

# Phenotypic evolution is more constrained in simpler food webs

Matthew A. Barbour<sup>1,2,\*</sup>

Christopher J. Greyson-Gaito<sup>1,3</sup>

Arezoo Sootodeh<sup>3</sup>

Brendan Locke<sup>4</sup>

Jordi Bascompte<sup>2</sup>

1. University of British Columbia, Department of Zoology, Vancouver, BC V6T 1Z4, Canada;
2. University of Zurich, Department of Evolutionary Biology and Environmental Studies, Winterhurerstrasse 190, 8057 Zurich, Switzerland;
3. University of Guelph, Department of Integrative Biology, Guelph, ON N1G 2W1, Canada;
4. Humboldt State University, Department of Biological Sciences, Arcata, CA 95521, USA.

\* Corresponding author; e-mail: matthew.barbour@ieu.uzh.ch

*Manuscript elements:* Figure 1, figure 2, figure 3, figure 4. All figures should be printed in color.

*Keywords:* fitness landscape, host-parasitoid, natural selection, G-matrix, community context, ecological networks, evolutionary ecology, eco-evolutionary dynamics.

*Manuscript type:* Article.

Prepared using an *Am. Nat.* inspired L<sup>A</sup>T<sub>E</sub>X template for Rmarkdown.

## Abstract

Global change is simplifying the structure of ecological networks; however, we are currently in a  
3 poor position to predict how these simplified communities will affect the evolutionary potential  
of remaining populations. Theory on adaptive landscapes provides a framework for predicting  
how selection constrains phenotypic evolution, but often treat the community context of evolving  
6 populations as a “black box”. Here, we integrate ecological networks and adaptive landscapes  
to examine how changes in food-web complexity shape evolutionary constraints. We conducted  
a field experiment that manipulated the diversity of insect parasitoids (food-web complexity)  
9 that were able to impose selection on an insect herbivore. We then measured herbivore survival  
as a function of three key phenotypic traits. We found that more traits were under selection in  
simpler vs. more complex food webs. The adaptive landscape was more neutral in complex food  
12 webs because different parasitoid species impose different selection pressures, minimizing relative  
fitness differences among phenotypes. Our results suggest that phenotypic evolution becomes more  
constrained in simplified food webs. This indicates that the simplification of ecological communities  
15 may constrain the adaptive potential of remaining populations to future environmental change.

“What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions.” [Janzen \(1974\)](#)

## <sup>18</sup> Introduction

The adaptive landscape provides a powerful framework for understanding how natural selection has shaped the evolution of biodiversity —from genes to phenotypes to species ([Wright, 1931](#); [Simpson, 1944](#); [Arnold et al., 2001](#)). More than a metaphor, the adaptive landscape links quantitative genetic and phenotypic variation to evolution by natural selection ([Lande, 1979](#); [Arnold and Wade, 1984a,b](#)). Ecological interactions often play a key role in shaping adaptive landscapes, as evidenced by the role of antagonistic ([Schluter, 2000](#); [Abrams, 2000](#)) and mutualistic ([Bronstein et al., 2006](#)) interactions in driving evolutionary change. Although there is clear evidence that pairwise interactions can shape the adaptive landscape, we do not know how the adaptive landscape is shaped by the community context ([McPeek, 2017](#); [terHorst et al., 2018](#)). Resolution on how the community context shapes phenotypic evolution is urgently needed though, given the rapid impacts of climate change on ecological communities ([Scheffers et al., 2016](#)).

<sup>30</sup> Ecological networks, such as food webs describing who-eats-whom in ecological communities, provide an explicit representation of the community context ([Bascompte and Jordano, 2014](#); [McCann, 2012](#)). Here, we integrate ecological networks and adaptive landscapes to understand how community context constrains evolutionary change ([Arnold, 1992](#)). Different aspects of evolutionary constraints can be inferred by quantifying the slope and curvature of the adaptive landscape. For example, the slope is determined by directional selection gradients acting on each phenotypic trait and influences the trajectory of evolutionary change ([Lande, 1979](#); [Arnold, 1992](#)). Evolutionary trajectories become more constrained with an increase in the number of traits under selection, as this diminishes the number of optimal solutions ([Arnold, 2003](#)). The curvature of the adaptive landscape can also constrain evolution through its indirect effect on genetic constraints ([Arnold, 1992](#); [Hansen and Houle, 2008](#)). Genetic constraints are largely governed by a population’s G-matrix

—the additive genetic variances and covariances between traits (Hansen and Houle, 2008). In  
42 general, genetic constraints will increase with the number of traits under directional or stabilizing selection, as this will decrease the additive genetic variance in those traits (Hansen and Houle, 2008). Genetic constraints may also increase with the number of trait combinations under correlational  
45 selection, as this type of selection decreases the evolutionary independence of traits (Hansen and Houle, 2008). If we want to predict how community context constrains evolutionary change, we must understand how ecological networks shape the adaptive landscape.

48 Global change is simplifying the structure of ecological communities, which may influence evolutionary constraints in a number of ways. For example, in a multitrophic community or food web, if different consumers impose directional selection on different traits of a shared resource, then more  
51 complex food webs may constrain evolution by increasing the number of traits under selection. Alternatively, if consumers impose selection on different values of a trait, then their selective effects would cancel each other out in more complex food webs. To examine these different possibilities  
54 (among others), we conducted a field experiment that manipulated the complexity of trophic interactions (hereafter food-web complexity) associated with an abundant insect herbivore (*Iteomyia salicisverruca*; Family Cecidomyiidae)(fig. 1). The larvae of this herbivore induce tooth-shaped  
57 galls when they feed on the developing leaves of willow trees (*Salix* sp., Russo, 2006). These galls protect larva from attack by generalist predators (e.g. ants, spiders), but they suffer high mortality from egg and larval parasitoids (Barbour et al., 2016). We manipulated food-web complexity  
60 by either excluding the guild of larval parasitoids (simple food web) or allowing both egg and larval parasitoids to impose selection on gall midge traits (complex food web; fig. 1). We then applied modern statistical methods to quantify the effect of food-web complexity on the slope and  
63 curvature of the gall midge's adaptive landscape. Taken together, our study gives insight to how local extinctions, and concomitant decreases in food-web complexity, may constrain the evolution of interacting populations.

66 **Methods**

### Study Site

We conducted our study within a four-year old common garden experiment of coastal willow (*Salix hookeriana*) located at Humboldt Bay National Wildlife Refuge (HBNWR) (40° 40' 53"N, 124° 12' 4"W) near Loleta, California, USA. This common garden consists of 26 different willow genotypes that were collected from a single population of willows growing around Humboldt Bay. Stem cuttings of each genotype (25 replicates per genotypes) were planted in a completely randomized design in two hectares of a former cattle pasture at HBNWR. Willows at our study site begin flowering in February and reach their peak growth in early August. During this study, willows had reached 5 - 9m in height. Further details on the genotyping and planting of the common garden are available in Barbour et al. (2015).

