

# Fungal endophyte increases the allelopathic effects of an invasive forb

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**Abstract** Endophytic plant symbionts can have powerful effects on the way their hosts interact with pathogens, competitors, and consumers. The presence of endophytes in plants can alter food webs, community composition and ecosystem processes, suggesting that endophyte-plant symbioses may represent unique forms of extended phenotypes. We tested the impact of the fungal endophyte *Alternaria alternata* (phylotype CID 120) on the allelopathic effect of the invasive forb *Centaurea stoebe* when in competition with the North American native bunchgrass *Koeleria macrantha* in a greenhouse competition experiment. The allelopathic effect of *C. stoebe* on *K. macrantha* when infected with the fungal endophyte was more than twice that of endophyte-free *C. stoebe*. However, this allelopathic effect was a small part of the very large competitive

effect of *C. stoebe* on *K. macrantha* in all treatments, likely because of the priority effects in our experimental design. To our knowledge, these results are the first experimental evidence for a symbiotic relationship between plants and fungal endophytes affecting allelopathic interactions between competing plants, and thus provide insight into the mechanisms by which fungal endophytes may increase the competitive ability of their hosts.

**Keywords** *Alternaria* · *Centaurea* · Community · Competition · Mutualism

## Introduction

Plants are host to a diverse array of mutualistic endophytic symbionts, including mycorrhizae, nitrogen-fixing bacteria, and fungal endophytes. These symbionts can have powerful effects on the way their hosts interact with pathogens, competitors, and consumers (Aschehoug et al. 2012; Callaway et al. 2011; Clay 1988; Marler et al. 1999; Musetti et al. 2007). Of these symbionts, we know the least about the ecological function of fungal endophytes. However, evidence is rapidly accumulating for the ubiquity of fungal endophytes in plants and trees, and for the frequent mutualistic benefits they confer via herbivore defense (Clay et al. 2005; Koh and Hik 2007; but see Faeth 2002), effects on rhizosphere microbial communities (Rudgers and Orr 2009), and increased tolerance to abiotic stress (Elmi and West 1995).

Beyond the strong direct effects that fungal endophytes may infer, cascading effects of fungal endophyte-plant symbionts across trophic levels also constitute unique forms of extended phenotypes (Dawkins 1982; Whitham et al. 2003). In this context, variation in both fungal

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endophyte and host plant genotype, as well as host plant infection rates, can have different effects on food webs, community composition, and ecosystem-level processes (Baynes et al. 2012; Cheplick and Faeth 2009; Clay et al. 2005; Rudgers et al. 2010; Xiao et al. 2012). These cascading effects of fungal endophytes also appear to play a role by increasing the competitive effects of infected plants on other species (Aschehoug et al. 2012; Marks et al. 1991; Rudgers and Orr 2009; Vázquez-de-Aldana et al. 2013; but see Faeth et al. 2004), but these effects are much less understood than herbivore-mediated benefits. Because the phenotypic synergism of plants and endophytes is potentially powerful ecologically, it is important to understand in detail how this complex symbiosis affects interspecific interactions among plants.

To date, most studies of fungal endophytes have focused on agronomically important cool-season grasses and the indirect benefits of deterring herbivores through qualitative or quantitative changes in leaf chemistry (Saikkonen et al. 2006). Fungal endophytes can produce many powerful biologically active chemicals that enhance overall plant resistance to herbivores (Bush et al. 1997), but there is also some evidence that fungal endophyte-induced plant chemistry may affect the allelopathic potential of plants (Sutherland et al. 1999; Vázquez-de-Aldana et al. 2011). However, this evidence is inconsistent and limited to laboratory trials of germination and growth of seedlings using infected tissue slurries from species of non-native forage grass. Sutherland et al. (1999) found that extract solutions made from ground up, fungal endophyte-infected tissues of *Lolium perenne* suppressed growth of *Trifolium repens* more than solutions made from uninfected tissues. Vázquez-de-Aldana et al. (2011) found that extracts made from infected root tissues of *Festuca rubra* slowed radicle growth more than extracts made from uninfected root tissue. In contrast, Renne et al. (2004) investigated the allelopathic potential of *Festuca arundinacea* on North American native prairie plants and found limited to no evidence of allelopathy regardless of endophyte infection. Studies of this nature can be useful for probing potential mechanisms by which plants and microbes may interact, but do not provide insight into the ecological relevance of these interactions. Further, the use of artificially produced leachates cannot separate the direct pathogenic effect of the endophyte from a potential endophyte-mediated chemical interaction. Because of this, it is important to test questions of endophyte-mediated plant interactions in an ecologically realistic way where plants experience both competition and microbially mediated interactions in whole soils. To our knowledge there are no studies that have explicitly tested the effects of fungal endophytes on the allelopathic interactions of competing plants. Interestingly, very little research has focused on how endophytes may enhance the success of invasive

