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Research

Measuring the contribution of evolution to community trait structure in freshwater zooplankton

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There are currently few predictions about when evolutionary processes are likely to play an important role in structuring community features. Determining predictors that indicate when evolution is expected to impact ecological processes in natural landscapes can help researchers identify eco-evolutionary 'hotspots', where eco-evolutionary interactions are more likely to occur. Using data collected from a survey in freshwater cladoceran communities, landscape population genetic data and phenotypic trait data measured in a common garden, we applied a Bayesian linear model to assess whether the impact of local trait evolution in the keystone species *Daphnia magna* on cladoceran community trait values could be predicted by population genetic properties (within-population genetic diversity, genetic distance among populations), ecological properties (Simpson's diversity, phenotypic divergence) or environmental divergence. We found that the impact of local trait evolution varied among communities. Moreover, community diversity and phenotypic divergence were found to be better predictors of the contribution of evolution to community trait values than environmental features or genetic properties of the evolving species. Our results thus indicate the importance of ecological context for the impact of evolution on community features. Our study also demonstrates one way to detect signatures of eco-evolutionary interactions in communities inhabiting heterogeneous landscapes using survey data of contemporary ecological and evolutionary structure.

Keywords: community trait structure, *Daphnia magna*, eco-evolutionary dynamics, evolutionary ecology, trait-based ecology, zooplankton

Introduction

Evolutionary and ecological processes have been shown to dynamically influence one another (Hairston et al. 2005, Pelletier et al. 2009, Hendry 2017) and there is increasing evidence that evolutionary trait change may explain species composition patterns

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that cannot be understood by considering ecology in isolation (Whitham et al. 2006, Urban et al. 2008, 2020). Several studies have demonstrated that contemporary evolution can in some cases explain as much variation in community structure as ecological processes (Palkovacs and Post 2009, terHorst et al. 2014, Pantel et al. 2015, Gómez et al. 2016). Although the magnitude of effect of evolutionary processes for community structure has been measured in some systems, there is not a clear understanding of what causes variation in this effect, especially in natural systems (De Meester et al. 2019).

Local and regional properties of communities can determine the degree to which evolutionary change occurs (Barraclough 2015). If evolution occurs, then these local and regional properties can also determine the magnitude of effect this evolutionary change can have on ecological processes. In other words, the strength of interacting eco-evolutionary processes (where evolution can impact community structure) depends not only on evolutionary drivers such as genetic diversity (Fisher 1958, Frank and Slatkin 1992), but also on ecological context (De Meester et al. 2019). For example, communities in isolated locations with infrequent dispersal from other sites may have unoccupied niche space, which can increase opportunities for evolutionary diversification of populations in these locations (Urban et al. 2008). Interactions with other species (e.g. competition, mutualism) can also promote or inhibit evolutionary responses of resident species (Fukami et al. 2007, de Mazancourt et al. 2008, Lawrence et al. 2012). To better understand the drivers of eco-evolutionary dynamics in natural landscapes, it is important to identify the landscape, genetic and ecological features that influence whether evolutionary change has a strong impact on communities.

Freshwater zooplankton are an interesting model system to study the impact of evolutionary change on ecology, as previous studies have shown that *Daphnia* evolution can have a profound impact on interactions with other species (Steiner et al. 2007) and on the overall diversity and composition of zooplankton communities (Howeth et al. 2013, Pantel et al. 2015). Zooplankton occur in ponds and lakes that form a patchy landscape, and can experience both significant shifts in community structure (Cottenie and De Meester 2004, Norlin et al. 2006) and phenotypic evolution in response to landscape features and environmental variation (Morgan et al. 2001, Chen et al. 2015). We therefore expect that trait distributions in local zooplankton communities will be impacted both by ecological and evolutionary processes. Traits such as age and size at maturity or number of offspring are closely linked to fitness and can respond strongly to changes in the environment (Lande 1982, Stearns 1989). These traits can influence population growth dynamics as well as community coexistence patterns (Bonsall et al. 2004, Sæther et al. 2013, Lancaster et al. 2017).

Trait-based ecology (Litchman et al. 2013) and evolutionary ecology are well developed in zooplankton (Miner et al. 2012), and life history traits play a central role in this research (Dodson 1974, Woodward et al. 2005). Body size is often under selection in zooplankton taxa (Lynch 1977) because of its role in grazing efficiency (Hall et al. 1976, Gianuca et al. 2016) and in susceptibility to predation (Brooks and Dodson 1965). Age at maturity is determined by development rate, which in zooplankton is highly dependent on temperature, food availability and predation pressure (Reede 1995, Beckerman et al. 2010). Clutch size represents an individual's reproductive output and is strongly influenced by food availability and predation (Vanni and Lampert 1992, Reede 1995). Together with fecundity, age at maturity is a key trait affecting population growth rate. Fast population growth rates are selected for in a wide variety of circumstances, such as in environments with high predation pressure, when organisms colonize new habitats, or when environments only allow for short growing seasons (Roff 2002, Stoks et al. 2016). These life history traits have also been shown to play a strong role for coexistence in some freshwater zooplankton communities (Spaak and Hoekstra 1995, Spaak et al. 2000). Overall, these studies suggest that understanding trait distributions in zooplankton communities will require knowledge of evolutionary trait change in resident species. The importance of intraspecific variation for community structure is well established (Ackerly and Cornwell 2007, Bolnick et al. 2011, Violle et al. 2012). However, the importance of phenotypic evolution in individual species for observed patterns of community trait distributions, as well as what determines the variation in the impact of phenotypic evolution in natural communities, is not well understood.

Studies have indicated rapid evolution in the keystone herbivore *Daphnia* (Hairston et al. 1999, Cousyn et al. 2001, Duffy and Hall 2008), and that such rapid evolution in *Daphnia* can have a large impact on communities and ecosystems (Walsh et al. 2012, Pantel et al. 2015). We therefore expect that evolutionary trait change in one species, *Daphnia magna*, can impact community trait structure in natural communities of freshwater cladocerans. The goals of our study were to quantify the magnitude of these impacts in natural pond communities, and to assess which factors determine the relative importance of evolutionary trait change for community trait composition. To our knowledge, there are no existing studies that attempt to identify which factors (i.e. properties of the evolving population or of the community) might determine this among-site variability. In this study, we 1) quantify the degree to which evolution in a focal species structures local community trait values in a natural, heterogeneous landscape, and 2) identify predictors of the magnitude of evolution's impact on community trait values. We combined a survey of genetic variation in life history traits and neutral molecular markers in *D. magna* with a metacommunity survey of trait and species composition of cladoceran communities in 20 ponds. Specifically, we answer two main questions: 1) to what extent does local evolution of *D. magna* contribute to among-community variation in life history traits?, and 2) how do landscape, population genetic and community properties influence the role of *D. magna* evolution for community trait composition? Our study thus moves beyond demonstrating that evolution can play an important

role in structuring communities and instead seeks to identify ways to determine when evolution plays an important role in structuring communities.

