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ARTICLE

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Pesticide exposure enhances dominance patterns in a zooplankton community

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Abstract

Exposure to pesticides can profoundly alter community dynamics. It is expected that dominance patterns will be enhanced or reduced depending on whether the dominant species is less or more sensitive to the pesticide than the subdominant species. Community dynamics are, however, also determined by processes linked to population growth as well as competition at carrying capacity. Here, we used a mesocosm experiment to quantify the effect of chlorpyrifos exposure on the population dynamics of four cladoceran species (*Daphnia magna*, *Daphnia pulicaria*, *Daphnia galeata* and *Scapholeberis mucronata*) in mixed cultures, testing for direct effects of chlorpyrifos and indirect effects mediated by interactions with other species on the timing of population growth and dominance at carrying capacity. We also quantified whether the pesticide-induced changes in community dynamics affected top-down control of phytoplankton. By adding a treatment in which we used different genotype combinations of each species, we also tested to what extent genetic composition affects community responses to pesticide exposure. Immobilization tests showed that *D. magna* is the least sensitive to chlorpyrifos of the tested species. Chlorpyrifos exposure first leads to a reduction in the abundance of *D. galeata* to the benefit of *D. pulicaria*, and subsequently to a reduction in densities of *D. pulicaria* to the benefit of *D. magna*. This resulted in *D. magna* being more dominant in the pesticide than in the control treatment by the end of the experiment. There was no effect of genotypic differences on community patterns, and top-down control of phytoplankton was high in all treatments. Our results suggest that in this community dominance patterns are enhanced in line with the observed among-species differences in sensitivity to the pesticide. Our results also show that the development of the community in pesticide treatment is a complex interaction between direct and indirect effects of the pesticide.

KEYWORDS
chlorpyrifos, Cladocera, competition, ecosystem functioning, genetic variation, interspecific interactions, mesocosm

INTRODUCTION

A profound understanding of the impact of anthropogenic stressors on the structure and functioning of biotic communities has become increasingly important in the face of global change (Groh et al., 2022). Indeed, a large number of ecosystems on Earth is exposed to different types of human disturbance. Among these, pesticides are especially important because they do not only impact target organism groups, but can also affect nontarget organisms in surrounding habitats (Bernhardt et al., 2017; Peters et al., 2013; Rumschlag et al., 2020; Schäfer et al., 2007; Yamamuro et al., 2019). Since agricultural industrialization, pesticide diversity and applied volumes continue to increase at alarming rates (Bernhardt et al., 2017). Pesticides are ubiquitous in agricultural and urban areas as well as in surrounding natural habitats (Gilliom et al., 2006; Stehle & Schulz, 2015; Tang et al., 2021) and they represent a major threat to biodiversity (Beketov et al., 2013; Geiger et al., 2010; Stehle & Schulz, 2015).

There is currently a rich and growing body of literature on how pesticides affect individuals and species. Most studies to date have focused on single-species approaches to assess the organismal responses to pesticide exposure (Delnat et al., 2019; Janssens & Stoks, 2020; Lal et al., 2013; Song et al., 2017; Thoré, Philippe, et al., 2021), or have relied on mesocosm experiments and field surveys to assess how pesticides affect biodiversity and community composition (Andrade et al., 2021; López-Mancisidor et al., 2008; Mcmahon et al., 2012; Pestana et al., 2009; Smith et al., 2018). Pesticides may not only induce direct lethal (Delnat et al., 2020; Hua et al., 2013; Kafula et al., 2022) but also sublethal effects such as physiological and life history changes (Aliouane et al., 2009; Palma et al., 2009; Thoré, van Hooreweghe, et al., 2021). These can alter biotic interactions, such as reduced top-down control on phytoplankton (Bengtsson et al., 2004) and altered predator–prey dynamics (Bianchi et al., 2006; J. J. Rasmussen et al., 2013), which can ultimately cascade to changes in community structure and ecosystem functioning (Rumschlag et al., 2020). To study such changes in biotic interactions, there is a need for controlled experiments with multiple interacting species in standardized communities. Several studies focusing on two competing species have shown that pesticide contamination can cause shifts in dominance patterns when the stronger competitor is more sensitive to the pesticide than the subdominant one (Cordeiro et al., 2014; Mohammed et al., 2019; Zhao et al., 2017). Other scenarios might be possible, however (Figure 1). More in general, it is important to understand how pesticide exposure affects community assembly and dynamics through time.

Freshwater ecosystems are often exposed to different types of pesticides through run-off from agricultural fields (Malaj et al., 2014; Stehle & Schulz, 2015). As freshwater ecosystems crucially contribute to global biodiversity (Dudgeon et al., 2006) and provide key ecosystem services (Biggs et al., 2017), contamination of these systems with pesticides is thus particularly concerning. In lentic waterbodies, such as lakes and ponds, zooplankton plays a central role in the food web, as they are an important food source for higher trophic levels and can exert strong top-down control on phytoplankton (Brett et al., 1994; Gianuca et al., 2016; Miner et al., 2012). In cladoceran zooplankton, the body size is an important trait that determines the competitive strength and the capacity to top-down control phytoplankton, with larger species being competitively superior and stronger grazers than smaller bodied ones (Brooks & Dodson, 1965; Kreutzer & Lampert, 1999; Miner et al., 2012). This implies that, in the absence of predation by fish, larger species generally outcompete smaller species and become dominant in the community (Figure 1A). There is, however, a trade-off between body size and speed of maturation. As a result, except in systems where negative size-selective predation imposes a shift in body size, smaller bodied species might show a peak in population abundance earlier than larger-bodied species, before they are outcompeted by the latter.

Competitive outcomes in freshwater communities are expected to be affected by pesticide exposure, as extensive interspecific variation in pesticide sensitivity has been shown among freshwater species, including in cladoceran zooplankton (Bossuyt & Janssen, 2005; Hayasaka et al., 2012; Mano et al., 2010). Several studies also report among-individual differences in sensitivity within the same species, which can be a result of differences in genetic features or phenotypic plasticity (Almeida et al., 2021; Barata et al., 2002; Bossuyt & Janssen, 2005; Cothran et al., 2013; Hayasaka et al., 2012; Mano et al., 2010; Shahid et al., 2018). Organisms with a lower pesticide resistance may become competitively weaker and might become suppressed by less sensitive species in the community when exposed to pesticides (Knillmann et al., 2012). Figure 1 illustrates different scenarios for the case of cladoceran zooplankton, where large-bodied species tend to be competitively superior. If the large-bodied species is less sensitive to the pesticide than the smaller bodied species, the smaller species will be suppressed by both the pesticide and by the better performance of the stronger competitor and will, therefore, not be able to reach high densities (Knillmann et al., 2012; Figure 1B,C). If the stronger competitor is more sensitive to the pesticide than the smaller bodied species, then the smaller bodied species may reach higher population growth due to competitive release under pesticide

