Multiple parasitoid species enhance top-down control, but parasitoid performance is context-dependent

Mélanie Thierry*[1,2], Nicholas A. Pardikes[2], Miguel G. Ximénez-Embún[2], Grégoire Proudhom[1,2] & Jan Hrček[1, 2]

[1] University of South Bohemia, Faculty of Science, České Budějovice, Czech Republic

[2] Institute of Entomology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic

[*] Corresponding author: melanie.thierry34@gmail.com

Running Head: Trophic interactions depend on context

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Abstract. Ecological communities are composed of a multitude of interacting species, forming complex networks of interactions. Current global changes are altering community composition and we thus need to understand if the mechanisms structuring species interactions are consistent across different species compositions. However, it is challenging to explore which aspects of species interactions are primarily driven by community structure and which by species identity. Here we compared the outcome of host-parasitoid interactions across four community modules that are common in host-parasitoid communities with a laboratory experiment using a pool of three *Drosophila* host and three larval parasitoid species, resulting in nine different species assemblages. Our results show general patterns of community structure for host-parasitoid interactions. Multiple parasitoid species enhanced host suppression without general antagonistic effects between parasitoid species. Presence of an alternative host species had no general effects on host suppression nor on parasitoid performance, therefore showing no evidence of indirect interactions between host species nor any host switching behavior. However, effects of community structure on parasitoid performance were species-specific and dependent on the identity of co-occurring species. Consequently, our findings highlight the importance of both the structure of the community and its species composition for the outcome of interactions.

Key words: community modules, multiple predator effects, community composition, interaction modification, *Drosophila*

Introduction

In nature, species interact in a variety of ways, forming complex ecological networks (Fontaine et al. 2011, Kéfi et al. 2012, 2015, Pilosof et al. 2017, García-Callejas et al. 2018, Miele et al. 2019). How species interact depends on the structure of the community, but also on identity of species in the assemblage (Bográn et al. 2002). With environmental changes such as climate warming, species are shifting their ranges and phenology (Parmesan and Yohe 2003). But species show differences in their sensitivity and responsiveness to these changes, disrupting historical patterns of interactions and co-occurrences, with communities of new species composition (Alexander et al. 2015). We thus need to determine which aspects of species interactions are primarily driven by community structure, and which are driven by species identity to accurately forecast the ecological consequences of changes in the biotic environment induced by global changes.

Together, trophic and non-trophic interactions, and their modifications by other co-occurring species act in combinations to shape communities (Thierry et al. 2019), and their dynamics (Kawatsu et al. 2021). A predator-prey interaction can be weakened by the presence of another predator via exploitative competition, interference or intraguild predation, enhanced via facilitation, or unchanged if predators have additive effects on prey suppression (Sih et al. 1998). Top-down control might also be driven by a single influential predator species independently of predator diversity (Letourneau et al. 2009), or be enhanced if predators show some degree of niche differentiation (Bográn et al. 2002, Pedersen and Mills 2004, Snyder et al. 2006, 2008). A predator might switch prey species with the presence of a competing predator, or with change in relative prey abundances (Siddon and Witman 2004, Randa et al. 2009). In addition, two competing species are able to coexist in nature, in part, because of indirect interactions through a shared natural enemy, which reduces the frequency of the dominant competitor that would otherwise exclude less competitive species (i.e., apparent competition) (Bonsall and Hassell 1999, Singh and Baruah 2020). Most studies looking at complex networks are observational (e.g., Tylianakis et al. 2007, Jeffs et al. 2021), and typically unable to disentangle the potential mechanisms driving species interactions described above. Experimental systems are thus needed to disentangle the mechanisms structuring networks of interacting species. For this purpose, community modules (i.e., a small number of species interacting in a specified pattern; Holt 1997, also referred to as “motifs” in the literature; Milo et al. 2002) represent a powerful tool to isolate certain key interactions that structure complex networks. They are the building blocks of natural communities (Gilman et al. 2010), and thus allow us to disentangle the mechanisms structuring them. Common community modules in food webs are pair of predator-prey, two prey species sharing a common natural enemy (i.e., apparent competition or mutualism; hereafter apparent competition module), or two predator species attacking the same prey (i.e., exploitative competition, interference, or facilitation; hereafter exploitative competition module). But experimental studies investigating the mechanisms structuring interactions with community modules rarely consider potential variations due to species-specific effects (but see Bográn et al. 2002, Snyder et al. 2006). Thus, it is unclear whether the mechanisms structuring interactions are consistent when looking at community modules of different species compositions (Cusumano et al. 2016).

Experiments manipulating interactions in different community contexts with different species assemblages are still rare, and usually manipulate species assemblage of one trophic level at a time. For instance, Bográn et al. (2002) revealed competitive interactions among predator species in some, but not all the predator assemblages studied. However, the study used only one prey species. Snyder et al. (2006) found varying strength in the effect of predator species diversity on aphid suppression depending on the aphid species considered, but did not vary species composition in multiple predator treatment. Understanding how the identity of co-occurring species at both trophic levels affects the outcome of consumer-resource interactions is of particular importance in the context of current global changes.