Material and methods

Environmental survey

Based on previous surveys (De Bie et al. 2012), we selected 20 ponds with zooplankton communities that contained populations of *Daphnia magna* and that are situated along gradients of fish predation and land use intensity. We selected 10 inland ponds, centered near the city of Leuven, and 10 coastal ponds, located near Belgium's North Sea coast (Supporting information). The sampled ponds ranged from 120 to 140 000 m^2 in surface area, but most were smaller than 35 000 m^2. In April 2007, we characterised 12 environmental variables at each site: O_2 concentration (mg l^{-1}), pH, conductivity (μsiemens per centimeter, μS cm^{-1}), macrophyte coverage (percent coverage by floating and submerged vegetation), surface area (m^2), suspended particulate matter (mg l^{-1}), chlorophyll a concentration (μg l^{-1}), total nitrogen (mg l^{-1}), total phosphorus (mg l^{-1}), percent of arable land within a 200 m radius, the distance (m) to the nearest crop field and fish predation intensity (detailed in Supporting information). Planktivorous fish abundance was based on electrofishing survey supplemented by fishing with fyke nets in larger ponds. Given that fish sampling by electrofishing gives biased results depending on the behaviour of species, we characterized fish predation intensity in broad categories: fish absent (0), *Gasterosteus aculeatus* present in samples at an abundance < 100 individuals (1), *G. aculeatus* > 100 individuals (2), *G. aculeatus* with other species present at low abundances (3) and at high abundances (4).

Zooplankton collection

To evaluate population genetic composition of *Daphnia magna* populations and cladoceran community composition, we collected 200–800 g of sediment from the upper 2 cm of each pond in March and April 2007. This depth likely encompasses dormant egg deposits from the previous two to four years (Cousyn and De Meester 1998). The sediment samples were stored at 4°C. Between January and April 2009, we filtered a variable mass of stored sediment through a 125 μm sieve to remove soil. The amount of sediment varied between 200 and 800 g for each pond, based on a previous pilot experiment that determined the estimated mass of sediment needed to obtain sufficient numbers of hatchlings for each pond. We then isolated the remaining dormant eggs using a sugar flotation method (Onbé 1978, Marcus 1990). An oversaturated sugar solution (1000 g l^{-1}) was added to the filtered sediment and this combination was placed in a 50 ml Falcon tube and centrifuged for three then ten minutes at 3000 rpm. Remaining dormant eggs were extracted manually.

All dormant eggs were transferred into containers filled with ADaM medium (Aachener Daphnien Medium Klüttgen et al. 1994), and placed in an environmental chamber at 20°C with a 16 h:8 h light:dark schedule. Every 8–9 days, the medium was refreshed. We collected hatched individuals daily for three weeks. All individuals were placed in 24 h aged tap water with 20°C and 16 h:8 h light:dark growth conditions and fed the unicellular algae *Acutodesmus obliquus* until they could be identified to species (Flössner 2000, Benzie 2005). The individuals hatched from each pond were randomly divided into two groups. We fixed and counted one group to estimate the community composition (expected number of hatchlings per species found in 1000 g of sediment). Individuals from the other group were placed in monoclonal culture and used to measure ecologically relevant traits in cladoceran communities and to estimate genetic diversity using molecular markers and using quantitative genetic analyses for traits in *Daphnia magna* populations.

Because community composition was inferred from dormant egg banks, it represents the potential diversity that could be observed in a community at the beginning of the growing season (Vandekerkhove et al. 2005), but can also reflect among-site variation in hatching cue sensitivity (Gómez and Carvalho 2000). Although using hatched communities from dormant egg banks can introduce some biases, the seven species that are most abundant among the hatchlings were also the species that are known to be regionally most abundant. We used relative abundances of hatchlings of the different species to evaluate local and regional variation in community composition by calculating alpha, beta and gamma diversity (calculated as the inverse of Simpson's diversity index; ^2D, Jost 2010; implemented in R, ver. 3.6.0, 2019, using the 'vegan' package, Oksanen et al. 2013). Among-site similarity in community composition was visualized using network plots with affinity scores calculated using Hellinger distance values, implemented in the R packages 'SNFTools' (Wang et al. 2014) and 'qgraphs' (Epskamp et al. 2012, 2017).

Zooplankton traits

All zooplankton trait values (for *D. magna*: local trait values for all 20 sites, capturing among-population genetic differentiation; for all other taxa: regional trait values based on a number of individuals drawn from subsets of populations across the landscape) were measured in a laboratory common garden environment. Trait values were measured after clonal lineages were purged of maternal effects by culturing them for at least one (for seven out of eight taxa) or two (for *D. magna*) generations under common garden conditions. Purging maternal effects for one generation means that for each individual hatched from a dormant egg, trait values were measured on a single second-clutch F1 individual. Purging maternal effects for two generations (*D. magna*) means that trait values were measured on a single second-clutch F2 individual (i.e. a random daughter of the F1 generation individual). Hence, all reported trait values represent phenotypic variation due to genetic variation in life history traits, and do

not reflect variation due to field conditions in the environment where samples were collected.

Daphnia magna traits were measured for all 20 populations using 15 hatched individuals per site. Each individual was cultured in 40 ml of aged tap water at 20°C with a 16 h:8 h light:dark schedule, fed 125 000 cells ml^{-1} of *S. obliquus* daily, and received fresh medium every other day. Those individuals were monitored daily to record the genotype-associated value of age at maturity (day; 24 h resolution), length at maturity (mm; 0.0485 mm resolution) and number of eggs in the first clutch using a life table experiment.

For six out of the seven other cladoceran taxa found regionally, 8–44 individuals (*Chydorus sphaericus*: 8, *Ceriodaphnia* (*quandrangula* and *pulchella*): 21, *Moina* (*brachiata*, *macropa* and *micrura*): 16, *Daphnia* (*pulex*: 44 and *curvirostris*: 11) and *Simocephalus vetulus*: 8) were isolated from 2 to 9 sites (Supporting information). For the seventh species, *Bosmina longirostris*, we isolated three individuals from one habitat (i.e. the only community in which this species was relatively abundant). These individuals were used to quantify life history traits in a life table experiment using the same laboratory conditions as for the assessment of *D. magna* trait values. These life history traits were then used to represent the regional phenotypic values for each of these species (Supporting information). Thus for these species, we did not assess local evolution. The eight taxa for which we measured trait values represented on average 97% of the total abundance of cladocerans among the hatchlings in our survey (Supporting information), and therefore are generally representative of the community trait distributions used in this study.

Molecular markers

To estimate genetic variation at putatively neutral microsatellite loci, we haphazardly selected 30 *D. magna* individuals from each site's hatched population, extracted their DNA (methods in Orsini et al. 2012) and genotyped individuals at 13 loci in two multiplexes: multiplex M01 with markers B050, B064, B074, B045, B030, B008 and B096, and multiplex M02 with markers B031, B065, B088, B174, B155, B135 (Jansen et al. 2011, Orsini et al. 2012). Alleles were identified using Genemapper 4.0 software. Outlier analysis indicated that none of the 13 loci showed evidence of being under selection (Orsini et al. 2012). Genetic data used for this analysis are a subset of data used previously to analyse the drivers of landscape genetic structure in *Daphnia* in the region (Orsini et al. 2013).

