Spiders might therefore aggregate in prey-rich patches of high-infested stands where they could encounter enough prey to satisfy these increased demands. Another possible explanation is that the invasive fungus changes habitat structure and consequently reduces functional complementarity and intensifies negative intraguild interactions among web-building spiders (Michalko et al. 2021). The higher prey availability might reduce the negative intraguild interactions and enable the coexistence of more spider individuals (Birkhofer et al. 2008).

The infestation by the invasive fungus cut off the trophic cascade from spiders on ash leaves as spiders significantly increased the dry leaf biomass in low-infested plantations during autumn, but this relationship was only marginal in high-infested plantations. It could be argued that the heavier leaves were larger and supported more spider individuals because there was no observable link through herbivores. If this were to be the case, however, we would observe this pattern consistently across the periods and infestations, but that was not the case. Moreover, it is known that the effect of spiders escalates from herbivores to plants rather than attenuating (Michalko et al. 2019) due to the non-consumptive effect when spiders reduce the per capita feeding rate of herbivores (Bucher et al. 2015). The loss of this trophic cascade may be explained again by the altered functional composition, reduced functional complementarity, and intensified negative intraguild interactions in heavily infested plantations, which might reduce the suppression efficacy of spiders (Michalko et al. 2021).

We found that LMA marginally increased with the density of earwigs in low-infested plantations but decreased significantly in highly infested plantations during the spring/summer period. Earwigs are omnivores (Kirstová et al. 2018) that can significantly reduce herbivores (Niedobova et al. 2021) as well as cause substantial damage to plants (Quarrell et al. 2021). Therefore, the observed pattern is difficult to explain as the changes may arise directly through the changes in leaves consumption by earwigs or indirectly through the effect of earwigs on herbivores. For example, lower LMA is assumed to be positively related to herbivory by leaf-chewing insects (Pellissier et al. 2012). Therefore, earwigs might prefer herbivorous prey in low-infested plantations. The fungus may increase the nutritional value of ash leaves for earwigs and as a consequence earwigs may prefer ash leaves over herbivores as food in high-infested stands.

Conclusion

The invasive pathogenic fungus *Hymenoscyphus fraxineus* seem to alter the top-down and bottom-up processes in local predator–herbivore–ash food webs. The impact of the invasive fungus seems to pervade the entire ecosystem and affect its functioning. The pathways through which the fungus affects the ecosystem functioning are complex and may include rather direct pathways by altering the food quality for consumers (Tack and Dicke 2013) as well as more indirect effects through altered habitat structure (Michalko et al. 2021). Further research is needed to disentangle these complex pathways, especially manipulative experiments that would provide more direct evidence. A previous study had documented that the fungus reduces the functional complementarity and intensifies negative intraguild interactions among spider species (Michalko et al. 2021). This, as the present study indicates, results consequently in increased bottom-up limitation of spiders and their reduced ability to suppress herbivores and herbivory.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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