exotic species (but see Baynes et al. 2012) despite allelopathy being implicated in their often unusually intense competitive effects on natives (Inderjit et al. 2011; Murrell et al. 2011).

*Centaurea stoebe* is an aggressive invader of western North American grasslands, and its seeds can be infected with a high diversity of non-clavicipitaceous endophytes in both its native and non-native ranges (Shipunov et al. 2008). Aschehoug et al. (2012) found that fungal endophytes in *C. stoebe* directly increased the competitive effect and response of *C. stoebe* when competing against North American native grass species, but not when in competition with grass species native to the same European grasslands as *C. stoebe*. Further, models exploring the community-level effects of endophyte infection in *C. stoebe* suggest that endophytes contribute to the expression of a highly dominant extended phenotype in North American grassland communities, but not in European grasslands (Xiao et al. 2012).

However, the mechanism by which the symbiosis increases competitive ability is not clear. There is evidence that *C. stoebe* is allelopathic (Chen et al. 2012; Ridenour and Callaway 2001; Thorpe et al. 2009); but, the allelopathic effects of *C. stoebe* are highly variable (Inderjit et al. 2008). Intriguingly, the fungal endophyte community infecting *C. stoebe* throughout its native and non-native range is very diverse taxonomically, and while the leaves, stems and roots of individual plants are consistently infected by endophytes, the proportion of seeds infected by fungal endophytes varies dramatically among populations (Shipunov et al. 2008). Thus variation in endophytic infection has the potential to cause variation in competitive outcomes, and perhaps helps to explain differences among experiments and variation within experiments. Similarly, different endophytic fungi might produce different allelopathic chemicals (Newcombe et al. 2009; Rudgers and Orr 2009) or stimulate different levels of allelochemical production.

Here we expand on previous work on how endophytes affect the general competitive ability of *C. stoebe* by investigating the link between fungal endophyte infection and the allelopathic effect of this invader. We hypothesized that endophyte infection would enhance the allelopathic effect of *C. stoebe* when in competition with a native North American grass species.

## Materials and methods

We grew *Centaurea stoebe* plants that were either endophyte-free or infected with the fungal endophyte *Alternaria* phylotype alt2b isolate CID120 (hereafter CID 120). CID 120 is closely related to *Alternaria alternata* and is

the most abundant fungal endophyte found in seeds of *C. stoebe* in the native range of *C. stoebe* and is common in seeds in the invaded range of North America as well (Shipunov et al. 2008). CID 120 has been previously shown to increase the competitive effect of *Centaurea* in competition experiments (Aschehoug et al. 2012).

We used seeds of *C. stoebe* obtained from greenhouse populations of plants known to be endophyte free (Raghavendra et al. 2013). To create the experimentally inoculated plants, seedlings of *C. stoebe* were placed in Petri dishes of fungal endophytes cultured on potato dextrose agar and allowed to remain in contact with fungal hyphae for 12 h to ensure adequate inoculation. CID 120 can colonize roots, leaves and seeds making our inoculation procedure a realistic experimental manipulation with previous results showing reliable colonization (Newcombe et al. 2009). Endophyte cultures were created using endophytes isolated from seeds of wild plants (Shipunov et al. 2008, Newcombe et al. 2009).

*C. stoebe* seedlings were grown in a mix of 50:50 native soil from the Missoula Valley and 20–30 grit silica sand (632- to 1,000- $\mu\text{m}$  grain size) for 124 days in 500-mL rocket pots in order to develop a large root system before being transferred to 2.4-L pots. When transplanting *Centaurea*, we filled the 2.4-L pots to 15 cm with the same 50:50 native soil/sand mix used in the 500-mL pots, placed the stem of the *C. stoebe* near the edge of the pot, and spread the extensive root system across the entire surface of the soil. We then covered the root system with an additional 7 cm of the same mixed soil/sand substrate. We intentionally created a scenario in which the roots of the native competitor (see below) in this experiment could not avoid the extensive root systems of *Centaurea* plants in order to increase the potential of detecting chemically mediated effects of *Centaurea*. Because of this design we expected the effects of *C. stoebe* on *Koeleria macrantha* (Ledeb.) Schult. to be intense regardless of treatment.