Life history trait variation in *D. magna*

To better understand how traits varied across the landscape, we estimated the within- and among-population variation in each of three quantitative traits measured for *D. magna*: age at maturity, length at maturity and number of individuals in the first clutch (analysis described in Supporting information), and combined these measures to calculate the proportion of trait variance found among populations, as opposed to within them (i.e. Q_{ST}; Spitze 1993; detailed in Supporting information). We also compared the average local trait value of *D. magna* to the community weighted mean trait values of the non-*D. magna* community using Bayesian estimation of difference in group means for each of the three traits (where a posterior distribution of the difference in group means that overlaps with zero indicates no difference among groups; see Kruschke 2013 for how this compares to a parametric t-test). Because the sites were sampled from two regions in Flanders (coastal and inland) along a mosaic of environmental gradients, we also used this Bayesian estimation of differences in means to evaluate whether the two regions differed in the trait values for *D. magna* and whether the two regions differed in the environmental variables measured. Both tests were implemented using the 'BEST' R package (Kruschke 2013, Kruschke et al. 2018). Among-population similarity in trait values were visualized using network plots, with affinity scores calculated based on Euclidean distances, implemented in the R packages 'SNFTools' (Wang et al. 2014) and 'qgraphs' (Epskamp et al. 2012, 2017).

The impact of local evolution in *D. magna* on community trait composition

We used our survey of zooplankton traits to address our first research goal, to determine whether the sampled communities differed in the impact of local evolution on community trait composition. To quantify the degree to which local evolution in a single species (in our study: *D. magna*) affects community trait values, we use a metric developed by Lepš et al. (2011) that can estimate the relative importance of intraspecific trait variation for community weighted means. As our application of the metric differs from its use in previous work, we start with detailing its calculation (Box 1) and demonstrating how it can be used to address eco-evolutionary research questions. We applied the metric first developed by Lepš et al. (2011) to trait values measured in a common garden environment after purging maternal environmental effects, rather than on phenotypic values obtained from field measurements that may include plasticity effects (Brans et al. 2017, Lajoie and Vellend 2018 for evolutionary applications of this metric). We thus quantify the degree of local evolution rather than phenotypic (genetic and non-genetic) effects. We also apply the metric to one species, instead of summing across all species in a community, because we only have trait data for all populations from one species. In the focal species approach applied here, we do not evaluate the importance of all evolutionary processes in the system relative to all ecological processes – we instead quantify the importance of evolution in a key interactor (here *D. magna*) and do not consider population-level differentiation for other species in the community (i.e. we use regional averages for the other species). Our metric ΔC thus quantifies the evolutionary contribution of a species i to the community average trait value (Box 1). We also measured the importance of *D. magna* evolution for community trait composition in a second way – by calculating the proportional change in

Box 1. Derivation of method

Average weighted community trait values, using species relative abundances as weights, are often used in analyses of among-community functional diversity (Lavorel et al. 2008). Similarly as in Lepš et al. (2011), we can calculate a community weighted mean (CWM) using local or regional species trait values (where the region is considered to be a group of local communities). A single CWM value can be calculated at the regional level, by using regional trait values and regional average relative abundances of species. This yields one value for the entire metacommunity. It can also be viewed as the expected CWM in the absence of local evolution and phenotypic plasticity, and by assuming that individuals are drawn at random from the entire region, i.e. trait variation within and among species is randomly structured. Considering deviations from this regional CWM by calculating a CWM using local species relative abundances with regional species trait values can thus reflect site-specific variation in community composition. For a trait z and site j, such a CWM C_j using each species local relative abundance and regional average trait value is then calculated as:

$$C_j = \sum_{i=1}^{s} \frac{n_{ij}}{n_j} z_i \qquad (1)$$

where s is the total number of species present in the metacommunity uniquely indexed as $i \in \{1, \ldots, s\}$, (n_{ij}/n_j) is the relative abundance of species i in the community at site j, $n_j = \sum_{i=1}^{s} n_{ij}$ is the sum of the n_{ij} values estimated as the number of hatchlings found in 1000 g of sediment in site j, and z_i is the regional average trait value of species i (i.e. species trait average taken across all sites). In this metric, site-specific variation in community average trait values are due only to variation in community composition. The deviation in the expected community trait value calculated due to using local versus regional trait values of species measured in a common garden quantifies the degree to which local evolution affects community trait values. A community weighted mean trait value using local relative abundances and local trait values of species can be calculated as follows:

$$Ce_j = \sum_{i=1}^{s} \frac{n_{ij}}{n_j} z_{ij} \qquad (2)$$

where z_{ij} represents the local trait value of species i in site j assessed in a common garden. While this formula is similar to the specific average calculated in Lepš et al. (2011), it differs because the trait values used when taking evolution into account were measured in a common garden environment after purging maternal environmental effects rather than on phenotypic values obtained from field measurements that may include plasticity effects. This ensures that the metric quantifies the degree of local evolution rather than phenotypic plasticity effects. Given that our phenotypic differences are due to genetic variation, any deviation observed from the regional trait value should be due to local evolution.

Equation 2 takes into account the contribution of total evolution across all species to CWM, and thus uses information on species local relative abundances and local trait values. However, one can also calculate the degree to which local evolution of a single species (in our study: *D. magna* indexed as *d*) affects community trait values. In this calculation, one would use local relative abundances of all species, local trait values of the focal species of interest and regional trait values of all non-focal species in the community. The community average trait value of a site j when *D. magna*'s local evolution is taken into account, Ce_j^d, was calculated using the regional trait value of the non-focal species and the local trait value of the focal species. Specifically, Ce_j^d is calculated as follows:

$$Ce_j^d = \left(\sum_{i=1;i\neq d}^{s-1} \frac{n_{ij}}{n_j} z_i \right) + \frac{n_{dj}}{n_j} z_{dj} \qquad (3)$$

where z_{dj} (resp. n_{dj}/n_j) is the local trait value (resp. relative abundance) of *D. magna* in site j. The difference between the community average trait value calculated using regional trait values versus *D. magna*'s local trait value reflects local evolution of the *D. magna* population at a specific site. We refer to this quantity as ΔC, calculated for a community at site j as:

$$\Delta C_j = Ce_j^d - C_j = \frac{n_{dj}}{n_j}\left(z_{dj} - z_d\right) \qquad (4)$$

ΔC_j is the difference between the community average trait value calculated using the focal species' metacommunity-wide average trait value (z_d in this instance) and using the focal species' local population trait value (z_{dj}), weighted by the species' relative abundance at site j. For any community at site j, ΔC_j quantifies the impact of local evolution of the focal species for community trait values. Note that for those sites that only contained *D. magna*, $n_{dj}/n_j = 1$ and ΔC_j simplifies to the difference between the local and regional trait value of *D. magna* (for detailed calculations see the Supporting information).

a site's community weighted mean (CWM) resulting from *D. magna* local evolution as the ratio between a site's community weighted mean using local and regional *D. magna* values. To assess the proportional increase or decrease in the CWM, we subtracted this ratio by 1. Thus, values lower than 0 indicate a proportional decrease in CWM, while values larger than 0 indicate a proportional increase in CWM due to local *D. magna* evolution.

