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ORIGINAL ARTICLE

Mycoparasitism of *Fomitopsis pinicola* (Sw.) P. Karst. by *Antrodiella citrinella* Niemelä & Ryvarden

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Abstract

Antrodiella species (*Agaricomycotina*, *Polyporales*) are often growing on or near to the living, dead, or dying fruitbodies of pioneer wood-inhabiting fungi. *Antrodiella citrinella* always occurs on wood that previously has been decayed by the polypore *Fomitopsis pinicola*. However, the underlying mechanism remained unclear. Based on field observations, it has been assumed that the succeeding species is not only a highly competitive wood decomposer but also a mycoparasite feeding on the preceding species. To investigate the interaction between *A. citrinella* and the putative host *F. pinicola*, the species were grown in dual cultures at different temperatures (5–25 °C). The interaction tests were complemented with qualitative enzymatic tests for both species and microscopic examination of the interaction zone. In the dual cultures, *A. citrinella* replaced *F. pinicola* only at low temperature (5 °C); at higher temperatures (25 °C), it was vice versa. Light microscopy revealed preferential growth of *A. citrinella* toward *F. pinicola*, hyphal contact, and finally death of *F. pinicola* hyphae. Enzymatic tests showed that *A. citrinella* is capable to degrade extracellular proteins, chitin, cellulose, and lignin. We interpret the interaction as mycoparasitism, as we suggest that *A. citrinella* is capable to recognize, kill, and feed from *F. pinicola*, beside its ability to degrade woody substrates. The results are discussed in an ecological context.

Keywords Mycelial interaction · Secondary resources capture · Deadwood · Strict successor species

Introduction

In deadwood, there is usually a succession of wood-inhabiting fungi, where pioneer species are successively replaced by secondary species. Patterns in fungal succession have been investigated in various studies using observational data (Renvall 1995; Jönsson et al. 2008; Ottosson et al. 2014), in vitro studies (e.g., Holmer et al. 1997; Hiscox et al. 2018), and deadwood experiments (e.g., Olsson et al. 2011; Weslien et al. 2011). Generally, the fungal community is shaped by biotic and abiotic conditions (Boddy 2000; Hiscox and Boddy 2017) and affected by the identity of dominant pioneer species (Dickie et al. 2012; Hiscox et al. 2015). One conspicuous observation is that some fungi, termed "successor species," seem to strongly depend on the presence of other preceding species, the "predecessor species," while other wood-inhabiting species seem to appear and disappear by chance (e.g., Pouska et al. 2013). Thus, beside general successional pathways, some species seem to follow a stricter kind of succession (Niemelä et al. 1995; Halbwachs et al. 2021). Although various explanations for this phenomenon exist (Jahn 1967; Niemelä et al. 1995; Gams et al. 2004), i.e., pioneer effects, dominance effects, competition, commensalism, and parasitism, to our knowledge, no replacement mechanism has been proven for any strict successor yet. In this study, the relationship between the two polypore species *Antrodiella citrinella* Niemelä & Ryvarden and *Fomitopsis pinicola* (Sw.) P. Karst. will be examined.

Antrodiella citrinella gained some attention in nature conservation issues in recent years because of its indicator function for old-growth forests (e.g., Blaschke et al. 2009; Holec et al. 2018; Braunisch et al. 2020). While the knowledge of

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its overall distribution (Niemelä and Ryvarden 1983; Vlasak 1990; Grosse-Brauckmann and Luschka 1991; Pieri et al. 2000; Ryvarden and Melo 2014), habitat requirements (Niemelä and Ryvarden 1983; Bässler and Müller 2010), cultural characteristics (David and Tortic 1986; Wieners et al. 2016), and phenology (Wieners et al. 2016; Holec et al. 2018) is growing, not much is known about the biotic interaction with the preceding polypore *F. pinicola*. In literature, the explanations for the strict succession of *A. citrinella* range from commensalism by means of resource complementary use (Holmer et al. 1997) over competition (Gams et al. 2004) to parasitism (Niemelä and Ryvarden 1983).

