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Survey of arthropod assemblages responding to live yeasts in an organic apple orchard

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Associations between yeasts and insect herbivores are widespread, and these inter-kingdom interactions play a crucial role in yeast and insect ecology and evolution. We report a survey of insect attraction to live yeast from a community ecology perspective. In the summer of 2013 we screened live yeast cultures of *Metschnikowia pulcherrima*, *M. andauensis*, *M. hawaiiensis*, *M. lopburiensis*, and *Cryptococcus tephrensis* in an organic apple orchard. More than 3000 arthropods from 3 classes, 15 orders, and 93 species were trapped; ca. 79% of the trapped specimens were dipterans, of which 43% were hoverflies (Syrphidae), followed by Sarcophagidae, Phoridae, Lauxaniidae, Cecidomyidae, Drosophilidae, and Chironomidae. Traps baited with *M. pulcherrima*, *M. andauensis*, and *C. tephrensis* captured typically 2.4 times more specimens than control traps; traps baited with *M. pulcherrima*, *M. hawaiiensis*, *M. andauensis*, *M. lopburiensis,* and *C. tephrensis* were more species-rich than unbaited control traps. We conclude that traps baited with live yeasts of the genera *Metschnikowia* and *Cryprococcus* are effective attractants and therefore of potential value for pest control. Yeast-based monitoring or attract-and-kill techniques could target pest insects or enhance the assemblage of beneficial insects. Manipulation of insect behavior through live yeast cultures should be further explored for the development of novel plant protection techniques.

Keywords: yeast baited traps, *Mestchnikowia*, *Cryptococcus*, hoverflies, drosophilids

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INTRODUCTION

Yeasts are widely distributed in most terrestrial and aqueous environments (Lachance, 2006). They are found on plant leaves (Limtong and Koowadjanakul, 2012), ephemeral flowers (Lachance et al., 2001), floral nectars (Pozo et al., 2011), as well as on animals (Ahearn, 1998; Yaman and Radek, 2008). Yeasts associated with insects not only provide nutritional services (Callaham and Shifrine, 1960; Barker et al., 1988; Rohlfs and Kürschner, 2010; Becher et al., 2012; Stensmyr et al., 2012; Witzgall et al., 2012) but also benefit from insects that disperse them to new habitats (Lachance et al., 2001; Ganter, 2006; Buser et al., 2014). Volatile yeasts metabolites mediate these mutualistic interactions with insects (Davis et al., 2013; Buser et al., 2014; Christiaens et al., 2014).

Metschnikowia yeasts are commonly found on fruits, flowers and in nectar (Ethiraj et al., 1980; Manson et al., 2007; de Vega et al., 2012; Kaewwichian et al., 2012), where they encounter insects (Lachance et al., 2005; Nguyen et al., 2006; de Vega et al., 2012). So far, 39 *Metschnikowia* species are known to be associated with flower-visiting insects (Kaewwichian et al., 2012; Guzmán et al., 2013). Among these, *M. pulcherrima* is associated with several species, including the codling moth

Cydia pomonella (Lepidoptera: Tortricidae) (Witzgall et al., 2012; Knight and Witzgall, 2013) and the green lacewing *Chrysoperla rufilabris* (Burmeister) (Neuroptera: Chrysopidae) (Woolfolk and Inglis, 2004).

Yeast species of the genus *Cryptococcus* can be found in the soil (Vishniac, 2002) or in the phyllosphere of several plants (Fonseca and Inácio, 2006). They are associated with bromeliads (Landell et al., 2009) as well as fruit trees including apple (*Malus domestica*), pear (*Pyrus* spp.), and plum (*Prunus* spp.) where they have been found on fruits, blossoms, or leaves (Vadkertiová et al., 2012). Some *Cryptococcus* species are associated with beetles (Ganter, 2006), and *C. tephrensis* has been isolated from frass and larval galleries of the codling moth (Witzgall et al., 2012).

