Article

The Evolution of Life History Traits and Their Thermal Plasticity in *Daphnia*

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Abstract: Few studies have explored the relative strength of ecogeographic versus lineage-specific effects on a global scale, particularly for poikilotherms, those organisms whose internal temperature varies with their environment. Here, we compile a global dataset of life history traits in *Daphnia*, at the species-and population-level, and use those data to parse the relative influences of lineage-specific effects and climate. We also compare the thermal response (plasticity) of life history traits and their dependence on climate, temperature, precipitation, and latitude. We found that the mode of evolution for life history traits varies but that the thermal response of life history traits most often follows a random walk model of evolution. We conclude that life history trait evolution in *Daphnia* is not strongly species-specific but is ecogeographically distinct, suggesting that life history evolution should be understood at the population level for *Daphnia* and possibly for other poikilotherms.

Keywords: zooplankton; phylogenetic generalized least squares; phylogenetic independent contrasts; *Daphnia* phylogeny; temperature; climate; metaanalysis

1. Introduction

Life history traits are among the most frequently studied traits of organisms because of their direct relevance to fitness via reproduction and survival. Variation among life history traits provides many solutions and strategies to similar problems. The diversity and specificity of life history traits provide glimpses into the evolutionary history of organisms, whereas the evolutionary history of organisms phylogenetically constrains the parameter space for those life history traits [1]. Predicting how organisms' life histories will respond to environmental changes is important for understanding the generation and maintenance of biodiversity broadly.

Despite the variability in life history traits across taxa, some life history traits are constrained by the evolutionary histories of specific lineages, deemed lineage-specific effects [1]. These effects are important constraints on organisms' ability to respond to their environment evolutionarily. However, many organisms have evolved ways to overcome environmental pressures by exhibiting phenotypic plasticity. Moreover, life history traits are among the most plastic traits and, while some are thought are thought to be highly heritable, others are not [2]. It is unclear how different life history traits and their plasticity are inherited in *Daphnia* and across the tree of life more broadly.

While life history traits are constrained by the evolutionary lineages in which they evolve and respond plastically to the environment, it is therefore interesting to understand the independent contributions of lineage-specific effects and climate on the evolution and expression of life history traits. For example, some traits like body size may be heavily constrained by lineage-specific effects, limited by deep ancestral divergences, such as endo-versus exoskeletons [3]. Other traits may exhibit strong variability due to local environmental conditions or resource availability, such as clutch size or interclutch (interlitter) intervals [4]. Finally, some traits may vary in response to both lineage and local environmental constraints, such as somatic (juvenile) growth rate [5].

Increasing and increasingly variable rates of global temperature change [6] are likely to interact strongly with the extreme plasticity of life history traits [7,8] to influence or mediate population and species responses to climate change [9]. Despite the central role of life history traits and their sensitivity to temperature variation, the extent of the plastic responses to temperature and subsequent trait evolution remains an open question. With variable changes in climate, life history trait plasticity and evolution will be especially important for invertebrates and poikilotherms, those organisms whose metabolism and internal temperature depend on the environmental temperature.

Temperature should affect poikilotherms and homeotherms differently [1], and for the purposes of this study, a common poikilotherm microcrustacean genus, *Daphnia*, is known to respond with dramatic plasticity to different temperatures making it a useful lens for exploring lineage-specific and latitudinal variation in life history traits [10–12]. *Daphnia* is particularly well-suited as a study system due to the deep understanding of their ecology and their use in thermal experiments and toxicology studies as indicator species (Table S1)—resulting in an abundance of life history data experimentally tested in different environments.

Prevailing theories from community and ecosystem ecology suggest that local conditions, or ecogeography, should be the strongest signal in predicting the life history variation in poikilotherms [13,14]. Meanwhile, population ecology theory suggests that there is significant intra-and interspecific variation, and therefore, lineage-specific effects and ecogeography must both be known to predict life history variation [15]. We hypothesize that life history traits follow a mixture of these trends with rate-limited traits, such as juvenile growth and interclutch intervals being closely aligned with climatic/latitudinal gradients [16] and other allometrically linked traits, like size and age at first reproduction and clutch size to be closely aligned with species identity [17].

Here, we test the effects of lineage, local environment, and the mode of evolution on life history traits in *Daphnia*. We use a phylogenetic framework to test for evolutionary constraint in life history traits across the *Daphnia* phylogeny. We then test for local environmental signals in life history trait evolution by incorporating precipitation, temperature, and latitude data. We repeat these analyses for thermal responses in life history traits to explore if there are lineage-specific or local environmental effects on the evolution of trait plasticity. Finally, we explore whether the evolutionary trends of life history traits and their plasticity is stronger at the species or population level for *Daphnia*. A mixture of local adaptation and evolutionary history undoubtedly influences life history traits [18], but exploring the relative effects of each on trait variation will allow for better predictions of how life history traits may evolve in a changing thermal environment.

2. Materials and Methods

2.1. The Life History Dataset and Literature Review

We collected data for this meta-analysis from a search of Web of Science and Google Scholar using the search term: temperature AND response AND *Daphnia*. The literature search returned 89 articles that were then assessed for quality standards, resulting in 70 studies useful for further analysis, representing 342 controlled laboratory temperature measurements from 75 individual populations across 20 species of *Daphnia* (Figure 1). A full set of articles used in these analyses can be found in the Supplement (Table S1). Quality standards included research studies reporting means, standard deviations, and sample sizes, (or means of extracting these values) for any of 8 life history traits, similar to methods in [19].
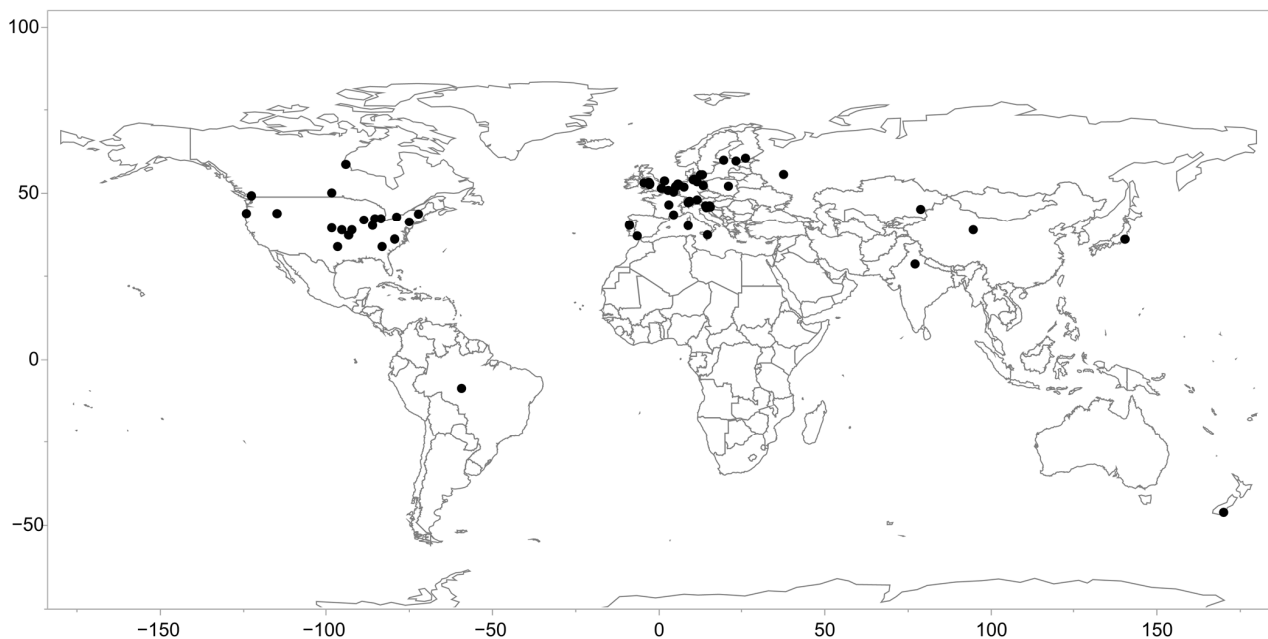
Figure 1. Sampling sites from data synthesis where life history traits were reported for *Daphnia*. Each marker represents an individual population (or set of populations) included in these analyses. *N* = 75. References for each location can be found in Table S1.

