Trait variation across biological scales shapes community structure and ecosystem function

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Abstract. Trait variation underlies our understanding of the patterns and importance of biodiversity, yet we have a poor understanding of how variation at different levels of biological organization structures communities and ecosystems. Here, we use a mesocosm experiment to test for the effects of a larval dragonfly functional trait on community and ecosystem dynamics by creating artificial populations to mirror within- and between-population trait variation observed in our study area. Specifically, we manipulate variation in activity rate, a key functional trait shaping food webs, across three levels of biological organization: within-populations (differences in trait variation in a population), among-populations (differences in population mean trait values), and among-species (species-level differences of co-occurring dragonflies). We show that differences in activity rate alter prey communities, trophic cascades, and multiple ecosystem processes. However, trait variation among populations had much larger effects than differences between co-occurring species or even the presence of a predator, whereas within-population variation had a relatively minor impact. Interestingly, combined with earlier work in the same system, our study suggests that the relative importance of species vs. individual level differences for ecosystem functioning will depend on the spatial scale considered. Ecological processes, including biodiversity–ecosystem-functioning relationships, cannot be understood without accounting for trait variation across biological scales of organization, including at fine scales.

Key words: animal behavior; eco-evo; ecosystem services; food web; individual to ecosystem; mesocosm; odonate.

INTRODUCTION

From fleeting changes in an individual's phenotype, to differences among entire communities, trait variation is ubiquitous across biological scales and is central to our understanding of ecological and evolutionary processes. Given the ubiquity of trait variation, biologists in particular sub-fields tend to focus on trait variation at specific biological scales: community ecologists tend to consider among-species differences while evolutionary biologists are primarily concerned with individual- or population-level differences. Because of this compartmentalization we often fail to consider the effects of processes occurring at different biological scales. However, trait variation occurs across biological scales in all natural systems (Sih et al. 2012, Des Roches et al. 2017, Garamszegi and Moller 2017), requiring a greater consideration of processes occurring across scales to understand realistic biological systems.

In ecological communities, functional traits are often important determinants of species interactions, community structure, and even ecosystem functioning (McGill et al. 2006). For example, predator species differing in body size may differently affect prey abundances, identities, and ultimately ecosystem function (Shurin et al. 2002). More recently, the importance of functional trait variation within species for ecological processes has been increasingly recognized (Post et al. 2008, Messier et al. 2010, Schreiber et al. 2011, Violle et al. 2012, Siefert et al. 2015, Hart et al. 2016, Des Roches et al. 2017, Start and Gilbert 2017, Rhoades et al. 2018). Indeed trait variation among populations (Post et al. 2008), and among individuals within a population (Hart et al. 2016, Siefert and Ritchie 2016), can alter species interactions, community structure, and even corresponding ecosystem processes (Morin 1983, Johnson and Stinchcombe 2007).

Functional trait variation across biological scales may be particularly important for the ecological dynamics of trophic systems (Post et al. 2008, Schreiber et al. 2011, Sih et al. 2012, Start and Gilbert 2017), where the cascading effects of predator traits can alter community composition and ecosystem function. There are numerous examples of predator species and populations that differ in key traits and ultimately create divergent prey and resource communities (Morin 1983, Post et al. 2008,

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Start and Gilbert 2017). Similar differences in predator functional traits among populations of the same species can also alter patterns of selection acting on prey, favoring species that are well defended but which consume relatively few resources, ultimately triggering trophic cascades (Post et al. 2008, Start and Gilbert 2017). Finally, within-population trait variation can also cause important shifts in average consumption rates. For instance, variable populations may feed on a greater variety of resources, having smaller effects on any one prey species but interacting with more species overall ("increased degree" in Bolnick et al. 2011, Harmon et al. 2009). Within-population intraspecific variation can also affect consumption independent of increasing the number of resources exploited. For instance, given a saturating relationship between a predator trait and prey consumption (e.g., Bolnick et al. 2011, Start 2018a), increasing intraspecific variation within a population will cause some individuals to consume many fewer prey, and other individuals to consume only incrementally more. As a result, more variable predator populations will on average consumer fewer prey, with this effect being attributed to nonlinear averaging (Jensen's inequality in Bolnick et al. 2011). While it is well understood that different predator functional traits can alter the strength of trophic cascades, studies tend to focus on trait variation at a single biological level, making it difficult to compare impacts across levels.

Behavioral traits may be particularly useful for multi-level comparisons of the impacts of functional trait variation because they can be ecologically significant and measured in common units across levels of biological organization (Sih et al. 2012, Start and Gilbert 2017, Start 2018a). Among predators, particularly, behavioral traits may have large effects (e.g., Griffen et al. 2012, Royauté and Pruitt 2015). For example, differences in movement behavior between populations of dragonfly larvae can create divergent zooplankton communities (Start and Gilbert 2017), and species-level differences in the same traits affect species distributions and community assembly (Start 2018a). Specifically, we hypothesize that increased activity rate augments attack rates, exacerbating the effects of predators on prey abundances and community composition (Griffen et al. 2012, Toscano and Griffen 2014, Start 2018b). Beyond this direct effect, reduced prey abundance and community reorganization can trigger trophic cascades (Griffen et al. 2012, Start and Gilbert 2017, Start 2018a). Ultimately, this shift in producer vs. consumer biomass should cause active dragonflies to increase total photosynthesis but reduce respiration (Start 2018a). Overall, variation in dragonfly activity rates is likely to have important consequences for prey and basal resources, with ultimate impacts on key ecosystem processes.