Yeast-invertebrate associations have been known for decades, yet only few specific ecological interactions are studied in depths (Ganter, 2006), and the potential of yeast for pest control has been rarely exploited. Yeasts play a crucial role in host finding in insect herbivores and a wide range of insects respond olfactorily to volatile emissions from yeasts (Witzgall et al., 2012; Davis et al., 2013; Buser et al., 2014). Herein, we report attraction of arthropods to traps baited with five yeast species in an organic apple orchard. The overall research objectives were to survey the arthropod species composition and abundance, and the specificity of attraction to different yeasts.

MATERIALS AND METHODS

Study Site

The study site was a 25-year-old organic apple orchard (cvs. Aroma and Discovery) located in Alnarp, Southern Sweden (55°39.602′N latitude, 13°4.688′E longitide; 7 m above sea level).

Yeast Species and Cultivation

The yeast species used in our study are shown in **Table 1**. Four species belonged to the genus *Metschnikowia* (Ascomycota, Saccharomycetes) and one species to the genus *Cryptococcus* (Basidiomycota, Tremellomycetes). Stocks of all yeast cultures were stored at −80°C in 15% glycerol.

Starting cultures (50 ml) for inoculation of Petri dishes (3.5 cm diameter) were grown in a defined synthetic minimal medium (Merico et al., 2007) in 250 ml Erlenmeyer flasks at 26°C with the aeration maintained by shaking at 380 rpm for approximately 40–44 h in a rotative shaker (VWR® Incubating Mini Shaker, VWR International, USA). Yeast growth was followed by measuring the optical density at a wavelength of 600 nm ($OD_{600\,nm}$) (SPECTROstar Nano, BMG LABTECH, Ortenberg, Germany).

Trapping with Live Yeast Cultures

Live yeast cultures were prepared for tests of arthropod attraction by streaking 100 µl of the fermented starting cultures (at $OD_{600\,nm}$ 1.2–1.4) from *M. pulcherrima*, *M. andauensis*, *M. hawaiiensis*, *M. lopburiensis*, and *C. tephrensis* isolates onto Petri dishes (3.5 cm diameter) containing 5–10 ml YPD agar (20 gL^{-1} peptone, 20 gL^{-1} glucose, 10 gL^{-1} yeast extract, and 20 gL^{-1} agar). The dishes were incubated in a dark climate chamber at 24°C for 72 h. Dishes containing only YPD agar were prepared as a control.

All trapping experiments using live cultures consisted of six treatments which were cultures of (i) *M. pulcherrima*, (ii) *M. andauensis*, (iii) *M. hawaiiensis*, (iv) *M. lopburiensis*, (v) *C. tephrensis*, and (vi) media control. Arthropod responses to these live culture treatments were tested six times from late June to early September 2013, every 2 weeks (Figure S1). Petri dishes were placed in delta traps (12 × 10 × 18 cm, white body and sticky bottom; PheroNet AB, Alnarp, Sweden) and traps were rotated within a site on each trapping date by shifting positions in the line (i.e., the first trap moved to the second trap's position, trap two moved to trap three's location, and so forth). Traps were hung from the apple tree branches at ca. 1.5 m height, with a distance of ca. 5 m between traps. Each treatment was replicated 10 times at each of the trapping dates. Traps were checked daily. After 5 days traps were collected and all captured specimens were determined. Most specimens were identified to family, many of them to genus and species, based on morphological criteria.

Statistical Analysis

All statistical tests incorporate a Type I error rate of $\alpha = 0.05$, and all parametric statistics were carried out using Proc GLM in SAS version 9.4© 2013 (SAS Institute, Cary, NC, USA). Specimen abundance, species richness, as well as the effect of yeast cultures on the attraction of individuals in the families Syrphidae, Chironomidae, Sarcophagidae, Cecidomyidae, Drosophilidae, Tephritidae, Phoridae, and Lauxaniidae were examined by a

TABLE 1 | Yeast strains used for trapping of arthropods in an organic apple orchard in Alnarp, Sweden, June–September 2013.