Life history traits included in the analysis were age at first reproduction (AFR), size at first reproduction (SFR), clutch size, juvenile growth rate, population growth rate, size at death, interclutch interval, and lifespan. Trait variation data were recorded across all reported temperatures. Where data were not reported directly in tabular form, they were extracted from plots using WebPlotDigitizer [20].

Latitude and longitude measurements were obtained from sampling locations reported in the original research studies. For a robust measurement of latitude, research must also have been conducted on wild-caught, lab-manipulated *Daphnia*. We did not include long-term lab-maintained clonal lines because of the potential effects of long-term lab culturing. We extracted climate data from the Global Climate Data (WorldClim) dataset [21]. These data include temperature, precipitation, and elevation information at a 10s latitude resolution. Variables BIO1-BIO11 were used in this analysis to define the temperature aspect of climate, and variable BIO12-BIO19 represent the precipitation aspect of climate, similar to [22]. We analyzed monthly temperature and precipitation readings from the last 50 years of available data—more information about individuals variables and how they are obtained can be found in [21].

We grouped all species together for most analyses for the interest of elucidating the importance of phylogenetic constraints on life history traits. We averaged across all population-level measurements with averages weighted for samples size and corrected using the standard error measurements calculated from the original research articles. For climate variables, we averaged all temperature and precipitation variables across these same populations to obtain a measurement of the average environmental condition experienced by the species. Thus, the final species-level dataset included in the phylogenetic analyses included single measurements for all life history traits and all climate variables. For population-level analyses, we used individual population measurements for life history traits, climate, and laboratory (experimental) temperature measurements.

2.2. Phylogeny

We created a *Daphnia* phylogeny for subsequent species-level analyses which account for shared ancestry in lineages [23] (Figure 2). We downloaded sequence data for

six loci from Genbank for the *Daphnia* species in our analyses. Our phylogeny contains data for three nuclear loci: 18 s, 28 s, 5.8 s and three mitochondrial loci: 12 s, COI, and ND2 (Supplemental Table S2). We downloaded *Simocephalus* sp. sequences and added them to the dataset as outgroups. We trimmed the resulting sequences by eye for low quality bases and created consensus sequences for each locus using Geneious v.11.1.5 (http//www.geneious.com, accessed on 1 December 2018). We created consensus sequences because subsequent phylogenetic analyses required single tips for each species and to avoid oversampling issues with more heavily sampled species. We aligned sequences using MUSCLE v.3.8.425 [24] with *Simocephalus* sp. as the outgroup. We used PartitionFinder 2 [25] to designate seven data partitions to correspond to the three separate codon positions for each of the six loci. Phylogenies were inferred using MrBayes v. 3.2 [26], and we ran the analysis on the concatenated dataset of all 6 loci for two independent runs of 10^7 MCMC generations, sampling every 1000 generations. We checked for convergence of the runs using Tracer v.1.7.1 (http://tree.bio.ed.ac.uk/software/tracer/, accessed on 1 December 2018) and plotted the final phylogeny using FigTree v.1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/, accessed on 1 December 2018).
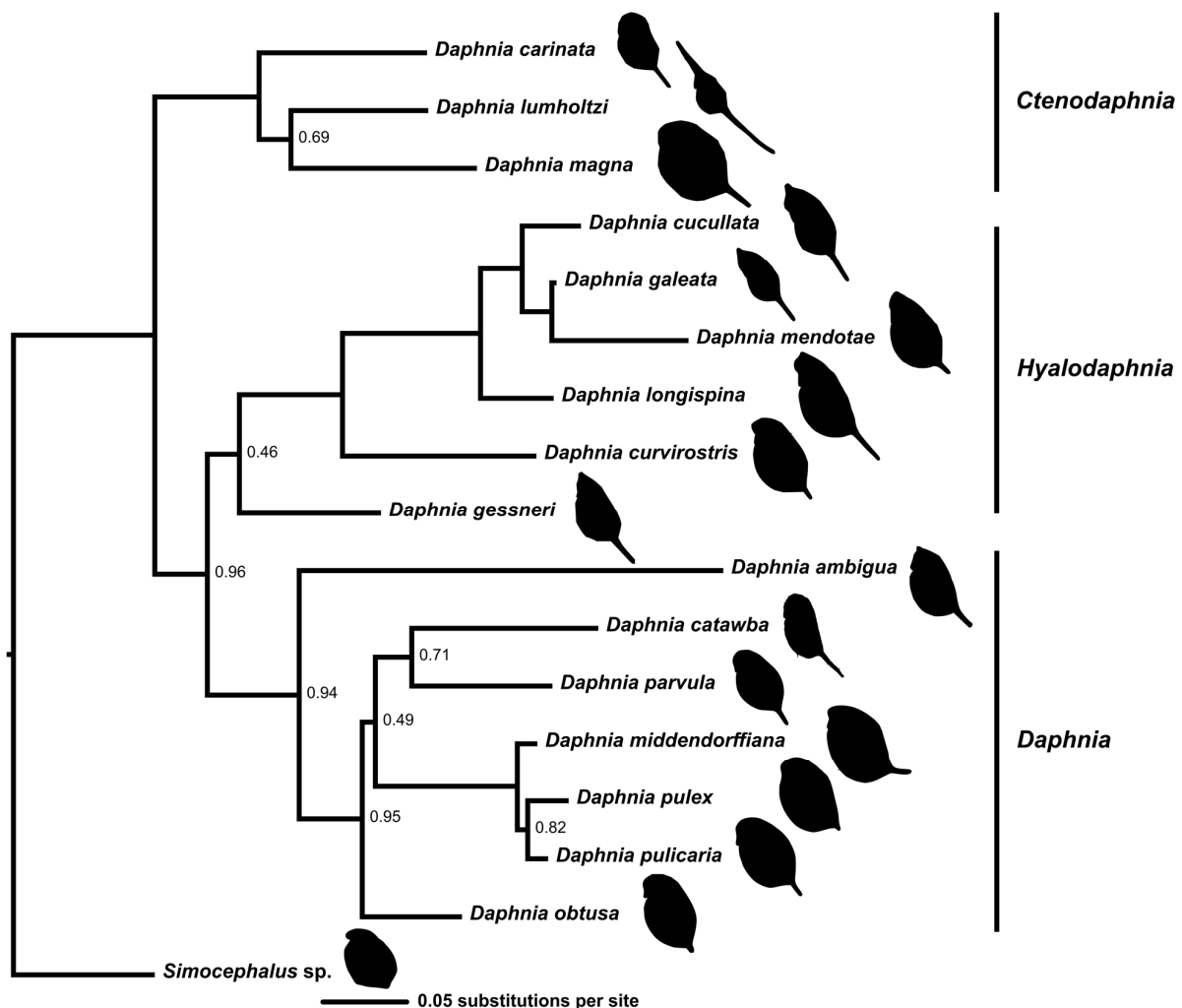
Figure 2. Bayesian-estimated molecular phylogeny of *Daphnia* from three nuclear (18 s, 28 s, 5.8 s) and three mtDNA (12 s, COI, ND2) genes (concatenated). Bayesian posterior probabilities appear at nodes; nodes without values are equal to 1. The tree is rooted at *Simocephalus* sp., which also serves as outgroup. The three major subgenera are labeled (right) and recapitulate findings from earlier molecular phylogenies [27–29].