In this study, we use aquatic mesocosms to test for the impact of functional traits across biological scales on communities and ecosystems. We chose to focus on activity rate differences among dragonflies, a trait that has already been linked to changes in species interactions (e.g., prey consumption; Start and Gilbert 2017, Start 2018b) and ecosystem functioning (e.g., net primary productivity; Start 2018a). We used a classic experimental design in which artificial populations and communities were seeded into mesocosms to create population-level and community-level differences in trait distributions (e.g., Hargrave et al. 2011, Rudman et al. 2015). In particular, we investigated the links between activity rate and ecological responses by manipulating (1) among-population differences, (2) within-population variation, and (3) activity rate differences that arise between species. While among- and within-population variation both represent intraspecific variation, the evolutionary sources of trait variation and their ecological consequences can differ markedly across spatial scales (i.e., among vs. within populations). We chose levels of among-population variation that are representative of ponds surrounding our research site (Start 2018b), and used our focal pond trait distribution for both our high within-pond population variation and also for comparing between co-occurring species. This latter between-species comparison represents but one potential species pair found in the region, but we note that, as in our focal pond, co-occurring species typically have very similar mean activity rates (Start 2018a), likely due to the overwhelming influence of fish predators on survival of individuals with different activity rates (Start et al. 2018). We then tested for the impacts of these treatments on prey communities and ecosystem functioning, demonstrating the surprising importance of trait variation across biological scales or organization.

Materials and Methods

Focal organisms

Epitheca canis (hereafter *Epitheca*) and *Leucorrhinia intacta* (hereafter *Leucorrhinia*) are common dragonfly predators in fishless ponds throughout northeastern North America. They were the first and second most abundant dragonfly larvae species (88% and 11% of all dragonfly individuals for *Epitheca* and *Leucorrhinia*, respectively) in the pond where they were collected (all individuals were collected from a single pond; Supporting Information), and co-occur in ~70% of fishless ponds in Southern Ontario (Start et al. 2018). Choosing co-occurring species informs our understanding of local dynamics, rather than changes that play out over broader scales or across habitat types (fish vs. fishless; see discussion of the implications of this choice in the discussion).

Variation in *Epitheca* activity rate has previously been shown to alter both prey communities and trophic cascades in microcosms (Start and Gilbert 2017), potentially indirectly influencing ecosystem functions such as net primary productivity (Start 2018b). Specifically, more active *Epitheca* tend to increase the relative

abundance of copepods by consuming more co-occurring *Daphnia* (Start and Gilbert 2017). Importantly, *Epitheca* populations also vary markedly in within-population activity rate and differ in average activity rate (Start 2018*b*), meaning that our manipulations of trait variation are concordant with natural patterns. Unfortunately, less is known about the effects of activity rate in *Leucorrhinia*, and the distribution of trait values in this species. Regardless, many odonates have heritable behavioral traits (implied from response to selection) that are consistent across ontogeny (Stoks et al. 2003, Brodin 2008, Start 2018*a*).

Activity assay

We began by collecting dragonfly larvae in early April using dip nets from a fishless pond at the Koffler Scientific Reserve, Ontario, Canada. We used individuals from a single pond to ensure that inferences made about the effects of activity rate were not confounded by other differences that may also occur among ponds, such as carry-over effects of differing resource environments. We immediately transferred each individual to a 9-cm Petri dish filled with pond water. We then used a simple open-field activity test to assay individual larval activity rates, our focal behavioral trait (following Start and Gilbert 2017, Start 2018*a,b*). Open-field tests are frequently used to measure movement patterns such as activity rate, including in larval odonates (Johansson and Rowe 1999, Brodin 2008, Start and Gilbert 2017, Start 2018*b*). We conducted assays on 307 haphazardly collected individuals (33 *Leucorrhinia* and 274 *Epitheca*) in the 9-cm Petri dishes to which they were immediately transferred. After allowing 24 h to become habituated, we recorded the position of each individual every 20 min for 3 h (10 observations; 12). We then calculated the minimum distance between each position, using the summation across all 10 observations as our measure of activity rate (i.e., the minimum total distance moved by an individual in 3 h). This measure of activity rate has previously been shown to be repeatable in *Epitheca* ($R^2 = 0.41$ in Start and Gilbert 2017) and *Leucorrhinia* ($R^2 = 0.35$ in Start 2018*b*). Note that all individuals were well below the theoretical maximum activity rate, meaning that constraints imposed by arena size are unlikely to affect our measure of activity rate.