Antrodiella species are often growing on or near to the living, dead, or dying fruitbodies of pioneer wood-inhabiting fungi, as summarized in Table 1. The association of *Antrodiella* species with their predecessor species is always specific, in most cases at the species or genus level, and in one case at the family level (e.g., Niemelä et al. 1995; Johannesson et al. 2000; Miettinen et al. 2006). This suggests that the interaction between successor and predecessor has a long evolutionary trajectory, and that the association may indicate an advantageous strategy to gain and maintain resources. When Niemelä and Ryvarden (1983) described *A. citrinella*, they considered mycoparasitism sensu Rayner and Todd (1979) and Lumsden (1981) as explanation for the strong successional link to *F. pinicola*. Interestingly, Vampola (1991) suggested for *A. parasitica*, which grows on living and dead basidiocarps of *Trichaptum* spp., that this species is a mycoparasite as well. However, a parasitic interaction for *A. citrinella* (or related taxa) has not been experimentally proven yet (Holec et al. 2018).

The aim of this study is to test experimentally whether *A. citrinella* has two modes of nutrition, a saprotrophic and a mycoparasitic one. Here, we use the term mycoparasitism as defined by Jeffries and Young (1994): a parasite can obtain nutrition in a parasitic manner from its host. To test this hypothesis, dual culture tests were complemented with tests for enzymatic activity and light microscopic examination of the interaction zone. Dual cultures were used to assess the combative abilities of both species. Since the polypore is already known to grow mainly in the cool season (Wieners et al. 2016; Holec et al. 2018), the dual cultures were incubated at different temperatures. Extracellular enzymes such as proteases and chitinase were investigated because they are involved in cell wall degradation and nutrition of mycoparasitic fungi (e.g., Gams et al. 2004; Hiscox and Boddy 2017). The interaction zone was studied to characterize the fungal interaction. This approach attempted to facilitate the interpretation of the results in an ecological context.

Table 1 Associations of *Antrodiella* species with preceding species in Europe. Note that information on some species is scarce, as some species are only known from a limited number of specimens from their type locality

Successor species	Predecessor species	Rot type (successor)	Rot type (predecessor)	Substrate	Literature
Antrodiella canadensis	unknown	WR		W, dB	1, 2
Antrodiella citrinella	*Fomitopsis pinicola*	WR	BR	W, dB	1, 2, 3, 4
Antrodiella faginea	*Phellinus* spp., *Inonotus* spp., *Hymenochaete* spp.	WR	WR	W, dB	1, 4, 5
Antrodiella foliaceodentata	unknown	WR		W	1, 6
Antrodiella fragrans	unknown	WR		W	1
Antrodiella ichnusana	unknown	WR		W	1
Antrodiella leucoxantha	unknown	WR		W	1
Antrodiella metschulensis	unknown	WR		W	1
Antrodiella niemelaei	*Hymenochaete* spp.	WR	WR	W, dB	1, 4, 7
Antrodiella onychoides	*Fomes fomentarius*	WR	WR	W, dB	1, 4
Antrodiella pallasii	*Trichaptum* spp.	WR	WR	W, dB	1, 2, 5
Antrodiella pallescens	*Fomes fomentarius*	WR	WR	W, dB	1, 5, 8
Antrodiella parasitica	*Trichaptum* spp.	WR	WR	W, dB, lB	1, 4, 9
Antrodiella pirumspora	*Trametes trogii*	WR	WR	dB	1
Antrodiella romellii	*Hymenochaete* spp.	WR	WR	W, dB	6, 8
Antrodiella semistipitata	unknown	WR		W	1, 10
Antrodiella serpula	*Inonotus radiatus, Inonotus nodulosus*	WR	WR	W, dB	1, 4, 11