We rooted the tree with *Simocephalus* sp. as an outgroup and checked the resulting tree with Colbourne and Hebert 1996 [27] for agreement. Hybrid species were dropped from phylogenetic (species-level) analysis, and trait values were separated into both of the species categories to which they purportedly belong. Additionally, more recent genetic analysis has grouped *Daphnia hyalina* and *D. rosea* into the *D. longispina* species complex [28,29], and these species are also grouped in our analysis.

2.3. Statistical Analyses

2.3.1. Phylogenetic Signal

We tested the phylogenetic signal of each life history trait against the phylogeny we generated using two different statistical models. We categorized all of our life history traits as continuous traits and used the R package phytools [23] to test for the signal of life history traits and climate variables on our phylogeny using two different phylogenetic statistics: Pagel's λ [30,31] and Blomberg's *K* [32] (Table 1). Both of these statistics calculate the phylogenetic independence probability given a null or random distribution of the tips in the tree. Values near zero indicate phylogenetic independence, or that traits are unrelated to inheritance; values closer to 1 indicate that the tested signal follows a random walk or Brownian motion model of evolution; values greater than 1 indicate that relatives show higher similarity to each other than Brownian motion would suggest, e.g., traits are highly conserved in lineages [22]. We then tested for significance of Blomberg's *K* by setting our null model to that of phylogenetic independence ($K \approx 0$) and simulated 1000 randomizations of the tree where species identities at the tips are randomly sampled [22,32].To test the significance of Pagel's λ, we used a likelihood ratio of our model (the true tree) to the null ($\lambda \approx 0$) and to a neutral model of evolution ($\lambda \approx 1$), similar to [22].

Table 1. Phylogenetic signal in life history traits and climatic data for *Daphnia* and mode of evolution that best describes current trait values as supported by best model AICc scores. BM = Brownian Motion; OU = Ornstein–Uhlenbeck.

Variable	N	Blomberg's K	p	Pagel's λ	p	Mode of Evolution
Life History Traits:						
Age at First Reproduction	111	0.773	0.09	1.00	0.08	BM
Size at First Reproduction	144	0.635	0.03 *	1.00	0.06	BM
Clutch Size	116	0.304	0.56	<0.001	1.0	OU
Juvenile Growth Rate	120	0.872	0.07	1.00	0.26	OU
Population Growth Rate	140	0.769	0.15	1.00	0.40	OU
Size at Death	28	10.14	0.08	1.00	0.26	BM
Interclutch Interval	37	0.718	0.58	<0.001	1.0	OU
Lifespan	38	0.671	0.83	<0.001	1.0	BM
Temperature Response						
Age at First Reproduction	111	0.799	0.13	0.536	0.33	BM
Size at First Reproduction	144	0.382	0.32	<0.001	1.0	BM
Clutch Size	116	0.257	0.61	<0.001	1.0	OU
Juvenile Growth Rate	120	0.397	0.45	<0.001	1.0	BM
Population Growth Rate	140	0.669	0.44	<0.001	1.0	BM
Size at Death	28	10.27	0.23	0.975	0.29	BM
Interclutch Interval	37	0.735	0.56	<0.001	1.0	BM
Lifespan	38	0.637	0.79	<0.001	1.0	BM
Climate:						
Temp PC1		0.337	0.50	0.354	0.69	
Temp PC2		0.355	0.39	<.001	1.0	
Precip PC1		0.526	0.17	0.809	0.56	
Precip PC2		0.297	0.59	<0.001	1.0	

* $p < 0.05$

2.3.2. Climate and Temperature Variables

We included studies that measured life history at experimentally manipulated (non-ambient) temperatures ($Temp_{exp}$) in order to understand the effect of temperature alone versus climate. To avoid overfitting, climate variables from the WorldClim database were condensed into two predictor variables via principal components analysis (PCA) for both temperature and precipitation, resulting in four principal components (PCs) used in subsequent regression analyses [22].

The temperature principal components (BIO1-BIO11) collectively explained 84.9% of the variation in the temperature data. $PC1_{temp}$ (51.0%) is positively correlated to the minimum and mean temperature of the coldest month(s) and negatively correlated to the annual temperature range and temperature seasonality, creating an axis from less variable and warmer to more variable and cooler climates. $PC2_{temp}$ (33.9%) is strongly positively correlated to maximum and mean temperature of the warmest month(s), creating a secondary axis from milder to hotter climates.

The precipitation principal components (BIO12-BIO19) collectively explained 84.3% of the variation in the precipitation data. $PC1_{precip}$ (50.5%) is positively correlated to annual precipitation and the wettest continuous 3-month period (quarter) creating an axis from drier climate to wetter climates. $PC2_{precip}$ (33.8%) is strongly negatively correlated to precipitation of the driest month, creating a secondary axis from driest to wettest absolute precipitation climates. The factor scores for the first two principal components were used for subsequent analyses for each population or species.

2.3.3. Life History Response Variables

We were also interested in the response of life history trait reaction norms to temperature. For each life history trait, we collected the reaction norms for each species and averaged their responses across the temperature span reported in the literature. We fit general linear models (GLMs) to the data accounting for differential sampling size among the reported data. We extracted the slope of the model as the species' average thermal reaction norm and used this as the life history response in subsequent species-level analyses. Because we expect several life history traits to exhibit nonlinear relationships with temperature (e.g., population growth rate), we also fitted generalized nonlinear models (GNLMs) to the data. Linear models explained significantly more variation in the data and were used for further analyses. We expect the linearity of our collected thermal responses was due to the restricted range of temperatures used in most studies, which does not explore the full thermal parameter space that *Daphnia* may tolerate.

2.3.4. Life History Traits and Climate Variables Regressions

- Species-level analyses—To test how climate affects life history traits, we used three different modeling structures. We used ordinary least squares (OLS) regressions to examine the predictive power of climate for life history traits. However, OLS models do not account for the known issues of phylogenetic relatedness among closely related lineages [33–35], more especially those that may have recent introgression events due to *Daphnia*'s elevated rate of hybridization. OLS models were conducted in JMP Pro 13.2 [36].