Here, we investigated the mechanisms structuring consumer-resource interactions using a host-parasitoid system. Parasitoids are a diverse group of insects that use other arthropods as a nursery for their offspring, killing their host to complete development (Godfray 2004). Parasitoids are important for top-down control in agricultural and natural ecosystems, and widely used as biological control agents. Interactions between hosts and parasitoids are easily observed, and host-parasitoid communities thus represent a good model system to study how the structure and composition of communities influence species interactions. We used a set of three *Drosophila* species and three of their larval parasitoids from a natural tropical community in Australia (Jeffs et al. 2021) in a laboratory experiment to isolate direct and indirect interactions within host-parasitoid communities. We aimed to uncover general effects of community modules in our *Drosophila*-parasitoid system, and detect any species-specific effects depending on the co-occurring species identity (using 9 species assemblages for each of the four common community modules in host-parasitoid networks: host-parasitoid pair, exploitative competition module, apparent competition module, and both exploitative and apparent competition module). Specifically, we tested the following hypotheses: (i) host suppression will be higher with the presence of multiple parasitoid species (i.e., exploitative competition module) because of increased chances to have an efficient parasitoid species (Pedersen and Mills 2004, Letourneau et al. 2009), (ii) despite potential multiparasitism events and therefore a decrease in parasitoid performance (Harvey et al. 2013). (iii) Pairwise interaction between a focal host-parasitoid pair will weaken with the presence of an alternative host in the apparent competition module because of trait- and density- mediated indirect effects (Werner and Peacor 2003). (iv) Combined effects of exploitative competition among parasitoids and apparent competition among hosts in the four-species module will differ from three-species modules depending on the identity of the co-occurring species because of species-specific effects (Bográn et al. 2002, Sentis et al. 2017).

Methods

Study system

The experiment used cultures of *Drosophila* species and their associated parasitoids collected from two tropical rainforest locations in North Queensland Australia: Paluma (S18° 59.031' E146° 14.096') and Kirrama Range (S18° 12.134' E145° 53.102') (< 100 m above sea level) (Jeffs et al. 2021). *Drosophila* and parasitoid cultures were established between 2017 and 2018, identified using both morphology and DNA barcoding, and shipped to the Czech Republic under permit no. PWS2016-AU-002018 from Australian Government, Department of the Environment. All cultures were maintained at 23°C on a 12:12 hour light and dark cycle at Biology Centre, Czech Academy of Sciences. Three host species (*Drosophila birchii*, *D. simulans* and *D. pallidifrons*), and three larval parasitoid species *Asobara sp*. (Braconidae: Alysiinae; strain KHB, reference voucher no. USNMENT01557097, reference sequence BOLD process ID:DROP043-21), *Leptopilina sp*. (Figitidae: Eucolinae; strain 111F, reference voucher no. USNMENT01557117, reference sequence BOLD process ID:DROP053-21), and *Ganaspis sp*. (Figitidae: Eucolinae; strain 84BC, reference voucher no. USNMENT01557102 and USNMENT01557297, reference sequence BOLD process ID:DROP164-21) were used (for more details on the parasitoid strains used see Lue et al. 2021). *Drosophila* isofemale lines were kept on standard *Drosophila* medium (corn flour, yeast, sugar, agar and methyl-4-hydroxybenzoate) for approximately 45 to 70 non-overlapping generations. To revive genetic variation, four to seven lines from each host species were combined to establish two population cages per species of mass-bred lines prior the start of the experiment. Single parasitoid isofemale lines were used, and maintained for approximately 25 to 40 non-overlapping generations prior to the start of the experiment by providing them every week with 2-days-old larvae of *Drosophila melanogaster*. This host species was not used in the experiment, thus avoiding potential bias due to maternal effects.

Experimental design

To investigate the effects of community structure and species composition on host-parasitoid interactions, we used four community modules, and 9 different species assemblages each (6 host and 6 parasitoid assemblages, from the pool of three host species and three parasitoid species) replicated 6 times (Figure 1). Each replicate was represented by a set of two vials in one box, for a total of 216 boxes. Either conspecific (Figure 1a and c) or heterospecific (Figure 1b and d) parasitoids were used. The two vials contained *Drosophila* larvae from either the same host species (Figure 1a and b) or different host species (Figure 1c and d). We also included control treatments for each host species to acquire baseline levels of survival in the absence of parasitoids (replicated 8 times).

To initiate the experiment, twenty-five eggs of each host species were placed in a single glass vial with 10mL of food media. To collect *Drosophila* eggs, an egg-wash protocol was developed based on Nouhaud et al. (2018). The day before the egg-washed protocol was conducted, two egg-laying mediums (petri dishes with agar gel topped with yeast paste) were introduced in each population cage for flies to laying eggs overnight. We used a #3 round paintbrush and distilled water to rinse out the yeast paste and collect the eggs on a fine black mesh that allowed only yeast and water to filter through, leaving the eggs on the surface. Eggs were transferred into petri dishes containing PBS (1 mM Calcium chloride dihydrate, 0.5 mM Magnesium Chloride Hexahydrate, pH = 7.4), and collected under microscope using a pipette to transfer eggs from the petri dish with PBS to the experimental vials.