Genus	Species	Accession no.	Origin	Substrate of isolation	References
Metschnikowia	*pulcherrima*	CBS 5833	CBS[a]	*Vitis labrusca* berries	Pitt and Miller, 1968
	andauensis	CBS 10809	CBS[a]	*Helicoverpa armigera* larval gut, *Ostrinia nubilalis* larval feces	Molnár and Prillinger, 2005
	hawaiiensis	CBS 7432	CBS[a]	*Ipomoea acuminate* flowers	Lachance et al., 1990
	lopburiensis	SPODO 4	SLU[b]	*Spodoptera frugiperda* larval feces	
Cryptococcus	*tephrensis*	NRRL Y 48787	ARS[c]	Apple orchard	

[a] *CBS stands for CBS Collection (Centraal Bureau voor Schimmelcultures, Utrecht, the Netherlands).*
[b] *SLU stands for SLU Collection (Swedish University of Agricultural Sciences, Alnarp, Sweden).*
[c] *ARS stands for Agricultural Research Service Culture Collection (United States Department of Agriculture, Peoria, IL).*

TABLE 2 | Summary table for the results of GLM analysis for the effects of live yeast cultures, trap date and tree location on capture of insects of different families in an organic apple orchard.

Factor	Syrphidae			Chironomidae			Sarcophagidae			Cecidomyiidae		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Yeast	5	6.04	< 0.001	5	8.65	< 0.001	5	4.04	0.0015	5	5.16	< 0.001
Date	4	72.26	< 0.001	4	11.83	< 0.001	5	7.48	< 0.001	5	8.97	< 0.001
Yeast*Date	20	5.31	< 0.001	20	8.52	< 0.001	25	2.57	< 0.001	25	2.43	0.0003
Location	9	1.57	0.1263	9	0.70	0.7085	9	1.59	0.1192	9	2.32	0.0159
Yeast*Location	45	0.81	0.8007	45	0.95	0.5680	45	1.21	0.1789	45	0.68	0.9372
	Drosophilidae			**Tephritidae[a]**			**Phoridae**			**Lauxaniidae**		
	df	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*	*df*	*F*	*P*
Yeast	5	2.91	0.0214	5	3.12	0.0102	5	2.02	0.0754	5	5.99	< 0.001
Date	1	20.02	< 0.001	4	9.24	< 0.001	5	31.87	< 0.001	5	2.68	0.0222
Yeast*Date	5	3.07	0.0164	20	2.89	< 0.001	25	0.80	0.7401	25	0.60	0.9350
Location	9	2.16	0.0401	9	0.99	0.4530	9	1.64	0.1033	9	1.39	0.1929
Yeast*Location	45	0.76	0.8295	45	0.77	0.8528	45	0.77	0.8549	45	1.06	0.3820

[a] *Tephritid fruit flies were mainly represented by Rhagoletis cerasi.*

TABLE 3 | Summary table for the results of GLM analysis for the effects of live yeast cultures, trap date and tree location on specimen abundance and species richness of arthropods in an organic apple orchard.

Factor	Specimen abundance			Species richness		
	df	*F*	*P*	*df*	*F*	*P*
Yeast	5	10.31	< 0.001	5	7.27	< 0.001
Date	5	52.99	< 0.001	5	11.57	< 0.001
Yeast*Date	25	4.20	< 0.001	25	1.69	0.0230
Location	9	1.65	0.1001	9	0.94	0.4950
Yeast*Location	45	0.84	0.7619	45	1.31	0.0988

generalized linear model (GLM) with a Poisson error distribution with treatment ($n = 6$) as a fixed effect, while trap position (tree location) ($n = 10$) and trapping date ($n = 6$) were considered as blocking factors. Multiple comparisons of means were made using Tukey's honestly significant difference (HSD) test. For analyses of individual arthropod families trap data were only considered for dates where specific catches were above zero since we were not as strongly interested in distinguishing effects of date of capture or tree location as we were in the efficacy of live yeast cultures, but we did wish to partition these sources of variation in the models (**Tables 2**, **3**) (Domingue et al., 2015).

TABLE 4 | Number of arthropods by order [classification is based on Tree of Life Web Project (Maddison and Schulz, 2007)] captured in trapping experiments with live yeast cultures of the genera *Metschnikowia* and *Cryptococcus*.