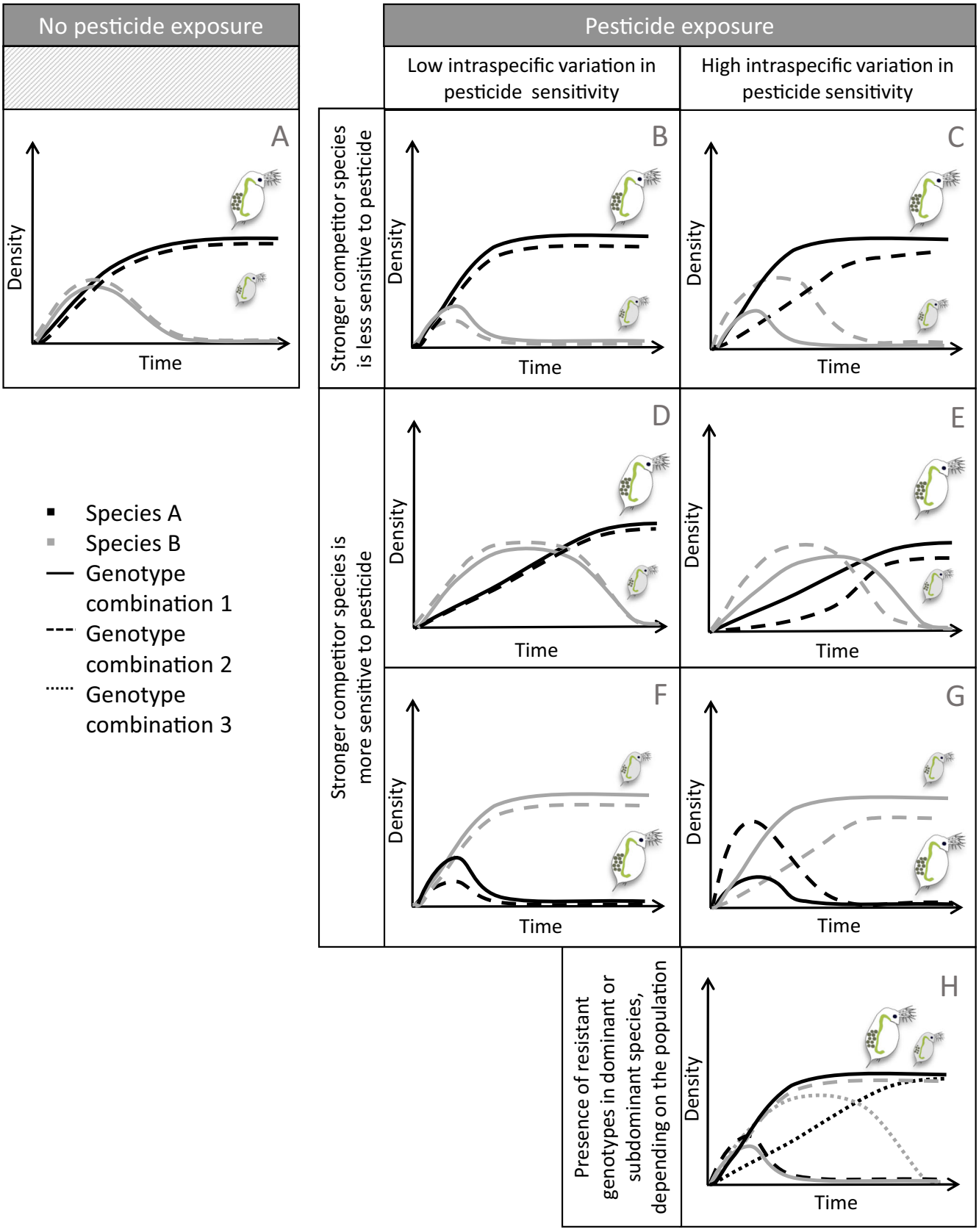


FIGURE 1 Legend on next page.

exposure than under control conditions (Fleeger et al., 2003; Figure 1D,E). If the larger species is very sensitive to the pesticide, a complete shift in community composition might occur, with the smaller species becoming dominant (Figure 1F,G). As different genotypes can respond differently to pesticide exposure, this can result in communities with the same species composition responding differently upon pesticide exposure (Bendis & Relyea, 2016). In the case of high intraspecific variation in pesticide sensitivity, communities may show different dynamics depending on the genotypic composition of the interacting species (Figure 1C,E,G). If intraspecific differential sensitivity is as large as the differences among species, the pattern of community dominance can be strongly dependent on the genetic composition of the different populations in the different communities (Figure 1H).

Here, we carried out an outdoor mesocosm experiment to study how exposure to pesticides affects the dynamics of four coexisting cladoceran species of the Daphniidae family and investigate how this translates into variation in community structure and ecosystem functioning. More specifically, we aimed to assess to what extent exposure to a model pesticide, chlorpyrifos (CPF), affects the population dynamics of four interacting cladoceran species that differ in competitive strength, and whether pesticide exposure affects competitive dominance. Given that chlorpyrifos sensitivity of *Daphnia magna* is reported to be lower than that of smaller *Daphnia* species (Palma et al., 2008; Raymundo et al., 2019; Simpson et al., 2015), we predicted that pesticide exposure would enhance the competitive dominance of *D. magna* at carrying capacity. However, as *D. magna* is also the species showing the longest development time, we also expected other species to dominate earlier in the experiment, and this pattern may also be impacted by chlorpyrifos exposure. More in general, we expected that the observed dynamics would reflect an interaction of direct effects of chlorpyrifos and indirect effects mediated by the presence of other species. In addition, we assessed whether variation in genetic composition within species contributed to differences in community responses. Finally, we tested whether altered community structure linked to pesticide exposure translated into a differential top-down impact on phytoplankton.

MATERIALS AND METHODS

Mesocosm experiment

We carried out an outdoor mesocosm experiment that lasted 6 weeks during the summer (July–August) of 2019. For this experiment, 30 mesocosms (210 L) were set up in an open field, and were filled with filtrated pond water (10%) and tap water (90%), enriched with nutrients (4.12 g of $NaNO_3$ and 0.37 g of KH_2PO_4). An inoculum of green algae *Acutodesmus obliquus* (85×10^8 cells/L) was added to each mesocosm after 1 week to stimulate the build-up of a phytoplankton food base for cladoceran grazers. The cladoceran community was added to the mesocosms 4 days later (this moment was considered day 0). We created five different sets of communities, each of them consisting of the same four species of the family Daphniidae (*Daphnia magna*, *Daphnia pulicaria*, *Daphnia galeata* and *Scapholeberis mucronata*), but being represented by different sets of four genotypes. This resulted in communities that varied in their genetic composition but were standardized in the amount of genetic diversity. Such design allowed us to account for variation in responses related to the genetic composition of the different populations making up the communities. As the different species have different maturation times and to avoid using sensitive juveniles, we isolated matured females of each species. In order to standardize the biomass for all species at the inoculation moment, the number of individuals added in the mesocosms for each species was adjusted to the average adult body size of the species. Hence, to each mesocosm we added, from each clonal lineage, two individuals from *D. magna* ($n = 8$, 2 individuals × 4 clonal lineages), six from *D. pulicaria* ($n = 24$), eight from *D. galeata* ($n = 32$) and 12 from *S. mucronata* ($n = 48$). These numbers were based on a length–weight regression published by

FIGURE 1 Representation of hypothetical scenarios of how pesticide exposure may affect the population dynamics of two coexisting and competing species. The larger species is represented by black lines and the smaller species is represented in gray. Line types (full, dashed, dotted) represent different genotype combinations and thus illustrate the effect of intraspecific variation, that is, the variation that is linked to the different species being represented by different genotypes (populations). In the absence of pesticides, the larger bodied species is expected to become dominant in the community because it is competitively superior (A). In the presence of pesticides, the trajectories change depending on whether the stronger competitor is more or less sensitive to the pesticide than the weaker competitor. When exposed to a pesticide, communities with the same species composition will have similar responses when there is low intraspecific variation in pesticide sensitivity (B, D, F). If intraspecific variation in pesticide sensitivity is high, different communities that are composed of different combinations of genotypes might show very different trajectories (C, E, G, H). *Daphnia* illustrations by Rafaela A. Almeida.

Dumont et al. (1975). All clonal lineages from all four species were obtained from the same pond in Belgium, Langerodevijver (50°49′42.2″ N, 4°38′23.7″ E). As a result, in this experiment we quantified the effect of exposure to a pesticide on the coexistence and population dynamics of four populations that naturally co-occur in the same pond. Similarly, the intraspecific genetic variation that we study in the genotype treatment refers to genetic variation within a single population (i.e., we did not study the effect of genetic variation linked to environmental gradients in landscapes).