### Manipulating Food-web Complexity

We setup our food-web manipulation across 128 plants soon after galls began developing on willows in early June of 2013. These 128 plants came from eight different plant genotypes that spanned the range of trait variation observed in this willow population (Barbour et al., 2015). For the complex food-web treatment (eight replicates per genotype), we used flagging tape to mark 14 galled leaves per plant (~30 larvae), allowing the full suite of egg and larval parasitoids to impose selection. Marking galls with flagging tape ensured that we compared control and treatment galls with similar phenology when we collected galls later in the season. For the simple food-web treatment, we enclosed 14 galled leaves with 10x15cm organza bags (ULINE, Pleasant Prairie, WI, USA) to exclude three parasitoid species that attack during larval development. This treatment did not exclude the egg parasitoid *Platygaster* sp., which attacks prior to gall initiation (larva initiate gall development in Cecidomyiid midges: Gagné, 1989). In late August, we collected marked and bagged galls from each plant, placed them into 30 mL vials and kept them in the lab for 4

90 months at room temperature. We then opened galls under a dissecting scope and determined  
91 whether larvae survived to pupation (our measure of fitness) or were parasitized. Since we were  
92 interested in selection imposed by parasitoids, we excluded unknown sources of mortality. For the  
93 food-web treatment that excluded larval parasitoids (simple food web), we further restricted our  
94 data by removing any incidental instances of parasitism by a larval parasitoid. This represented  
95 less than 3% of the observations in this food-web treatment and allowed us to focus our inferences  
96 of selection on those imposed by the egg parasitoid. Our final dataset contains survival estimates  
for 1285 larvae from 613 galls and 111 plants.

## Measuring Phenotypic Traits

99 We collected data on three different traits that we expected to influence larval survival based on  
100 our previous work (Barbour et al., 2016) and others work with gall midges (Weis et al., 1983; Heath  
et al., 2018). First, we measured gall diameter as the size of each gall chamber to the nearest 0.01  
102 mm at its maximum diameter (perpendicular to the direction of plant tissue growth). Our previous  
work has shown that larger galls are associated with higher survival (Barbour et al., 2016). Second,  
103 we measured clutch size by counting the number of chambers in each gall (Weis et al., 1983; Heath  
et al., 2018). All larvae collected from the same multi-chambered gall were scored with the same  
105 clutch size. Third, we measured oviposition preference as the density of larvae observed on a plant  
in an independent survey. We did this by randomly sampling five branches per tree and counting  
108 the number of individual gall chambers (number of larvae). We then converted these counts to a  
measure of larval density per 100 shoots by counting the number of shoots on the last branch we  
sampled. All larvae collected from the same plant were scored with the same oviposition preference.  
111 Measuring larval densities on plants in the field is a common method for measuring oviposition  
preference (Gripenberg et al., 2010); however, caution must be taken in inferring ‘preference’ as  
113 larval densities can be influenced by processes other than preference (Singer, 1986). Fortunately,  
114 a couple of features of our study system suggest that larval densities may be a good proxy for

oviposition preference. For example, since our data comes from a randomized placement of plant genotypes in a common garden, there is no consistent bias in which plant genotypes females are exposed to while searching for oviposition sites. Also, egg predation is a minor source of mortality for galling insects in general ([Hawkins et al., 1997](#)); therefore, we do not expect any prior egg predation to bias our estimates of observed larval densities.

## [120 Quantifying the Adaptive Landscape](#)

Our analyses consisted of three parts. First, we used generalized linear mixed models (GLMM) to quantify selection surfaces —linear and nonlinear relationships between absolute fitness ( $W$ ) and phenotypic traits ( $z_i$ ) of individuals —in each food-web treatment. Second, we translated selection surfaces into the scale of relative fitness ( $w$ ) in order to calculate selection gradients. Third, we used our estimates of selection gradients to characterize the slope and curvature of the adaptive landscape. Note that inferring adaptive landscapes from selection surfaces assumes that trait distributions are multivariate normal ([Lande and Arnold, 1983](#)). To approximate this assumption, we log-transformed clutch size and square-root transformed oviposition preference. We then scaled all phenotypic traits (mean=0 and SD=1) in order to calculate standardized selection gradients that were comparable across traits and with other studies of natural selection.

**Selection surface:** Since larval survival was our measure of absolute fitness, we used a GLMM that assumed a binomial error distribution (and logit-link function). To approximate the selection surface, we modelled larval survival as a function of food-web treatment as well as linear ( $\alpha_{z_i}$ ), quadratic ( $\alpha_{z_i z_i}$ ), and linear interactions ( $\alpha_{z_i z_j}$ ) between each trait. We also allowed these trait-fitness relationships ( $\alpha$ ) to vary between food-web treatments. Note that to obtain valid estimates of linear trait-fitness relationships, we removed nonlinear terms prior to estimating linear relationships ([Lande and Arnold, 1983](#)). Other approaches have been advocated for approximating selection surfaces ([Schluter, 1988](#)); however, our approach enables us to calculate selection gradients, and thus is more appropriate for approximating the adaptive landscape ([Arnold, 2003](#)). To account for

the nonindependence of clutch size (measured at gall level) and oviposition preference (measured  
141 at plant level) as well as any independent effects of willow genotype on larval survival, we  
modelled gall ID nested within plant ID nested within genotype ID as random effects. Although  
statistical models with random effects are not common in analyses of natural selection, we think  
144 that modelling random effects can mitigate biased estimates of selection due to environmental  
covariances between traits and fitness ([Rausher, 1992](#)). Since our end goal was to characterize  
the relationship between mean trait values and mean fitness (adaptive landscape), we assumed  
147 the mean value of our random effects (i.e., setting them to zero) when calculating trait-fitness  
relationships. We then used parametric bootstrapping (1,000 replicates) to estimate the effect  
of food-web treatment on larval survival as well as trait-fitness relationships in each food-web  
150 treatment. To determine whether trait-fitness relationships differed between food-web treatments,  
we calculated the difference in bootstrapped replicates between treatments.

**Selection gradients:** We used the method of [Janzen and Stern \(1998\)](#) to translate trait-fitness rela-  
153 tionships ( $\alpha$ ) into the scale of relative fitness in order to calculate directional ( $\beta_{z_i}$ ), quadratic ( $\gamma_{z_i:z_i}$ ),  
and correlational ( $\gamma_{z_i:z_j}$ ) selection gradients. Briefly, this method calculates the average gradient  
of selection surfaces by multiplying the average of  $W(z)[1 - W(z)]$  by each regression coefficient  
156 (e.g.  $\alpha_{z_i}$ ,  $\alpha_{z_i:z_i}$ , or  $\alpha_{z_i:z_j}$ ). We then divided this average gradient by mean fitness ( $\bar{W}$ ) to put it on  
the scale of relative fitness, and thus interpretable as a selection gradient. We estimated selection  
gradients separately for each food-web treatment. Note that we doubled all quadratic terms prior  
159 to calculating selection gradients to put them on the same scale as estimates of directional and  
correlational selection ([Stinchcombe et al., 2008](#)).