After 48 hours, two vials with *Drosophila* second instar larvae (initially eggs) were placed in a hermetically sealed plastic box (15x11x19 cm) with four 3-to-5-days-old parasitoids (1:1 sex ratio). Twenty-four hours later, parasitoids were removed, and vials were removed from the boxes and plugged for rearing (Figure S1). Every vial was checked daily for emerges until the last individual emerged (up to 41 days for the species with the longest developmental time). We stopped collecting host emerges after 5 consecutive days without emerges to avoid collecting the second generation. All emerges were collected, identified, sexed, and stored in 95% ethanol. A total of 11,400 host eggs were collected across 456 experimental vials, of which 7,494 (65.7%) successfully emerged as adults (3,702 hosts and 3,792 parasitoids).

Data analysis

We characterized the outcome of host-parasitoid interactions by a combination of degree of infestation (DI) for each host species (i.e., the probability of a larvae to be parasitized and die), and successful parasitism rate (SP) for each host-parasitoid pair representing parasitoid performance (i.e., the probability of a parasitized host to give rise to an adult parasitoid) (Carton and Kitano 1981, Boulétreau and Wajnberg 1986). Degree of infestation (DI) was calculated as the proportion of host attacked (the difference between adult hosts emerging from the controls without parasitoids and from the experiment) among the total of hosts (set to 0 if the number of hosts emerging from the experiment was greater than the controls). Successful parasitism rate (SP) was calculated as the proportion of parasitoid adults emerging among the number of hosts attacked (Carton and Kitano 1981, Boulétreau and Wajnberg 1986). If no parasitoid emerged or if the number of hosts attacked was estimated to be zero, SP was set to 0. If the number of parasitoids that emerged was greater than the estimated number of hosts attacked, SP was set to 1. For treatments with one parasitoid species, we assumed that each of the two parasitoid individuals were attacking hosts equally, therefore the number of parasitoid adults emerging was divided by two to allow comparison of parasitism rates between single and multiple parasitoid species.

Data were analyzed using generalized linear mixed-effects models (GLMMs). Model assumptions were verified with the *DHARMa* package (Hartig 2019). To correct for overdispersion of the residuals and zero inflation, data were modeled using zero-inflation models with a beta binomial error distribution and a logit link function using the *glmmTMB* function from the *TMB* package (Lüdecke et al. 2019). Three model types were used to investigate general effects of community modules, species-specific responses, and effects of community composition for each focal species. (i) "Community module models" used two explanatory variables and their two-way interaction to account for the fully-factorial design of the experiment that resulted in four community modules (exploitative competition treatment with two levels: presence or not of a parasitoid heterospecific, and apparent competition treatment with two levels: presence or not of an alternative host species). Box ID (214 levels) was included as a random factor to remove the variation between the different species assemblages and thus extract general effects of community modules. Host species (three levels) for DI, and host-parasitoid pairs for SP were also included as random factors to remove the variation between different species. (ii) "Species-specific community module models" used the same explanatory variables than previously described, and Box ID as a random factor, but host species and host-parasitoid pairs were included as fixed factors to test if effects varied depending on the focal species. All three and two-way interactions between treatments (exploitative and apparent competition), host species, and host-parasitoid pairs were tested and kept in our models if found to be significant based on backward model selection using

Likelihood-ratio tests. Models for SP were also run for each host-parasitoid pair separately to quantify differences in the sign and magnitude of the effects of community structure on pairwise interaction depending on the focal species. (iii) "Community composition models" used species assemblages rather than community modules as explanatory variables (host species assemblage: 6 levels, and parasitoid species assemblage: 6 levels). The two-way interaction between host and parasitoid assemblages was always kept in the models to account for the fully-factorial design of the experiment. Models for DI were run for each host species, and models for SP were run for each host-parasitoid pair separately. Blocks (6 levels) were included in all models as a random effect. Significance of the effects was tested using Wald type III analysis of deviance with Likelihood-ratio tests. Factor levels of community modules and species assemblages were compared to the reference module and species assemblages of the host-parasitoid pair in isolation by Tukey's HSD *post hoc* comparisons of all means, using the *emmeans* package (Lenth 2018). All analyses were performed using R 4.0.2 (Team 2017).