Taxa	Order	Total no. of specimens per treatment[a]						
		MP	*MA*	*MH*	*ML*	*CT*	C	Total
Entognatha	Collembola	36	35	54	53	38	32	248
Insecta	Dermaptera	10	2	3	4	8	5	32
	Orthoptera	5	2	5	1	4	0	17
	Psocoptera	0	0	1	1	2	0	4
	Thysanoptera	15	7	9	5	4	4	44
	Hemiptera	14	11	10	10	6	5	56
	Neuroptera	0	0	1	0	1	0	2
	Coleoptera	4	2	4	3	2	2	17
	Mecoptera	2	1	3	4	1	5	16
	Diptera	547	581	307	346	602	197	2580
	Lepidoptera	10	5	7	10	4	6	42
	Hymenoptera	16	22	28	17	17	17	117
Arachnida	Acari	9	7	6	5	4	7	38
	Aranea	4	4	7	7	5	7	34
	Opioliones	5	3	3	4	4	0	19

[a] *MP, M. pulcherrima; MA, M. andauensis; MH, M. hawaiiensis; ML, M. lopburiensis; CT, C. tephrensis; C, control.*

RESULTS

A total number of 3266 arthropods were captured during the sampling period, 89.6% Insecta, 7.6% Entognatha, and 2.8% Arachnida. Concerning insect orders, the composition of trap catches was 88.1% Diptera, 4.0% Hymenoptera, 1.9% Hemiptera, 1.5% Thysanoptera, and 1.4% Lepidoptera (**Table 4**). The family-level composition within Diptera was 42.8% Syrphidae, 10.1% Sarcophagidae, 9.9% Muscidae, 7.7% Phoridae, 6.9% Lauxaniidae, 5.9% Cecidomyiidae, and 2.5% Drosophilidae (**Table 5**).

Traps baited with *M. pulcherrima*, *M. andauensis*, and *C. tephrensis* captured significantly more individuals of the family

TABLE 5 | Number of Diptera by family [classification is based on Tree of Life Web Project (Maddison and Schulz, 2007)] captured in trapping experiments with live cultures of *Metschnikowia* and *Cryptococcus* yeasts.

Family	Main species/genus	Larval habitat	Total no. of specimens per treatment[a]					
			MP	*MA*	*MH*	*ML*	*CT*	C
Chironomidae	*Chironomus* sp.	Aquatic	36a[b]	3b	5b	3b	5b	5b
Culicidae	n.s.[c]	Aquatic	0	1	0	0	0	0
Cecidomyiidae	*Dasineura mali*	Plant tissue	43ab	50a	10c	16bc	23bc	25bc
Tipulidae	n.s.	Saprophagous	1	1	1	3	1	1
Phoridae	n.s.	Saprophagous	37	33	30	42	37	18
Syrphidae	*Episyrphus balteatus*	Predatory, insectivorous	237a	292a	64b	138ab	294a	60b
–/–	*Sphaerophoria scripta*	Predatory, insectivorous	3	2	0	2	5	0
Lonchaeidae	n.s.	Mainly phytophagus	12	24	7	0	5	7
Tephritidae	*Rhagoletis cerasi*	Frugivorous	2b	9ab	4b	3b	14a	3b
Piophilidae	n.s.	Saprophagous	2	0	1	0	0	0
Lauxaniidae	n.s.	Saprophagous	34ab	24bc	37ab	24bc	50a	7c
Chloropidae	*Chlorops pumilionis*	Phytophagous	0	1	2	0	2	0
Drosophilidae	*Drosophila* sp.	Saprophagous, frugivorous	20a	25a	7ab	5ab	7ab	1b
Muscidae	n.s.	Mainly saprophagous	20	28	11	19	24	5
Sarcophagidae	*Sarcophaga* sp.	Saprophagous	37ab	43ab	52a	46ab	66a	10b
Tachinidae	n.s.	Mainly parasitoids	30	19	16	19	32	30
Calliphoridae	*Lucilia* sp.	Saprophagous	1	0	1	0	0	0
Calliphoridae	*Calliphora vicina*	Saprophagous	0	0	0	0	2	1
Other	n.s.		32	26	59	26	35	25