*Centaurea* plants were randomly assigned to one of two fully factorial treatments: with endophyte infection (E+), and without endophyte infection (E-); and in each endophyte treatment soil was treated with activated carbon or not. Phosphorus-free activated carbon (Calgon Carbon, PA) was applied at a rate of 40 mL L<sup>-1</sup> to the soil-sand mixture. Activated carbon has a high affinity for organic compounds, such as potentially toxic or allelopathic chemicals, and a weak affinity for inorganic electrolytes, such as those present in nutrient solution, and has been previously shown to reduce the negative belowground effects of *Centaurea* and other species (Callaway and Aschehoug 2000; Mahall and Callaway 1992; Ridenour and Callaway 2001) which allows us to experimentally separate the effects of allelopathy from the effects of resource competition. Once assigned to treatments, individual pots were relocated into

new random positions every 2 weeks to minimize microsite differences within the greenhouse.

After *Centaurea* plants were allowed to establish for 21 days in the 2.4-L pots, we sowed ten seeds of the North American native *K. macrantha* (hereafter *Koeleria*) 1–3 mm below the surface of each pot and 10 cm from the stem of the *Centaurea*. All seeds were collected from local populations in the Missoula valley of western Montana, USA, mixed, and haphazardly assigned to treatments. Watering displaced many *Koeleria* seeds and after 5 weeks, germinants were thinned to focus on the largest seedling in each pot regardless of its distance to the stem of *Centaurea*. *Centaurea* leaves were manipulated so that *Koeleria* seedlings were in full light. Because activated carbon has the potential to confound allelopathic interpretations (Callaway and Aschehoug 2000), we also planted *Koeleria* without *Centaurea* in ten pots with and without activated carbon.

All plants were grown in a greenhouse at the University of Montana, Missoula, USA. Greenhouse temperatures were kept between 15 and 30 °C and photosynthetically active radiation fluctuated between  $\approx 500$  and 1,700  $\mu\text{mol m}^2 \text{s}^{-1}$ . All plants were watered regularly during the experiment using tap water.

Our final replications in each treatment were affected by the number of plants that survived each step of the complex experimental design. At harvest replications were as follows:

1. *Koeleria* with *Centaurea* infected with CID 120 in activated-carbon soils,  $n = 20$ .
2. *Koeleria* with *Centaurea* infected with CID 120 without activated carbon in soils;  $n = 11$ .
3. *Koeleria* with *Centaurea* not infected with CID 120 and in activated-carbon soils,  $n = 34$ .
4. *Koeleria* with *Centaurea* not infected with CID 120 without activated carbon in soils,  $n = 34$ .
5. *Koeleria* grown alone in activated-carbon soils,  $n = 10$ .
6. *Koeleria* grown alone without activated carbon in soils,  $n = 10$ .

Previous studies have shown that *K. macrantha* is not sensitive to direct infection by CID 120 (Aschehoug et al. 2012); therefore we did not include treatments of direct infection in this experiment.

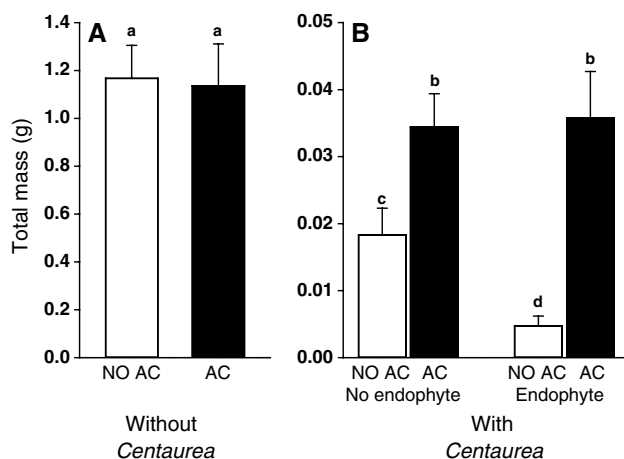
We harvested whole *Koeleria* plants 77 days after sowing. Plants were dried for 72 h at 80 °C, and each plant was weighed. We did not weigh above- and belowground biomass separately. We used a log (10) transformation of biomass data to improve the normality of the data set. We tested the effects of activated carbon on total *Koeleria* biomass grown alone using a one-way ANOVA. For *Koeleria* grown with *Centaurea*, we tested the effects of endophyte and activated carbon combined on total *Koeleria* biomass