**Evolutionary constraints:** We quantified the effects of food-web complexity on evolutionary con-  
162 straints by inspecting the slope and curvature of the adaptive landscape. The number of selective  
constraints is determined by the slope of the adaptive landscape, which in our study corresponds  
to:

$$\text{Slope} = \beta = \begin{pmatrix} \beta_{\text{Diam}} \\ \beta_{\text{Clutch}} \\ \beta_{\text{Pref}} \end{pmatrix}$$

- <sup>165</sup> By comparing the number of traits that determine the slope (i.e., nonzero directional selection gradients) in simpler vs. more complex food webs, we can infer the effect of food-web complexity on selective constraints.
- <sup>168</sup> The indirect effects of selection on genetic constraints is governed by the curvature of the adaptive landscape ( $C = \gamma - \beta\beta^T$ ), which in our study corresponds to:

$$\mathbf{C} = \begin{pmatrix} \gamma_{\text{Diam:Diam}} & & \\ \gamma_{\text{Clutch:Diam}} & \gamma_{\text{Clutch:Clutch}} & \\ \gamma_{\text{Pref:Diam}} & \gamma_{\text{Pref:Clutch}} & \gamma_{\text{Pref:Pref}} \end{pmatrix} - \begin{pmatrix} \beta_{\text{Diam}}\beta_{\text{Diam}} & & \\ \beta_{\text{Clutch}}\beta_{\text{Diam}} & \beta_{\text{Clutch}}\beta_{\text{Clutch}} & \\ \beta_{\text{Pref}}\beta_{\text{Diam}} & \beta_{\text{Pref}}\beta_{\text{Clutch}} & \beta_{\text{Pref}}\beta_{\text{Pref}} \end{pmatrix}$$

$$\mathbf{C} = \begin{pmatrix} C_{\text{Diam:Diam}} & & \\ C_{\text{Clutch:Diam}} & C_{\text{Clutch:Clutch}} & \\ C_{\text{Pref:Diam}} & C_{\text{Pref:Clutch}} & C_{\text{Pref:Pref}} \end{pmatrix}$$

- <sup>171</sup> Note that we omitted the upper triangle of each matrix for clarity since it is simply the reflection of the lower triangle. The sign of diagonal terms of the curvature matrix dictate whether selection will increase (+), decrease (-), or cause no change (0) in the additive genetic variance of a trait. Similarly,
- <sup>174</sup> any nonzero covariance terms (off-diagonal) are indicative of selection for trait integration (i.e., less independence). Therefore, we can infer the indirect effects of selection on genetic constraints by counting the number of negative signs along the diagonal (decrease in additive genetic variance)
- <sup>177</sup> and the number of nonzero terms along the off-diagonal (trait integration) of the curvature matrix.

## **Adjusting for biased measurements of selection**

Rather than imposing selection, parasitoids may influence the expression of herbivore traits which

180 could bias measurements of selection. In our system, it was plausible that parasitoids may influence  
chamber diameter by altering larval feeding behavior or killing larvae before they complete their  
development. To estimate this potential bias, we subset our data to only include galls where there  
183 was variation in larval survival within the same gall (i.e.  $1 > \text{mean survival} > 0$ ). If we assume  
that larvae within each gall should have similar chamber diameters because they come from the  
same clutch and experience the same local environment (an assumption our data supports: gall ID  
186 explains 54% of the variance in chamber diameter), then the relationship between chamber diameter  
and larval survival in this data subset represents the effect of parasitism on trait expression (i.e. bias).

We used a GLMM with the same structure as described above except that we only modelled a  
189 linear relationship between chamber diameter and larval survival ( $\alpha_{\text{Diam}}$ ). We detected a positive  
bias in both food-web treatments (complex  $\alpha_{\text{Diam}} = 0.36 [0.05, 0.67]$ ; simple  $\alpha_{\text{Diam}} = 0.42 [0.01, 0.82]$ ),  
indicating that unadjusted relationships would overestimate the strength of selection on chamber  
192 diameter. To account for this bias, we subtracted our mean estimates of bias from our estimates  
with the full dataset prior to calculating chamber diameter's trait-fitness relationship and directional  
selection gradient.

## **195 Measuring selection on the extended phenotype of egg parasitoids**

Once parasitized, the gall phenotype becomes the extended phenotype of the egg parasitoid. This

extended phenotype may influence the egg parasitoid's survival in the face of larval parasitoids,

198 and thus experiences selection. Our food-web manipulation allows us to measure selection imposed  
by larval parasitoids on the extended phenotype of egg parasitoids. Using the same models as  
described above, we substituted egg parasitism as our response variable to quantify trait-fitness  
201 relationships and selection gradients acting on the egg parasitoid. Note that we cannot test the  
effect of food-web complexity on the egg parasitoid's adaptive landscape —we can only estimate

the selection imposed by larval parasitoids. This comparison is still useful though in determining  
204 the extent to which the community context may have indirect evolutionary effects by altering  
selection on multiple interacting populations.

All analyses and visualizations were conducted in R ([R Core Team, 2018](#)). Unless otherwise noted,  
207 we report mean estimates of trait-fitness relationships and selection gradients with 95% confidence  
intervals in brackets. Note that for visualizing the adaptive landscape we restrict trait axes to  $\pm 1$   
SD of the mean trait value. This emphasizes the fact that we can only reliably estimate the shape of  
210 the adaptive landscape near the mean phenotype of the population ([Arnold et al., 2001](#)). We also  
plot mean larval survival on a natural log scale to accurately reflect the mathematical definition of  
the adaptive landscape ([Arnold, 2003](#)).

## 213 Results

### Simpler food webs increase selective constraints

We found that more gall midge traits experienced directional selection in the simple (3 of 3)  
216 vs. complex food-web treatment (1 of 3)(table 1). For example, we observed directional selection  
for smaller clutch sizes in the simple food web, but there was no evidence of selection acting on  
this trait in the complex food web (table 1; fig. 2C). This absence of selection appeared to be a  
219 result of conflicting selection pressures imposed by each guild of parasitoids (fig. 2). Specifically,  
when we subset our data to focus on differences between parasitoid guilds, we found that larval  
parasitoids actually impose directional selection for larger clutch sizes ( $\beta_{\text{Clutch}} = 0.13 [0.03, 0.23]$ ). In  
222 the simple food web, we also observed clear evidence of directional selection for midges to avoid  
ovipositing on plants with high densities of conspecifics (table 1; fig. 2B); however, this relationship  
was weaker in complex food webs (table 1). This was likely a result of larval parasitoids imposing  
225 greater mortality on egg parasitoids at high gall midge densities (see Selection on the extended  
phenotype of egg parasitoids section), and thus a less than additive effect on gall midges. Chamber

diameter experienced positive directional selection in both food-web treatments, but selection was  
 228 65% higher in complex food webs (table 1; fig. 2). This was not due to any difference between egg  
 and larval parasitoids (fig. 2), but was due to the lower average survival in complex food webs  
 (contrast -0.26 [-0.12, -0.42]).