Results

Effects of community structure on host suppression

The presence of multiple parasitoid species in the module significantly increased the probability of host being infested (DI) by 48% (CI 26-70%) (community module model: $\chi2_{(1)} = 7.08$, $P = 0.008$; Post Hoc Odds Ratio (OR) exploitative competition module/pairwise interaction = 1.58, $P = 0.076$; OR exploitative and apparent competition module/pairwise interaction = 1.32, $P = 0.376$). However, DI did not significantly change with the presence of an alternative host species ($\chi2_{(1)} = 0.56$, $P = 0.452$; OR apparent competition module/pairwise interaction = 0.96, $P = 0.984$), and the two-way interaction between apparent and exploitative competition treatments had no significant effect (community module model: $\chi2_{(1)} = 0.22$, $P = 0.638$) (Figure 2a).

Effects of host species and community composition on host suppression

Host DI did not differ significantly across host species (species-specific community module model: $\chi2_{(2)} = 0.07$, P = 0.965). The directionality of the effect of parasitoid diversity did not vary depending on species assemblages (community composition models; Figure S2 and Appendix S2).

Effects of community structure on parasitoid performance

Community modules had no general effects of successful parasitism rates (SP) (community module model; Figure 2b), but the effects significantly varied across host-parasitoid pairs (species-specific community module model; three-way interaction: $\chi2(8) = 36.81$, $P < 0.0001$; Table 1). The interaction between exploitative and apparent competition treatments had a significant effect on SP for one out of the nine host-parasitoid pairs (*Ganaspis sp*. on *D. simulans*). SP of two other host-parasitoid pairs significantly decreased with exploitative competition between parasitoid species (*Ganaspis sp*. on *D. birchii* and on *D. pallidifrons*). SP of one host-parasitoid pair significantly increased with apparent competition (*Asobara sp*. on *D. simulans*). SP for the rest of the host-parasitoid pairs did not significantly changed between community modules when compared to the host-parasitoid pair in isolation (Table 1).

Effects of community composition on parasitoid performance

Effects of an alternative host and a parasitoid competitor on parasitoid performance varied depending on co-occurring species identity, both in term of magnitude and direction of their response (community composition models). The interaction between host and parasitoid species assemblages had a significant effect on SP for four out of the nine host-parasitoid pairs: *Asobara sp*. on *D. simulans*, *Leptopilina sp*. on *D. birchii*, and *Ganaspis sp*. on *D. birchii* and on *D. simulans*. Effects of species assemblages on SP for each host-parasitoid pair are summarized in Table 2 and Figure 3, and presented in Appendix S3.

Discussion

Our results confirm some general effects of community structure on consumer-resource interactions over a number of species combinations, but also reveal important species-specific effects linked to the identity of species composing the community. Specifically: (i) the presence of multiple parasitoid species consistently increased host suppression, showing the prevalence of synergistic effects between consumer species in our system. On the contrary, (ii) the presence of an alternative host had no general effect on host suppression, but increased or decreased successful parasitism rate depending on host-parasitoid pairs and co-occurring species identity.

Positive effects of consumer diversity on top-down control

The presence of multiple parasitoid species generally increased host suppression. An increase in top-down control compared to single-species treatments with one consumer species is predicted when the different natural enemies present a certain degree of niche differentiation, therefore complementing each other (Pedersen and Mills 2004), which have been reported in several experimental studies (reviewed in Letourneau et al. 2009). Here, we observed a general positive effect of consumer diversity on top-down control independently of the number of host species present in the community. No general effects were detected on parasitoid performance, suggesting no general difference between intra- and interspecific competition between consumers. Moreover, the positive effects of parasitoid diversity on host suppression were mainly driven by the presence of the most efficient parasitoid species for the focal host (e.g., presence of *Ganaspis sp*. for *D. simulans*). These results match the sampling effect model suggesting that an increase in top-down control with an increase in consumer diversity is explained because of an increasing probability that a superior natural enemy species will be present in the community (Myers et al. 1989).

No indirect interactions detected among prey species

Contrary to the presence of an additional parasitoid species, we did not detect any effect of an additional host species on host suppression, reveling no host switching behavior nor any indirect interactions between host species over this one generation experiment. Another empirical study failed to uncover any evidence of indirect interactions in natural host-parasitoid food webs (Kaartinen and Roslin 2013). Indirect interactions between prey, mediated by a shared natural enemy, is supposedly common in nature (e.g., Morris et al. 2001), and an important mechanism for prey species coexistence via density- and trait-mediated effects (Holt 1977, Fleury et al. 2004, van Veen et al. 2005, McPeek 2019). But direct exploitative competition between host species, which was not allowed in our experiment, might have a stronger effect on host population and community structure than apparent competition (Jones et al. 2009). Furthermore, frequency-dependent attack rate, in which a predator switches between two prey species depending on their relative densities, through aggregative behavior (Bonsall and Hassell 1999), and through learning (Ishii and Shimada 2012), is another important mechanism determining the strength of predator-prey interactions (van Veen et al. 2005), but was not tested in the present study. Varying host and non-host densities could also change parasitoid foraging behavior (Kehoe et al. 2016). In our study, potential effects of an alternative host (i.e., apparent competition module and both exploitative and apparent competition module) on host-parasitoid interactions were tested over a single generation and with constant host density. Therefore, experimental studies manipulating alternative prey density over several generations might be needed to detect indirect interactions between host species.