using a two-way ANOVA and as a one-way ANOVA with Tukey honest significant difference (HSD) Kramer post hoc test. We tested the effect of activated carbon within the endophyte treatment using a one-way ANOVA. For percent mortality (the number of seedlings that died in each pot after 5 weeks) and percent germination, we used an arcsin square root transformation of the data. We tested the effects of endophyte and activated carbon as fixed factors on percent mortality and percent germination in a separate two-way ANOVA, and also with a one-way ANOVA with Tukey HSD Kramer post hoc tests. All analyses were conducted using IBM SPSS statistics 20.0 (San Jose, CA).

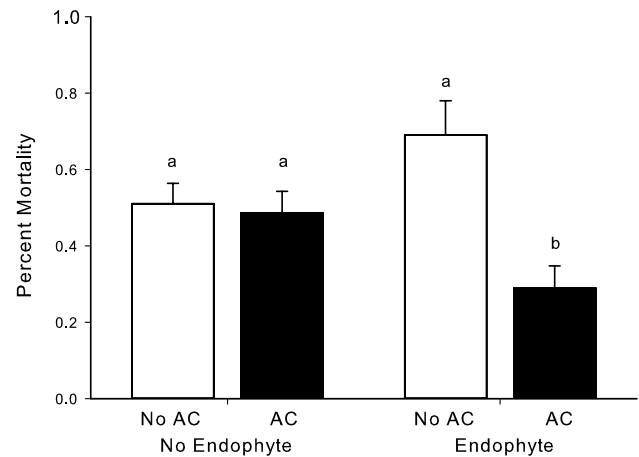
## Results

*Centaurea* dramatically reduced the size of individual *Koeleria* plants in all conditions (Fig. 1a vs. b; note different scales on y-axes). The mean total mass of *Koeleria* across all treatments when grown alone was  $1.15 \pm 0.10$  g ( $\pm 1$  SE) versus  $0.023 \pm 0.004$  g when grown with *Centaurea*. This very large difference was likely due to the priority effects that favored *Centaurea* in our experimental design.

When grown without *Centaurea*, the total mass of *Koeleria* was not affected by activated carbon ( $F_{1,18} = 0.004$ ;  $P = 0.951$ ; Fig. 1a). When competing against *Centaurea* when activated carbon was added to the soil, the mass of *Koeleria* plants was significantly larger than that of *Koeleria* competing against *Centaurea* without activated carbon across both E+ and E– treatments ( $F_{1,86} = 47.79$ ;  $P < 0.001$ ). There was a significant effect of endophyte on *Koeleria* biomass when competing with *Centaurea* across both with and without activated carbon soil treatments



**Fig. 1** Total mass of *Koeleria macrantha* when **a** grown alone or **b** with *Centaurea stoebe*, with (AC) or without activated carbon (NO AC) in the soil. Error bars show 1 SE and shared letters indicate no significant difference between the means



**Fig. 2** Mortality of germinated *K. macrantha* per pot planted with *C. stoebe*, either infected with fungal endophytes or not, and either in AC or NO AC soil. For abbreviations, see Fig. 1

( $F_{1,86} = 7.177$ ;  $P = 0.009$ ). There was also a significant interaction between the endophyte treatment and the activated-carbon treatment ( $F_{1,86} = 8.676$ ;  $P = 0.004$ ; Fig. 1b). The total mass of *Koeleria* plants competing with *Centaurea* with activated carbon in the soil was not significantly different in the E+ ( $0.034 \pm 0.01$  g) and in the E– ( $0.036 \pm 0.01$  g) treatments ( $P = 0.996$ ). However, without activated carbon the mass of *Koeleria* plants was significantly smaller when *Centaurea* was infected with the endophyte than when *Centaurea* was not infected with the endophyte ( $P = 0.004$ ; Fig. 1b). When *Centaurea* was not infected with the endophyte, the biomass of *Koeleria* was significantly larger when activated carbon was in the soil ( $P = 0.002$ ). The biomass of *Koeleria* plants grown in competition with *Centaurea* infected with the endophyte was also significantly larger when activated carbon was in the soil ( $P < 0.001$ ).