Each mixture was combined in a cross-factorial design with two treatments: a control and a chlorpyrifos treatment. Each condition (treatment × mixture) was replicated three times, resulting in a total of 30 mesocosms (Appendix S1: Figure S3). During the experiment, three chlorpyrifos pulses were given. The first CPF pulse (0.3 μg/L) was given 10 days after the inoculation of the zooplankton communities. The second pulse of CPF (0.45 μg/L) was given on day 24, and the third pulse (0.675 μg/L) on day 38. We chose to apply pulses of increasing concentrations (each time ×1.5) because this was expected to better reveal the effect of differences in sensitivity among species by ensuring that the most sensitive species would not be eliminated from the first pulse while preventing the more resistant species would not be affected. CPF solutions were prepared following the protocol outlined below.

Clone isolation and rearing

The four cladoceran species used in this experiment were *D. magna*, *D. pulicaria*, *D. galeata* and *S. mucronata*. These species vary in their body size: large-bodied *D. magna* (size at maturity ~3–4 mm, Błędzki & Rybak, 2016; De Meester, 1995), intermediate-sized *D. pulicaria* (~2.0 mm, Vanvelk et al., 2020) and *D. galeata* (~1.7 mm, Vanvelk et al., 2020) and the much smaller *S. mucronata* (~1 mm, Chang & Hanazato, 2005). They also vary in average development time (egg till maturation): shortest in *S. mucronata* (5.4 days at 20°C; Lemke & Benke, 2003), intermediate (5.5–6.5 days at 20°C) in *D. galeata* and *D. pulicaria*, and longest in *D. magna* (~8 days at 20°C, De Meester, 1995; van Doorslaer et al., 2009). Given that there is genetic variation in sensitivity to pesticides and that all four species were isolated from the same pond, we verified using an immobilization test whether the gradient in sensitivity to chlorpyrifos reported in the literature was also present in the specific *Daphnia* populations we used in our experiment. We indeed observe that also for the populations used, *D. magna* was less sensitive to chlorpyrifos than the smaller *Daphnia* species, and *D. galeata* is slightly more sensitive than *D. pulicaria* (for the results of these immobilization tests, see Appendix S1: Box S1).

The clonal lineages of the four species used in this experiment were hatched from dormant eggs collected from one shallow eutrophic pond in Flanders, Belgium (50°49′42.2″ N, 4°38′23.7″ E). Resting eggs of Daphniidae species are formed through sexual reproduction (Ebert, 2005), hence being genetically unique. The eggs were harvested in April–May 2018 by sampling the upper 2 cm sediment layer of the pond. To hatch the dormant eggs in the laboratory, the sediment was thinly spread on white trays filled with dechlorinated tap water and incubated at 20 ± 1°C and under a photoperiod of 16 h light/8 h dark. The trays were checked every second day for new hatchlings. From these hatchlings, we randomly isolated 20 unique clonal lineages for each species ($20 \times 4 = 80$), which were randomly allocated to five groups of four clones per species (five genetic mixtures).

All clonal lineages were cultured under standardized laboratory conditions (20 ± 1°C, 16 h light/8 h dark) for multiple generations to avoid interference of maternal effects in our experiment. Prior to inoculation in the mesocosms, the animals were reared in 2-L aquariums filled with dechlorinated tap water. The aquariums were rinsed twice a week and the water was refreshed once a week. The animals were fed every second day by restoring the food concentration of 1×10^5 *Acutodesmus obliquus* cells/mL. From these monoclonal cultures, individuals of each clone were randomly selected for the mesocosm experiment. The 20 clonal lineages of each species were randomly distributed over five different mixtures, each mixture representing a different combination of four unique lineages of each species.

Pesticide preparation

Chlorpyrifos (CPF; CAS 2921-88-2, purity >99%, Sigma-Aldrich) is a broad-spectrum organophosphorus insecticide commonly used in agriculture (Eaton et al., 2008; Racke, 1993). Chlorpyrifos is a neurotoxic pesticide that acts as an acetylcholinesterase inhibitor and impairs neurotransmission at cholinergic synapses (Eaton et al., 2008). Environmentally relevant concentrations of chlorpyrifos were chosen that covered the sensitivity range that was expected to affect the different species (López-Mancisidor et al., 2008; Palma et al., 2008; Raymundo et al., 2019; Simpson et al., 2015; see also Appendix S1: Box S1 for differential impact on the study species). We implemented the pulses such that there was a ×1.5 increase with each pulse: 0.3, 0.45 and 0.675 μg/L. At the beginning of the experiment, a stock solution was prepared at a concentration of 1 mg/mL and was stored in

the dark and in the cold in a dark-colored glass vial. The stock solution was used throughout the whole experiment. The final concentrations were prepared on the day on which they were added to the mesocosms.

Collection of data

Samples from the zooplankton community were collected every week from all mesocosms. Before taking the samples, the water in the mesocosm was gently mixed and 5 L of water was subsequently collected and filtered through a plankton gauze sieve (mesh size: 64 μm). Samples (final volume 42 mL) were fixed with formaldehyde (4%) until further processing in the laboratory. Twice per week, the biomass of phytoplankton and cyanobacteria were estimated by measuring the concentration of in vivo chlorophyll *a* (Chl *a*) and phycocyanin, respectively, using a handheld fluorometer (Turner Designs). Conductivity and pH were measured using a HACH HQ40 probe (for values see Appendix S1: Table S1). The temperature was registered for six randomly chosen mesocosms using data loggers, which recorded hourly data throughout the entire experiment. Nutrient samples were taken in weeks 1, 3, and 6. The concentration of total phosphorous (TP) and total nitrogen (TN) was measured after persulfate digestion. Zooplankton samples were processed in the laboratory by identifying and counting at least 200 animals per sample using a stereomicroscope (Olympus SZx12). Zooplankton abundances were converted into biomass data using the body size–dry weight regressions reported by Bottrell et al. (1976). Body size data were collected by measuring 10 adults from each species in each mesocosm during the two last time points of the experiment. However, *D. galeata* and *S. mucronata* were extinct in most of the mesocosms under pesticide treatment at these time points. Therefore, we retrieved body length values from Dumont et al. (1975) for these two species. Population biomasses of *D. magna* and *D. pulicaria* were determined using the mean of the measured body sizes across all mesocosm and both time points as we did not encounter systematic differences in body size between treatments for both species.

Statistical analysis

We developed a Bayesian hierarchical model to study the impact of pesticide exposure on community dynamics. Specifically, we aimed to assess the variation in temporal dynamics of the community between the control and the pesticide treatment by taking into account the hierarchical nature of the experimental design (i.e., replicates nested within genetic mixtures, nested within treatment). For this, we tailored a hierarchical Gaussian process model to parsimoniously model biomass time series data (C. E. Rasmussen & Williams, 2006). The outcome of interest is $y_{m,s,d}$, the $\log(1+.)$-transformed observed biomass of the different cladoceran species, phytoplankton and cyanobacteria $s \in \{D.\,magna, D.\,galeata, D.\,pulicaria, S.\,mucronata, \text{Chl } a, \text{phycocyanin}\}$ in mesocosm $m \in \{1,2,...,30\}$ during day d. We define $t(m) \in \{\text{control}, \text{pesticide},\}$ and $g(m) \in \{1,2,...,5\}$ as the pesticide treatment and the genetic mix of mesocosm m, respectively.

Gaussian processes (GP) are uniquely defined by a mean and a covariance function. While the mean function is often set to zero for convenience reasons, the covariance function is important as it describes the covariance between any two data points as a function of their distance (C. E. Rasmussen & Williams, 2006). We used an exponentiated quadratic covariance function to describe the covariance in log-biomass between two time points as a function of the number of days $\Delta d = |d - d'|$ that separates them:

$$k(\Delta d) = \alpha^2 \exp\left(-\frac{1}{2}\left(\frac{\Delta d}{\rho}\right)^2\right),$$

where α^2 is a marginal variance parameter that controls the amplitude in log-biomass fluctuations, and ρ is a length scale parameter that controls the rate at which the covariance decays with increasing Δd.