To avoid confounding body size with activity rate, we measured the head width of each individual using ImageJ software (NIH and LOCI, University of Wisconsin). Consistent with past work (McCauley 2008, Start and Gilbert 2017, Start 2018*b*), we found no correlation between these traits ($r = -0.05$, $P = 0.98$). We detected no difference in mean body size among treatments ($P = 0.87$), including our species-level comparisons. We also did not find any difference in the variance in body size among treatments ($P = 0.97$). We therefore analyzed data without controlling for body size, although all analyses are qualitatively identical when including this factor.

All other sources of trait variation (e.g., ontogeny, sex) were uncontrolled. After measuring activity rate, we immediately grouped individuals into one of five predator treatments and introduced them into mesocosms (in the Experimental Design section).

Feeding trial

Nonlinear relationships between a trait and its function (e.g., activity rate and consumption) can cause trait variance to affect function via nonlinear averaging (see Bolnick et al. 2011 for a simple graphical example). As such, we used a feeding trial to quantify the effect of larval activity rate on consumption. We conducted feeding trials for 10 *Epitheca* selected to represent a range of high and low activity rate individuals. We began by introducing each individual to a separate 4-L tank filled with filtered pond water. After allowing individuals to acclimate for 24 h, we introduced ten adult *Daphnia* sp., counting the number of *Daphnia* remaining after one hour.

Statistically, we aimed to quantify the relationship between activity rate and consumption. Specifically, we log transformed both dragonfly activity rate and the number of *Daphnia* consumed, then estimated consumption using a linear model (LM). In this model, the coefficient of ln-transformed activity rate is equivalent to the exponent in a power function, such that a coefficient that is significantly different from 1 signifies a nonlinear response.

Mesocosm experiment

Experimental communities.—We performed the experiment in artificial mesocosms created to mimic the structure of local fishless ponds where invertebrate predation is predominant. We established mesocosms in 416-L plastic cattle watering tanks in a fully randomized design in a field at the Koffler Scientific Reserve, Ontario, Canada. We half-filled tanks with filtered pond water (5-μm pore size) in early April 2017 immediately after ice-off in local ponds, then allowed water levels to fluctuate naturally throughout the experiment (tank levels rose, but never to the top). We excluded colonization by non-focal predators and other organisms (e.g., tadpoles) by covering all tanks with 0.066-cm fiberglass mesh.

Immediately after filling tanks we began to establish experimental communities. We first added 500 g of air-dried white oak leaves to serve as litter. We then introduced 250 mL of concentrated zooplankton and phytoplankton collected using 64-μm plankton nets from the same fishless pond where dragonfly larvae were collected. Note that while we did not identify or count aquatic invertebrates, similar collections from the same pond have included > 30 morphospecies spanning > 10 families (Start 2018*b*, Start and De Lisle 2018). We also added 100 g of aquatic macrophytes (*Hydrilla* sp.) to each tank after ensuring that we had removed all

dragonfly larvae, but while leaving in place all other aquatic invertebrates. We allowed these communities to establish for three weeks prior to initiating treatments.

Experimental design.—Our experimental design allowed us to test for the community and ecosystem level consequences of predator activity rate, while controlling for predator abundance. We introduced seven individual dragonfly larvae to each mecosom, but while manipulating activity rates. More specifically, we imposed treatments that allowed us to test for the effects of intraspecific variation among communities (difference in mean activity rate among mesocosms), intraspecific variation with communities (identical mean activity rate but with high or low variation within a mesocosm), and interspecific variation among communities (mesocosms with either *Epitheca* or *Leucorrhinia*). We tested for the effects of these differing types of variation using six treatments: (1) no predators, (2–4) low, medium, or high mean activity rate of *Epitheca* predators with low variance, (5) medium activity rate of *Epitheca* with high (natural) variance, and (6) presence of the same number of *Leucorrhinia* sampled from the natural distribution of activity rates (*Leucorrhinia* has an intermediate activity rate; Appendix S1).

Note that population mean activity rates and variance in activity rates were not manipulated in a factorial design. We have instead included three different population mean activity rates with low variances, and contrasted only the medium average activity rate treatment with low and high variances. This limitation occurs because, consistent with patterns observed in nature, it was impossible to create treatments where there existed high within-population trait variation with high or low mean trait values. This is because having a large variance with an extreme mean phenotype would change the shape in addition to the raw variance in traits. Put simply, if a population has a low mean trait value, variation can only be so high because a given individual cannot have a substantially lower trait value than the mean.

Also note that for logistical reasons, we were not able to replicate manipulations of trait means and variances for both species, as this would have required an experiment that was twice as large. Instead, we suggest that readers compare the *Leucorrhinia* treatments to the medium-mean high-variance *Epitheca*. This comparison is appropriate because these treatments represent the natural distribution of trait values in the collection pond, thus recapitulating patterns observed in the wild. Our treatments are therefore likely to be representative of dynamics occurring in real systems.