Importance of community composition for consumer-resource interactions

Our study was based on a particular set of interacting species, yet even the relatively small number of species used in our experiment allowed us to uncover species-specific response within a given community module. Community modules have been extensively used as a tool to study the mechanisms structuring and stabilizing complex natural communities (Bascompte and Melián 2005, Rip et al. 2010), yet the effects of species identity in such studies is often ignored. Our results highlight the variation in directionality and magnitude of the effects of a particular community module on host-parasitoid interactions depending on the species assemblage considered.

Successful parasitism rate increased in modules with a parasitoid competitor compared to the pairwise interaction in 6 species combinations (out of the 67 species combinations representing host-parasitoid pairs in modules with either or both exploitative and apparent competition), suggesting that some parasitoid species benefit from presence of an heterospecific. According to a recent review on interspecific interactions among parasitoids (Cusumano et al. 2016), and to the best of our knowledge, only one study showed facilitation between two parasitoid species on cabbage white caterpillars (Poelman et al. 2014). Our case seems to be different because successful parasitism rates did not increase for both parties. Here, modules with the pairwise interaction in isolation had two parasitoid conspecifics, and our results therefore suggest that in these 6 cases, interspecific competition between parasitoids was weaker than intraspecific competition. Parasitoids can compete both as adults for oviposition and as larvae within an host (Harvey et al. 2013). Extrinsic competition would have negative effects on parasitoid attack rates, linked to search efficiency and handling time, leading to a potential decrease in host mortality (Xu et al. 2016), which seems to not be the case in our study. Intrinsic competition is the result of a super- or multiparasitism event when two parasitoids (conspecifics or heterospecific, respectively) parasitize the same host individual. It is usually detrimental for the host survival, and therefore the most likely interaction between parasitoids happening in our experiment that would explain an increase in host suppression. Furthermore, parasitoids can inflict non-reproductive effects on their hosts (i.e., ovipositor probing and egg laying without successful parasitism) that can lead to host death (reviewed in Abram et al. 2019). This could also explain that host suppression increased with multiple parasitoids while successful parasitism rate did not generally increase. Our contrasting results on successful parasitism rate depending on the host-parasitoid pair and the other parasitoid species present in the community are likely due to differences in traits (e.g., immune response of the hosts, and oviposition behavior and virulence of the parasitoids; Carton et al. 2008). The different trait combinations and trade-offs across host and parasitoid species are likely an important mechanism driving species interactions and co-occurrences in natural communities (Wong et al. 2019).

Conclusion

Our study is the first to our knowledge to investigate the effects of community module of different species assemblages on consumer-resource interactions at both trophic levels. Studies looking at interaction between predator species on single prey (e.g., Valente et al. 2019, Ortiz-Martínez et al. 2019), or studies looking at the effect of an alternative prey with single predator species (e.g., Ishii and Shimada 2012, De Rijk et al. 2016), will overlook important mechanisms present in nature where a number of species co-occur. With current global changes such as climate warming, the structure and composition of communities is changing, either via direct effects on species performance (Thierry et al. 2021), via effects on interactions (Hance et al. 2007, Thierry et al. 2019), or due to shift in ranges and phenology, and an increase in invasive species. It is therefore imperative to take into account the context in which species interact, both abiotic and biotic, as all those factors are likely to act together in influencing the outcome of the interaction between focal species (Gilman et al. 2010).

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Author contributions

MT conceived the project; NP and JH contributed to the experimental design; MT, NP, MG, and GP collected the data; MT analyzed the data. All authors contributed critically to the draft and gave final approval for publication.

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Table 1. Odds ratios of having a successful parasitism event in each community module (exploitative competition, apparent competition, and both exploitative and apparent competition) compared to the host-parasitoid pair in isolation for each pair (host abbreviations: b: *D. birchii*, p: *D. pallidifrons*, s: *D. simulans*, and parasitoid abbreviations: A: *Asobara sp.*, L: *Leptopilina sp.*, G: *Ganaspis sp.*). Odds Ratios superior or inferior to 1 translate an increased or a decreased probability of having successful parasitism, respectively. Results come from the species-specific community module models run for each host-parasitoid pair separately. Significant Odds Ratios are highlighted in bold.