To account for common ancestry, we used two phylogenetic least squares regression approaches [37] using the R package nlme [38], one with an underlying Brownian motion model of evolution and the other with an Ornstein–Uhlenbeck model of evolution [22]. The phylogenetic generalized least squares model with Brownian motion ($PGLS_{BM}$) accounts for phylogenetic relatedness while trait variance increases linearly through time [39]—this represents an evolutionary model where evolution occurs as a random walk, indicative of either drift or adaptation to a variable adaptive peak. The phylogenetic generalized least squares model with Ornstein–Uhlenbeck evolution ($PGLS_{OU}$) similarly accounts for phylogenetic relatedness while trait variance does not change over time [40]—this represents an evolutionary model where evolution occurs as a process whose value may

vary around a mean but whose mean trait value remains constant over evolutionary time, indicative of a trait that is evolving to an invariable adaptive peak [22]. We used these two models to elucidate not only the specific signals of these traits across the phylogeny but also to understand the evolutionary constraints on these traits.

Both PGLS models were constructed using phytools [23] in R with the corresponding variance-covariance matrices built in the R package ape [41] using the corBrownian function for Brownian motion (based on [42]) and the corMartins function for Ornstein–Uhlenbeck (based on [43]). Prior to running each model, input trees were trimmed to include only species with complete data, i.e., missing data were excluded from the analyses. We performed Box-Cox transformations on variables whose data did not pass tests for normality and homoscedasticity [22] using the R package MASS [44]. Finally, we account for model efficiency using an information theory approach using the Akaike information criterion (AIC) for model choice using the R package geiger [45] (Tables 2 and 3).

Table 2. Results from species-level regressions comparing life history traits and climate variables. PCs as defined in Methods from BioClim variables.

Response Variable and Model	Regression Summaries				β (Explanatory Variables)					
	Adj r^2	F/χ^2	df	p	Intercept	$PC1_{temp}$	$PC2_{temp}$	$PC1_{precip}$	$PC2_{precip}$	AIC [†]
Age at First Reproduction										
OLS	0.478	3.06	5, 10	0.126	8.60 ***	1.16 *	0.946	−0.292	−1.98 *	639
PGLS$_{BM}$	0.640	5.03	5	0.039	8.40	1.20	1.22	−0.190	−2.12	47.75
PGLS$_{OU}$	0.930	13.2	5	<0.001	8.47 **	1.26	1.12	−0.219	−2.24	50.50
Size at First Reproduction										
OLS	−0.133	0.678	4, 11	0.628	1.52 ***	0.167	0.656	0.222	0.019	304
PGLS$_{BM}$	0.335	1.81	4	0.460	1.52 **	0.058	−0.223	0.202	−0.046	37.67
PGLS$_{OU}$	0.868	10.4	4	<0.001	1.55 **	0.035	−0.258 *	0.173	−0.050	39.97
Clutch Size										
OLS	0.606	5.22	4, 11	0.246	14.9 ***	0.089	1.70 *	1.68 *	0.850	730
PGLS$_{BM}$	0.633	4.91	4	0.043	10.3	0.669	−1.36	2.79	0.662	44.99
PGLS$_{OU}$	0.597	4.46	4	0.063	10.6 **	0.534	−1.43	2.89	0.946	47.07
Juvenile Growth Rate										
OLS	−0.210	0.740	4, 6	0.644	−0.161	0.075	0.033	0.349	0.161	147
PGLS$_{BM}$	0.993	15.0	4	<0.001	1.25	0.446	1.04	−0.973	−0.275	9.94
PGLS$_{OU}$	−0.315	10.3	4	<0.001	1.25	0.449	1.05	−0.975	−0.278	11.94
Population Growth Rate										
OLS	−0.565	0.368	4, 7	0.821	0.125	0.394	0.037	0.271	0.373	517
PGLS$_{BM}$	0.663	3.81	4	0.107	0.274	0.101	−0.027	−0.085	0.016	19.61
PGLS$_{OU}$	0.494	2.39	4	0.189	0.273	0.111	−0.027	0.064	. . .	17.18
Size at Death										
OLS	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
PGLS$_{BM}$	0.659	1.74	2	0.175	2.10	−0.249	0.337	. . .	. . .	11.09
PGLS$_{OU}$	0.621	1.59	2	0.075	2.50*	−0.943	. . .	. . .	. . .	11.05
Interclutch Interval										
OLS	0.119	1.20	4, 6	0.501	8.06	0.282	0.521	0.300	0.483	234
PGLS$_{BM}$	0.368	1.38	4	0.601	5.80	1.78	−0.827	−1.41	−2.03	29.53
PGLS$_{OU}$	0.072	0.224	4	0.930	6.51	0.115	−0.976	−0.430	. . .	31.93
Lifespan										
OLS	0.042	1.09	4, 8	0.468	−0.484	0.716	0.134	0.090	0.629	352
PGLS$_{BM}$	0.756	3.52	3	0.070	29.0	2.45	−6.65	−9.22	. . .	27.14
PGLS$_{OU}$	0.391	1.24	3	0.290	31.5	−0.665	−6.80	. . .	. . .	32.46

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. [†] For OLS models, Akaike Information Criterion corrected for finite sample sizes (AICc) are reported. Omitted values (. . .) represent models with insufficient power.

Table 3. Results from species-level regressions comparing life history reaction norm responses and climate variables. PCs as defined in Methods from BioClim variables.

Response Variable and Model	Regression Summaries				β (Explanatory Variables)					
	Adj r^2	F/χ^2	df	p	Intercept	$PC1_{temp}$	$PC2_{temp}$	$PC1_{precip}$	$PC2_{precip}$	AIC [†]
Age at First Reproduction										
OLS	0.042	1.09	5, 8	0.468	−0.484 *	0.104	0.031	0.017	−0.143	52.1
$PGLS_{BM}$	0.290	0.687	5	0.849	−0.425	0.030	0.048	0.032	−0.047	31.64
$PGLS_{OU}$	0.999	3.18	5	0.174	−0.480 *	0.098	0.032	−0.021	−0.140	31.66
Size at First Reproduction										
OLS	0.810	5.34	4, 9	0.047	−0.015	−0.112 *	−0.215 *	0.347 *	0.296 *	25.1
$PGLS_{BM}$	0.964	16.7	4	<0.001	0.048	−0.120 **	−0.201 **	0.342 **	−0.329 **	15.14
$PGLS_{OU}$	0.423	2.75	4	0.139	−0.136	−0.004	−0.183	0.112	. . .	23.51
Clutch Size										
OLS	0.581	4.82	4, 11	0.035	−0.125	0.099	0.169	0.019	−0.214	32.7
$PGLS_{BM}$	0.914	11.15	4	<0.001	−0.414	0.260 *	−0.214	−0.178	−0.551 *	34.13
$PGLS_{OU}$	0.910	7.94	4	0.003	−0.128	0.101	0.169	0.016	−0.216	33.83
Juvenile Growth Rate										
OLS	−0.192	0.799	4, 5	0.674	−0.196	0.069	−0.033	−0.234	−0.051	. . .
$PGLS_{BM}$	0.838	5.47	4	0.027	−0.090	0.153	0.043	−0.228	−0.116	11.10
$PGLS_{OU}$	0.601	2.76	4	0.238	−0.101	0.130	0.022	−0.212	−0.095	13.10
Population Growth Rate										
OLS	0.883	12.3	4, 6	0.076	−0.017	0.023	0.004	−0.053 *	−0.049 *	. . .
$PGLS_{BM}$	0.951	10.6	4	<0.001	−0.015	0.022	0.003	−0.050 *	−0.047	7.39
$PGLS_{OU}$	0.588	3.10	4	0.102	0.013	−0.003	−0.006	−0.011	. . .	4.60
Size at Death										
OLS	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
$PGLS_{BM}$	0.283	0.665	2	0.514	0.034	−0.077	0.018	. . .	. . .	6.06
$PGLS_{OU}$	0.257	0.595	2	0.275	0.012	−0.040	. . .	. . .	. . .	0.90
Interclutch Interval										
OLS	−0.488	0.508	4, 6	0.746	−0.520	−0.209	0.113	0.168	0.225	. . .
$PGLS_{BM}$	0.677	2.36	4	0.316	−0.538	−0.234	0.129	0.200	0.220	27.69
$PGLS_{OU}$	0.430	1.31	4	0.455	−0.630	−0.057	0.156	0.099	. . .	25.53
Lifespan										
OLS	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .	. . .
$PGLS_{BM}$	0.868	4.82	3	0.022	−1.03	−0.839	0.348	1.32	. . .	22.06
$PGLS_{OU}$	0.138	0.370	3	0.691	−1.39	−0.392	0.369	. . .	. . .	24.04