Note that treatments 2–4 differed in mean activity rate ($P < 0.001$ using a linear model) but not variance (Appendix S1; $P = 0.74$ using an F test). Conversely treatments with average mean activity rates (3 and 5) did not differ in mean activity rate (Appendix S1; $P = 0.67$ using a linear model) but did differ in variance ($P < 0.001$ using an F test). Differences in the variance

and mean activity rates of *Epitheca* were consistent with observed differences among natural populations (Start 2018*b*). The natural distribution (mean and variance) of *Epitheca* activity rates did not differ from *Leucorrhinia* (both $P > 0.25$ using linear models and F tests, respectively), a pattern consistent for co-occurring dragonfly species in our study area (Start et al. 2018). We introduced all individuals to mesocosms on 29 April 2017, then allowed community dynamics to play out for 33 d before *Epitheca* began to emerge, at which point we ended the experiment. All treatments were replicated seven times, except the *Leucorrhinia* treatment, which had five replicates owing to a lack of available animals.

Community composition.—1. Primary producer abundance.—We aimed to quantify the abundance of primary producers in two ways. First, at the end of the experiment, we measured chlorophyll concentration using an AquaFluor probe (Turner Designs, San Jose, California, USA), which relies on spectrophotometry. We repeated these measurements five times, always drawing water from the center of the tank in the middle of the water column. These measurements principally quantify the abundance of phytoplankton suspended in the water column (pelagic phytoplankton). Our second measure of primary producer abundance aimed to quantify the biomass of periphyton (benthic phytoplankton). At the end of the experiment, we removed all floating biomass, and all algae that had accumulated on the sides and bottom of the tank. We dried this biomass in a drying oven for one week at 60°C then recorded dry biomass.

2. Invertebrate community composition.—At the end of the experiment, we used a pipe-sampler (10 L) to sample aquatic invertebrates from each tank, filtering each sample through 64-μm mesh. We took five samples across the length of each tank, including one from each edge of the tank, totaling ~50 L or ~12% of the total tank volume, then pooled the samples and preserved invertebrates in 80% ethanol for identification. We later counted and identified all individuals to genus and then morphospecies level. All morphospecies are likely to be eaten by both species of dragonfly (the largest morphospecies was in the genus *Chaoborus* along with some early instar damselflies), and no species was large enough to consume dragonfly larvae.

Ecosystem functions.— We estimated a suite of ecosystem functions, aiming to link differences in ecosystem function to activity treatments and corresponding changes in community structure.

1. Decomposition.—We estimated decomposition rates of oak leaves over the duration of the entire experiment. Immediately upon initiating experimental treatments we added one leaf litter bag (mesh size: 64 μm) filled with 2.5 g of oven-dried leaves (72 h at 60°C) to each

mesocosm. Leaves were collected from the ground surrounding our experimental mesocosms. At the end of the experiment we removed leaf litter bags, then dried all leaves for one week at 60°C before weighing the remaining leaf tissue. We then calculated decompositions rates (k) using the exponential decay curve model $M_t = M_0 e^{-kt}$, where M_0 is the initial mass, M_t the final mass, and t is the duration of the experiment in days (Rudolf et al. 2014).

2. Net primary productivity, photosynthesis, and respiration rates.—We measured NPP and its components (photosynthesis and respiration) using changes in dissolved oxygen (DO) over the course of a diurnal cycle. All DO measurements were performed using an oxygen probe (Professional Plus; YSI, Yellow Springs, Ohio, USA). Specifically, we measured DO at sunset on 31 May, then again at sunrise and sunset on 1 June. We then calculated NPP and its components based on changes in DO between these time periods. Respiration is simply the decrease in DO between sunset and sunrise when photosynthesis cannot occur. NPP is the net change in DO between sunrise and sunset, representing the cumulative effects of photosynthesis (producing oxygen) and respiration (using oxygen). Finally, photosynthesis is then simply the sum of NPP and respiration, after having multiplied respiration to account for differences in night and day length.

3. Water quality and chemistry.—We equally measured a suite of physical and chemical water variables. Specifically, we used a YSI probe (YSI Professional Plus, Hoskin) to measure pH, conductivity, turbidity, and oxidation-reduction potential.

Statistical methods

Community composition.— Our goal was to describe the effects of predator treatments on prey community abundance and composition and ecosystem functions, then to describe the relationships among these measures. We began by using linear models to test for the effect of predator treatments on prey abundance, the proportion of the community composed of copepods, and algal abundance in mesocosms. We used a generalized linear model (GLM) with a Poisson error distribution to test for differences in total prey abundance among treatments. We used an LM to estimate the ln-transformed proportion of the prey community composed of copepods, again using treatment as a main effect. We next tested for treatment-level differences in algae abundance, using separate LMs to estimate ln-transformed chlorophyll concentration (pelagic algae) and algal dry mass (benthic algae)