Specifically, we modeled the log-transformed observed biomasses for each mesocosm m, species s and day d as the sum of three smooth function realizations and a noise term:

$$y_{m,s,d} = f^{\text{main}}_{s,t(m)}(d) + f^{\text{gen}}_{s,g(m),t(m)}(d) + f^{\text{meso}}_{s,m}(d) + \varepsilon_s,$$

where $f^{\text{main}}_{s,t}$ is the main temporal pattern of species s under treatment t, $f^{\text{gen}}_{s,g,t}$ is the deviation in the temporal pattern of species s for genetic mix g under treatment t, $f^{\text{meso}}_{s,m}$ is the deviation in the temporal pattern of species s in mesocosm m, and $\varepsilon_s \sim \mathcal{N}(0, \sigma_s)$ is a species-specific, normally distributed measurement error. We assume the three smooth functions to follow a GP distribution:

$$f^{\text{main}}_{s,t} \sim \mathcal{GP}\left(0, k^{\text{main}}_{s,t}(\Delta d)\right),$$

$$f^{\text{gen}}_{s,g,t} \sim \mathcal{GP}\left(0, k^{\text{gen}}_{s,t}(\Delta d)\right),$$

$$f^{\text{meso}}_{s,m} \sim \mathcal{GP}\left(0, k^{\text{meso}}_{s,t}(\Delta d)\right),$$

where $k^{\text{main}}_{s,t}(\Delta d)$, $k^{\text{gen}}_{s,g,t}(\Delta d)$ and $k^{\text{meso}}_{s,m}(\Delta d)$ are the GP covariance functions. We consider the exponentiated

quadratic covariance functions to be different among GPs (main GP, genetic mix GP and mesocosm GP), as well as among species and treatments. Hence, $k_{s,t}^{\text{main}}(\Delta d)$, $k_{s,t}^{\text{gen}}(\Delta d)$ and $k_{s,t}^{\text{meso}}(\Delta d)$ have the following marginal variance (α) and length scale (ρ) parameter for each species s and experimental condition t: $\alpha_{s,c}^{\text{main}}$ and $\rho_{s,t}^{\text{main}}$, $\alpha_{s,t}^{\text{gen}}$ and $\rho_{s,t}^{\text{gen}}$, and $\alpha_{s,t}^{\text{meso}}$ and $\rho_{s,t}^{\text{meso}}$. By combining three GP layers into a single model, we obtain a hierarchical Gaussian process (HGP) model, similar to the approach of Hensman et al. (2013).

We chose a vague StudentT$^{+}(3,0,5)$-prior for the observation noise term's species-specific standard deviation parameter σ_s, and a vague standard half-normal $\mathcal{N}^{+}(0,1)$ prior for the three sets of marginal standard deviation parameters $\alpha_{s,t}^{\text{main}}$, $\alpha_{s,t}^{\text{gen}}$ and $\alpha_{s,t}^{\text{meso}}$. For the three sets of length scale parameters $\rho_{s,t}^{\text{main}}$, $\rho_{s,t}^{\text{gen}}$ and $\rho_{s,t}^{\text{meso}}$, we chose a moderately informative inverse gamma prior: an InvGamma$(6.5,2.0)$-prior for the zooplankton species and InvGamma$(3.6,0.6)$-prior for the photosynthetic pigments, which place most prior mass on length scales between the shortest and longest distance between any two time points. Additionally, we softly constrained $f_{s,t}^{\text{main}}$ to be equal for both treatments at days prior to the first pesticide pulse by means of a tight, zero-centered normal prior (with SD 0.05) on their difference, as any difference among mesocosms cannot be attributed to a treatment effect due to the randomization procedure.

While the model likelihood is only informed by the days on which the biomass was observed, our HGP model can provide posterior predictions for any set of time points to achieve interpolation, here chosen to be a daily grid spanning the experiment's duration, for visualization purposes. Wherever needed, more fine-grained interpolations were achieved through cubic splines (post hoc, fitted for each posterior iteration separately) as GP scale cubically with the number of time points and hence would quickly become too computationally intensive. As data on phytoplankton and cyanobacteria biomass were only available from the first pesticide pulse onwards, extrapolations for earlier time values were omitted from visualizations and interpretation.

For each species and experimental treatment, we investigated the differential impact of the pesticide on key population characteristics by calculating three derived quantities: the maximum biomass (at an hourly resolution), the day at which maximum biomass is reached (also at an hourly resolution) and the cumulated biomass over the experiment's duration (at a daily resolution). Comparing posteriors of these derived quantities enabled us to investigate the differential impact of pesticides on key population dynamics characteristics across species and treatments. In addition, hourly growth rates (i.e., the first derivative of the biomass curves) were calculated by evaluating the biomass change at 1 s time intervals using the finite difference method. Phase portraits based on the hourly biomasses and growth rates were constructed to obtain insights into how interspecific interactions affected temporal patterns in biomass, and how these were affected by exposure to pesticides. The hourly growth rates were plotted against the corresponding biomasses of the different interacting species (Seip, 1997).

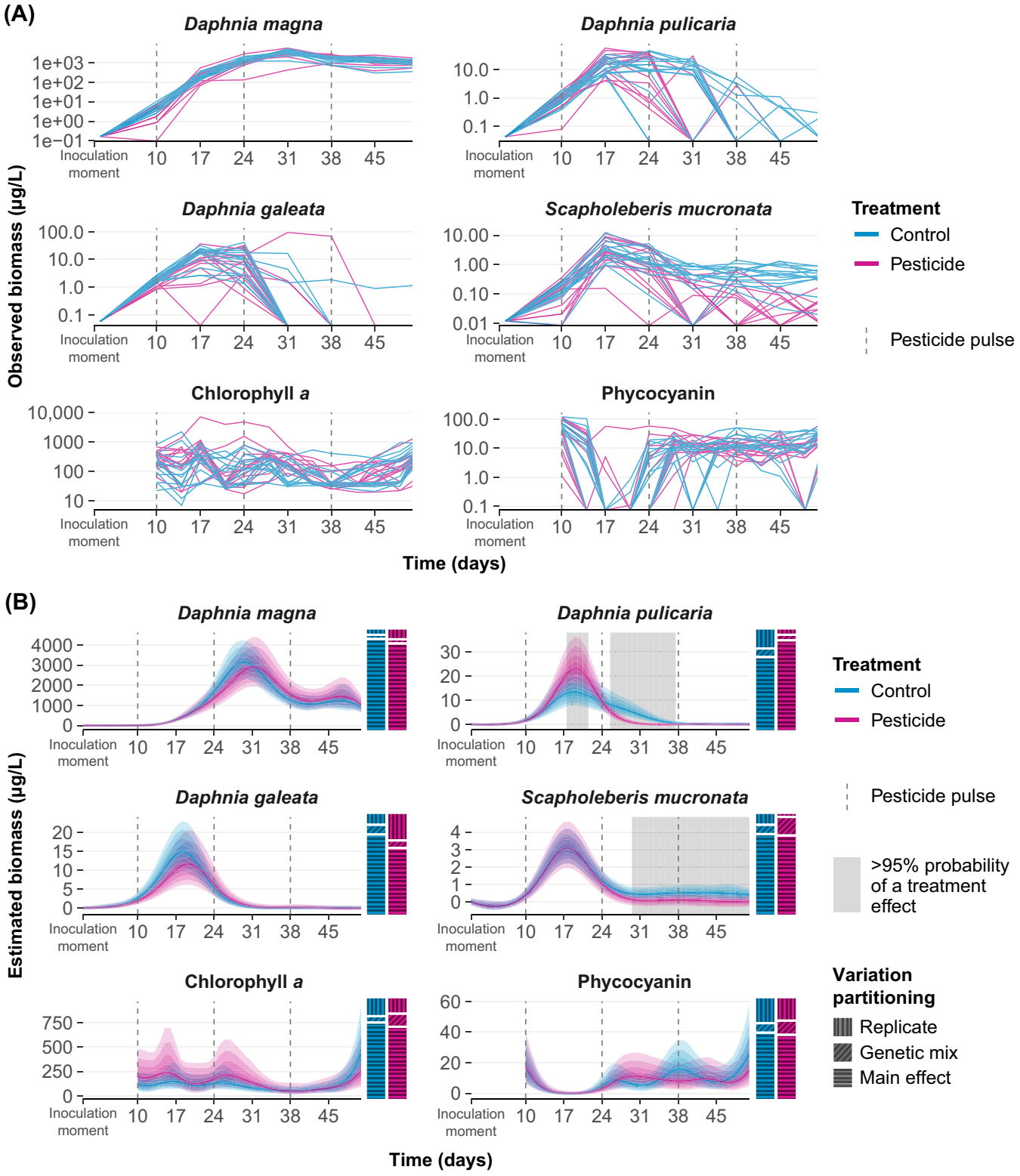
We implemented the HGP model using the probabilistic programming language Stan and the *rstan* v.2.21.2 package (Stan Development Team, 2020) in R v.4.0.3 (R Development Core Team, 2020). Stan performs Bayesian inference by means of dynamic Hamiltonian Monte Carlo (HMC), a gradient-based Markov chain Monte Carlo (MCMC) sampler (Carpenter et al., 2017). We ran four chains with 5000 iterations each, of which the first 2500 were discarded as a warm-up. The resulting 10,000 posterior samples are summarized using posterior medians and 95% equal-tailed credible intervals (bounded by the 2.5% and 97.5% samples from the distribution), unless otherwise specified. We used the *tidybayes* v.2.3.1 package (Kay, 2020) to visualize the posterior distributions. Cubic spline interpolation of the inferred biomass curves was achieved through the "spline" function of the *stats* package in R v.4.0.3 (Somanathan et al., 2004), using default settings.