231 **Simpler food webs increase genetic constraints**

The curvature of the adaptive landscape indirectly affects genetic constraints and is influenced by  
 directional, quadratic, and correlational selection gradients. Our food-web treatment did not alter  
 234 correlational selection for any combination of traits (table 1). Similarly, our food-web treatment  
 did not influence quadratic selection on either chamber diameter or clutch size (table 1; fig. 2A,C).  
 In contrast, our food-web treatment did alter quadratic selection acting on oviposition preference  
 237 (table 1). The negative relationship between oviposition preference and larval survival damped  
 at high densities in complex, but not simple food webs (fig. 2B). This damped relationship was  
 partly due to a trend for nonlinear selection imposed by larval parasitoids ( $\gamma_{\text{Pref:Pref}} = 0.18$  [-0.01,  
 240 0.42]), but was also magnified by the lower average survival in complex food webs.

To estimate the net effect of food-web complexity on the curvature ( $C$ ) of the adaptive landscape,  
 we only retained nonzero selection gradients (i.e. 95% CI did not overlap zero) prior to calculating  
 243 the curvature ( $\gamma - \beta\beta^T$ ) in each food-web treatment. We found that the curvatures of the adaptive  
 landscape exhibited the following structures:

$$\mathbf{C} = \begin{pmatrix} C_{\text{Diam:Diam}} & & \\ C_{\text{Clutch:Diam}} & C_{\text{Clutch:Clutch}} & \\ C_{\text{Pref:Diam}} & C_{\text{Pref:Clutch}} & C_{\text{Pref:Pref}} \end{pmatrix}$$

$$\mathbf{C}_{\text{Complex}} = \begin{pmatrix} -0.12 & & \\ 0 & 0 & \\ 0 & 0 & 0.33 \end{pmatrix}$$

$$\mathbf{C}_{\text{Simple}} = \begin{pmatrix} -0.04 & & \\ 0.02 & -0.01 & \\ 0.03 & -0.01 & -0.03 \end{pmatrix}$$

Remember that we can infer the indirect effects of selection on genetic constraints by counting the  
 246 number of negative signs along the diagonal (decrease in additive genetic variance) and the number  
 of nonzero terms along the off-diagonal (trait integration) of the curvature matrix. The structure of  
 these matrices indicates that there are more selective constraints imposed on the gall midge in the  
 249 simpler (6 of 6) vs. more complex (1 of 6) food web. Simpler food webs acted to decrease genetic  
 variance for all three phenotypic traits (negative diagonal terms), whereas only one trait (chamber  
 diameter) experienced a decrease in additive genetic variance in the more complex food web. For  
 252 genetic covariances, the simpler food web favored integration among all three phenotypic traits  
 (nonzero off-diagonal terms), and thus constraints along all three axes of covariance (fig. 3). In  
 contrast, there was no strong evidence of trait integration in the more complex food web (fig. 3).

255 **Selection on the extended phenotype of egg parasitoids**

Gall midge preference influenced the probability of observing egg parasitoids in complex vs. simple  
 food webs (contrast  $\alpha_{\text{Pref}} = 1 [0.03, 2.22]$ ). Specifically, larval parasitoids decreased the probability of  
 258 observing egg parasitoids at high gall midge densities (fig. 4). Note however that this trait-fitness  
 relationship did not translate into a significant difference in selection (contrast  $\beta_{\text{Pref}} = 0.24 [-0.09,$   
 $0.62]$ ). This was likely because there was a tendency (albeit not statistically significant) for a  
 261 lower probability of egg-parasitoid survival in complex vs. simple food webs (contrast=0.1 [ -0.08,  
 $0.31]$ ), which masks this trait-fitness relationship. We also observed two other interesting trends,  
 although neither significantly differed between treatments. Specifically, there was a tendency for the  
 264 impact of larval parasitoids to increase nonlinearly at higher gall midge densities (fig. 4; complex  
 $\alpha_{\text{Pref:Pref}} = -0.49 [-1.08, -0.1]$ ; but contrast  $\alpha_{\text{Pref:Pref}} = 0.46 [-0.03, 1.1]$ ). There was also a tendency for

egg parasitoids to obtain a refuge in large gall chambers at high gall midge densities (complex  
267  $\alpha_{\text{Pref:Diam}} = 0.25 [0.02, 0.5]$ ; but contrast  $\alpha_{\text{Pref:Diam}} = -0.25 [-0.57, 0.04]$ ).

## Discussion

Our key finding was that phenotypic evolution in gall midges was more constrained in simpler  
270 food webs. More traits contributed to the slope of the adaptive landscape in the simpler food web, suggesting that the trajectory of phenotypic evolution is more constrained. Similarly, the simple food-web treatment indirectly increased the number of genetic constraints, which could  
273 act to constrain the gall midge's adaptive potential in the face of novel selection pressures. We also found evidence of indirect selection pressures in more complex food webs, suggesting that the adaptive landscape may be more dynamic in complex food webs. Taken together, our study  
276 provides experimental evidence from the field that the simplification of ecological communities may constrain the adaptive potential of remaining populations.

All three phenotypic traits we examined experienced directional selection in the simpler food web,  
279 indicating that there is an optimal phenotype that maximizes larval survival (i.e. large chamber diameter, small clutch size, and avoidance of conspecifics). In contrast, we did not observe selective constraints on clutch size and oviposition preference in the more complex food web. This suggests  
282 that there are many optimal phenotypes (adaptive peaks), or in this case, a flat adaptive landscape where there are no fitness consequences for phenotypic change in these traits. This also implies that as selective constraints dampen in more complex food webs, then the trajectory of evolution  
285 becomes more determined by genetic constraints. This is made clear if we inspect the 'Lande equation',  $\Delta z = G\beta$ , where  $G$  corresponds to the population's  $G$ -matrix. As the components of  $\beta$  go to zero, then  $\Delta z$  is more influenced by the  $G$ -matrix. Interestingly, this corresponds to  
288 [Schluter \(1996\)](#)'s hypothesis that phenotypic evolution often follows 'genetic lines of least resistance'. [Schluter \(1996\)](#) found support for this hypothesis from data on natural populations of several vertebrate species, including threespine sticklebacks, a few species of songbirds, and mice from the

291 genus *Peromyscus*. All of these species occupy intermediate trophic levels and are likely embedded  
in complex food webs, which is consistent with our suggestion that genetic constraints may have a  
stronger influence in more complex food webs.