* $p < 0.05$; ** $p < 0.01$; [†] For OLS models, Akaike Information Criterion corrected for small sample sizes (AICc) are reported or are unable to be calculated due to small *N*. Omitted values (. . .) represent models with insufficient power.

- Population-level analyses—We expected climate variables to be good predictor variables on a global scale or species-level, but when assessing individual populations, we were interested in whether climate, temperature, or latitude alone were enough, regardless of species, to predict variation in life history traits. We used a stepwise model selection approach for our population-level analysis. We built a full model for each life history trait that included the four climate variables ($PC1_{temp}$, $PC2_{temp}$, $PC1_{precip}$, $PC2_{precip}$), the reported experimental temperature, the latitude, and species identity as a fixed effect. Then, we added and reduced the model by individual variables and compared the Akaike information criterion corrected for small sample sizes (AICc) scores to choose the optimum model for each trait (Table 4). Individual species identity coefficients can be found in the Supplement (Table S3). All statistical analyses were performed in JMP Pro 13.2 [36] or R [46]; we used a 5% significance level to reject null hypotheses.

Table 4. Results from population-level ordinary least squares (OLS) regressions comparing life history reaction norms and climate variables. PCs as defined in Methods from BioClim variables.

Response Variable and Model	Regression Summaries					β (Explanatory Variables)							
	Adj r^2	F/χ^2	df	p	Intercept	$PC1_{temp}$	$PC2_{temp}$	$PC1_{prec}$	$PC2_{prec}$	$Temp_{exp}$	Lat	Species [†]	AICc
Age at First Reproduction													
OLS_{Full}	0.232	2.97	17, 111	<0.001	23.7 ***	−0.073	−0.270	0.119	−0.442	−0.383 ***	−0.196	✓	629
OLS_{Best}	0.265	21.0	2, 111	<0.001	18.9 ***	. . .	. . .	. . .	. . .	−0.377 ***	−0.069 ***	. . .	602
Size at First Reproduction													
OLS_{Full}	0.832	38.7	19, 144	<0.001	3.81 ***	−0.018	−0.117 *	−0.002	0.028	−0.005	−0.055 ***	✓	97.8
Clutch Size													
OLS_{Full}	0.563	9.33	18, 116	<0.001	46.9 ***	−0.026	−1.24	0.387	0.684 *	−0.180 *	−0.691 **	✓	674
Juvenile Growth Rate													
OLS_{Full}	0.395	7.03	13, 120	<0.001	−3.37 *	0.232 *	0.374 *	0.123 **	−0.060	−0.005	0.084 *	✓	95.4
Population Growth Rate													
OLS_{Full}	0.123	2.52	13, 140	0.004	4.26	−0.192	−0.044	0.002	0.011	0.034	−0.010	✓	509
OLS_{Best}	0.022	4.16	1, 140	0.043	−0.152	. . .	. . .	. . .	. . .	0.041 *	. . .	. . .	509
Size at Death													
OLS_{Full}	0.936	82.7	5, 28	<0.001	−0.656	−0.353	0.295	. . .	. . .	−0.040 ***	0.074	✓	8.73
OLS_{Best}	0.938	107.1	5, 28	<0.001	0.243	−0.406	0.220	. . .	. . .	−0.040 ***	0.056	. . .	5.39
Interclutch Interval													
OLS_{Full}	0.812	17.0	10, 37	<0.001	−42.5	2.94 **	−4.05 ***	8.11 *	7.71 *	−0.560 ***	1.49 *	✓	218
OLS_{Best}	0.798	25.3	6, 37	<0.001	4.69	1.40	−1.64	−0.184	1.46	−0.490 ***	0.433 **	. . .	210
Lifespan													
OLS_{Full}	0.724	12.1	9, 38	<0.001	9.32	6.48	−2.20	−9.33	−13.0	−1.85 ***	1.81	✓	336
OLS_{Best}	0.747	19.7	6, 38	<0.001	5080 ***	−35.1 **	−364 ***	−142 ***	40.3 **	−1.91 ***	−93.4 ***	. . .	325

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; [†] Individual species identity coefficients can be found in the Supplement Table S3. Omitted values (. . .) represent models with insufficient power.

3. Results

3.1. Phylogeny

Our phylogeny recapitulated all of the major groups outlined by [27] (Figure 2). We were able to reconstruct the Ctenodaphnia including *Daphnia lumholtzi and D. magna* with the addition of *D. carinata*, not appearing in the Colbourne and Hebert tree [27]. Colbourne and Hebert [27] had weak support for the separation between the Hyalodaphnia and the Daphnia, which we greatly improve in our tree (0.96 posterior probability). Finally, as expected, we see close grouping between readily hybridizing species *D. galeata* and *D. longispina* and the *D. pulex–D. pulicaria* group which also includes *D. middendorffiana*, commonly found at high northern latitudes (Figure 2).

3.2. Life History Traits and Climate

Daphnia have a cosmopolitan global distribution, but most reported research in strongly represented by northern hemisphere studies (Figure 1). Most life history traits examined did not exhibit a strong phylogenetic signal (Table 1). Size at first reproduction was the only life history trait we found to have strong phylogenetic signal among life history traits (Table 1). We also found no phylogenetic signal of climate, temperature, or precipitation.

The modes of evolution varied among the life history traits that we examined. Age at first reproduction, size at first reproduction, size at death, and lifespan were all better predicted by simple Brownian motion models, while clutch size, juvenile growth rate, population growth rate, and interclutch interval were all better predicted by the Ornstein–Uhlenbeck models (as determined by AIC values; Table 2). However, the thermal plasticity of life history traits was better explained by Brownian motion, except for clutch size which was better explained by the Ornstein–Uhlenbeck model (Table 3).