Activated carbon also decreased the percent mortality of *Koeleria* seedlings in pots growing with *Centaurea* ( $F_{1,95} = 8.842$ ;  $P = 0.004$ ; Fig. 2), but there was no effect of endophyte treatment ( $F_{1,95} = 0.026$ ;  $P = 0.871$ ). There was a significant interaction between the activated carbon and endophyte treatments ( $F_{1,95} = 5.745$ ;  $P = 0.018$ ). Activated carbon significantly reduced the mortality of *Koeleria* seedlings when in competition with *Centaurea* infected with the endophyte ( $F_{1,29} = 12.780$ ;  $P = 0.001$ ), but did not have an effect on the mortality of seedlings in competition with *Centaurea* not infected with the endophyte ( $F_{1,66} = 0.259$ ;  $P = 0.612$ ).

There were no significant effects of activated carbon ( $F_{1,95} = 0.025$ ;  $P = 0.875$ ) or endophyte infection ( $F_{1,95} = 0.054$ ;  $P = 0.817$ ) on the germination rate of *Koeleria* seedlings when in competition with *Centaurea*, although there was a significant interaction between



endophyte and activated carbon ( $F_{1,95} = 5.848$ ;  $P = 0.017$ ). When *Centaurea* were grown without the endophyte, *Koeleria* germination rates were 63 % without activated carbon and 48 % with activated carbon in the soil. Similarly, when *Centaurea* were grown with the endophyte, *Koeleria* germination rates were 45 % without activated carbon and 62 % with activated carbon in the soil.

## Discussion

The competitive effects of *Centaurea stoebe* on *Koeleria macrantha* were very strong regardless of treatment, likely because our experimental set-up mimicked conditions in the field where the recruitment of native grasses is heavily suppressed by *C. stoebe*. Previous experiments conducted without priority effects have not shown such strong competitive effects of *Centaurea* on native bunchgrasses (Besaw et al. 2011; Marler et al. 1999; Ridenour and Callaway 2001). *C. stoebe* also had strong allelopathic effects on *K. macrantha* in the absence of endophyte infection, confirming the findings of previous work in this system (Chen et al. 2012; Ridenour and Callaway 2001). However, the allelopathic effects of *C. stoebe* on *K. macrantha* were much stronger when *C. stoebe* was infected with the CID120 fungal endophyte, suggesting that endophyte infection enhances the allelopathic effects of *C. stoebe* on its competitors. It is also important to note that the contribution of the allelopathic effect to the total effect of *C. stoebe* on *K. macrantha* in our experiment was small. To our knowledge this is the first experimental evidence of a symbiotic relationship between plants and fungal endophytes affecting allelopathic interactions between competing plants.

Our results help to resolve one mechanistic question about how mutualistic endophytes may, in some cases, improve the competitive effects of their hosts (Aschehoug et al. 2012; Marks et al. 1991; Rudgers and Orr 2009). However, it is hard to determine whether the enhanced competitive effect of *C. stoebe* (or any other species) by fungal endophytes was due to changes in the phenotype of *C. stoebe* (e.g., quantity of chemical), the extended phenotype of the fungal endophyte (e.g., novel chemical signature), or direct infection of the competitor by the endophytes themselves. Aschehoug et al. (2012) found that horizontal transfer from *C. stoebe* to grasses occasionally occurred but this did not correlate with the increased competitive effect of the invader. In addition, Aschehoug et al. (2012) found no effect of direct infection by CID 120 on *Koeleria*. We did not check for horizontal transfer of the endophyte to *Koeleria* in this experiment although this may have occurred. However, since activated carbon so strongly alleviated the allelopathic effect of the *C. stoebe*-endophyte

symbiosis and significantly reduced *Koeleria* seedling mortality, it seems unlikely that fungal infection of the grasses caused their suppression. Also, we did not control for the possible indirect effects that might be mediated through soil biota. *C. stoebe* can have substantial effects on soil biota that may affect other species (Callaway et al. 2004; Thorpe and Callaway 2011) and it is possible that our apparent allelopathic effects were confounded in some way by the effects of endophyte infection on soil biota (but see Aschehoug et al. 2012).