294 We also found evidence for more genetic constraints in simpler food webs due to indirect effects  
of selection on the population's G-matrix. The ability of a population to adapt to novel selection  
pressures (evolvability) is largely governed by the structure of its G-matrix (Hansen and Houle,  
297 2008). When selection favors genetic covariance between traits (positive or negative), this results in  
less autonomy of evolutionary responses to changing environments. Similarly, decreases in genetic  
variance constrain potential for the trait itself to evolve. Together, this suggests that simpler food  
300 webs may decrease the evolutionary potential of populations by indirectly selecting for decreases  
in genetic variance in multiple traits and favoring trait integration. Current theory often assumes  
genetic variances and covariances remain constant over time rather than dynamically changing  
303 with the community context (McPeek, 2017; Guimarães et al., 2017). Our empirical results highlight  
the need to explore the evolutionary consequences of not only direct effects of selection, but indirect  
effects on genetic constraints that are shaped by the community context.

306 The generality of our results likely depends on the relative abundance and functional differences  
between consumers in a community. In the simplest case, when consumers do not differ from  
each other, then we do not expect changes in food-web complexity to modify selective constraints.  
309 Also, many consumers may be at too low of abundances to impose selection on their resources.  
Rank abundance curves (Preston, 1948) and the disproportionate number of weak interactions in  
diverse communities (Paine, 1992) support this notion. When consumers are abundant though,  
312 the effect of food-web complexity will depend on whether different species impose conflicting  
selection pressures or select for distinct traits. For example, parasitoids and birds impose conflicting  
selection pressures on the size of galls induced by the fly *Eurosta solidaginis* (Weis and Abrahamson,  
315 1985; Abrahamson and Weis, 1997; Start and Gilbert, 2016). Recent studies in this system have  
shown that decreases in the relative abundance of birds, due to either small patch sizes (Start and

Gilbert, 2016) or proximity to urban areas (Start et al., 2018) causes a shift from neutral to directional  
318 selection on gall size. On the other hand, different consumers may impose selection on different traits, favoring trait integration and increasing genetic constraints. Examples of this include strong genetic covariances in plant resistance to different insect herbivores (Maddox and Root, 1990; Wise,  
321 Wise and Rausher, 2013), although there are also examples where these covariances are weak (Roche and Fritz, 1997; Barbour et al., 2015), or vary from year-to-year (Johnson and Agrawal, 2007). We suggest that gaining predictive insight to the effects of food-web disassembly requires an  
324 understanding of the mechanisms governing the assembly of trophic interactions.

Our results suggest that the simplification of ecological communities may not only directly affect connected species, but also result in indirect evolutionary effects. In our study, this indirect effect  
327 arises from egg parasitoids being released from intraguild predation in simpler food webs. This release occurs more on trees with high larval densities, which could intensify selection on gall midge oviposition preference. A growing number of experiments over the past two decades have  
330 demonstrated the presence and potential importance of indirect evolutionary effects that emerge in a community context (Juenger and Bergelson, 1998; Stinchcombe and Rausher, 2001; Lankau and Strauss, 2015; Walsh and Reznick, 2008, 2010; terHorst, 2010; Sahli and Conner, 2011; Lau, 2012;  
333 TerHorst et al., 2015; Schiestl et al., 2018). If indirect evolutionary effects are common (Walsh, 2013), then predicting evolutionary trajectories resulting from the simplification of food webs will require evolutionary studies to explicitly account for the ecological networks that species are embedded in.  
336 There are a growing number of theoretical studies on adaptation to directional environmental change that incorporate species interactions (e.g. de Mazancourt et al., 2008; Johansson, 2008; Norberg et al., 2012; Osmond et al., 2017). This work has given insight to the mechanisms by  
339 which pairwise interactions modify the adaptive potential of species. Our study hints at a novel mechanism, whereby food-web complexity flattens the adaptive landscape, thus facilitating future adaptation by allowing genetic and phenotypic variation to persist. This mechanism only emerges  
342 once we move beyond pairwise interactions to consider selection on multiple traits in a community

context. However, a study on competition has highlighted that we may expect the opposite effect of species diversity in competitive communities (de Mazancourt et al., 2008). This negative effect of  
345 species diversity on adaptation occurs because there is a greater chance that the optimal phenotype is already occupied by a competitor in a more diverse community. More work is needed to examine how the distribution of different interaction types affects adaptation to environmental change in  
348 species-rich communities.

Our study gives insight to how local extinctions, and concomitant decreases in food-web complexity, increase evolutionary constraints. This hints at a potential insidious effect of local extinctions that  
351 compromises the robustness of remaining populations to future environmental change. Our work also highlights some key challenges for predicting phenotypic evolution in the face of global change. First, the simplification of ecological communities may actually reduce the predictability  
354 of phenotypic evolution, because knowledge is required of both selective and genetic constraints, rather than potentially just genetic constraints in more complex systems. Second, many theoretical models of eco-evolutionary dynamics focus on phenotypic change in a single trait, yet our results  
357 highlight that the number of traits under selection may change with the community context. Importantly, while the net effects of selection in complex communities may be damped, we still found that different species/guilds imposed different selection pressures. Knowing these  
360 hidden selection pressures is critical for prediction, because the trajectory of evolution will depend on the nature of change in the community context. We expect that a continued integration of adaptive landscapes and ecological networks will enhance our ability to predict the evolutionary  
363 consequences of changes in ecological communities.

## Acknowledgements

We thank the staff of Humboldt Bay National Wildlife Refuge (U.S. Fish and Wildlife Service) for  
366 facilitating experimental logistics. For assistance with fieldwork, we thank Ruthie Espanol and Andrew MacDonald. For funding support, we thank the University of British Columbia (James

Robert Thompson Fellowship and Four-Year Fellowship to M.A. Barbour), NSERC (Discovery  
369 grant to Greg Crutsinger), and the Swiss National Science Foundation (grant 31003A\_160671 to J.  
Bascompte).

## References

<sup>372</sup> **Tables**

Table 1: Standardized selection gradients acting on gall midges in complex vs. simple food webs.