3.3. Species-Level Analyses

Climate variables showed no phylogenetic signal in our species-level analysis. Climatic variables were not significant predictors of life history variation (generalized least squares regressions), except for size at first reproduction which was negatively correlated to maximum and mean summer temperatures ($\beta = -0.364$, Table 2, Figure 3A). Best performing models were effective at explaining variance in the dataset (R2 = 0.38–0.99), but climate (PCs) had little explanatory power for all other life history traits (Table 2).

In contrast, climate variables explained significant variation in the thermal response of life history traits models, including thermal response of size in first reproduction, thermal response of clutch size, and thermal response of population growth rate (Table 3). All four of climate variables were significant predictors of the thermal response of size at first reproduction (negative correlation with temperature; positive correlation with precipitation; Table 3, Figure 3B). Thermal response of clutch size was positively correlated with mean and maximum summer temperatures (Table 3, Figure 3C). Thermal response in population growth rate was negatively correlated with minimum and maximum precipitation (Table 3, Figure 3D).
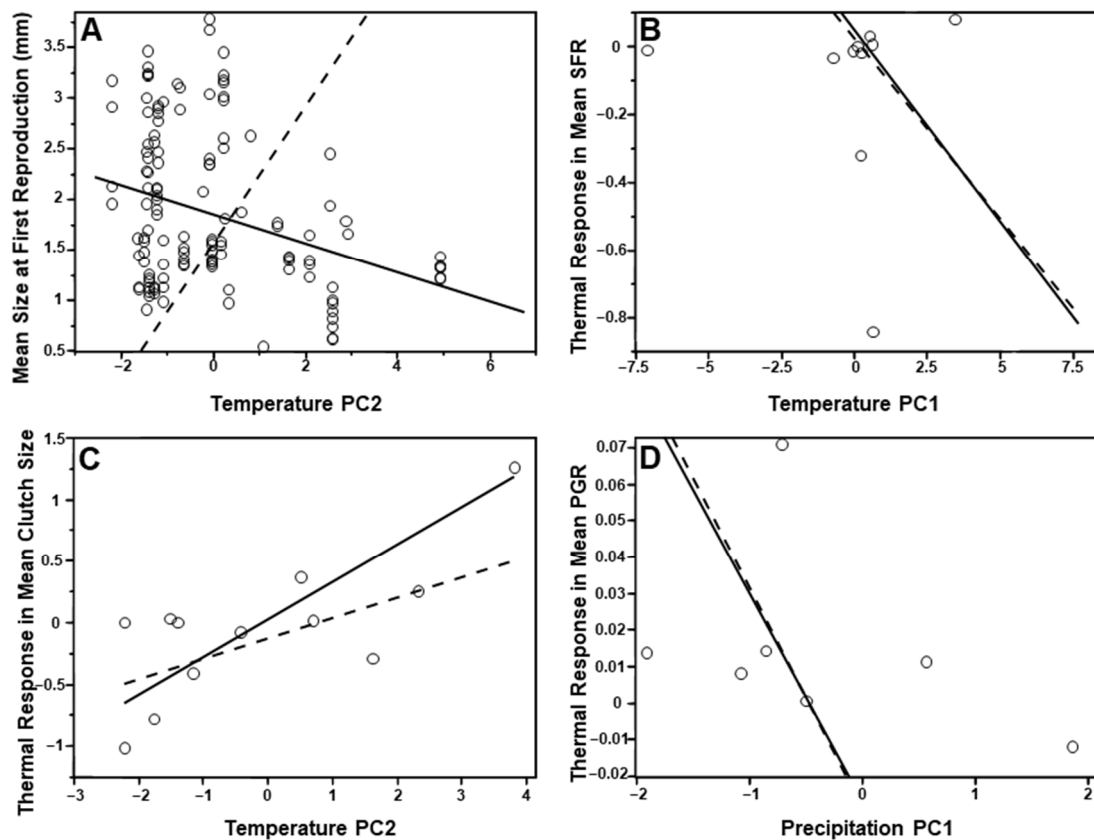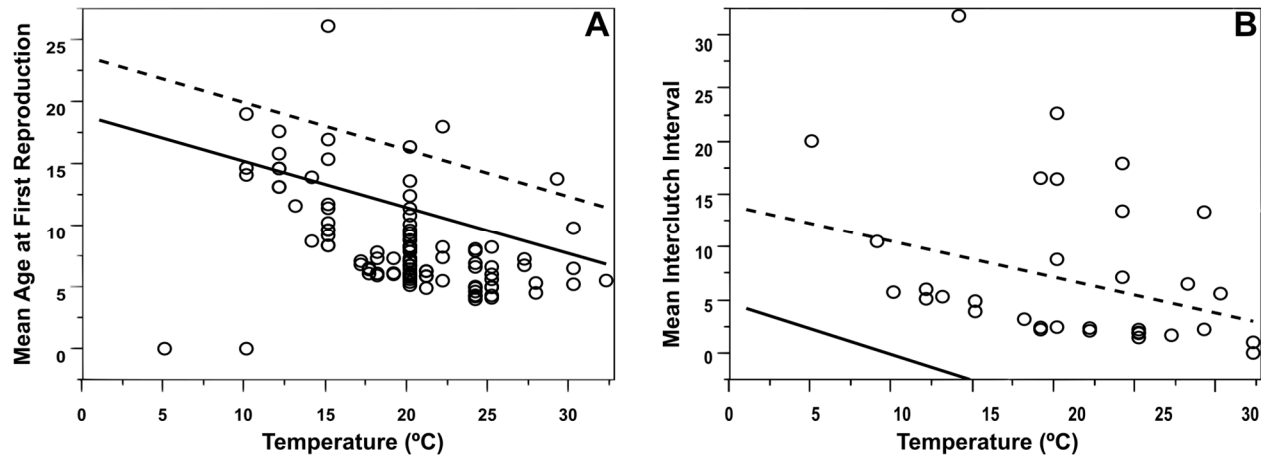
Figure 3. Bivariate scatterplots of select life history traits exhibiting high correlations with climatic variables at the species-level. Climatic principal components (PCs) as defined in Methods. Mean size at first reproduction (**A**) and the thermal response of mean clutch size (**C**) to temperature PC2, their most significant predictive variable. Thermal response in mean of size at first reproduction (SFR) against temperature PC1 (**B**), and the thermal response of population growth rate (PGR) against precipitation PC1 (**D**), their highest predictive variables, respectively. Solid lines represent the intercept and slope (partial regressions) from the phylogenetic generalized least squares models. Dashed lines represent partial regressions for ordinary least squares models. See Tables 2 and 3 for more info; all relationships $p < 0.05$.