Literature: (1) Ryvarden and Melo (2014); (2) Johannesson et al. (2000); (3) Niemelä and Ryvarden (1983); (4) Niemelä et al. (1995); (5) Miettinen et al. (2006); (6) Spirin and Zmitrovich (2003); (7) Kout et al. (2014); (8) Vampola and Pouzar (1996); (9) Vampola (1991); (10) Bernicchia et al. (2007); (11) Jahn (1967). *WR* white rot, *BR* brown rot, *W* wood, *dB* dead basidiocarps, *lB* living basidiocarps

Material and methods

Origin of isolates, reference material, and culture maintenance

Four *A. citrinella* and two *F. pinicola* isolates were used to test the hypothesis. Four dikaryotic strains (SBUG-M 1723, SBUG-M 1724, SBUG-M 1737, and SBUG-M 1738) were collected as part of the mycological inventory of the core zone of the Black Forest National Park (Germany) (Scholler & Popa 2021). One dikaryotic strain (Acit1) originated from the Bavarian Forest National Park (Germany). And one monokaryotic strain (Acit5) was obtained from germinated basidiospores of an in vitro fructification of SBUG-M 1737. The four isolates SBUG-M 1723, SBUG-M 1724, SBUG-M 1737, and SBUG-M 1738 were deposited in the fungus collections of the Department of Bacterial Physiology SBUG, University of Greifswald (Greifswald, Germany). The isolate SBUG-M 1723 was additionally deposited in the German Collection of Microorganisms and Cell Cultures (DSMZ) under the number DSM 108506. Basidiocarps for strain isolation (SBUG-M 1737: KR-M-0049005; SBUG-M 1738: KR-M-0049209) and *A. citrinella* isolate reference material (KR-M-0049247 to KR-M-0049250) were air dried (40 °C) and stored in the fungus collections of the Natural History Museum Karlsruhe (Karlsruhe, Germany) (KR). All isolates were maintained at 20 °C and 70(±5) % relative humidity on 2% malt extract agar (MEA: 20 g/l malt extract, 20 g/l agar) and regularly transferred to new MEA plates (9 cm in diameter). Circular inocula (1 cm in diameter) were cut out of the active growth zone using a cork borer and then used for the experiments.

Dual culture and hyphal interaction tests

To characterize the interspecific interaction, the effect of temperature (5 °C; 15 °C; 25 °C) on the competitive abilities of *A. citrinella* and *F. pinicola* was investigated by using dual cultures on MEA. For the dual cultures, inocula (1 cm) of both species were placed in the same petri dish (9 cm) at opposing sites with a distance of 6 cm. All possible combinations of *A. citrinella* and *F. pinicola* isolates were tested, and three technical replicates per combination were used. The dual cultures were documented photographically in a weekly interval for ten weeks. The mycelia of both species were distinguished by their appearance; *F. pinicola* formed dense, white aerial mycelium, while the mycelium of *A. citrinella* was less dense, and more cottony.

In a preliminary test, no gross mycelial contact, but hyphal interaction was observed on nutrient-poor substrata. For the light-microscopical documentation of the interaction between *A. citrinella* and *F. pinicola*, dual cultures according to Helfer (1991) were prepared. Sterilized microscope slides were placed in empty petri dishes and then covered with 2% MEA to create a medium layer as thin as possible. Here, a nutrient-rich substrate (2% MEA) was used instead of a nutrient-poor substrate (0.5% MEA) to ensure sufficient mycelial growth. Inocula of *A. citrinella* and *F. pinicola* were placed at opposing sites and incubated at 15 °C and observed up to four weeks. The interaction was documented using a Zeiss Primo Star and a Zeiss Imager. Z1 light microscope (Germany, Oberkochen). The hyphae of both species were distinguished by diameter and wall thickness. Also, the hyphae of the monokaryon had septa without clamps.