Module	**b-A**		**p-A**		**s-A**		**b-L**		**p-L**		**s-L**		**b-G**		**p-G**		**s-G**	
Expl. comp.	1.49	(ns)	0.63	(ns)	1.56	(ns)	0.85	(ns)	1.36	(ns)	0.00	(ns)	0.30	*	0.19	*	0.67	(ns)
App. comp.	0.95	(ns)	1.03	(ns)	4.29	***	1.16	(ns)	1.65	(ns)	0.00	(ns)	0.94	(ns)	0.92	(ns)	0.83	(ns)
Expl. + app. comp.	0.65	(ns)	038	(ns)	0.76	(ns)	1.44	(ns)	1.82	(ns)	0.00	(ns)	0.73	(ns)	0.45	(ns)	4.12	***
Df residuals	65		65		65		65		65		65		64		64		65	

Table 2. Effects of community composition on the probability to have a successful parasitism event for each host-parasitoid pair. Effects are shown by the summary of Likelihood-ratio chi-square tests on the community composition models with the effects of host and parasitoid species assemblages (3 levels each) (host abbreviations: b: *D. birchii*, p: *D. pallidifrons*, s: *D. simulans*, and parasitoid abbreviations: A: *Asobara sp.*, L: *Leptopilina sp.*, G: *Ganaspis sp.*). For p-A and s-L models contain only host species assemblage as a fixed effect due to convergence problem with the full model. Degrees or freedom (Df) are given for each factor and for the residuals. χ2 values are presented with the significance of the effect: (***) P < 0.001, (**) P < 0.01, (*) P < 0.05, (ns) P > 0.05.

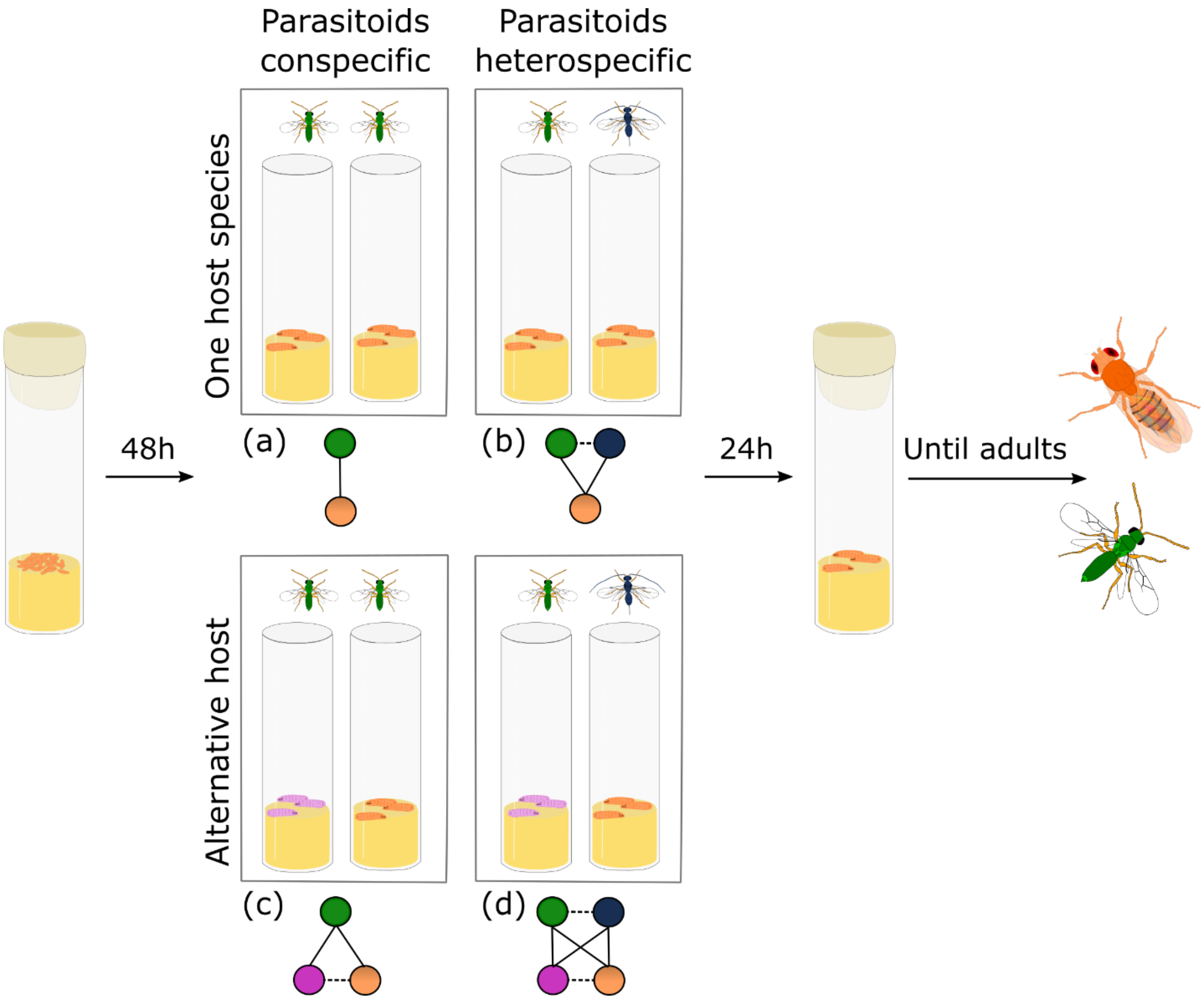
Effects	**Df**	**b-A**		**p-A**		**s-A**		**b-L**		**p-L**		**s-L**		**b-G**		**p-G**		**s-G**	
Host sp.	2	11.14	**	1.12	(ns)	15.56	***	4.80	(ns)	4.83	(ns)	10.08	**	34.14	***	2.23	(ns)	19.71	***
Parasitoid sp.	2	6.63	*	-		0.11	(ns)	38.32	***	4.36	(ns)	-		2.57	(ns)	1.73	(ns)	13.81	**
Host x para	4	7.80	(ns)	-		24.19	***	40.57	***	7.81	(ns)	-		25.22	***	9.01	(ns)	20.51	***
Df residuals		60		66		60		60		60		66		59		59		60	