Our results also provide an example of how allelopathic interactions can be conditional. Demonstrating and explaining conditionality has made important contributions to understanding interspecific interactions among plants in the context of abiotic stress (Callaway et al. 2002; Gurevitch 1986) and variation in resource supply (Besaw et al. 2011). Karban (2007) found that the allelopathic effects of volatiles emitted from *Artemisia tridentata* were stimulated by clipping, thus demonstrating potential herbivory-induced allelopathic conditionality. Allelopathic effects can also be attenuated or enhanced by the abiotic and biotic components of soil (Kaur et al. 2009; Pollock et al. 2009; Tharayil et al. 2009), the relative abundance of different neighbors (Lankau and Strauss 2007), and temperature (Wang et al. 2011). For *C. stoebe*, allelopathic effects have also been shown to vary with light intensity (Chen et al. 2012; Tharayil and Triebwasser 2010). Understanding such allelopathic conditionality is important because a growing body of evidence indicates that allelochemicals may contribute to the way plant species interact with each other (Barto et al. 2011; Jensen and Ehlers 2010; Lankau and Strauss 2007) and has been implicated as a mechanism in a number of exotic plant invasions (Inderjit et al. 2011; Murrell et al. 2011).

The symbiosis reported here and by Aschehoug et al. (2012) suggests that *C. stoebe* benefits in competitive interactions with other species by harboring specific fungal endophytes, and therefore this symbiosis may be mutualistic. As with most mutualisms, the *C. stoebe*-fungal endophyte symbiosis investigated here is generalized and facultative, not obligate, because the seeds of many *C. stoebe* individuals in nature are not infected and many different types of fungal endophytes can infect *C. stoebe* (Shipunov et al. 2008) with dramatically different consequences for the host (Aschehoug et al. 2012; Newcombe et al. 2009). This suggests the potential for amazing ecological complexity in this symbiosis, but in order to fully understand this *C. stoebe*-fungal endophyte symbiosis, we must know the degree to which the fungus benefits from being housed by *C. stoebe* and gain a more complete picture of the relative benefits and costs of endophyte infection for *C. stoebe* (Bronstein 2001; Faeth 2002). Aschehoug et al. (2012) did not find any growth costs to *C. stoebe* of housing either of

two endophyte haplotypes, but in these experiments plants were well watered, well fertilized and in greenhouses. The cost of hosting endophytes in stressful conditions may outweigh the kinds of competitive or allelopathic advantage we detected in our highly controlled experimental conditions. Endophytic infection may also impose reproductive costs or costs realized in other interactions. In addition, little is known about how the extended phenotype of the fungal endophytes *C. stoebe* hosts may influence the balance of community-level costs and benefits.

In order to understand the evolutionary consequences of mutualisms, such as the one proposed here, it is critical to evaluate the net cost–benefit ratio for the species involved (Bronstein et al. 2004). Mutualisms are favored evolutionarily and become stable when individuals that engage in the relationship perform better overall than individuals that do not. Xiao et al. (2012) found that models of plant–plant interactions involving different *C. stoebe*-fungal endophyte symbioses favored endophyte-infected *C. stoebe* against North American grasses, suggesting a potential stable mutualism in invaded range communities. However, *C. stoebe*-fungal endophyte symbioses were not favored in native range communities, suggesting that there may be a powerful biogeographic context for the stability of the symbiosis. Mutualisms become unstable when there is a selective advantage to individuals who benefit from their partner species without providing a benefit in return (Bronstein et al. 2004). Such cheating can arise because of genetic mutation or even ecological conditionality, resulting in a shift from mutualism to parasitism. This gap in knowledge is important because mutualisms can substantially increase diversity (Bronstein et al. 2004), but in the context of invasions, mutualisms such as we describe between *C. stoebe* and specific fungal endophytes may lead to a loss of biodiversity via the extended phenotype of the fungal endophyte. Whether the *C. stoebe*-fungal endophyte symbiosis represents a stable mutualism or not, or whether the nature of the symbiosis changes in the native and non-native ranges of the invader (Aschehoug et al. 2012), our results reveal a unique, indirect and conditional mechanism by which an invasive plant may suppress species in its new ranges.

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