While simple metrics of community composition (proportion of community composed of copepods) may adequately describe some ecological patterns, we next aimed to formally test for multi-variate differences in community

composition among treatments. After testing for differences in variance of community composition among treatments, and finding no difference, we tested whether prey communities differed among treatments using permutational multivariate analysis (PERMANOVA). We permuted analyses 999 times based on centroids, comparing Bray-Curtis similarity indices. We then visualized any potential multivariate differences in community composition using nonmetric multidimensional scaling plots (NMDS) using the package vegan in R (Oksanen et al. 2017, R Core Team 2017). Note that for all analyses comparing treatments with high and low within-population trait variation, we repeated tests while including mean activity rate as a random effect. These additional tests are to ensure that small and insignificant differences in mean trait values (e.g., between treatments with high and low within-population variation) were not driving any observed among-treatment patterns. We also repeated these alternative test for ecosystem analyses (Ecosystem Functioning section), but invariable found qualitatively identical results to those not including random effects. As such, we chose to report results from the simpler analyses.

Finally, we tested for a potential trophic cascade by aiming to link changes in zooplankton communities to algal abundance. Specifically we used LMs to predict each measure of algal abundance using zooplankton abundance, the proportion of the community composed of copepods, and their interaction as main effects, dropping nonsignificant terms to arrive at the final model. We repeated this analysis using scores generated from PERMANOVA rather than proportion of copepods, with the former measure representing a multivariate description of prey community composition.

Ecosystem functions.— We tested for treatment-level effects on ecosystem functions, and for relationships between ecosystem functions and various measure of invertebrate and primary producer community structure. We first used an LM with treatment as a main effect to estimate respiration. We repeated this analysis to estimate NPP, photosynthesis, decay rate, and our suite of water chemistry measurements, ln-transforming the response variable when appropriate.

After quantifying treatment-level differences, we aimed to link any observed changes in ecosystem function to corresponding changes in community composition. For example, we estimated NPP, photosynthesis, and respiration rates using an LM with invertebrate abundance, one measure of algal abundance, and one measure of invertebrate community composition as main effects. We repeated this model for all measures of ecosystem function that differed among treatments, selecting the variables retained in the final model using P values (i.e., we repeated models using chlorophyll concentration or algal dry mass, with the final model retaining the variable with the lowest P value). When model selecting using Akaike's information criterion corrected for sample size (AIC_c), the same final models were
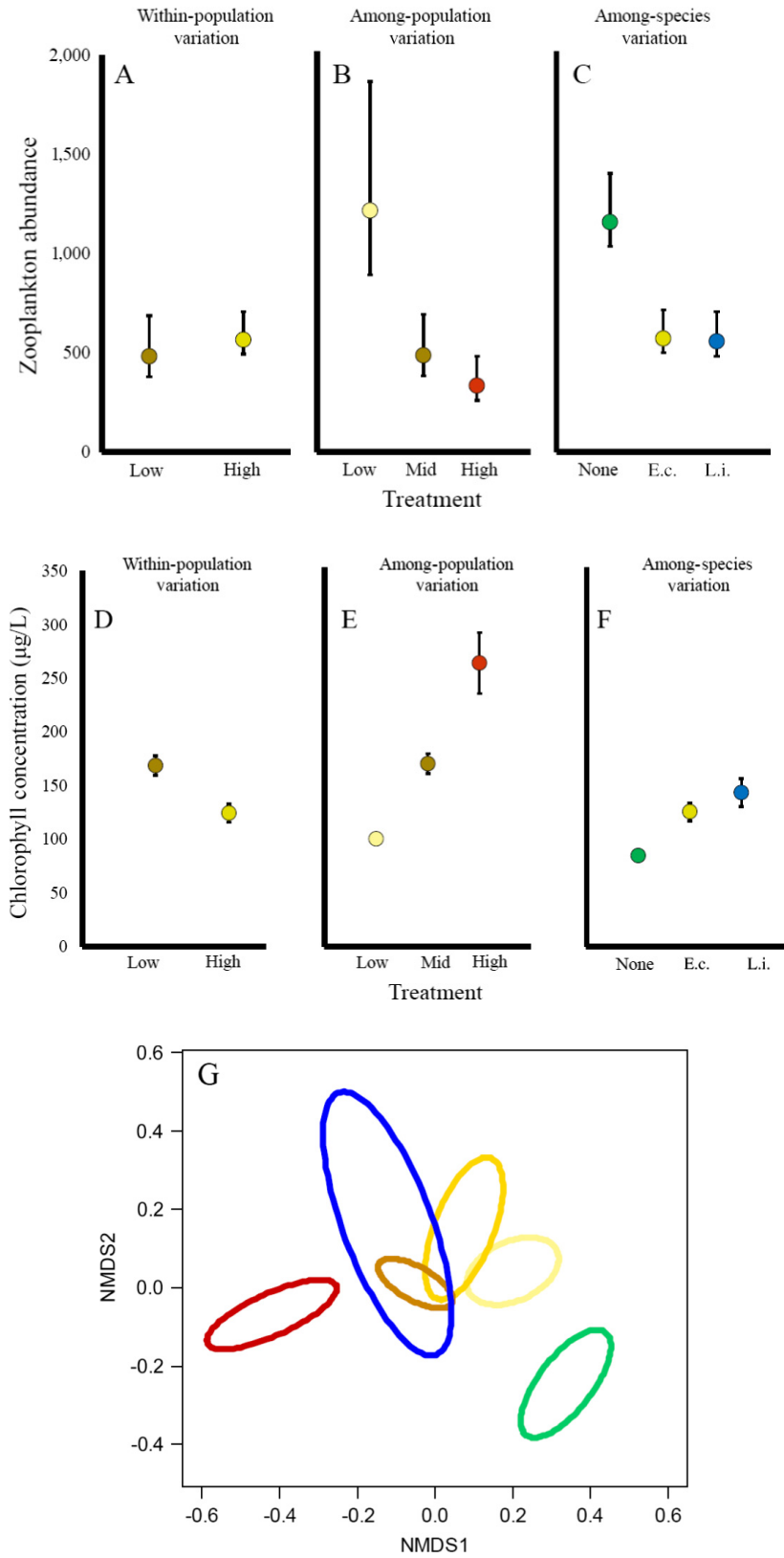
Fig. 1. Treatment-level effects on prey and resource communities. Dragonfly larvae (A–C) reduced zooplankton abundance, (D–F) increased chlorophyll concentration, and (G) shifted prey community composition. Zooplankton abundance was affected by