Figure legends

Figure 1. Schematic representation of the experimental treatments with the potential direct and indirect interactions in each community module. Orange and pink nodes and larvae represent different *Drosophila* host species, and green and blue nodes and wasps represent different parasitoid species, assembled in a fully factorial design in four different community modules represented schematically below their corresponding experimental box: a) host-parasitoid pair (one host and one parasitoid species), b) exploitative competition module (one host and two parasitoid species), c) apparent competition module (two host and one parasitoid species) and, d) both exploitative and apparent competition module (two host and two parasitoid species). In the community module schemas, solid lines represent trophic interactions, and dashed lines represent non-trophic interactions (in b) either exploitative competition, interference, or facilitation between parasitoids, c) either apparent competition or mutualism between hosts, and d) potential for all the above). Direct interaction between host species were not allowed. See Thierry et al. (2019) for a detailed description of each interaction type

Figure 2. Effects of community structure (represented by the community module bellow each treatment) on (a) degree of infestation and on (b) successful parasitism rate. Different capital letters denote significant differences between community structure from the community module models. The small points represent the observed values, and the large points represent the predicted values with their 95% confidence intervals

Figure 3. Effects of community composition (identity of the alternative host and the parasitoid heterospecific) on the successful parasitism rate of each parasitoid species on each host species [rows are host species (host abbreviations: b: *D. birchii*, p: *D. pallidifrons*, s: *D. simulans*), and columns are parasitoid species (parasitoid abbreviations: A: *Asobara sp.*, L: *Leptopilina sp.*, G: *Ganaspis sp.*)]. Host assemblages are represented by the different colors, and parasitoid assemblages are on the x axis. For SP p-A and SP s-L, only effect of host assemblages was analyses due to convergence problem with the full model, and are represented for all parasitoid assemblages combined. The small points represent the observed values, and the large points represent the predicted values with their 95% confidence intervals from the community composition models



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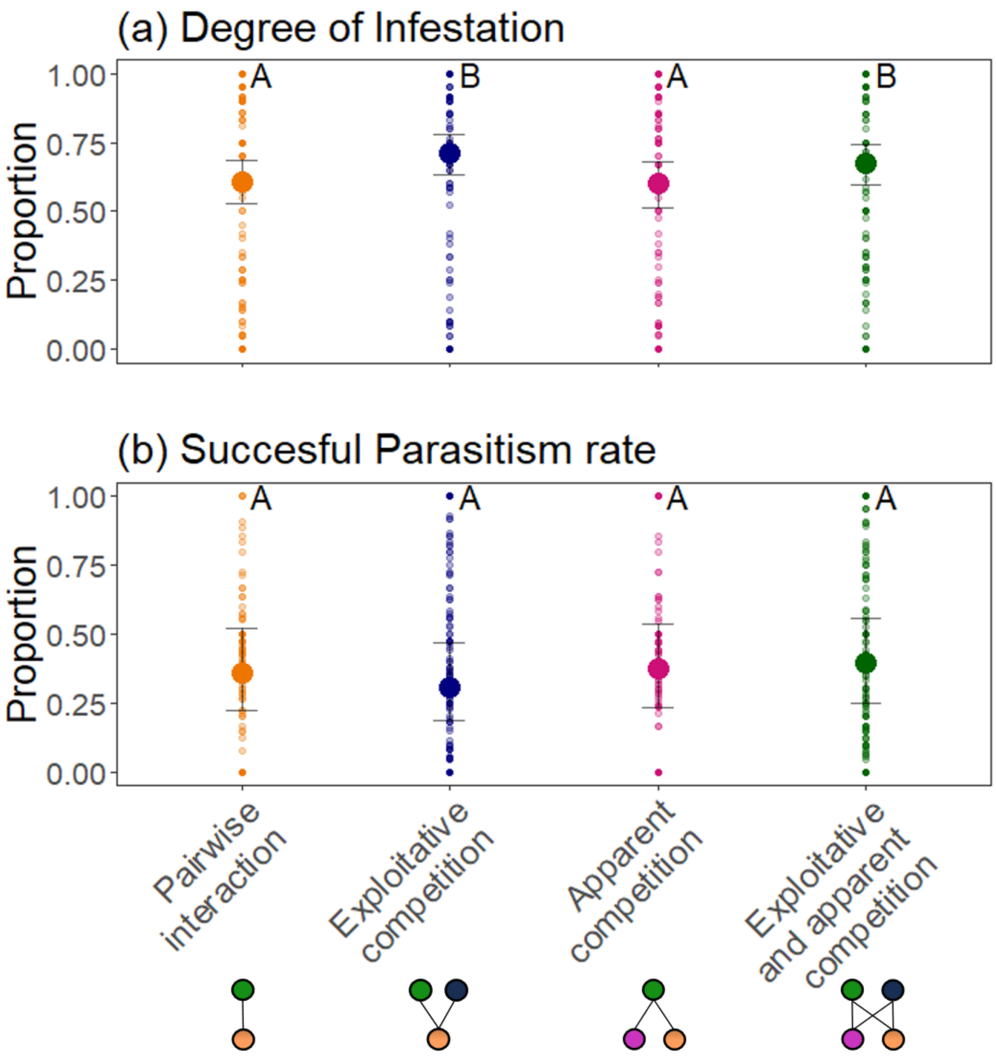
538 **Figure 1.**