Identifying the drivers of the variation in evolutionary contributions to community trait change

Our second research goal was to identify predictors of the magnitude of evolution's impact on community trait values. For the response variable, we quantified the evolutionary contribution of *D. magna* to community trait change for age and length at maturity, and first clutch size as the absolute value of ΔC_j (i.e. $|\Delta C_j|$) (Box 1). Before testing predictors of our response variable, $|\Delta C|$, we first tested whether $|\Delta C|$ values differed between regions using Bayesian estimation of group means, standard deviations and differences in group means (detailed in the Supporting information; $|\Delta C|$ values did not differ between regions, so we did not include region as a covariate in subsequent analyses). We also tested for relationships of $|\Delta C|$ values among traits using Bayesian estimation of group means, standard deviations and correlation coefficients (detailed in the Supporting information). We then evaluated whether $|\Delta C_j|$ is associated with five potential drivers that also vary among our sample sites: *D. magna* population genetic distance based on neutral molecular markers (D_C), within-population genetic diversity (D_G), species diversity (D_S), the degree of phenotypic divergence (i.e. the distance between the local non-*D. magna* community weighted mean and the regional average *D. magna* trait value, which captures an axis of niche divergence; $D_{T_{C\setminus d}}$), and the environmental divergence of the local patch from the landscape mean (D_E) (Box 2). These predictors represent different mechanistic hypotheses for why the impact of evolution on communities might vary among sites: this could be influenced primarily by *D. magna* genetic properties (i.e. D_C, D_G), by species diversity and phenotypic divergence of other species in the local community (e.g. D_S,$D_{T_{C\setminus d}}$) or by site environmental variation (e.g. D_E). Our hypotheses for the effects of these drivers are given in Box 2; how to calculate them using our data is given in the Supporting information.

To assess the association between *D. magna*'s evolutionary contribution and the five potential drivers, we used Bayesian regression analysis implemented in JAGS (Plummer et al. 2003, Plummer 2015) with stochastic search variable selection (SSVS; George and McCulloch 1993, O'Hara et al. 2009). SSVS is used to assess how frequently predictors appear in the Markov-chain Monte–Carlo (MCMC) samples of the posterior distribution, and thus indicates the overall likelihood of each predictor contributing to the response variable. We chose an SSVS threshold of 0.6 to retain variables in a most credible model, indicating that the model was considered more credible when the predictor was included in > 60% of the samples of the posterior distribution ($X > 0.6$). The response variable ($|\Delta C|$) was log-transformed to increase its fit to a normal distribution and then standardised to mean 0 and standard deviation 1 to facilitate comparison among the three traits. Two of the five predictor variables (environmental distance and genetic distance) were log-transformed to improve their fit to a normal distribution, and all were re-scaled to mean 0 and standard deviation 1 to facilitate comparison across drivers. The prior distribution for the intercept was $\sim N(0,10^6)$. In the SSVS procedure, each of the p predictors can be either excluded or included by using a prior distribution for the regression coefficient of $\beta_p \sim (1-\gamma_p)N(0,10^{-4}) + \gamma_p N(0,1)$, and a Bernoulli prior distribution with a mean of 0.5 for γ_p. For each trait, a model was run using five chains and inferences of intercept and regression coefficients were based on 100 000 samples from the posterior distribution of parameters, after 5000 iterations as a burn-in period and 1000 adaptation steps. Model diagnostics were checked by visually inspecting trace plots to evaluate proper convergence of the chains, and by calculating autocorrelations of lag 1. When autocorrelations exceeded values of 0.1, we increased the thinning index of the model to reduce autocorrelations until they approximated zero. In the regression model, sites only including *D. magna* were excluded from analysis as no local non-*D. magna* community weighted mean could be assessed for those sites (n = 16). Last, the regression analysis was run for two separate diversity measures: the exponential of Shannon's entropy and the inverse Simpson's diversity index. The inverse Simpson's index places an increased weight on more abundant species compared to the Shannon entropy (Hill 1973, Jost 2006).

Results

Overview of trait and community composition

Site-specific values of measured environmental variables are given in the Supporting information. Inland and coastal ponds did not differ in environmental variables except for fish predation intensity and surface area (Supporting information). A total of 19 species occur in the 20 cladoceran communities within the ponds surveyed in this region, with species richness varying from 1 to 6 species. The regional diversity was ${}^2D_\gamma = 1.96$, with some variation among sites (${}^2D_\beta = 1.27$) and an average local diversity of ${}^2D_\alpha = 1.55 \pm 0.52$ (average ± SD; alpha diversity and pairwise beta diversity among sites are given in the Supporting information). Only a few sites showed strong similarity in community composition (Supporting information) and these tended to be sites with high *D. magna* abundance. Overall, *D. magna* was the most abundant (> 50%) species in 18 out of the 20 sites (Fig. 1a). Local *D. magna* values for all three traits did not differ between regions (Fig. 1b–d, Supporting information). Overall, network plots of among-population similarity in *D. magna* traits showed no signature of a higher within- compared to among-region (inland and coastal) similarity,

Box 2. Overview of potential drivers of evolutionary contributions to community trait value

The degree to which evolutionary trait change occurs and how it influences ecological processes may depend on local and regional properties of the populations. We evaluated five potential drivers of the impact of local evolution on community trait variation, more specifically corresponding to population genetic (e.g. evolutionary potential), community ecological (e.g. amount of available niche space) and environmental properties at each site. These drivers evaluate whether the impact of *D. magna* evolution on community traits was determined primarily by evolutionary properties, the context created by the other species in the community or the environmental variation. Here we describe our hypotheses for how we expected these properties to influence the importance of local evolution for community traits.

1. Population genetic distance (D_C)
   Strong connectivity of sites might constrain local evolution because of gene flow from neighbouring populations (Wright 1943). Increased genetic divergence for neutral genetic variants of local populations may thus potentially be associated with a greater capacity for local evolutionary trait change (Nosil et al. 2008). In this study, population genetic distance was calculated as Jost's D (Jost 2008).
2. Within-population genetic diversity (D_G)
   Genetic variability is the basis of evolution and allows a population to respond to environmental changes (Fisher 1930). If populations are constrained in their evolutionary response by the available genetic variation, we expect that in populations with higher within-population genetic diversity evolutionary trait divergence might play a stronger role in community trait distribution. In this study, within-population genetic diversity was calculated following Nei (Nei 1972, 1987).
3. Species diversity (D_S)
   Evolution in a focal species might be associated with the properties of other species in the community. This is based on the theoretical findings of de Mazancourt et al. (2008) that biodiversity can constrain species evolution. This inhibition occurs because the presence of several species increases the likelihood that one of the species is well suited to the environmental conditions, leading to less available niche space to allow evolutionary expansion. These theoretical results have been supported in experimental adaptive radiation studies in the bacteria *Pseudomonas fluorescens* (Fukami et al. 2007, Gómez and Buckling 2013). To evaluate the hypothesis that community context influences the importance of local evolution for community trait structure, we used the reciprocal of Simpson's diversity index as a predictor in our model. The diversity property is an indication of the overall level of taxonomic diversity in the zooplankton community that *D. magna* interacts with and competes with for resources.
4. Degree of phenotypic divergence ($D_{T_{C\setminus d}}$)
   We expected that trait evolution's impact on communities might also be enhanced if the trait values of the other species in a local community are different from that of the focal species, thus providing niche space for the focal species to evolve. To test this hypothesis, we also included the difference between *D. magna*'s regional trait value and the local community-weighted mean trait value of the non-*D. magna* zooplankton community as a predictor in our model. This driver captures the divergence in life history strategy between *D. magna* and the rest of the cladoceran community, and provides an estimate of the available niche space associated with the trait.
5. Environmental divergence (D_E)
   Local divergence in environmental properties from the regional average environment might show a positive correlation with the degree of evolutionary responses of local populations, as it might capture the overall environmental selection pressure. *Daphnia* often show strong and rapid evolutionary responses to environmental variation (Tessier et al. 1992, Cousyn et al. 2001). We therefore hypothesized that more distinct environments will have larger impacts of local evolution in *D. magna* on community trait values. In this study, environmental divergence was calculated as the multivariate Euclidean distance of a site from a regional multivariate environmental average.