Fig. 1. (Continued)
the presence/absence and among-population variation (i.e., differences in population mean activity rate), but did not diverge among treatments with differing within-population (i.e., differences in population variance in activity rate) or among-species trait variation (A–C). Chlorophyll concentration varied among treatments manipulating within-population, among-population, and the presence/absence of predators, but was unaffected by among-species trait differences (D–F). For both zooplankton abundance and chlorophyll, among-population variation had the largest effect. Beyond shifting abundances, treatments also differed in multivariate community composition, with among-population variation again having the largest effect (G). Error bars represent 95% confidence intervals (A–F), ellipses show two standard errors about each treatment's centroid with colors corresponding to those in the other panels (G). L.i., *Leucorrhinia intacta*, which has a similar activity rate to E.c., *Epitheca canis*.

reached. Treatments had no effect on our suite of water quality and chemistry metrics or decay rate (all $P > 0.4$), but large effects on other ecosystem processes (reported in main text). We tested all models and calculated significance values using log-likelihood ratio tests. All analyses were done in R (R Core Team 2017) using the vegan (Oksanen et al. 2017) and lme4 (Bates et al. 2015) packages.

Results

Active *Epitheca* consumed more *Daphnia* ($P < 0.001$; Appendix S1), but this relationship was concave down (slope = 0.16, SE = ±0.018). Note that the slope is significantly less than one, meaning that the relationship is concave down (Appendix S1: Fig. S10). The concave-down relationship between activity rate and consumption means that increasing variation should reduce total consumption through nonlinear averaging (Ruel and Ayres 1999, Bolnick et al. 2011). Conversely, high average activity rates should increase population mean consumption.

Variation in predator activity rate altered prey communities, trophic cascades, and ecosystem function, but the effects depended on the scale at which we were examining trait variation (within populations vs. among populations vs. among species). In a simple feeding trial, high activity individuals consumed 66% more *Daphnia* (Appendix S1; $P < 0.001$, $n = 10$). This function mirrored the impact of dragonflies on prey communities and the broader ecosystem. First, the simple presence of dragonfly predators halved prey abundance and altered community composition (Fig. 1C, G, both $P < 0.001$; Appendix S1), doubling chlorophyll concentration (i.e., a trophic cascade; Fig. 1F, $P < 0.001$; Appendix S1) that ultimately reduced respiration and increased photosynthesis and net primary productivity (NPP; Fig. 2C, all $P < 0.001$; Appendix S1). Beyond the simple presence or absence of a predator, *Leucorrhinia* and *Epitheca* populations with realistic trait distributions (average activity rate with high variance) had similar effects on prey, resources, and ecosystem functions (Figs. 1C, G, and 2, Appendix S1, all $P > 0.2$). *Epitheca* populations with high mean activity rates had greater impacts on prey communities, trophic cascades, and ecosystem function than inactive populations (Figs. 1B and 2B, Appendix S1; all $P < 0.01$). Among treatments differing in individual (within-population) variation, the impact

of predators on prey abundance did not differ (Fig. 1A; $P = 0.42$), but within-population differences did restructure prey communities (multivariate community composition) and ecosystem function (Figs. 1D, G and 2A; all $P < 0.05$). In all cases, treatment affected photosynthesis, respiration, and NPP, but had no effect on other measures of water quality (all $P > 0.3$). All treatments were replicated seven times, save the *Leucorrhinia* treatment, which was replicated five times. Please see figures for pairwise comparisons with 95% confidence intervals, as well as to assess effect sizes.