Enzymatic activity

To gain qualitative information on the mode of nutrition of *A. citrinella* and *F. pinicola*, chemical detection reactions were carried out to characterize the physiological-biochemical properties of the study organisms. The production of proteases (F19), cellulase (F22), polyphenol oxidase (F28), laccase (F31), and peroxidase (F34) was investigated according to Kreisel and Schauer (1987). For the detection of chitinase, an enzyme test according to Helfer (1991) was adapted and performed. For the protease test, an agar medium turbid with gelatin was prepared. Similarly, chitin agar was prepared for the chitinase test. A clear zone around the inoculum indicated a positive test. The other tests were chemical detection reactions conducted with the whole culture. Positive results were indicated by color changes.

Results

Mycelial interaction

The outcome of interactions of *A. citrinella* and *F. pinicola* was strongly dependent on the temperature (Table 2). At 5 °C, all *A. citrinella* isolates were more competitive than the *F. pinicola* isolates, and a slow and steady replacement process was observed (Fig. 1A). Different outcomes were documented at 15 °C (Fig. 1B): mostly, *A. citrinella* was partly or completely overgrown by *F. pinicola*. Generally, the *F. pinicola* isolate SBUG-M 1738 was slightly more competitive than the isolate SBUG-M 1724. And at 25 °C, both *F. pinicola* isolates replaced *A. citrinella* within less than two weeks (Fig. 1C). At 5–15 °C, the hyphae of *F. pinicola* were stained brownish in the interaction zone. At 15 °C, the complete agar medium was darkened. And at 25 °C, no change in color of the agar medium was observed. Samples taken from the interaction zone and dying, dead, or lysed hyphae were observed under the microscope.

Hyphal interaction

Light microscopy revealed hyphal interaction of *A. citrinella* and *F. pinicola* (Fig. 2). In some cases, the hyphae

Table 2 Competitive abilities of *A. citrinella* and *F. pinicola* isolates

Combination	5 °C	15 °C	25 °C
Fp1724 vs. Ac1723	PR of Fp by Ac	Differing outcomes	R of Ac by Fp
Fp1724 vs. Ac1737	PR of Fp by Ac	PR of Ac by Fp	R of Ac by Fp
Fp1724 vs. Acit1	PR of Fp by Ac	PR of Ac by Fp	R of Ac by Fp
Fp1724 vs. Acit5	PR of Fp by Ac	PR of Ac by Fp	R of Ac by Fp
Fp1738 vs. Ac1723	PR of Fp by Ac	R of Ac by Fp	R of Ac by Fp
Fp1738 vs. Ac1737	PR of Fp by Ac	R of Ac by Fp	R of Ac by Fp
Fp1738 vs. Acit1	PR of Fp by Ac	R of Ac by Fp	R of Ac by Fp
Fp1738 vs. Acit5	Differing outcomes	R of Ac by Fp	R of Ac by Fp

Abbreviations: *R* replacement, *PR* partial replacement, *Ac Antrodiella citrinella*, *Fp Fomitopsis pinicola*

of *A. citrinella* conducted only short contact via infection hypha (Fig. 2A and B); in other cases, the hyphae of *A. citrinella* grew along the hyphae of *F. pinicola*. In both cases, preferential growth of *A. citrinella* toward *F. pinicola* was observed. After physical contact, death of single *F. pinicola* hyphal segments was regularly observed (Fig. 2C and D). This process took less than 2 h. Dead hyphal segments (single cells) were recognized by the darker color and a granular lumen. Hyphal death was often followed by cell lysis (Fig. 2E–H). Death of single hyphae was observed immediately after hyphal contact; after 48 h, the hyphae were almost completely lysed (Fig. 2A–H). In some regions, *F. pinicola* formed chlamydospores that were also attacked by *A. citrinella*. No penetration and no growth inside *F. pinicola* hyphae were observed.