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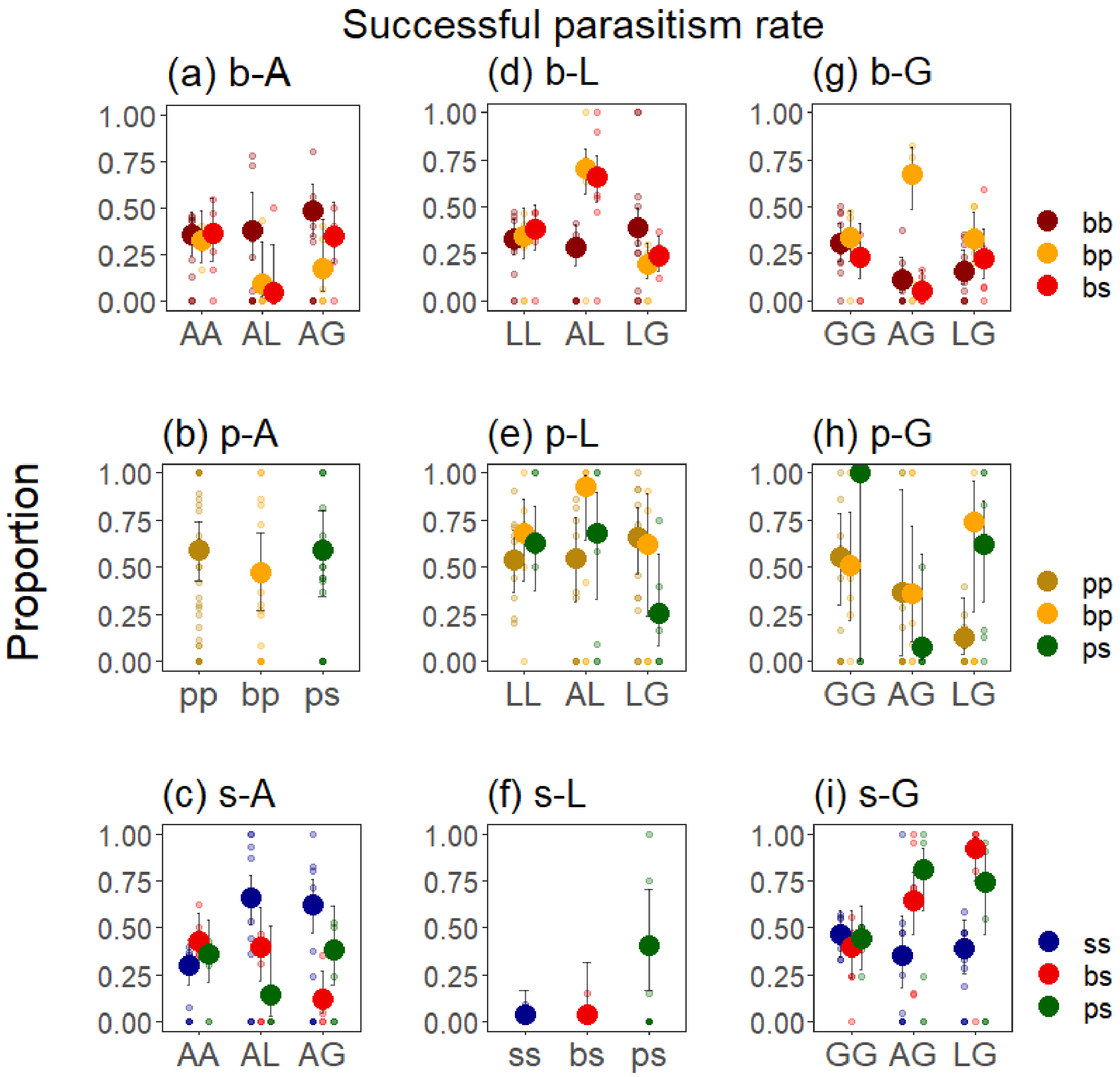
540 **Figure 3**.



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542 **Figure 3.**