We assessed model convergence both visually by means of traceplots and numerically by means of effective sample sizes, divergent transitions, and the Potential Scale Reduction Factor, for which all parameters had $\widehat{R} < 1.1$ (Vehtari et al., 2021). For two mesocosms, data were missing for one time point (one replicate of genetic mixture 2 and one replicate of genetic mixture 5, both under the pesticide treatment at day 16). The HGP model can easily deal with missing data, as the model likelihood is only conditioned on the observed data (Rubin, 1991).

The full code for the analysis is available at https://github.com/mfajgenblat/hgp-chlorpyrifos.

RESULTS

Data on zooplankton biomasses and photopigment concentrations (as a proxy for biomass of phytoplankton and cyanobacteria) as well as the estimated biomasses using the Bayesian hierarchical model are shown in Figure 2. All zooplankton species showed an initial increase in biomass, followed by a reduction and stabilization or, in some cases, extinction (Figure 2; see also Appendix S1: Figure S4). The rate of biomass increase was similar for the three smaller species (with a peak at around day 18), but was slower in the largest-bodied species *D. magna*.



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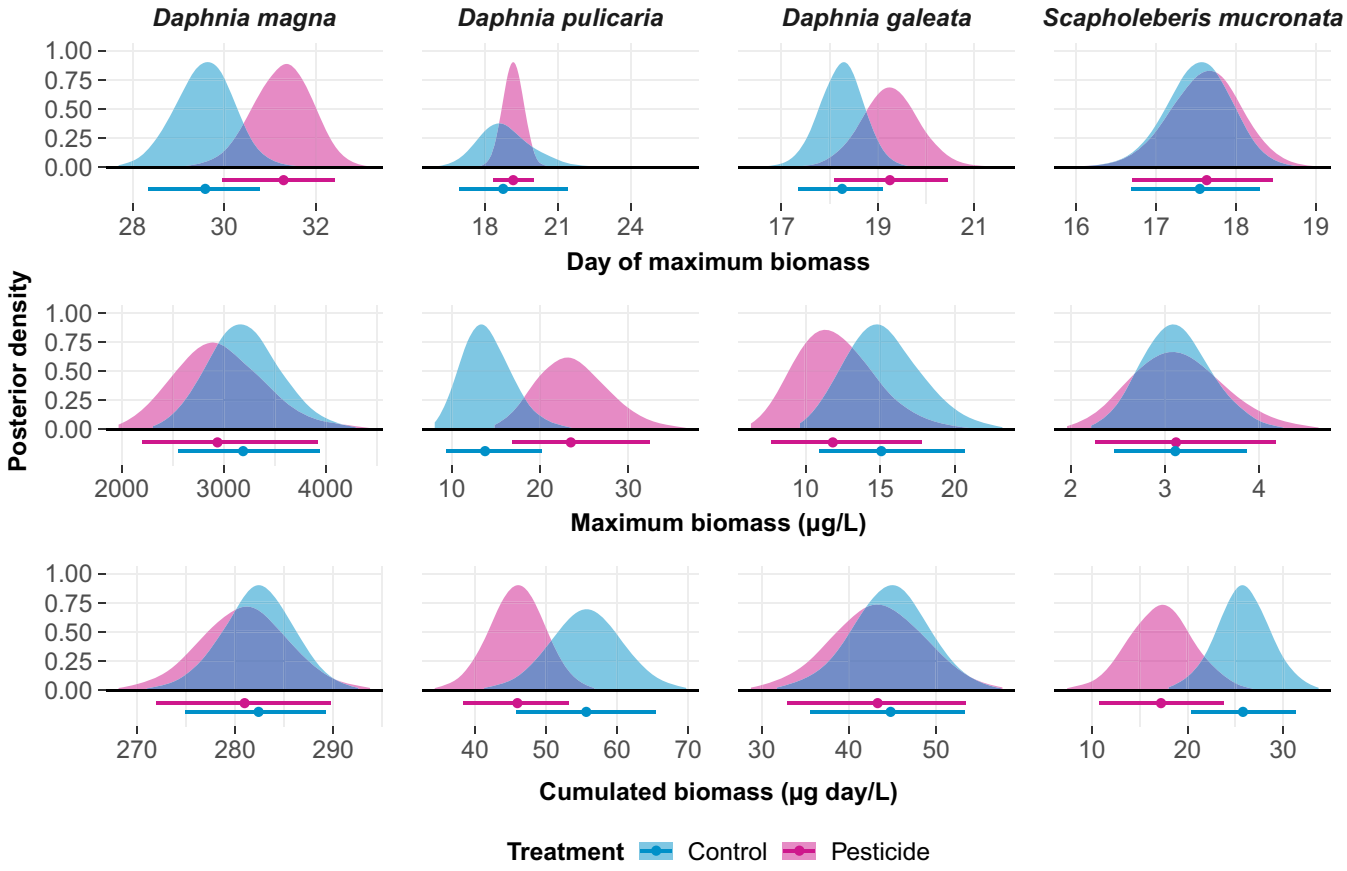

FIGURE 3 Posterior densities for the maximum biomass, the day at which maximum biomass is reached and the cumulated biomass (i.e., summed daily biomasses throughout the experiment's duration) for each species, for the control (blue) and pesticide (pink) treatment. The horizontal bars represent 95% credible intervals, while the dots represent the posterior medians.

Mesocosms exposed to chlorpyrifos showed a delay in the initial increase for two of the *Daphnia* species, *D. magna* and *D. galeata* (Figure 3), whereas *D. pulicaria* reached a higher biomass peak in the chlorpyrifos compared with the control treatment. After the initial peak, *D. magna* biomass remained quite high, and this species dominated the community from approximately day 30 onwards. Phytoplankton biomass varied over time, with biomasses of phytoplankton generally being lower when cladoceran biomass is higher, suggesting top-down control (Figure 2; see also Appendix S1: Figure S5). Chlorophyll *a* concentrations were generally higher than those of phycocyanin (cyanobacteria), but starting on day 24 phycocyanin concentrations tend to become higher.