Enzymatic activity

Both species, *F. pinicola* and *A. citrinella*, had enzymes for cellulose degradation. The latter also produced polyphenol oxidase, laccase, and peroxidase, three enzymes that are involved in the degradation of lignin. In addition to the enzymes directly involved in wood degradation, the production of chitinase and proteases was investigated. It could be shown that *A. citrinella* forms chitinase and proteases. The tests for *F. pinicola* were both negative.

Discussion

In this study, we provided experimental results that suggest a mycoparasitic interaction between *A. citrinella* and *F. pinicola*. The results of this study indicate that *A. citrinella* can recognize, kill, and feed on *F. pinicola*, which are key features of necrotrophic parasites (Gams et al. 2004). The ability of *A. citrinella* to produce chitinase and proteases generally supports this interpretation. In the following, the different aspects of the fungal interaction are outlined in more detail.

Outcome of interactions

Based on field observations, especially the occurrence of *A. citrinella* only in the cold season (Wieners et al. 2016; Holec et al. 2018), we expected that the temperature has an effect on the outcome of interactions in dual cultures. The results of this study show that *A. citrinella* was more competitive

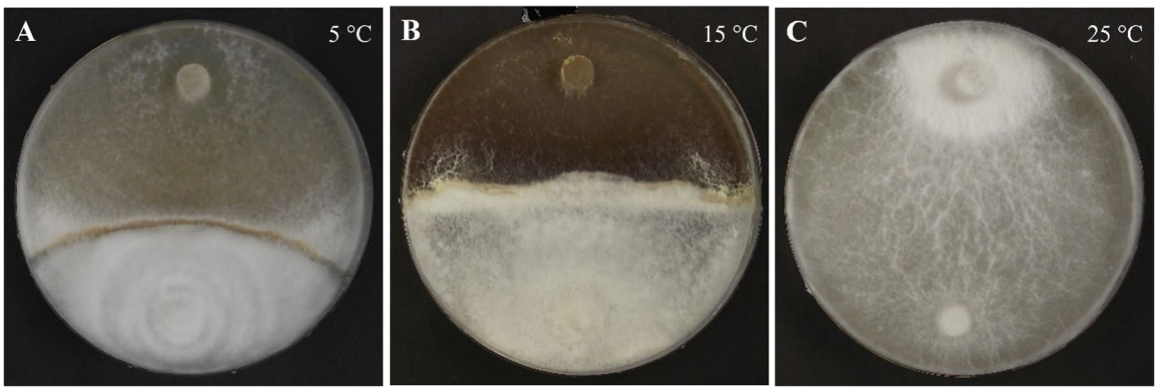

Fig. 1 Dual cultures of *A. citrinella* (top) and *F. pinicola* (bottom) at different temperatures. **A**: At 5 °C. *A. citrinella* slowly replaced *F. pinicola*. The interaction zone was stained brownish. **B**: Deadlock at 15 °C. The complete agar medium was darkened. **C**: At 25 °C *F. pinicola* replaced *A. citrinella* within two weeks. Diameter: 9 cm