indicating that *D. magna* populations from these regions did not differ in their trait values (Supporting information). Life history traits diverged among populations (Supporting information). Posterior modes of Q_{ST} estimates were 0.02, 0.26 and 0.46 for traits length at maturity, age at maturity and first clutch size with highest posterior density intervals of (0.00, 0.45), (0.03, 0.76) and (0.12, 0.89), respectively (detailed in the Supporting information). The wide confidence intervals reflect the uncertainty in the data and are often observed for Bayesian estimates of Q_{ST} (O'Hara and Merilä 2005). *Daphnia magna* had significantly higher age at maturity, length at maturity and first clutch size compared to the average non-*D. magna* community (detailed in the Supporting information).

The impact of local evolution in *D. magna* on community trait composition

The impact of local evolution of *D. magna* for community weighted mean trait values ($|\Delta C_j|$) varied among traits and among sites (Fig. 2; Supporting information). Mean non-standardised impact of *D. magna* local evolution

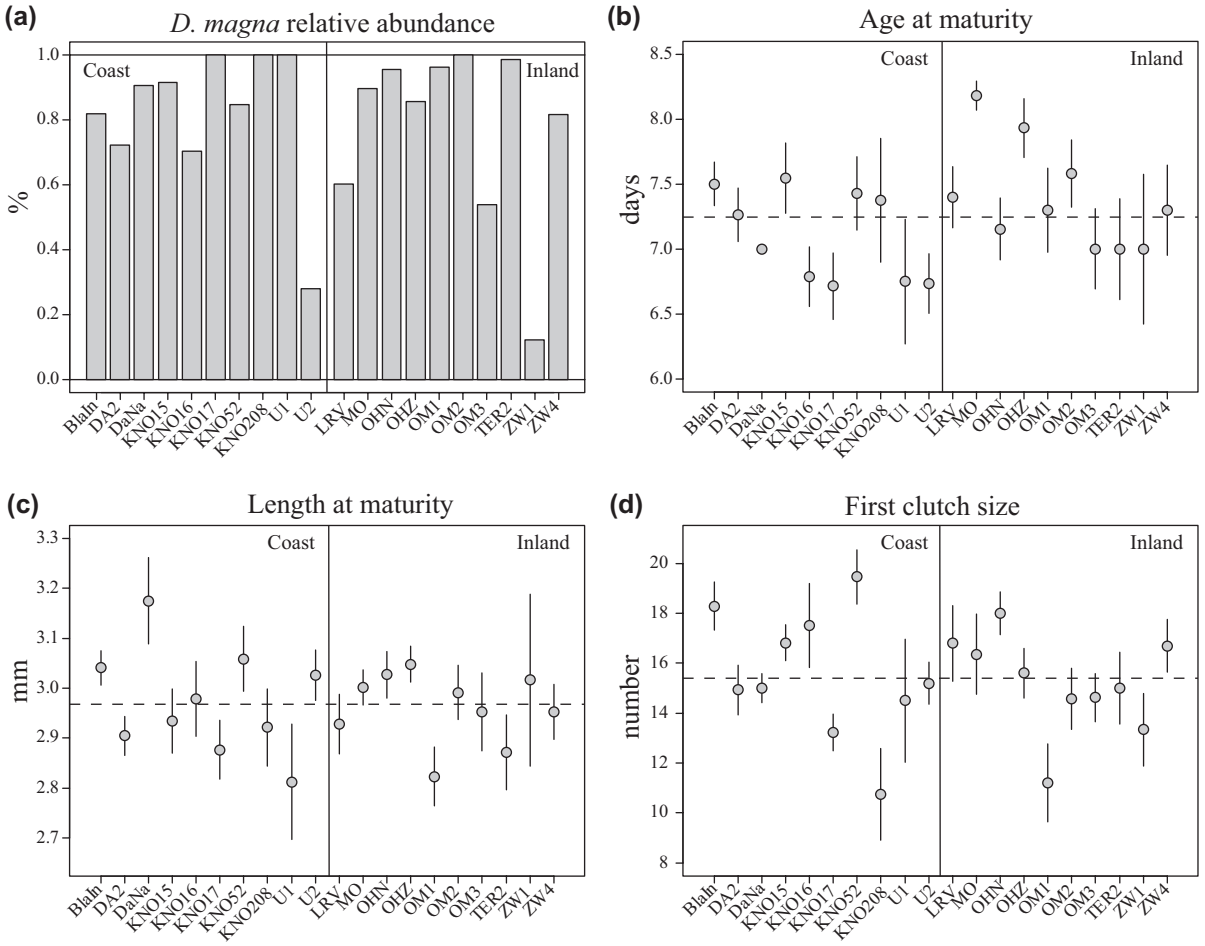

Figure 1. (a) *Daphnia magna* relative abundance in each community. *Daphnia magna* population mean values ± 1 standard error for (b) age and (c) length at maturity, and (d) first clutch size for 10 coastal and 10 inland populations. The dashed line gives the regional trait value (i.e. average across all populations).

($|\Delta C|$ ± standard deviation) varied among traits and equaled 0.06 ± 0.05 for length at maturity, 1.37 ± 1.33 for first clutch size and 0.23 ± 0.17 for age at maturity. For some sites, the impact of local evolution of *D. magna* for the average community trait mean was very low for all three traits (e.g. DA2, OHN, ZW1 and ZW4), while for other sites *D. magna* local evolution had a substantial effect on at least one trait (e.g. KNO52), or even for all three traits (e.g. KNO17; Fig. 2). The impact of *D. magna* local evolution for community trait mean was not correlated among traits (i.e. 95% HPDI for correlation coefficients included zero; Supporting information), and did not differ between regions for any of the three traits (Supporting information). Considering local evolution in *D. magna* alters estimates of community weighted mean (CWM) trait values. In some sites this was as high as 9% for age at maturity, 7% for length at maturity and 30% for first clutch size. On average, *Daphnia magna* local evolution altered community weighted means of local sites by 2.13 ± 1.68% (mean ± standard deviation) for length at maturity, 3.37 ± 2.43% for age at maturity and 9.79 ± 8.74% for first clutch size (Supporting information).