FIGURE 2 Observed (A; logarithmic scale) and estimated (set of panels B; natural scale) biomass patterns throughout the experiment's duration of the four cladoceran species and observed and estimated patterns of changes in chlorophyll *a* and phycocyanin pigment concentrations as a proxy for phytoplankton and cyanobacteria biomass, respectively. Blue lines: control treatment; pink lines: pesticide treatment. Each line in (A) represents an individual mesocosm. Pesticide pulses are indicated by vertical dashed lines. In the panels of estimated biomasses (B), the full lines indicate the posterior median evolution, while the colored bands represent the 50%, 80%, 95% and 99% credible intervals. The gray shaded zones visualize timer periods at which the estimated probability of a difference between the control and the pesticide treatment is at least 0.95. The curves for phytoplankton and cyanobacteria only start at day 10, as their biomasses were not determined at the time of zooplankton inoculation ($t = 0$). The vertically stacked bars indicate the posterior mean fraction of variation explained by each hierarchical level of the experimental design, each represented by a different striped pattern. The "main effect" bar (bottom) shows the explained fraction of the biomass dynamics curve's amplitude that is shared across all genetic mixes and experimental units belonging to a specific treatment. The "genetic mix" bar (middle) represents the fraction of explained variation that is shared within but not across mixes. The "replicate" bar (top) shows the fraction of variation that is not shared across or within genetic mixes, but that can still be explained by the smooth function capturing the replicate-level variation (and, hence, does not concern unstructured residual noise). The left blue bar corresponds to the control and the right pink bar refers to the pesticide treatment.

In our model, temporal variation in each mesocosm's biomass curves is partitioned across three hierarchical levels (Figure 2). Across all species and treatments, most temporal variation in biomass across mesocosms can be attributed to the main effect of the pesticide treatment (fraction of explained temporal variation contributed by pesticide treatment: 75.89%; 95% CrI [56.57;92.93]). Genetic mixture (9.04%; 95% CrI [0.47;22.95]) and replicate identity (15.07%; 95% CrI [1.26;32.02]) only modestly affected temporal biomass patterns in individual mesocosms (averaged across all species and treatments; see Appendix S1: Figure S6 for species-specific and treatment-specific results). Genetic mixture and mesocosm identity thus did not strongly impact temporal patterns in zooplankton and phytoplankton biomass in our experiment.

We identified important differences in population biomass between the control and pesticide treatment for *D. pulicaria* and *S. mucronata* during specific periods of the experiment (areas in gray in Figure 2). Initially, *D. pulicaria* reached a higher population biomass in the pesticide treatment compared with the control (98.24% posterior probability of difference at the moment of maximal difference). Subsequently, differences lessen and higher biomasses are observed in the control treatment after the 24th day of the experiment. *D. pulicaria* goes extinct on approximately day 29 in the pesticide treatment (100.00% posterior probability of a difference at the moment of maximal difference), whereas it can co-occur with other species in the control treatment until the end of the experiment (see Figure 2A; see also Appendix S1: Figure S4). For *S. mucronata*, the difference between both treatments became apparent only after day 24 of the experiment (99.13% posterior probability of difference at the moment of maximal difference). *S. mucronata* tended to become extinct in the pesticide treatment, while it remained present in the control treatment (see Figure 2A). We did not identify periods with clear differences in biomass between the control and pesticide treatment for *D. magna* and *D. galeata*. In the second half of the experiment, there was some evidence that *D. magna* showed a higher biomass in the pesticide treatment compared with the control treatment (83.66% posterior probability that the cumulated biomass throughout this period is higher in the pesticide treatment).

The timing at which the maximum biomass is reached was delayed in the pesticide treatment compared with the control mesocosms for two of the four cladoceran species (Figure 3). For *D. magna*, this effect was strongest, with a posterior mean delay of 1.70 days (95% CrI [1.20;3.37], 97.62% probability of a delay), followed by *D. galeata*, with a posterior mean delay of 1.02 days (95% CrI [0.23;2.39], 94.17% probability of a delay). For *D. pulicaria* and *S. mucronata*, the delay was minimal, with a posterior probability of a delay equaling 64.04% and 55.59%, respectively.

With respect to the biomass at the moment of highest density (maximum biomass in Figure 3), *D. pulicaria* showed the strongest treatment effect, with a posterior mean increase in biomass of 9.73 μg/L (95% CrI [0.32;19.84], 97.82% probability of an increase) in pesticide compared with the control mesocosms (Figure 3). For the other zooplankton species, the posterior mean maximum biomass was lower in the pesticide mesocosms, but this effect was highly uncertain (Figure 3; 32.72%, 17.77% and 50.22% for *D. magna*, *D. galeata* and *S. mucronata*, respectively). The cumulated biomass throughout the experiment was similar in the pesticide and control treatment for *D. magna* and *D. galeata*, but was considerably lower for *D. pulicaria* and *S. mucronata* in the pesticide compared with the control mesocosms (Figure 3). For the two latter species, the posterior mean decrease in cumulated biomass equaled 9.74 μg·day/L (95% CrI [−2.63;21.70], 94.09% posterior probability of a decrease) and 8.59 μg·day/L (95% CrI [0.49;16.8], 98.09% posterior probability of a decrease), respectively.

We did not identify periods with clear differences in biomass of phytoplankton and cyanobacteria between both treatments. Nevertheless, in the early weeks of the experiment, there was a tendency for higher phytoplankton biomass in the pesticide mesocosms compared with the control mesocosms (94.27% posterior probability of difference at the moment of maximal difference).

The phase portraits involving *D. magna* were strongly different compared with the ones involving the other three zooplankton species (Figure 4). More specifically, we observed that a higher biomass of *D. magna* suppressed the growth rate of all other species, as illustrated by the strong decrease in the growth rate of *D. pulicaria*, *D. galeata* and *S. mucronata* once the populations of *D. magna* reached critical biomass (Figure 4A,E,I,M). The growth rate of *D. magna* showed no apparent relationship with the biomass of any of the other species (Figure 4A–D). When considering the effect of the biomass of *D. pulicaria* and *D. galeata* on their own growth rates and the growth rates of the other species (Figure 4F,G,J,K), we observed strong but opposite differences between the pesticide treatments. When exposed to pesticides, the growth rate of *D. pulicaria* was seemingly less suppressed by *D. galeata* biomass than in control conditions (Figure 4G). We observed the opposite pattern for *D. galeata*: under pesticide conditions we observed a stronger negative association between the biomass of *D. pulicaria* and the growth rate of *D. galeata* than under control conditions (Figure 4J). Although *S. mucronata* had the lowest growth rate, it was the only species besides *D. magna* that is not completely excluded by others under control conditions (Figure 4P).