[a] *MP, M. pulcherrima; MA, M. andauensis; MH, M. hawaiiensis; ML, M. lopburiensis; CT, C. tephrensis; C, control.*

[b] *Numbers in a row followed by the same lowercase letter are not significantly different (GLM with Poisson error distribution followed by Tukey's honestly significant difference, $P < 0.05$).*

[c] *Not specified.*

Syrphidae [mainly *Episyrphus balteatus* (De Geer)] compared with traps baited with *M. hawaiiensis* and control traps, while traps baited with *M. lopburiensis* were of intermediate attractivity and not different from any treatment or control (GLM, $F = 6.04$; $df = 5, 216$; $P < 0.001$) (**Table 5**). Yeast-baited traps containing *M. pulcherrima* caught significantly more individuals of the family Chironomidae compared with those of the other treatments and control traps, while captures of chironomids among traps baited with *M. andauensis*, *M. hawaiiensis*, *M. lopburiensis, C. tephrensis* and control traps did not differ significantly (GLM, $F = 8.65$; $df = 5, 216$; $P < 0.001$) (**Table 5**). Secondary growth of yeasts from the environment, which was observed only on control plates, may have resulted in attraction of chironomid flies. Traps baited with *M. hawaiiensis* and *C. tephrensis* captured significantly more individuals of the family Sarcophagidae (mainly *Sarcophaga* sp. Meigen) compared with control traps, while traps baited with *M. pulcherrima*, *M. andauensis,* and *M. lopburiensis* were not different from control traps (GLM, $F = 4.04$; $df = 5, 270$; $P < 0.01$) (**Table 5**). Traps with *M. andauensis* caught similar numbers of individuals of the family Cecidomyiidae [mainly specimens of the apple leaf gall midge, *Dasineura mali* (Kieffer)] as *M. pulcherrima* and significantly more compared to traps baited with *M. hawaiiensis*, *M. lopburiensis, C. tephrensis* and control traps (GLM, $F = 5.16$; $df = 5, 270$; $P < 0.001$) (**Table 5**). Moreover, yeast-baited traps containing *M. andauensis* or *M. pulcherrima* caught significantly more individuals of the family Drosophilidae (mainly *Drosophila* sp. Fallén) compared with control traps. Captures of drosophilids among traps baited with *M. hawaiiensis*, *M. lopburiensis, C. tephrensis* and control traps did not differ significantly (GLM, $F = 2.91$; $df = 5, 54$; $P < 0.05$) (**Table 5**). Tephritid fruit flies were mainly represented by the European cherry fruit fly, *Rhagoletis cerasi* (L.) (Diptera: Tephritidae). Traps baited with *C. tephrensis* caught similar numbers of *R. cerasi* as *M. andauensis,* and significantly more individuals, compared to traps baited with *M. pulcherrima, M. hawaiiensis*, *M. lopburiensis* and control traps (GLM, $F = 3.12$; $df = 5, 216$; $P < 0.05$) (**Table 5**). Phoridae were attracted to all yeast-baited traps, however catches were not significantly different to control traps (GLM, $F = 3.147$; $df = 5, 270$; $P = 0.0754$) (**Table 5**). Finally, traps baited with *M. pulcherrima*, *M. hawaiiensis*, and *C. tephrensis* captured significantly more individuals of the family Lauxaniidae compared with control traps, while attraction to traps baited with *M. andauensis* and *M. lopburiensis* were not different from control traps (GLM, $F = 5.99$; $df = 5, 270$; $P < 0.001$) (**Table 5**).

Differences in specimen abundances as a function of trap baits were significant (GLM, $F = 10.31$; $df = 5, 270$; $P < 0.001$), and, traps with *M. pulcherrima*, *M. andauensis*, and *C. tephrensis* captured 2.4, 2.3, and 2.4-fold, respectively, more specimens than control traps (**Figure 1A**). Likewise, significant differences were observed in species richness due to trap baits (GLM, $F = 7.27$; $df = 5, 270$; $P < 0.001$). Traps baited with *M. pulcherrima*, *M. andauensis*, *M. hawaiiensis*, *M. lopburiensis* and *C. tephrensis*