Identifying the drivers of the variation in evolutionary contributions to community trait change

To better understand the variation in the impact of *D. magna* local evolution for community trait structure, we assessed whether it is random with respect to sites, or whether there was structure imposed by site properties. We tested the importance of genetic, ecological and environmental predictors for explaining variation in the magnitude of the impact of evolution on community trait values as quantified by our response variable $|\Delta C|$. We used a Bayesian regression model, and evaluated the inclusion of five predictors using a stochastic search variable selection threshold of $\gamma > 0.6$ and considering 95% highest probability density intervals (95% HDPI) for regression coefficients (β_X) that do not overlap with zero. Using these criteria, the most credible model of standardised $|\Delta C_j|$ retained two out of the five proposed drivers for age at maturity (Table 1). We found that species diversity of the non-*D. magna* community ($\beta_{D_S} = 0.54$, HPDI = (0.03, 1.02), $\gamma_{D_S} = 0.71$; Table 1) and phenotypic divergence

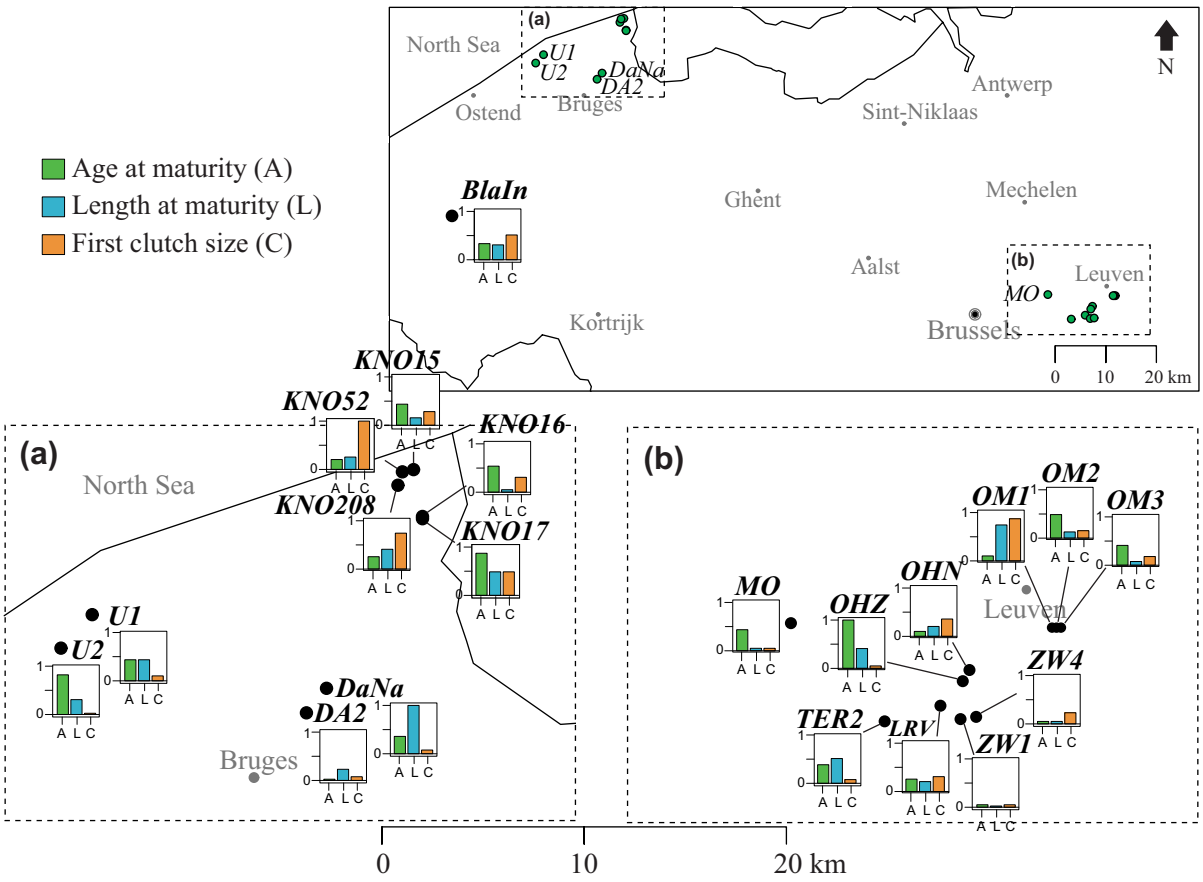

Figure 2. Site-specific variation in the impact of evolution for community average trait values on three life history traits for 20 ponds sampled in Flanders (Belgium). Spatial locations of the ponds are indicated by black filled circles. At each site, bar plots display the relative magnitude of the effect of local evolution in *D. magna* on the average trait value of the cladoceran community ($|\Delta C|$) for age (A; green) and length at maturity (L; blue), and first clutch size (C; orange) scaled to maximum value of 1. Absolute values of minima and maxima are 0.01 and 0.61 days for age at maturity, 0.01 and 0.18 mm for length at maturity and 0.19 and 4.64 number of offspring for first clutch size, respectively. To show the full variation across sampled sites, values for all sites are displayed in the figure (n = 20), but note that some sites had only *D. magna* present (KNO17, KNO208, U1, OM2). For these sites non-*D. magna* community properties (species diversity and phenotypic divergence) could not be calculated (detailed in Supporting information).

between *D. magna* trait values and those of the non-*D. magna* communities ($\beta_{D_{TC\setminus d}} = 0.68$, HPDI = (0.11, 1.20), $\gamma_{D_{TC\setminus d}} = 0.82$; Table 1) positively influenced the impact of local evolution of *D. magna* (Fig. 3). Hence, the impact of *D. magna* local evolution was larger in sites where communities were more diverse and where local cladoceran communities had trait values that were more different from *D. magna* trait values. For length at maturity and first clutch size, none of the drivers were retained in more than 60% of the posterior distribution models (Table 1). When using the exponential of Shannon's instead of the Simpson's diversity index, only the distance between the non-*D. magna* community weighted mean and the regional *D. magna* trait value ($D_{T_{C\setminus d}}$) was retained (Supporting information).

Discussion

An increasing number of studies have reported contemporary evolution of a focal species and quantified its feedback on ecological processes (Hairston et al. 2005, Pelletier et al. 2007, Declerck et al. 2015, Pantel et al. 2015, Hendry 2017). While several of these studies documented pronounced effects of evolution on population, community and ecosystem features, most of them have illustrated these effects in proof-of-principle experiments under relatively simplified conditions (Hendry 2019). It thus remains unclear to what extent evolution impacts ecological processes in complex natural settings and landscapes, and also which drivers determine variation in the importance of evolution for ecological processes. In this study, we altered an existing metric to quantify the degree to which evolution in one species influences a community average trait. In addition, we explore to what extent variation in the values obtained by this metric may be explained by variables that represent population genetic, community and environmental properties of the different sites. Our goal was to quantify when evolution plays an important role in structuring communities, and whether site-specific properties such as local population genetic diversity, community diversity and ecological opportunity and local environmental properties can determine the strength of this impact. Our

Table 1. Results of the Bayesian linear models regressing the impact of evolution for community trait values ($|\Delta C|$) against five predictor variables: population genetic distance (D_C), within-population genetic diversity (D_G), species diversity of the non-*D. magna* community (D_S) calculated as the inverse of Simpson's diversity index, the distance between the non-*D. magna* community weighted mean (CWM) and the regional *D. magna* value ($D_{T_{C\setminus d}}$), and environmental divergence of the local patch from the landscape mean (D_E). Three life history traits were evaluated: age at maturity, length at maturity and size of first clutch. For each predictor variable X the regression coefficient β_X, its corresponding parameter γ (the proportion of Bayesian models that included each covariate based on the stochastic search variable selection; number between brackets) and the 95% highest posterior density interval (HPDI) are given. Values in bold indicate 95% HPDI that do not include zero. Four sites containing only *D. magna* were excluded resulting in n = 16 sites.