Discussion

Variation in predator activity rate altered prey communities, trophic cascades, and ecosystem function, but differences within species tended to be far more consequential than equivalent differences among species. Specifically, among-population differences in activity rate had the largest impacts, greater even than the presence vs. absence of dragonflies (Figs. 1 and 2). Interestingly, even within-population variation generated larger trophic cascades than activity rate differences between the species considered here (Figs. 1 and 2), although we consider only the two species that co-occur locally and have similar trait distributions. As a result, and consistent with previous work (Start 2018a), we contend that the relative importance of within- vs. among-species will depend on the spatial scale of the community and the definition of the regional species pool. In short, if we consider all species in the regional species pool, among-species differences far exceed intraspecific variation, causing interspecific differences to have larger ecological effects (Start 2018a). This effect arises because species tend to specialize on different habitat types, meaning interspecific variation will exceed intraspecific variation when many types of habitats are sampled. Beyond the dichotomy of intra- vs. interspecific trait differences, we demonstrate that intraspecific variation within and among populations can have divergent effects on ecological processes (Figs. 1 and 2), requiring ecologists to consider the distribution of trait variation both across biological scales and across the landscape. Overall, achieving a deeper understanding of functional trait variation at different levels of organization allows for a more complete understanding of ecological systems

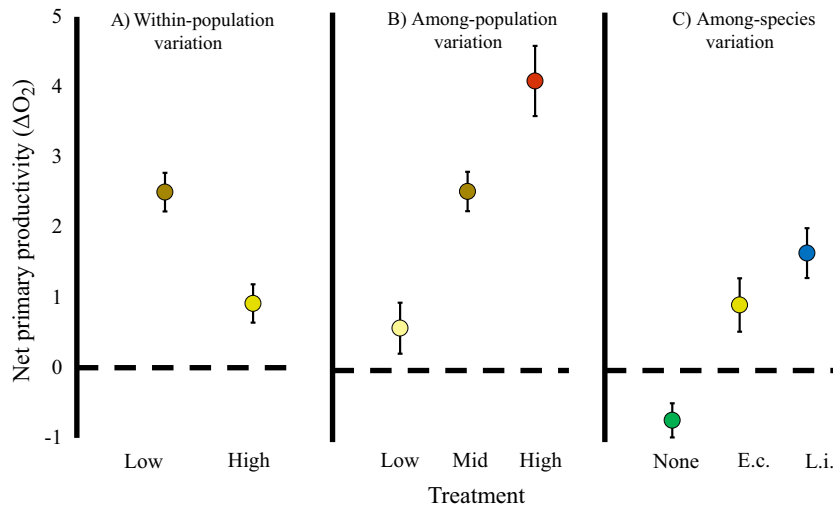Functional trait variation at multiple scales of biological organization (within populations to species-level

Fɪɢ. 2.   Treatment-level effects on ecosystem functions. Dragonfly larvae increased NPP (A–C), a pattern driven by changes in respiration and photosynthesis (Appendix S1), and ultimately underlain by shifting patterns of community composition driven by predator trait variation. Again, among population differences (i.e., population mean differences in activity rate) have the largest effect and among species differences are the least consequential. Error bars show 95% confidence intervals. L.i., *Leucorrhinia intacta*, which has a similar activity rate to E.c., *Epitheca canis*.

differences) cascaded through ecological communities, causing large shifts in distant processes (e.g., ecosystem function). High activity rates increase attack rates (Appendix S1), thus directly reducing prey abundance. Beyond simple differences in prey abundance, high activity rate shifted invertebrate communities to favor copepods over *Daphnia* (Fig. 1G, Appendix S1), likely because copepods are less susceptible to predation (Start and Gilbert 2017). While copepods are consumed less frequently, they are outcompeted in the absence of predation and have a smaller impact on resource abundance (e.g., Morin 1983, Start and Gilbert 2017). High activity rate thus changed the abundance and composition of prey communities, ultimately increasing resource abundance (Fig. 1, Appendix S1). These differences in trophic community structure had corresponding effects on ecosystem processes (Fig. 2, Appendix S1). High prey abundance and shifts in prey community composition increased respiration, and corresponding changes in algal abundance reduced photosynthesis (Appendix S1). Jointly, changes in both ecosystem processes determine net primary productivity (Fig. 2, Appendix S1). These links between predators, prey, resources, and ecosystem processes are broadly consistent with observed patterns of trophic cascades, particularly in aquatic systems (Paine 1966, Post et al. 2008, Start and Gilbert 2017, Start 2018*a,b*). Given the common effects of increasing activity rate, an understanding of the effect of a trait at one level of biological organization may inform our understanding of the same trait at other scales.