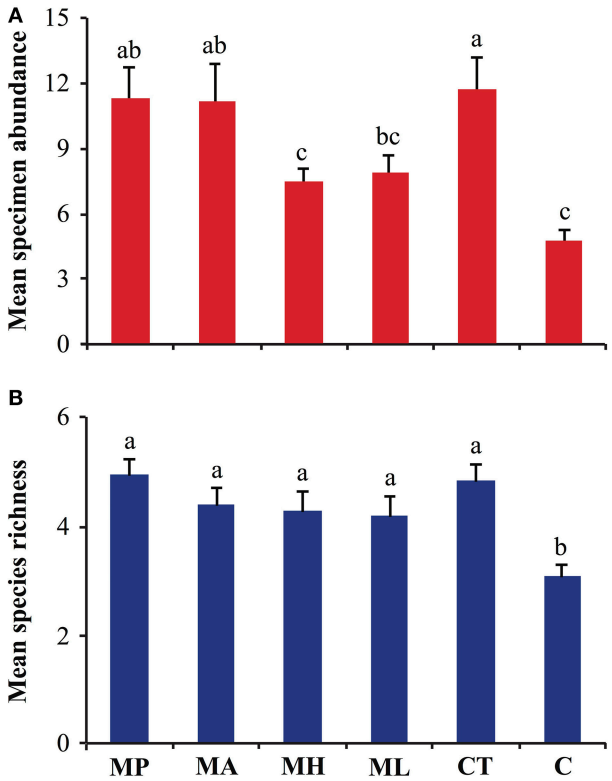

FIGURE 1 | Analysis of (A) specimen abundance, and (B) species richness of arthropod assemblages trapped with live yeast cultures ($n = 6$) in an organic apple orchard in Alnarp (Sweden), from late June to early September 2013. Bars show mean values per trap plus/minus standard error, and different lettering denotes significant differences among means (GLM with Poisson error distribution followed by Tukey's honestly significant difference, $P < 0.05$). MP, *M. pulcherrima*; MA, *M. andauensis*; MH, *M. hawaiiensis*; ML, *M. lopburiensis*; CT, *C. tephrensis*; C, control.

were 1.6, 1.4, 1.4, 1.4, and 1.6-fold, respectively, more species-rich than control traps (**Figure 1B**).

DISCUSSION

Organic apple orchards harbor a remarkable diversity of arthropods and our trapping study shows that a diverse assemblage of 93 arthropods species, belonging to 15 orders of Insecta, Collembola, and Arachnida were attracted to traps baited with *Metschnikowia* and *Cryptococcus* live yeast cultures. Similarly, the ubiquitous yeast-like fungus *Aureobasidium pullulans* attracted a variety of insect taxa in spearmint fields (Davis and Landolt, 2013). This attraction was not indiscriminate, attraction to specific yeasts differed between arthropod taxa.

The majority of arthropods that were trapped in our experiments were insects (89.6%), of which approximately 79% were flies, and most of these were hoverflies. Significantly more hoverflies were captured with traps baited with *M. pulcherrima*, *M. andauensis*, and *C. tephrensis,* compared with controls. Hoverflies exhibit a preference with respect to trap color as well as to trap height (Chen et al., 2004; Rodriguez-Saona et al., 2012). Optimizing trap color and trap placement likely could further enhance attraction of hoverflies to yeast.

Traps baited with live cultures of *M. pulcherrima* caught significantly more chironomids, compared with the other yeasts tested and control. Chironomids are known to be highly attracted to visual and acoustic cues (Hirabayashi and Ogawa, 1999). Our report adds evidence for microbial attraction of chironomids. Furthermore, yeasts attracted flesh flies (Sarcophagidae), whereas blow flies (Calliphoridae), colonizing similar habitats (Hall and Doisy, 1993), were not significantly attracted.