	Age at maturity	Length at maturity	First clutch size
Genetic distance			
β_{D_C} (γ)	0.3567 (0.46)	−0.3296 (0.36)	0.0287 (0.21)
95% HPDI	(−0.1620, 0.8271)	(−0.9365, 0.2679)	(−0.5429, 0.5800)
Within-population genetic diversity			
β_{D_G} (γ)	0.2977 (0.35)	−0.1367 (0.26)	−0.0266 (0.23)
95% HPDI	(−0.2444, 0.8449)	(−0.8004, 0.4879)	(−0.6134, 0.5678)
Species diversity			
β_{D_S} (γ)	**0.5385 (0.71)**	0.2558 (0.30)	0.0381 (0.22)
95% HPDI	(0.0318, 1.0156)	(−0.2943, 0.8444)	(−0.5388, 0.6106)
Phenotypic divergence			
$\beta_{D_{T_{C\setminus d}}}$ (γ)	**0.6781 (0.82)**	−0.2058 (0.28)	−0.3919 (0.46)
95% HPDI	(0.1130, 1.2000)	(−0.8770, 0.4478)	(−0.9485, 0.1507)
Environmental divergence			
β_{D_E} (γ)	−0.0932 (0.20)	−0.1241 (0.23)	−0.3563 (0.44)
95% HPDI	(−0.5972, 0.3859)	(−0.6851, 0.4234)	(−0.8140, 0.1385)

application to zooplankton communities ultimately serves as a case study demonstrating a way to quantify eco-evolutionary interactions in natural systems. It also emphasizes the need for more studies that collect this type of data in other systems in order to find generalities for the role of evolution in natural (meta)communities.

Our results indicate that the evolutionary contribution to local community trait values does not necessarily depend on the capacity of the local populations to evolve. Instead, we found that properties of the cladoceran communities of direct competitors best explained the degree to which evolution impacted local community trait composition for one trait, age at maturity. The impact of evolution on community trait values for age at maturity was positively related to phenotypic divergence (i.e. the effect of *D. magna* evolution on communities was higher when those communities had larger differences between regional *D. magna* and local non-*D. magna* community trait values) and positively related to species diversity in the non-*D. magna* community. The positive relationship with phenotypic divergence indicates that large differences in life history traits of species may create ecological opportunity to evolve (de Mazancourt et al. 2008, Urban et al. 2008).

The positive relationship between the impact of *D. magna* evolution for community mean age at maturity and species diversity was contrary to our expectation. We predicted a negative relationship, based on findings from theoretical (de Mazancourt et al. 2008) and experimental (Fukami et al. 2007, Gómez and Buckling 2013) studies showing that diversity can inhibit trait evolution. However, some additional studies have shown that species interactions may either inhibit (de Mazancourt et al. 2008, Fiegna et al. 2015) or promote (Liow et al. 2011, Osmond and de Mazancourt 2013) evolutionary responses. For example, Osmond and de Mazancourt (2013) showed that the degree of adaptation in the presence of competition in their evolutionary rescue model was contingent on the degree of niche overlap (defined as the overlap between selection from the local environment and from competition). Their study concluded that partial niche overlap promoted adaptation, while strong niche overlap hindered adaptation. In line with this, the theoretical study of Fielding and Pantel (2020) demonstrated among-site variation in niche overlap and associated variation in the impact of community features on trait evolution in a spatially structured metacommunity. *Daphnia magna* is by far the largest species of the cladoceran metacommunity and is characterized by a longer developmental time, larger clutch sizes and a larger particle size range that can be grazed than other cladocerans (Lampert 1987). It is possible that *D. magna* demonstrate partial rather than strong niche overlap with other cladocerans in this study. The effect of niche overlap for degree of adaptive evolution predicted by Osmond and de Mazancourt (2013) may also be reflected in our observed positive relationship between the contribution of *D. magna* evolution to community trait values and distances between the non-*D. magna* community weighted mean and regional *D. magna* trait values. Further studies would be necessary to explore and test this idea in other systems.

The other two traits we evaluated, size at maturity and number of offspring, did show among-site variation in the contribution of *D. magna* evolution to community traits, but our model did not provide clear evidence that the hypothesized drivers structured this variation. One possible