While species differences did not have detectable impacts on ecological processes, intraspecific variation (among and within population differences) had sometimes large effects on prey abundance, community composition, and ecosystem processes (Figs. 1 and 2; Des Roches et al. 2017). The disproportionate importance of intraspecific variation is particularly marked given that community ecologists tend to consider the mean species trait value as adequately representing the role of a species in a community (although intraspecific variation is gaining renewed appreciation; Johnson and Stinchcombe 2007, Post et al. 2008, Bolnick et al. 2011, Sih et al. 2012, Hart et al. 2016, Siefert and Ritchie 2016). From an applied perspective, the effects of trait variation across scales on ecosystem functioning suggests that biodiversity–ecosystem-function relationships may stem from trait differences at multiple scales (Johnson and Stinchcombe 2007). Overall, these results suggest a need to further incorporate intraspecific variation into models of community and ecosystem dynamics (Bolnick et al. 2011, Des Roches et al. 2017).

While the incorporation of intraspecific variation into community ecology can result in a novel and more profound understanding of biological systems, our results further suggest that the current dichotomy of intra- and inter-specific variation is overly simplistic (Sih et al. 2012). In our study, intraspecific variation had quantitatively different ecological consequences depending on the scale being considered; differences in activity rate among populations had much larger effects on community and ecosystem processes than did variation within populations (Figs. 1 and 2). From an eco-evolutionary perspective, we may then predict that local adaptation resulting in population differences should have a large effect on community and ecosystem dynamics (Post et al. 2008) whereas the maintenance or loss of variation within populations should be less consequential. A more thorough understanding of the scale of intraspecific

functional trait variation and its consequences will deepen our understanding of eco-evolutionary dynamics.

Despite their small quantitative effect relative to population-level differences, within-population variation in activity rate did cause larger shifts in community structure and ecosystem processes than equivalent differences among species (Figs. 1D and 2A). Subsequent analyses of these data showed that this trend persisted when any differences in mean trait values were accounted for, highlighting the role of within-population variation. The greater impact of intermediate predator populations lacking individual variation may be owing to Jensen's inequality (Ruel and Ayres 1999). Because the relationship between activity rate and consumption is saturating (Appendix S1: Fig. S10), nonlinear averaging should reduce the effect of predators on their prey when predators exhibit variation in activity rate (Bolnick et al. 2011). Although we could not detect an impact of within-population variability on prey abundances, it caused a clear change in lower trophic levels and caused concordant shifts in ecosystem processes (Figs. 1 and 2). Hence, the evolutionary loss of variation from a population owing to stabilizing selection or genetic drift could have effects on ecological dynamics independent of any change in mean trait value (Bolnick et al. 2011, Sih et al. 2012). Importantly, the effect of nonlinear averaging on prey communities will depend on the shape of the relationship between ecologically relevant predator traits and prey consumption (Bolnick et al. 2011). More broadly, many mechanisms link predator traits (and their variation) to prey consumption (for a review see Bolnick et al. 2011), necessitating a greater understanding of the mechanisms underlying the ecological impacts of intraspecific variation.

An important consideration is the degree to which the species being considered affect the importance of different components of functional trait variation. Indeed, earlier work has demonstrated that, contrary to the present study, dragonfly species can have extremely divergent effects on aquatic communities and ecosystems (Start 2018a). However, the vast majority of this variation arises between species that specialize on fish vs. fishless habitats. For instance, when considering only the four fishless pond specialists present in the regional species pool, there were no differences in any measured community or ecosystem response (Start 2018a). The lack of among-species differences in fishless pond specialists suggests a certain degree of ecological equivalence, a pattern consistent with other work in odonates (Siepielski et al. 2010). More generally, the relative importance of species-level differences will depend on the breadth of the regional species pool. In essence, when considering local communities that are environmentally similar and thus support ecologically similar species (e.g., fishless ponds with fishless pond specialists), intraspecific variation should be relatively more consequential. Conversely, if we simply consider a more general regional species pool (e.g., all species including fish pond specialists), then interspecific variation should

become increasingly important as among-species trait differences are inflated (Start 2018a). Overall, the relative importance of different biological scales of trait variation may largely depend on the definition of the regional species pool. Regardless, in this system and in the absence of dispersal from dissimilar habitats (i.e., those with fish), changes to within rather than among species trait variation appear to be more consequential for communities and ecosystems.

By considering functional trait variation across biological scales, this study has demonstrated the implication of traits for communities and ecosystems. At the most basic level, we have shown that realistic differences in predator traits can alter trophic cascades, shifting the abundance and composition of prey communities, resource abundance, and ultimately shifting ecosystem processes. While increasing activity rate at the among-population and among-species levels had similar effects, the relative importance of intraspecific variation was much greater (Figs. 1A–C and 2A–C), suggesting a need to incorporate trait variation at all levels into models of communities and ecosystems (Bolnick et al. 2011, Sih et al. 2012, Violle et al. 2012). Beyond the simple dichotomy of variation within and among species, we suggest that intraspecific variation can have different effects within and among populations, requiring a deeper understanding of both the causes and distribution of trait variation, and the many mechanisms by which variation can affect population, community, and ecosystem dynamics. Although achieving a deeper understanding of functional trait variation across biological levels is challenging, our study shows that such an understanding can fundamentally shift the dynamics of ecological communities and associated ecosystem functions.

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