Selection gradient	Complex	Simple	Contrast
$\beta_{\text{Diam}}$	<b>0.34 [ 0.22, 0.47]</b>	<b>0.21 [ 0.13, 0.3]</b>	-0.13 [ -0.26, 0.01]
$\beta_{\text{Clutch}}$	0.06 [ -0.04, 0.17]	<b>-0.09 [ -0.18, -0.02]</b>	<b>-0.15 [ -0.29, -0.02]</b>
$\beta_{\text{Pref}}$	-0.12 [ -0.29, 0.05]	<b>-0.16 [ -0.25, -0.07]</b>	-0.04 [ -0.22, 0.14]
$\gamma_{\text{Diam,Diam}}$	0.14 [ -0.06, 0.32]	0.1 [ -0.03, 0.25]	-0.04 [ -0.27, 0.2]
$\gamma_{\text{Clutch,Clutch}}$	-0.05 [ -0.25, 0.16]	-0.12 [ -0.27, 0.03]	-0.06 [ -0.33, 0.19]
$\gamma_{\text{Pref,Pref}}$	<b>0.33 [ 0.06, 0.64]</b>	0.01 [ -0.14, 0.17]	<b>-0.32 [ -0.66, 0]</b>
$\gamma_{\text{Diam,Clutch}}$	-0.05 [ -0.17, 0.08]	-0.07 [ -0.15, 0.02]	-0.02 [ -0.16, 0.13]
$\gamma_{\text{Diam,Pref}}$	-0.13 [ -0.28, 0]	-0.02 [ -0.09, 0.06]	0.12 [ -0.05, 0.29]
$\gamma_{\text{Clutch,Pref}}$	0.03 [ -0.11, 0.18]	0 [ -0.07, 0.07]	-0.03 [ -0.19, 0.12]

Note: Values in brackets represent 95% confidence intervals. Bold values indicate that the 95% CI does not overlap zero.

$\beta_{\text{Diam}}$  has been adjusted for bias.

Table 2: Relationship between absolute fitness (larval survival) and phenotypic traits of gall midges in complex vs. simple food webs.

Coefficient	Complex	Simple	Contrast
$\alpha_{\text{Diam}}$	<b>1.14 [ 0.73, 1.57]</b>	<b>1.1 [ 0.68, 1.58]</b>	-0.04 [ -0.57, 0.51]
$\alpha_{\text{Clutch}}$	0.21 [ -0.13, 0.57]	<b>-0.47 [ -0.94, -0.09]</b>	<b>-0.68 [ -1.27, -0.13]</b>
$\alpha_{\text{Pref}}$	-0.41 [ -0.97, 0.15]	<b>-0.84 [ -1.35, -0.36]</b>	-0.43 [ -1.16, 0.25]
$\alpha_{\text{Diam},\text{Diam}}$	0.23 [ -0.1, 0.54]	0.27 [ -0.07, 0.65]	0.04 [ -0.43, 0.52]
$\alpha_{\text{Clutch},\text{Clutch}}$	-0.09 [ -0.42, 0.26]	-0.31 [ -0.71, 0.08]	-0.22 [ -0.77, 0.31]
$\alpha_{\text{Pref},\text{Pref}}$	<b>0.56 [ 0.1, 1.07]</b>	0.03 [ -0.38, 0.46]	-0.52 [ -1.18, 0.09]
$\alpha_{\text{Diam},\text{Clutch}}$	-0.16 [ -0.57, 0.25]	-0.35 [ -0.78, 0.08]	-0.19 [ -0.78, 0.44]
$\alpha_{\text{Diam},\text{Pref}}$	-0.44 [ -0.95, 0.01]	-0.09 [ -0.5, 0.3]	0.36 [ -0.27, 0.97]
$\alpha_{\text{Clutch},\text{Pref}}$	0.1 [ -0.37, 0.59]	0 [ -0.37, 0.38]	-0.1 [ -0.69, 0.49]

Note: Values in brackets represent 95% confidence intervals. Bold values indicate that the 95% CI does not overlap zero.

$\alpha_{\text{Diam}}$  has been adjusted for bias.

## References

- Abrahamson, W. G., and A. E. Weis. 1997. Evolutionary Ecology Across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies. Princeton University Press.
- Abrams, P. A. 2000. The evolution of predator-prey interactions: Theory and evidence. *Annual Review of Ecology and Systematics* 31:79–105.
- Arnold, S. J. 1992. Constraints on phenotypic evolution. *The American Naturalist* 140:S85–S107.
- . 2003. Performance surfaces and adaptive landscapes1. *Integrative and Comparative Biology* 43:367–375.
- Arnold, S. J., M. E. Pfrender, and A. G. Jones. 2001. The adaptive landscape as a conceptual bridge between micro- and macroevolution. *Genetica* 112:9–32.
- Arnold, S. J., and M. J. Wade. 1984a. On the measurement of natural and sexual selection: Applications. *Evolution* 38:720–734.
- . 1984b. On the measurement of natural and sexual selection: Theory. *Evolution* 38:709–719.
- Barbour, M. A., M. A. Fortuna, J. Bascompte, J. R. Nicholson, R. Julkunen-Tiitto, E. S. Jules, and G. M. Crutsinger. 2016. Genetic specificity of a plant–insect food web: Implications for linking genetic variation to network complexity. *Proceedings of the National Academy of Sciences* 113:2128–2133.
- Barbour, M. A., M. A. Rodriguez-Cabal, E. T. Wu, R. Julkunen-Tiitto, C. E. Ritland, A. E. Miscampbell, E. S. Jules, and G. M. Crutsinger. 2015. Multiple plant traits shape the genetic basis of herbivore community assembly. *Functional Ecology* 29:995–1006.
- Bascompte, J., and P. Jordano. 2014. Mutualistic Networks. Princeton University Press.
- Bronstein, J. L., R. Alarcón, and M. Geber. 2006. The evolution of plant–insect mutualisms. *New Phytologist* 172:412–428.