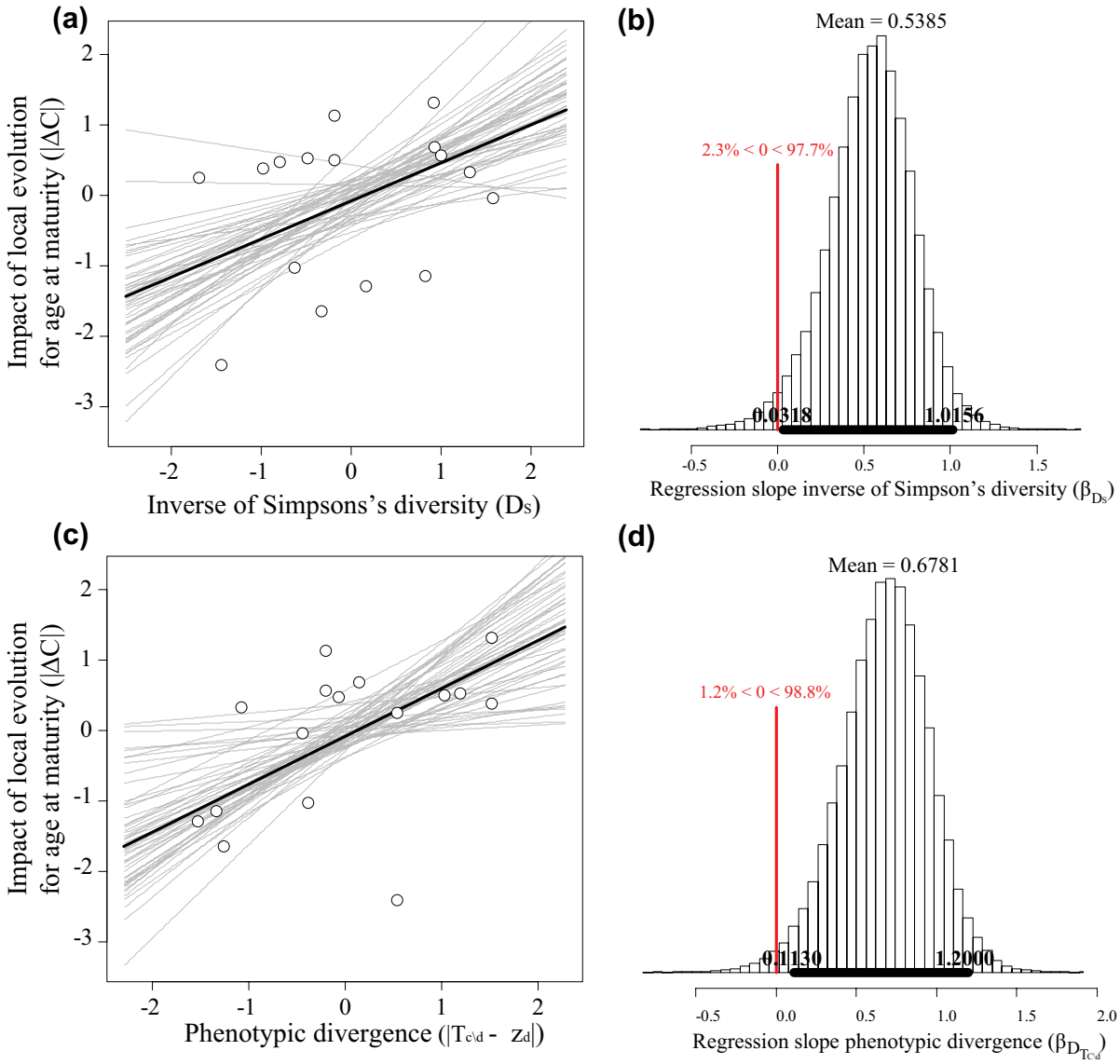

Figure 3. Effects of predictors for the impact of *D. magna* evolution on community mean trait values (|Δ*C*|) for age at maturity. Credible regression lines (drawn by randomly selecting a subset of values from the posterior distribution of the regression coefficient) and posterior distributions with their corresponding posterior mean and 95% highest posterior density interval (bold line and numbers) are given for the regression coefficient of (a, b) species diversity of the non-*D. magna* community (D_S, calculated as the inverse of Simpson's diversity index), and (c, d) phenotypic divergence ($D_{T_{C\backslash d}}$, calculated as the difference between the non-*D. magna* community weighted mean and regional *D. magna* value). Solid black lines in (a, c) represent the regression line using the posterior mean coefficient value. Red numbers in (b, d) represent the percentage of values in the posterior distribution below and above zero. Four sites containing only *D. magna* were not included in the regression models (n = 16) because these community properties of the non-*D. magna* community could not be calculated (for detailed information see Supporting information). Posterior distributions of the three remaining predictors (that showed no evidence of impact) are shown in the Supporting information.

explanation for this lack of evidence could be that there are unmeasured drivers of the impacts of *D. magna* evolution on these traits (e.g. coevolution with other species). Alternatively, it is also possible that this variation is not structured and instead has a random distribution (Laroche et al. 2015). It is thus important in future studies to establish the nature of the null distribution underlying observed effect sizes of evolution for ecological processes and patterns. It is also possible that the trait values measured in the common garden environment do not capture the range of trait values encountered at local sites throughout the growing season (e.g. they may only reflect conditions early in the growing season, when densities of competitors and fish are low). Reciprocal transplant experiments across study sites or measurement of phenotypic reaction norms would better capture landscape heterogeneity (Benito Garzón et al. 2019). We also did not

a priori expect that only age at maturity would respond to the predictors in our model. However, it has previously been shown that individual *Daphnia* populations can adaptively respond to selection pressures via variable contributions of traits (Boersma et al. 1998), which means that life history strategies can arise via a number of trait combinations. The trait of age at maturity is highly heritable (Spitze 1995), and is strongly driven by access to resources and by whether *Daphnia* are exposed to invertebrate or vertebrate predators (Beckerman et al. 2010). Given the presence of these multiple selection pressures in many ponds, age at maturity may thus represent a niche axis that partitions zooplankton species employing distinct life history strategies, but this requires laboratory experiments to confirm.

In this study, we only quantified the evolutionary contribution of one focal species, *Daphnia magna*, to community trait values. Estimating the total impact of evolution requires having local population-specific trait values for all species in the community, i.e. common garden experiments involving all populations of each of the (dominant) species. This would vastly increase the amount of work. In addition, if species are sexually reproducing (as opposed to our cyclically parthenogenetic focal species, which allows working with clones), appropriate breeding designs need to be performed. Although *Daphnia* species have been found to be an important driver of community and ecosystem dynamics in small ponds (Walsh et al. 2012, Pantel et al. 2015), it is likely that the single-species approach may not always reflect the true impact of evolution on the community (terHorst et al. 2018, De Meester et al. 2019). This may be the case because, for example, site properties can select both for optimal traits within populations of a single species and for particular combinations of traits in assemblages of multiple species (Leibold and Norberg 2004). In natural systems, the impact of evolution in one species for the structure of trait distributions in the community may vary not only in magnitude, but also in whether the effects are negative or positive. While the cumulative effect of evolution in multiple species (which is not captured in this study) might often be higher than that of a single species, the net effect of the total evolutionary contribution might be lower than the sum of the individual effects of the different species (De Meester et al. 2019). This would reflect an example of cryptic eco-evolutionary dynamics (Luo and Koelle 2013, Kinnison et al. 2015), and is a key reason why studies involving diverse communities is an important avenue for future research in eco-evolutionary dynamics (terHorst et al. 2018, De Meester et al. 2019).

Previous studies have found that zooplankton community composition responds to landscape-level variation in site connectivity and environmental gradients (Cottenie and De Meester 2003, Xiong et al. 2017) and that multiple species in zooplankton communities can be genetically adapted to local environmental conditions (Yampolsky et al. 2014, Brans et al. 2017). Here, we found that the impact of local evolution in *D. magna* – a key ecological interactor in this system – for community average trait values showed substantial among-site variation, and that this variation was associated with properties of the non-*D. magna* community and not with population genetic properties of the *D. magna* population. This finding suggests that the influence of evolution on ecological dynamics might be more dependent on ecological than on genetic constraints. If our findings are corroborated by more studies, then the study of how community features impact evolution and how this feeds back on ecology should become a central topic in the field of eco-evolutionary dynamics. These studies could consider additional aspects of a species' genetic architecture to more explicitly capture genetic constraints on adaptive phenotypic evolution. Other interesting next steps involve 1) more clearly isolating adaptive phenotypic evolution in response to a particular selection pressure, which will require an increased number of sites sampled along a gradient of that selection pressure and 2) generating testable predictions about which communities are more or less likely to influence, or be influenced by, evolutionary dynamics, which can be informed by the candidates for drivers of eco-evolutionary processes in natural systems considered in this study. Our results suggest that community context is an important mediator of how and when evolution impacts ecological processes and that landscapes may harbour eco-evolutionary 'hotspots', where eco-evolutionary interactions are more likely to occur.

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Author contributions

Lynn Govaert: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Methodology (supporting); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Luc De Meester**: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (lead); Investigation (supporting); Project administration (equal); Resources (equal); Supervision (equal); Writing – review and editing (equal). **Sarah Rousseaux**: Conceptualization (equal); Data curation (equal); Investigation (lead); Project administration (equal); Resources (equal); Writing – review and editing (equal). **Steven A. J. Declerck**: Conceptualization (equal); Investigation (supporting); Project administration (supporting); Writing – review and editing (equal). **Jelena H. Pantel**: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Methodology (lead); Supervision (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data accessibility statement

Data are available at Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.rxwdbrv8s> (Govaert et al. 2021).

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