Volatiles emitted by *M. andauensis* captured gall midges (Cecidomyiidae) in significant numbers, especially the apple leaf gall midge. An interaction between cecidomyiid midges and microbes was first suggested by Herman et al. (1993), who observed that *A. pullulans* participates in gall formation by *Lasioptera ephedricola*. Taken together with gall midge attraction in our study, this hints at a role of microbes in associations between phytophagous gall midges and their host plants. This is of basic interest, since many gall midges are rather specifically associated with their respective host plants. In addition, many gall midges are of economic importance (Barnes, 1951). Thus, yeast attraction may become useful in gall midge monitoring or control, for example by enhancing attractiveness of pheromone-mediated methods (Boddum et al., 2009; Hall et al., 2012).

Drosophilid fruit flies were attracted to *M. pulcherrima* and *M. andauensis*. It has been demonstrated that yeast attracts the fruit fly *Drosophila melanogaster* (Diptera: Drosophilidae) more than fruit (Becher et al., 2012). Hamby et al. (2012) showed that the spotted-wing drosophila, *D. suzukii* is preferentially associated with the yeast *Hanseniaspora uvarum*, while Cha et al. (2012, 2014) suggest fermentation volatiles to be involved in food-finding behavior. Moreover, cup traps baited with yeast plus sugar captured more spotted-wing drosophila and nontarget organisms than vinegar baited cup traps in berry crops (Iglesias et al., 2014).

Yeast is a food resource for tephritid fruit flies (Christenson and Foote, 1960; Yee, 2008) and it is conceivable that yeast volatiles contribute to host location in these flies as well. Live cultures of *C. tephrensis* attracted a significantly higher number of European cherry fruit fly individuals than traps baited with *M. pulcherrima* and *M. andauensis* as well as control traps. Significant captures of *R. cerasi* in an apple orchard are remarkable as the flies are known to be a stenophagous species that primarily infests *Prunus* and *Lonicera* spp. (White and Elson-Harris, 1992); it could be worthwhile to investigate a possible use of *C. tephrensis* volatiles for monitoring or control.

All baited traps with live yeast cultures attracted flies of the families Lauxaniidae and Phoridae. Lauxaniid larvae are known to feed on microorganisms such as fungi, yeast, and bacteria (Silva and Mello, 2008). Larval feeding on fungi is also known for phorids, and adults are regarded as efficient vectors of diseases, especially in mushroom cultures. Moreover, other species such as *Apocephalus borealis* Brues (Diptera: Phoridae) parasitize and eventually kill bumble bees, paper wasps, and honey bees (Core et al., 2012). Leblanc et al. (2010) observed a significant attraction of phorid flies toward traps baited with *Candida utilis* (torula yeast) compared with traps baited only with water. Thus, baiting traps with behaviorally active yeast volatiles possibly could allow

monitoring of the presence and abundance of phorids or even control of their population.

Our trapping study adds evidence that yeast volatiles attract a wide range of insect species. Attraction to fermentation compounds has been shown earlier for various insects (e.g., Landolt and Alfaro, 2001; Landolt et al., 2005; Becher et al., 2010; Davis et al., 2013; Cha et al., 2014). To further improve the efficacy of yeast-baited traps, additional research should be conducted to enhance attractiveness and specificity of trap lures, e.g., by using other or additional microbes, by enhancing volatile production and release, or by improving trap design. Yeast semiochemicals might contribute to improve monitoring of pest populations and establishing their economic thresholds, which is key for the implementation of successful integrated pest management (IPM) programs. Thus, we strongly suggest future work should aim at identification of yeast volatiles that elicit insect attraction. Recent work has shown that understanding of ecological interactions between yeasts and insects can lead to the development of new control strategies like efficient attract-and-kill methods (Witzgall et al., 2012; Knight and Witzgall, 2013; Knight et al., 2015). Future tests might show whether additional economically important orchard insects, such as lepidopteran, tephritid, or drosophila species, can be targeted by development of innovative yeast-based control strategies. A better understanding of the behavioral physiology and ecology of insect attraction to associated yeasts will undoubtedly contribute to the development of new tools for monitoring and population control.

AUTHOR CONTRIBUTIONS

All authors participated in the design of the study and interpretation of the data. SA and PB prepared the yeast baits. SA performed the trapping experiments. SA wrote the first draft of the manuscript, which was edited and approved by all authors. PW supervised the project.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fevo.2015.00121

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