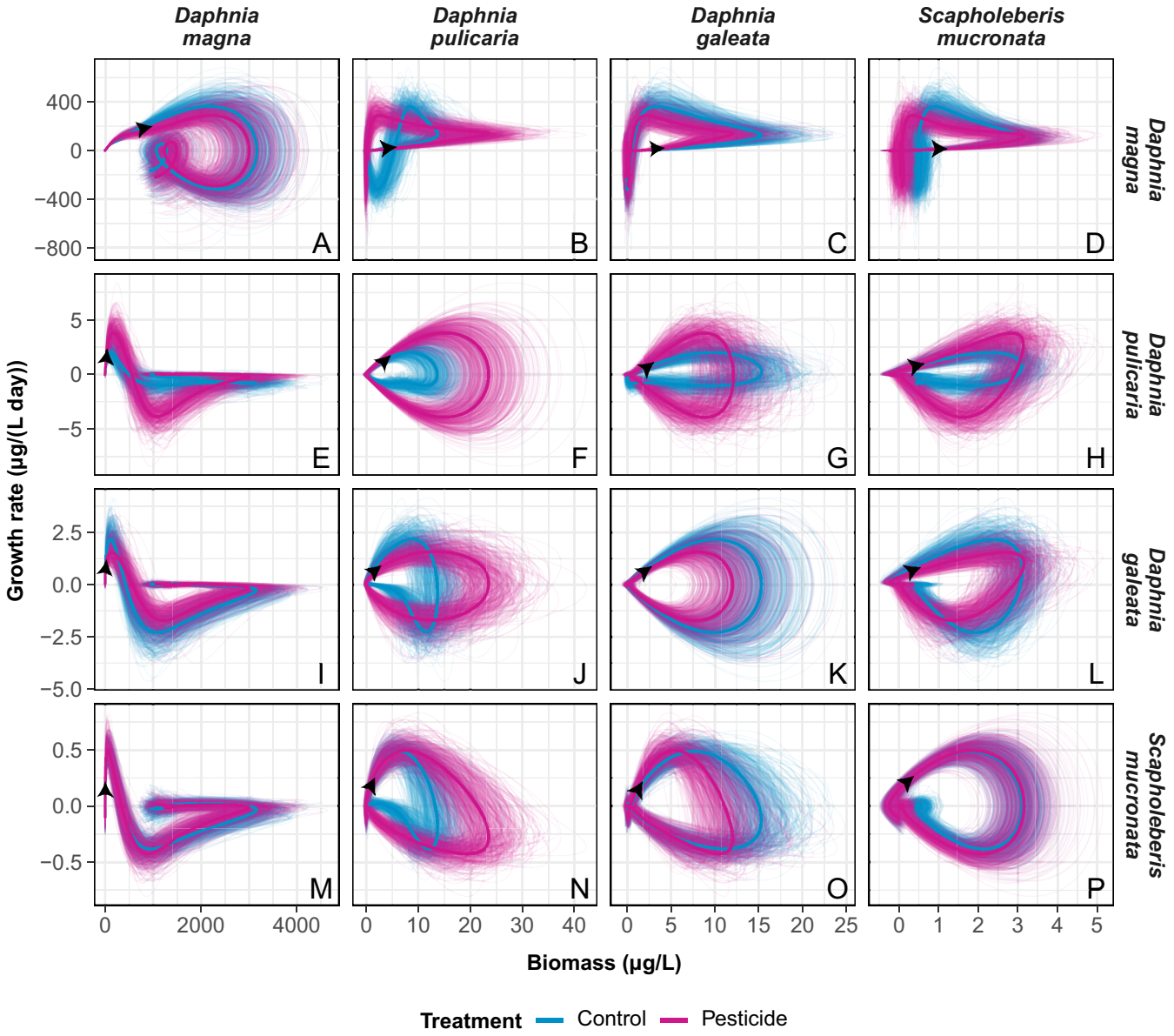

FIGURE 4 (A–P) Phase portraits showing the relationship between the biomass of a given species (columns) and the growth rate (rows) of itself and the other three species in the community, for the control (blue) and pesticide (pink) treatment. Faint lines represent individual posterior phase portrait trajectory draws (thinned to every 20th iteration). Thick lines represent the posterior mean phase portrait trajectories. Black arrowheads indicate temporal directionality.

DISCUSSION

Our results revealed that exposure to chlorpyrifos affected the dynamics of different cladoceran zooplankton species of the family Daphniidae. More specifically, it led first to a shift in dominance between the two smaller *Daphnia* species and subsequently to a more pronounced dominance of the strongest competitor, the large-bodied *D. magna*. This implied that the dominant competitor in the system became even more dominant in the presence of chlorpyrifos, in line with our data showing that *D. magna* was also the most tolerant to this pesticide of the three *Daphnia* species used in this study (scenario Figure 1B,C). Variation in genetic composition did not strongly affect community responses to chlorpyrifos exposure (scenario Figure 1B). There was no strong effect of chlorpyrifos exposure on phytoplankton biomass, although there was a trend for a higher Chl *a* concentration in the mesocosms exposed to pesticides compared with the ones in the control condition during the first half of the experiment. The observed community response of the Daphniidae to chlorpyrifos exposure (Figures 2 and 3) reflected a complex interaction between direct differential effects of the pesticide on the different

species, as well as indirect effects mediated through changed interactions with other species (Figure 4). The changes involved both changes in the timing of peak densities as well as in biomasses.

D. pulicaria populations reached higher densities in the chlorpyrifos compared with the control conditions in the first half of the experiment. Dominance in terms of biomass around day 18, the period when both smaller bodied *Daphnia* species reached their peak density, switched from *D. galeata* dominating in the control condition to *D. pulicaria* dominating in the pesticide treatment (Figure 2). This reflected the higher sensitivity of *D. galeata* compared with *D. pulicaria* to chlorpyrifos (Appendix S1: Figure S1), such that *D. galeata* was hindered in its population growth following application of the first pulse of pesticide exposure while *D. pulicaria* could grow to higher densities because of competitive release. This switch in the interaction between the two species is also clearly illustrated in the phase portraits (Figure 4). Other authors have similarly reported a high sensitivity of *D. galeata* to chlorpyrifos at concentrations similar to those used in our experiment (van den Brink et al., 1995). The largest species, *D. magna*, was dominant in the second half of the experiment, both in the pesticide and the control treatment. This reflects that *D. magna* is both a strong competitor and is relatively less sensitive to chlorpyrifos compared with the other species in our experiment. We indeed observed that this species was also able to withstand the highest concentration of chlorpyrifos applied in the current experiment (0.675 μg/L), whereas the other species were drastically reduced after the second pulse of chlorpyrifos (0.45 μg/L). This is in line with the results of our immobilization tests at these three concentrations (Appendix S1: Figure S1). Likely to be linked to the suppression of the other species, *D. magna* was able to reach slightly higher densities in the pesticide than in the control treatment mesocosms during the second half of the experiment. The fact that *D. magna* only started to dominate after day 17 reflected its longer development time (Vanvelk et al., 2020). *Scapholeberis* was hardly affected by the pesticide treatment in the first half of the experiment. In the second half of the experiment, its densities were drastically reduced in the pesticide treatment, most likely due to the high concentration of chlorpyrifos after the third pulse. In the control treatment, the species was still present, although in low densities, most likely to be because of food limitation due to the high densities of *D. magna*.

Our study clearly shows how pesticide exposure and competition interact to shape the changes in community structure. Pesticide exposure had multiple effects, such as a delay in peak densities of *D. galeata* and *D. magna*, a reduced peak density in *D. galeata* and an enhanced peak density of *D. pulicaria*, extinction of *D. galeata*, *D. pulicaria* and *Scapholeberis* in the second half of the experiment, and enhanced densities of *D. magna* in the second half of the experiment. Pesticide exposure did not cause a collapse in community-wide biomass, but rather a shift in species composition. Hébert et al. (2021) similarly observed that, even though other zooplankton groups were more susceptible, cladoceran biomass was not affected by pesticide exposure, as more tolerant species were able to compensate for the loss in biomass of more sensitive ones. This led to changes in community composition after pesticide exposure, but not to a reduction in total biomass. Our results also indicated that some responses were the direct consequence of pesticide exposure, whereas others were indirect effects linked to the differential sensitivity of the different species to chlorpyrifos resulting in shifts in competitive interactions. Our phase portrait analyses show, in general, that the dynamics of *D. magna* are not negatively influenced by higher biomasses of the other species (Figure 4B–D), whereas the population growth rates of the other species are negatively affected by the increase in biomass of *D. magna* in the first half of the experiment (Figure 4E,I,M). This shows that indirect effects are important, and that the strongest competitor plays an important role in the observed dynamics. The timing of this effect is determined by the somewhat longer generation time of the competitively dominant species, leaving a time window for the other species to reach peak densities earlier in the experiment. The observed patterns also suggested that the delay in the peak density of *D. magna* in the pesticide treatment was due to a direct response to the pesticide. Indeed, earlier studies have shown that chlorpyrifos reduces the reproductive capacity of *D. magna* both by reducing brood size (Palma et al., 2009) and delaying reproductive timing (Song et al., 2017).