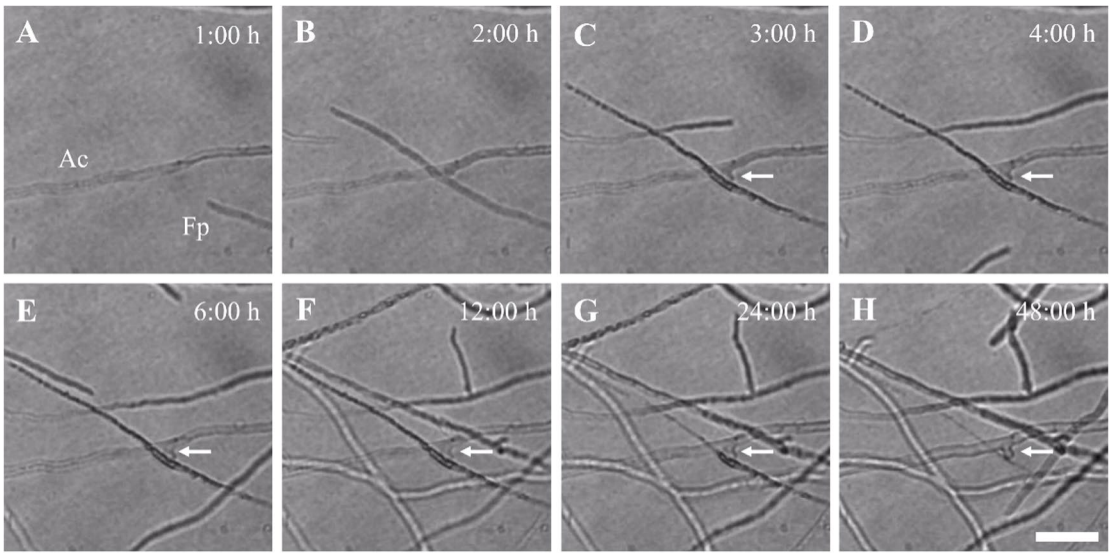

Fig. 2 Hyphal interaction of *A. citrinella* and *F. pinicola*. **A**, **B**: *A. citrinella* (Ac) and *F. pinicola* (Fp) before contact in close proximity. **C**, **D**: Formation of infection hypha. *A. citrinella* is growing toward *F. pinicola* hypha and contacts it (arrow). Death of *F. pinicola* hypha is recognized by dark granular cell lumen. **E**–**H**: Lysis of *F. pinicola* hypha. After two days, the hypha is almost completely dissolved. *A. citrinella* hypha including infection hypha is alive. Bar: 20 µm

than *F. pinicola* at 5 °C; at 25 °C, it was vice versa. At 15 °C, *F. pinicola* was slightly more competitive. Based on single culture growth rates at different temperatures, Wieners et al. (2016) already assumed that replacement only takes place at low temperatures, namely, below 10 °C. The results of the current study point into the same direction. Growth rates and competitive abilities of wood-inhabiting fungi have been reported to correlate well (Fryar et al. 2002; Hiscox et al. 2016). This relation seems to apply for *A. citrinella* and *F. pinicola*, too. Thus, the results indicate a realized niche of *A. citrinella* at low temperature.

Parasitic interaction

As the fruiting bodies of *A. citrinella* usually occur on or close to the dead fruiting bodies of *F. pinicola*, we expected a mycoparasitism that is mediated by hyphal contact. By using the experimental setup described by Helfer (1991), we studied the replacement mechanism and identified the following three steps: (1) *A. citrinella* made physical contact with *F. pinicola*. It was regularly observed that the former species made short contact or grew along the hyphae of the later. (2) Many hyphae of *F. pinicola* died after contact with *A. citrinella*. This step was recognized by the protoplasmic destruction of the dead hyphae. And (3) subsequently, nutrients from *F. pinicola* were exploited by *A. citrinella*. The last step was concluded from the lysis of the dead hyphae together with the production of chitinase and proteases.

Rayner and Webber (1984) distinguish between two basic replacement mechanisms following hyphal contact that are mycoparasitism and hyphal interference. The latter is very common in antagonistic interactions between wood decaying basidiomycetes (Rayner & Boddy 1988). Hyphal interference is mediated by non-enzymatic, diffusible metabolites and leads to growth inhibition at close proximity (< 50 µm) or after contact. It may also cause the death of involved hyphal compartments, followed by protoplasmic destruction. In contrast, mycoparasitism is a trophic interaction, where the parasite obtains nutrition in a parasitic manner from its host. In this study, system physical contact and death of single hyphal segments, but no growth inhibition in dual cultures, were observed. Also, lysis of *F. pinicola* hyphae after contact with *A. citrinella* was observed, which was also reported for the mycoparasitism of *Trametes* spp. by *Lenzites betulina* (Rayner et al. 1987). Thus, we suggest that mycoparasitism can explain the findings of this study better than hyphal interference.