3.4. Population-Level Analyses

At the population level, most life history traits were strongly correlated to climate, temperature, and latitude; however, adding species identity to the models increased the predictive power of the model for size at first reproduction, clutch size, and juvenile growth rate (Tables 4 and 5). Age at first reproduction was strongly negatively correlated to experimental temperature ($Temp_{exp}$), temperature, and latitude, independent of species identity (Table 4, Figure 4A). Size at first reproduction was negatively correlated to minimum temperatures and latitude; clutch size was positively correlated with annual precipitation seasonality and experimental temperature, and negatively correlated with latitude; and juvenile growth rate was positively correlated with maximum temperatures, minimum temperatures, annual precipitation, and latitude (Table 4). Population growth rate was positively correlated with experimental temperature, but the effect size was very low, predicting 2% of the variance in the data (Table 4); the full model performed equally as well (similar AICc values) but explained little more variance at 12% (Table 4).

Table 5. Data with highest explanatory power for predicting *Daphnia* life history evolution. Numerical results can be found in population-level analyses (Table 4).

Life History Trait	Species Identity	Population/Latitude	Temperature
Age at First Reproduction	✗	✓	✓
Size at First Reproduction	✓	✓	✗
Clutch Size	✓	✓	✓
Juvenile Growth Rate	✓	✓	✗
Population Growth Rate	✗	✗	✓
Size at Death	✗	✗	✓
Interclutch Interval	✗	✓	✓
Lifespan	✗	✓	✓

Figure 4. Bivariate scatterplots of select life history traits exhibiting high correlations with climatic variables at the population-level. Temperature is experimentally controlled rearing temperature as reported in the literature, see Methods. Mean age at first reproduction (**A**) and mean interclutch interval (**B**) to Temperature, their most significant predictive variable. Solid lines represent the intercept and slope (partial regressions) from the best ordinary least squares model after stepwise model selection (via AICc, see Methods). Dashed lines represent partial regressions for full ordinary least squares models. See Table 4 for more info; all relationships $p < 0.05$.

Size at death, interclutch interval, and lifespan all were highly correlated with experimental temperature ($Temp_{exp}$) and the model fits were not improved by adding species identity as a fixed effect. Size at death was strongly negatively correlated to experimental temperature, which explained >93% of the variance in the data (Table 4). Interclutch interval was strongly correlated with experimental temperature and negatively correlated with latitude with 80% effect size (Table 4, Figure 4B). Meanwhile, lifespan was highly correlated to all climatic variables, experimental temperature, and latitude, but was not improved by adding species identity (Table 4). Lifespan was negatively correlated with maximum and minimum temperatures, annual precipitation, experimental temperature, and latitude; and positively correlated with precipitation seasonality (Table 4).

4. Discussion

We found little support for phylogenetic or climatic signals in life history trait evolution but strong support for the effects of climate on life history trait plasticity at the species-level in *Daphnia*. We found strong support for the effects of climate, rearing temperature, and latitude on individual *Daphnia* populations, and species identity improved the predictive power of few models. Therefore, the evolution of life history traits and their thermal

plasticity may best be tested and understood at the level of individual populations rather than generalizing across species or even groups of species (Table 5). We found little support for the general rules that allometric life history traits are associated with phylogenetic lineage and rate-limited life history traits are associated with temperature. Instead, life history trait evolution and thermal plasticity may better be predicted by mode of evolution in *Daphnia* (Table 1) and possibly other poikilotherms.

4.1. Species-Level Analyses

Life history traits can vary considerably among species, yet we find that species groups perform less like their closest relatives than predicted [22,31,32,47]. This could be explained by the group's cosmopolitan distribution or the extreme climate variability across its range [48]. We found that the size at first reproduction was highly dependent on their species identity—a commonly held theoretical prediction [49–52]. We did not find that groups that were more closely related were more similar in their size at first reproduction, simply that species identity has a strong effect.

Both of our phylogenetic approaches (Blomberg's K and Pagel's λ) indicated that juvenile growth rate has a marginally significant phylogenetic signal, and therefore closely related species were more similar in their juvenile growth rate than a null Brownian motion evolution model would predict. This suggests that there is a strong selective pressure on juvenile growth rate in certain clades, and given *Daphnia*'s long-documented history of portfolio effects [53–55], allee effects [56,57], and seasonal growth [16,58–62], our findings corroborate a strong selective pressure for *Daphnia* species to grow quickly in order to reproduce early and often. Size-dependent life history traits seem to be phylogenetically constrained, and of course, juvenile growth rate and size at first reproduction are linked traits, supporting previous assertions that body size is particularly phylogenetically constrained [63–65].

The weak phylogenetic signal ($p = 0.13$) in the thermal response of age at first reproduction where again, groups that are more closely related have more similar responses to temperature (Table 1) deserves further investigation. This signal may be due to *Daphnia*'s phenotypic plasticity [66] ability to change reproductive strategies dependent on the current environment [67,68]. *Daphnia* have two major reproductive strategies: asexual reproduction resulting in genetic clones of the mother and sexual reproduction resulting in genetically distinct individuals. However, these two strategies also represent income versus capital breeding strategies, respectively [69–71]. If environmental (particularly temperature) conditions are beneficial, *Daphnia* tend to grow and reproduce rapidly [72,73]; whereas, if environmental conditions (temperature) are suboptimal, *Daphnia* can store resources as lipids or reduce growth rates [74], resulting in longer times to first clutch or sexual mating, producing resting eggs (ephippia) instead of a first clutch. The plasticity necessary to invoke these two strategies may explain why we see a strong phylogenetic signal particularly in the thermal response (plasticity) to age at first reproduction with but not the trait itself.

We also make meaningful inferences about life history trait evolution modes from these results. Age at first reproduction, size at first reproduction, size at death, and lifespan are all better predicted by the phylogenetic generalized least squares model with Brownian motion (Table 2). This suggests that these four traits are randomly walking (drift) to shifting optima through time. This result may be attributable to the phenotypic plasticity we see across the *Daphnia* clade [75]. We expect these traits to have variable optima due to the wide range of environments that *Daphnia* inhabit [48,75], resulting in the variation we see in these traits. Notably, it has been suggested that individual lake environments can produce independently evolving *Daphnia* lineages based on local environmental differences, such as predation [76,77], and our results strongly support that assertion for these life history traits.

Conversely, clutch size, interclutch interval, and juvenile and population growth rates are all better predicted by the phylogenetic generalized least squares model with Ornstein–Ulhenbeck evolution (Table 2). This suggests that these traits have an absolute evolutionary adaptive peak, and though individual lineages may deviate from the peak, the mean trait value is maintained through time [78,79]. We might expect this to be true for clutch-related

traits given the physical limitations of making vast changes to clutch size [80,81], and, as previously stated, growth rates are phylogenetically constrained but likely faster growth rates are always selected for given *Daphnia*'s ecology [82]. Our model outputs support stationary mean trait values for these life history traits, where the elevation of the adaptive peak is always evolving to become steeper (faster rates or a specific egg number/frequency) but not moving from specific mean trait values.

If we consider that the thermal response of life history traits represents phenotypic plasticity to locally variable environments [83], then the near unanimous output that thermal response traits evolve under Brownian motion makes intuitive sense. The thermal response in all life history traits (except clutch size) evolve as a random walk (Table 2), further supporting the assertion that individual *Daphnia* species are ecological distinct yet locally adapted [84]. Individual lakes present specific and different selective pressures, be them predatory size-selection [85], thermal variation [15,86], or extreme seasonality [87,88]. These local selective pressures likely result in an evolutionary random walk for phenotypic plasticity in life history traits [89]. However, we do see the phylogenetic generalized least squares (PGLS) models under Ornstein–Uhlenbeck evolution again being more predictive for clutch size, further underscoring the physical constraints on an optimum egg number per species, as previously stated (Table 2).