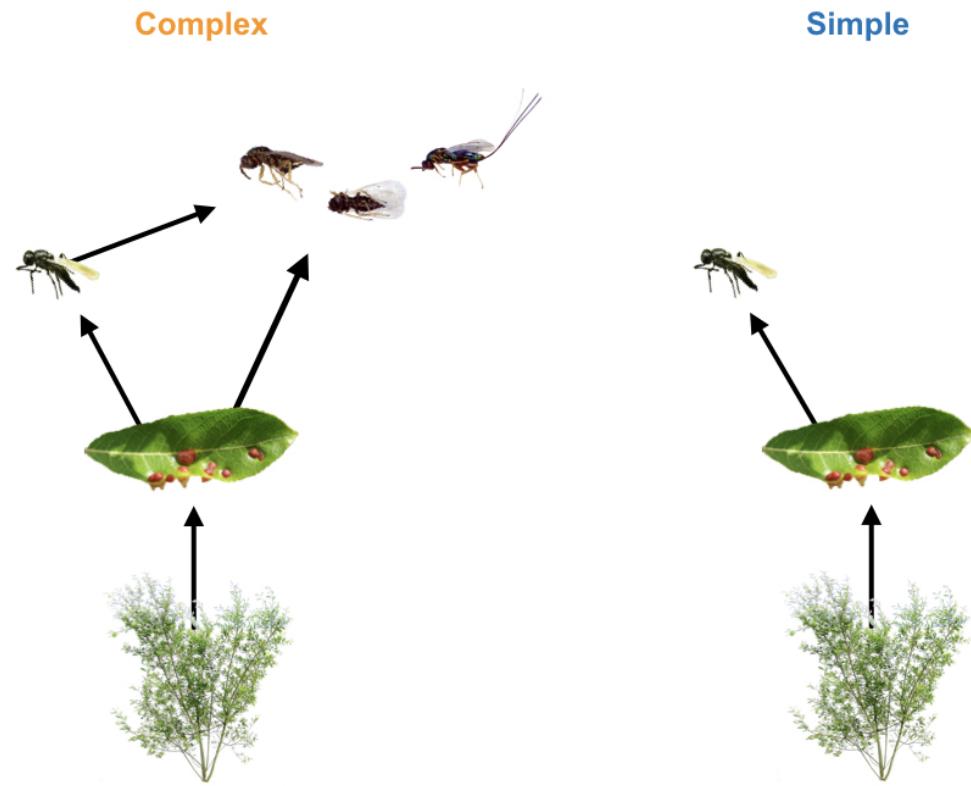


Figure 1: Experimental manipulation of food-web complexity associated with a leaf-galling midge (*Iteomyia salicisverruca*) feeding on the willow *Salix hookeriana*. Black arrows denote the flow of energy in this network of trophic interactions. In the complex food-web treatment, we allowed the full suite of egg and larval parasitoids to impose selection. In the simple food-web treatment, we used mesh bags to exclude the guild of larval parasitoids, only allowing the egg parasitoid (*Platygaster* sp.) to impose selection. Larval parasitoids include the following species (from left to right): *Mesopolobus* sp. (Family: Pteromalidae); *Tetrastichus* sp. (Family: Eulophidae); and *Torymus* sp. (Family: Torymidae).

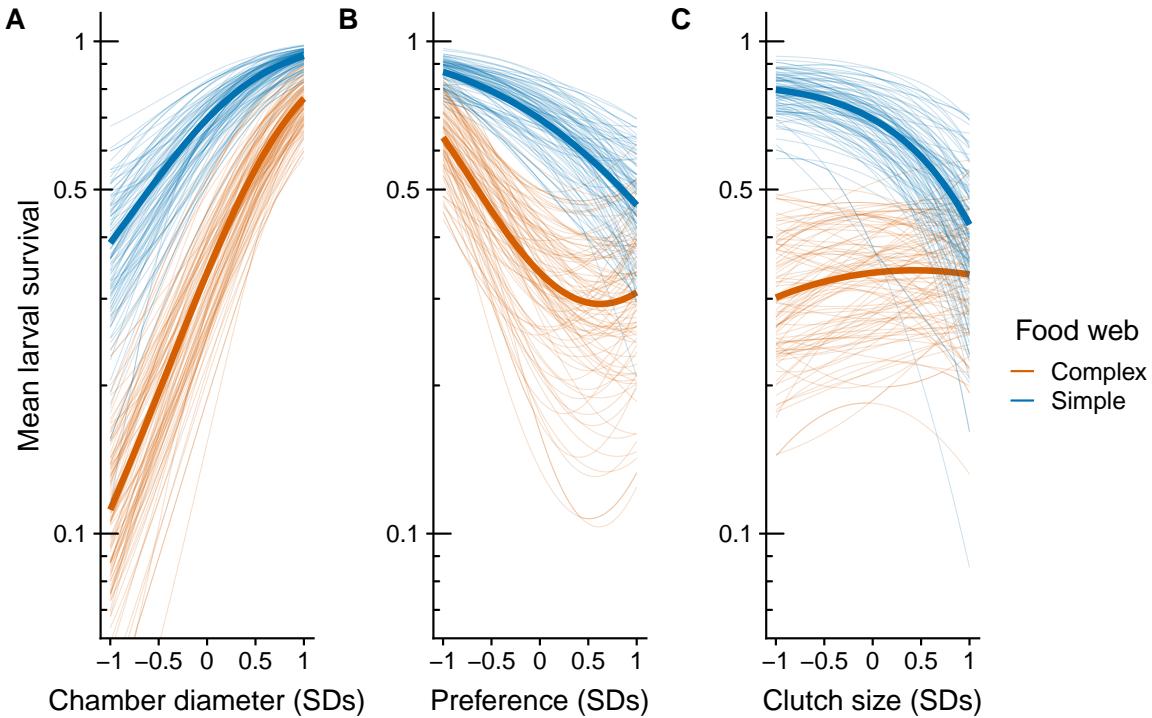


Figure 2: Adaptive landscape of gall midge phenotypes in complex vs. simple food webs. Each panel corresponds to a different phenotypic trait: chamber diameter (A); oviposition preference (B); and clutch size (C). Solid lines represent selection experienced in complex (orange) and simple (blue) food webs. Transparent lines represent bootstrapped replicates to show the uncertainty in selection. For clarity, we only display 100 bootstraps even though inferences are based on 1,000 replicates. Note that mean larval survival is plotted on a natural log scale to reflect the mathematical definition of the adaptive landscape.