There are two types of necrotrophic mycoparasites that are characterized by the host-parasite-interface, contact necrotrophs, and invasive necrotrophs (Jeffries and Joung 1994). In dual cultures, protoplasmic destruction and cell lysis were observed regularly. But specialized interfaces, i.e., haustoria, or the penetration of hyphae by appressoria or the invasion into the complete thallus, known from other mycoparasitic genera (Jeffries and Young 1994; Gams et al. 2004), were not observed. Accordingly, we assume a contact necrotrophic interaction. This would be a rather unspecific mode of interaction and only the first evolutionary step of a true mycoparasite. But even though the association of *A. citrinella* with *F. pinicola* seems to be rather specific,

dual culture experiments showed that *A. citrinella* is an overall strong competitor in natural and artificial species-species combinations (Holmer et al. 1997).

Ecological implications

From an ecological perspective a mycoparasitic, wood-inhabiting polypore may use its ability to specifically replace a dominant pioneer species as a strategy for secondary resource capture (Rayner et al. 1987). This consideration would suggest that the presence of the pioneer species is more important than the host tree species. For *A. citrinella*, this seems to be the case: although it is mainly encountered on conifers (*Picea*, *Abies*, and *Pinus*), which constitute the main substrate of *F. pinicola*, the polypore follows *F. pinicola* also on *Fagus*, *Betula*, and *Populus* (Bässler and Müller 2010; Ryvarden and Melo 2014; Holec et al. 2018). Also, the explanation provided by Holmer et al. (1997), who assumed a rather unspecific link and therefore suggested resource complementary use (a white rotter follows a brown rotter), seems unsatisfying. The observation that nine out of ten *Antrodiella* species with known associations to other wood decomposers follow a white rotting predecessor strengthen the point that the successional link is rather specific and mainly mediated by the species identity of the predecessor species, not the tree species identity or decay capability.

Potential reasons for the relative rarity of *A. citrinella* are of interest to nature conservation. Despite the occurrence of *F. pinicola* throughout coniferous forests in Europe, the distribution of *A. citrinella* is disjunct. One reason for this might be that *A. citrinella* occurs only at high host abundances: Bässler and Müller (2010) found in their threshold analysis that *A. citrinella* mainly occurs in forest stands with more than 180 *F. pinicola* basidiocarps per hectare. Such high abundances are very unlikely in managed forests. Another factor to consider is microclimate. The species seems to be restricted to moist habitats (Niemelä and Ryvarden 1983; Ryvarden and Melo 2014). And based on the results of this study, we suggest that *A. citrinella* is capable to parasitize and thereby replace *F. pinicola* only at low temperatures. Nevertheless, we expect that *A. citrinella* can build stable populations wherever those conditions are met, as particularly in protected forest areas with high deadwood amounts in Central European mountains or in North Europe.

Cautionary notes

In this study, we presented results that indicate a parasitic mode of nutrition for the polypore *A. citrinella*. Nevertheless, we are aware of some shortcomings of the applied set of qualitative methods, which motivated us to formulate some steps to further investigate the interaction of *A. citrinella* and *F. pinicola*: to gain a deeper, more mechanistic understanding of the interaction, methods from the OMICs toolbox could be applied (i.e., gene expression in interaction zone, quantitative enzyme assays in time series, and screening of the genomes for functionally relevant enzymes). Also, stable isotope analysis or staining of living cells with fluorescent dyes could be used to trace nutrients that are transferred from one organism to the other. With this, we hope to stimulate much more exiting research with the study organisms *A. citrinella* and related taxa.

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Author contribution Conceptualization: Max Wieners and Markus Scholler; methodology: Max Wieners, Claus Bässler, and Markus Scholler; formal analysis and investigation: Max Wieners; writing—original draft preparation: Max Wieners; writing—review and editing: Claus Bässler and Markus Scholler.

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Data availability The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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