Our results of the community response experiment were largely in line with predictions one could make based on the differences in the sensitivity shown by the results of our immobilization tests. This indicates that the immobilization tests on juveniles do capture more general differences in sensitivity of the species at different life stages and endpoints. Demographic trajectories and community assembly do indeed integrate features of a whole suite of traits (survival, reproduction, development time, competitive strength, energy allocation, etc.). Yet, without the knowledge of other traits (cf. competitive strength, development time, niche overlap), one would predict a stronger dominance of *D. magna* (cf. Figure 1B), but not the shifts in timing at which peak densities are reached. The fact that the communities would first be dominated by the smaller species and that in the first instances of the experiment the relative

abundances of *D. galeata* and *D. pulicaria* would reverse depending on exposure to chlorpyrifos (Figure 2), means that the interaction between *D. magna* and the other species is highly asymmetric, whereas that between the two smaller species is more symmetric. Another aspect that the immobilization tests do not account for is the possibility of variation in toxicity associated with food availability. Resistance of *Daphnia* individuals to pesticides has been shown to increase (Ieromina et al., 2014; Shahid et al., 2019) or decrease (Folt et al., 1999) with higher food concentrations, and the direction of this correlation can vary between pesticides and the route of exposure (i.e., water and/or food-borne; Barry et al., 1995; Folt et al., 1999), as well as among species (Antunes et al., 2004) and life stage (Reyes et al., 2015). Yet, the results of our mesocosm experiment generally conformed to predictions based on the differences in pesticide tolerance among species as observed in the immobilization tests. This indicates that food availability probably did not change the relative differences in pesticide tolerance for the species and pesticide tested.

While the main focus of our experiment was to disentangle community responses to chlorpyrifos exposure, we also tested whether genetic differences influenced these responses. Differences in the genetic composition of the communities did not translate into strongly different species responses to pesticide exposure. Previous studies have shown high intraspecific variation in pesticide sensitivity, for instance when comparing populations inhabiting agricultural areas compared with populations located in less disturbed areas (Bendis & Relyea, 2014, 2016; Coors et al., 2009; Hua et al., 2015; Jansen et al., 2015; Shahid et al., 2018). Bendis and Relyea (2014) showed that *D. pulex* collected from ponds located in agricultural settings were more resistant to chlorpyrifos compared with populations from more natural areas. In a follow-up study (Bendis & Relyea, 2016), the same authors showed that communities that included *D. pulex* populations with evolved resistance to chlorpyrifos showed significantly higher abundances under pesticide exposure (at a concentration of 0.5 μg/L) compared with communities with sensitive populations. In another experiment that focused on community assembly, evolution in *D. magna* to specific environmental conditions, namely the presence of fish and macrophytes, was shown to influence the community composition of zooplankton (Pantel & Duvivier, 2015). More in general, multiple studies have shown eco-evolutionary dynamics where evolution in one species influences population dynamics or community composition (Crutsinger et al., 2008; Fridley & Grime, 2010; Hendry, 2017). In our experiment, we did not observe an effect of manipulating the genotype composition of the different species on population and community dynamics. This is not necessarily in contrast with earlier evidence of ecological consequences of evolutionary change, because our test was very conservative. In our experiment, we compared settings in which populations differed in genotypic identity by randomly allocating groups of four clones to treatments. By randomly picking clones we tested for the average effect of differences in genetic identity within a given population, which is the proper design if one wants to assess the relative contribution of interspecific and intraspecific variation to the observed patterns. Yet, this underestimates the potential for genotypic effects. For a proof-of-principle that genotypic differences can impact community dynamics, it would have been more effective to select genotypes that differed in sensitivity to chlorpyrifos or to use genotypes from different populations (as in Bassar et al., 2010; Bendis & Relyea, 2014; Harmon et al., 2009). In summary, our results did not refute the possibility that genetic composition might influence the community responses to chlorpyrifos exposure, but rather indicated that its effect was low when working with groups of randomly picked clones from a single population. Future studies including populations with different backgrounds in pesticide exposure might show a stronger potential for pesticide adaptation to influence community dynamics and ecosystem features upon pesticide exposure.

Changes in zooplankton community structure in response to pesticide exposure have been shown to cause a reduction in the capacity to top-down control phytoplankton growth and thus maintain the clear water state in freshwater ecosystems (Mcmahon et al., 2012; Relyea, 2005; Rumschlag et al., 2020). Large *Daphnia* species are key grazers in pond systems (Gianuca et al., 2016; Miner et al., 2012) and a reduction in their population growth rates and densities can have cascading effects on ecosystem functioning by reduced top-down control of phytoplankton communities (Relyea & Diecks, 2008; Rumschlag et al., 2020). While we expected higher concentrations of Chl *a* in mesocosms treated with pesticide compared with control ones, we did only observe a trend for higher Chl *a* concentrations during the first half of the experiment. The reason for this weak response is likely to be that, after an initial phase in which the smaller *Daphnia* species still represented a considerable fraction of total biomass, *D. magna*, the most efficient grazer (Gianuca et al., 2016), became dominant and reached equal or higher densities as in the control treatment. The absence of a strong phytoplankton response in our experiment is thus linked to the fact that *D. magna* is not only the least sensitive and competitively dominant species, but also the most efficient grazer on phytoplankton. Other studies similarly have shown that, even when anthropogenic stressors led to the local extinction of a subset of species, this did not always

translate into significant changes in ecosystem functioning (Mcmahon et al., 2012; Rodrigues et al., 2018). This can happen when the species that are eliminated are not the main contributor to a particular ecosystem function (Rodrigues et al., 2018). It is also important to consider that pesticide exposure can have indirect impacts on phytoplankton concentrations by reducing the grazing efficiency of *Daphnia* individuals. Several studies have shown that feeding behavior in *Daphnia* species can be affected by pesticides (Bengtsson et al., 2004; Pestana et al., 2010) including chlorpyrifos (Loureiro et al., 2010). Although variation in densities of the different species was an important factor determining differences in Chl *a* concentrations between treatments, it is also likely that other sublethal effects contributed to these dynamics, such as reduced grazing efficiency under pesticide exposure. Lower concentrations of chlorpyrifos may have stronger impacts on the grazing efficiency of smaller species due to their higher sensitivity. This could further explain the stronger variation in Chl *a* densities at the beginning of the experiment, as the grazing efficiency of more sensitive species may have been affected even at low pesticide concentrations.

Our experiment showed clearcut differences in community trajectories in simple communities of coexisting zooplankton species between pesticide-exposed and control treatments. While the communities we studied were simplified, the community trajectories upon pesticide exposure reflected the interaction between direct effects of the pesticide on the different species and indirect effects mediated by changes in the competitive environment. This highlights the complementary between highly standardized and simplified single-species tests and community assessments and their combined importance for disentangling the direct effects of toxicants and indirect effects on and mediated by biotic interactions.

AUTHOR CONTRIBUTIONS

Rafaela A. Almeida, Pieter Lemmens and Luc De Meester conceived and designed the study. Rafaela A. Almeida executed the data collection. Maxime Fajgenblat performed the data analyses in interaction with Rafaela A. Almeida and Luc De Meester. Rafaela A. Almeida led the writing of the manuscript, with input from Luc De Meester, Maxime Fajgenblat and Pieter Lemmens in different rounds of editing. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Almeida et al., 2023) are available in Dryad: https://doi.org/10.5061/dryad.7pvmcvf00.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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