Though the PGLS models account for phylogenetic dependence, we also calculated simple phylogenetic independent contrasts (PICs) pairwise for each life history trait (Supplemental Table S4). We found significant differences in pairings of size at first reproduction and size at death; population growth rate and interclutch interval; and growth rate and size at death (Supplemental Figure S1). We found a marginally significant difference in age at first reproduction and clutch size (Supplemental Figure S1A).

All other pairwise comparisons were not significant (Supplemental Table S4), implying that most life history traits in *Daphnia* are phylogenetically independent across species. For size at first reproduction and size at death (trait pairs that showed significant phylogenetic dependence) there was overdispersion of those life history traits in closely related taxa (Supplemental Figure S1). Species that are more closely related to each other show more divergent life history traits than one would expect via evolutionary history, suggesting that some species pairs may be undergoing niche partitioning or that the evolution of these life history traits were important in speciation.

4.2. Phylogeny

Though we constructed this phylogeny primarily for subsequent analyses, the phylogeny demonstrates the need to understand species delimitation in extremely plastic and readily hybridizing groups such as the *Daphnia*. We left low bootstrap support branches in our analysis to test for species-level effects but recognize that many of these clades would be condensed to single species or need more concerted sampling for proper delimitation (Figure 2). With species known to be readily hybridizing, it is extremely difficult to delimit them based on genetic analyses alone, and this phylogeny supports that notion [90–92]. The evolutionary history of this group is yet complicated by an extremely skewed sex ratio, identification issues due to phenotypic plasticity, mixtures of sexual and asexual reproduction, and historic and recent introgression events, all making genetic species delimitation very difficult.

4.3. Life History Traits and Climate Dataset

The final dataset constructed here is, to our knowledge, the largest repository of *Daphnia* life history traits. Over 360 individual populations of *Daphnia* from over 75 research articles were assembled for eight life history traits across 20 species. Our final dataset captured an important portion of *Daphnia* species (*N* = 20), but there are also notable weaknesses including an overabundance of studies on *D. magna* and *D. pulex-pulicaria*, accompanied by an abundance of Northern hemispheric sampling.

One of the attractive advantages of *Daphnia* is their extreme accessibility for meaningful ecological and evolutionary research; however, much like in *Drosophila*, we are missing much of the naturally occurring genetic and phenotypic variability in this group due to a lack of sampling in the Southern hemisphere, particularly with species of invasive concern like *D. lumholtzi*, believed to be native to central Africa. Capturing more parameter space in these ecological and evolutionary contexts may enable us to better understand this group's incredible ability to adapt to changing environments and hybridize between divergent lineages.

4.4. Population-Level Analyses

Most of our ordinary least squares models were improved by adding species identity as a fixed effect, despite the fact that most life history traits have no phylogenetic signal (Tables 4 and 5). This would be consistent with species identity having strong predictive power for how local population respond to their environment, particularly temperature, but that pattern is not recapitulated across the phylogeny in a meaningful way. This result also may be indicative of population-level signals being masked at the global (species) level due to averaging [93], particularly in large ecological datasets [94].

At the population level, we observed the temperature at which the *Daphnia* are reared (local temperature) has significant predictive power in all life history traits except size at first reproduction and clutch size (Table 4), consistent with our previous conclusions that size at first reproduction is particularly constrained by phylogeny and that thermal response in clutch size has low variability and species-dependence.

The models generated by the population-level analyses explain between 27% (age at first reproduction) to 94% (size at death) of the variation in the dataset (Table 4), with the exception of population growth rate with very low predictive power at 12%. We understand this high effect size to be attributable to the importance of temperature to the evolution of life history traits. All models contain temperature (either annual or experimental) as significant predictors with high predictive power.

Only half of the population-level life history trait models were improved by the addition of species identity as a fixed effect (Table 4). Even in cases where the model was improved (via AICc score), the predictive value did not substantially improve nor was AICc value substantially decreased by adding species identity. This suggests that species identity is valuable information, even at the population level, but that temperature is a significantly more important driver in life history trait evolution for *Daphnia*, as can be seen by the effect size and significance values for experimental temperature (Table 4). This phenomenon has been well-documented for decades (Table S1), but this analysis, in particular, adds further evidence that it is rarely climatic temperature or temperature variability that predicts life history traits, but absolute temperature instead [95,96]. Notable exceptions to this include size at first reproduction and juvenile growth rate which are more significantly correlated with temperature range ($PC2_{temp}$) than constant absolute temperature ($Temp_{exp}$). Given these two traits' phylogenetic signal and thermal response at the species-level, these findings support their susceptibility to variation in temperature. Additionally, the high predictive value of our population-level life history models (Table 4) along with their species-specific coefficients (Supplement Table S3) will be a valuable resource for understanding *Daphnia* populations and local adaptation broadly.

5. Conclusions

Life history traits are some of the most complex traits yet most important for organisms' evolutionary success [1]. Understanding how they evolve is of utmost importance particularly for cosmopolitan species that experience wide ranges of environmental conditions and those that exhibit life history plasticity [88], particularly to temperature variability [10,12,97]. Especially for poikilothermic organisms, such as *Daphnia*, we expect environmental changes to have drastic implications for their ongoing success due to global climate change [88] and yet their important trophic position to many freshwater ecosystems makes them of

particular concern [98]. Our analyses are an attempt to understand *Daphnia* life history traits through several different lenses: species versus populations and traits versus trait responses (to temperature). *Daphnia* is a particularly useful system in this regard because we have studied the thermal phenotypic plasticity of *Daphnia* for more than 5 decades (Table S1) which gives an abundance of data to test for not only the phylogenetic signal of life history traits but also the phylogenetic signal of the thermal response of life history traits. These analyses add to previous work in understanding global trends in life history trait evolution [1,22,99], but make important additions to our understanding of life history trait evolution in aquatic system, which we know are warming on increased climate trajectories [100], and to the global phylogenetic trends in thermal plasticity of life history traits.

We found that our hypotheses about rate-limited life history traits versus allometric life history traits is too simplistic to fully capture the evolution of life history traits that we see in *Daphnia*. We find that a more apt hypothesis is that considering the mode of life history trait evolution may be a more illustrative way of predicting life history trait response to temperature. Identifying whether traits having shifting optima versus static optima may be more indicative of life history trait trends than allometry or rate limitations alone. However, our global analysis is consistent with previous work with global terrestrial groups [22] that mode of evolution may be more useful than trait associations with allometry or rate limitation, which concurs with findings from small studies [101,102]. Unlike previous global analyses with terrestrial groups [22], we have high predictive power on the majority of our models, despite having few traits with phylogenetic signal, suggesting that these life history trait conclusions may be especially pertinent to aquatic systems or to poikilothermic organisms, more broadly. Despite the successful predictive power of many of our models, in most cases, they remain quite complex, needing to retain long-term temperature and precipitation data, rearing temperature (Temp$_{exp}$), latitude, and species identity, further underscoring the complexity of life history traits and their evolution.

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