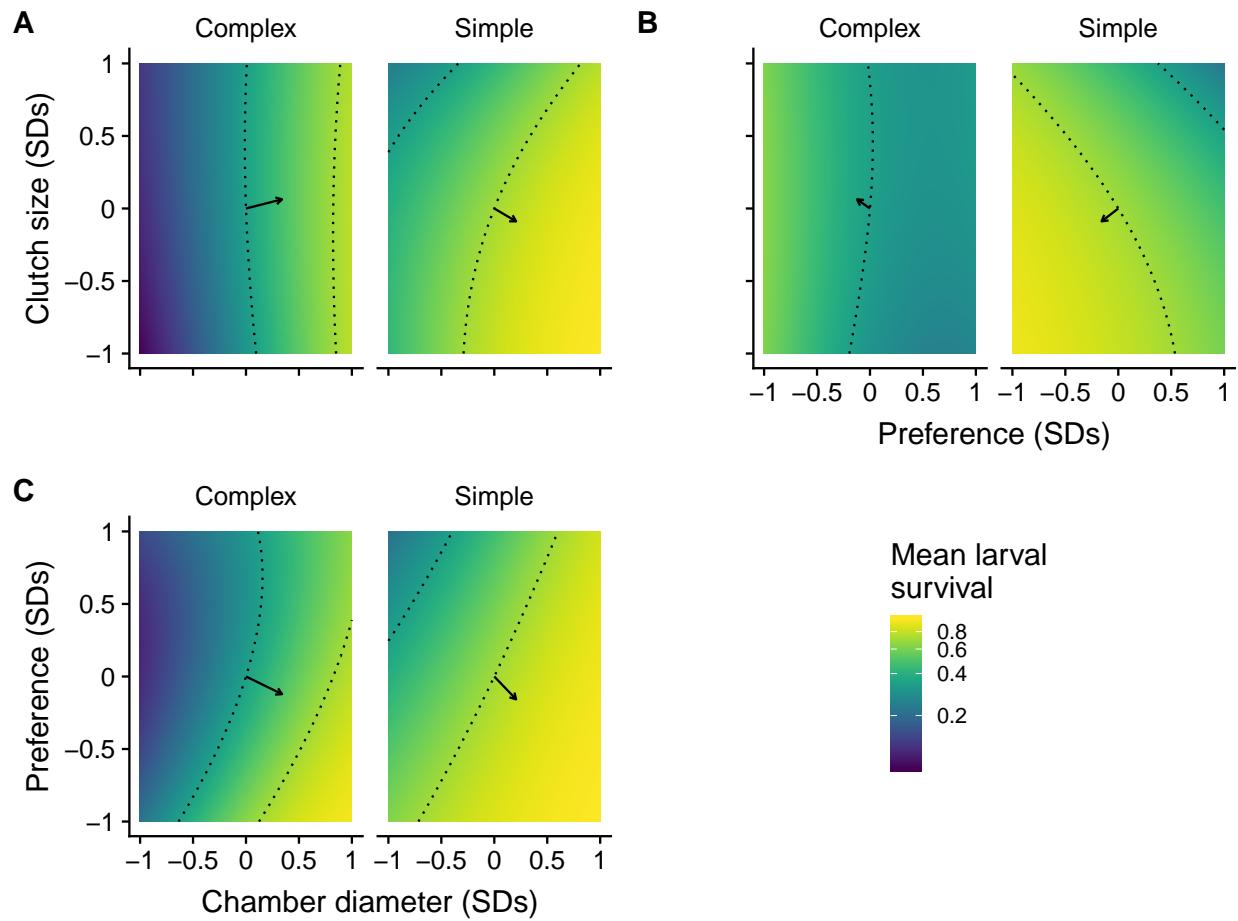


Figure 3: Two dimensional view of adaptive landscapes of gall midge phenotypes in complex vs. simple food webs. Each panel corresponds to a different combination of phenotypic traits: clutch size and chamber diameter (A); clutch size and oviposition preference (B); oviposition preference and chamber diameter (C). Arrows represent mean estimates of directional selection gradients, while contours represent predicted larval survival of the mean phenotype (i.e., all traits = 0) in each food-web treatment. Notice that arrows point more toward a corner of the adaptive landscape for each combination of traits in the simple vs. complex food-web treatment. This indicates that trait integration (covariance) is more strongly favored in simpler vs. more complex food webs. Note that mean larval survival is plotted on a natural log scale to reflect the mathematical definition of the adaptive landscape.

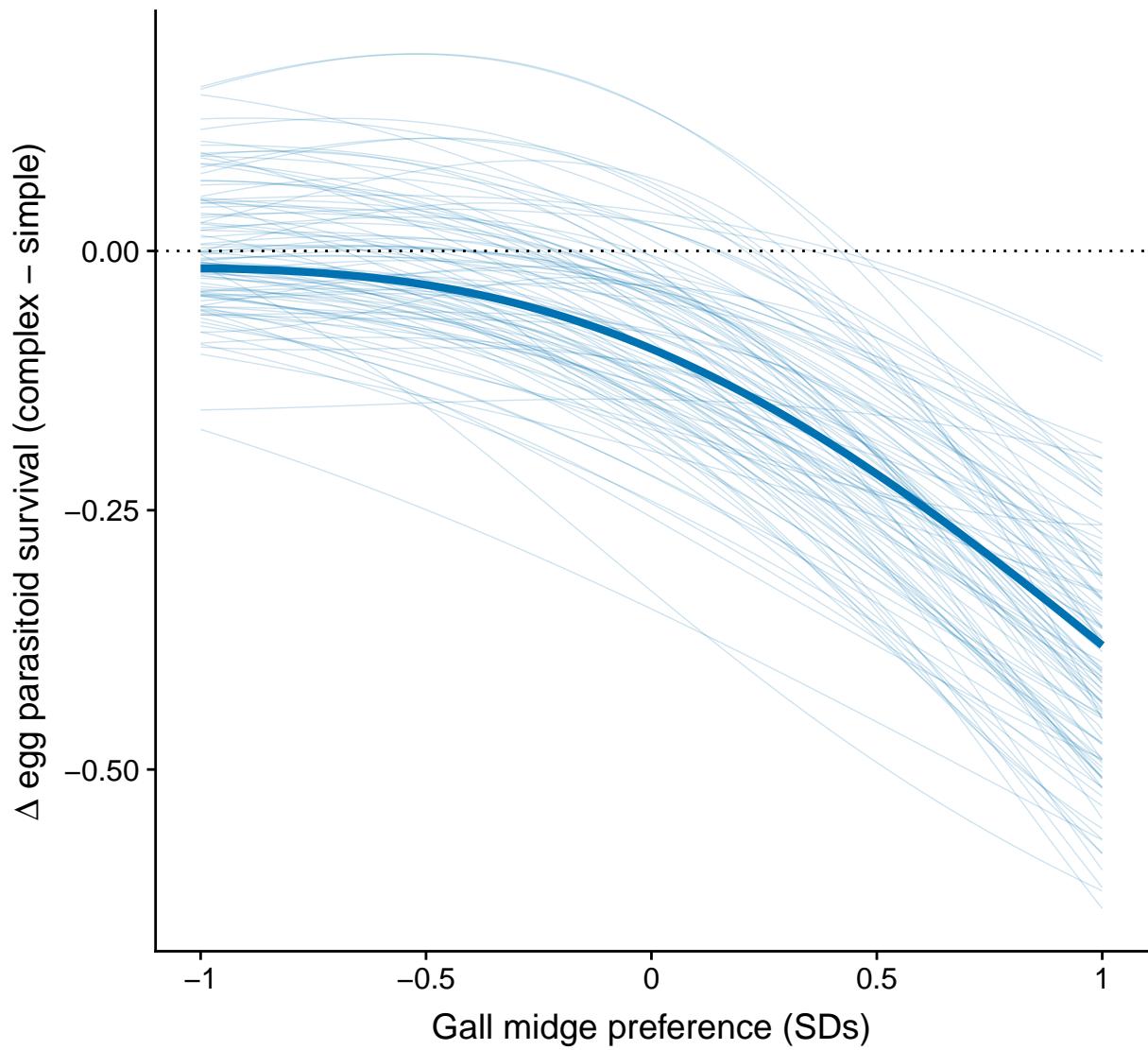


Figure 4: Selection imposed by larval parasitoids on the extended phenotype of egg parasitoids (*Platygaster* sp.). The solid line represents the average difference in the probability of observing the egg parasitoid in complex vs. simple food webs as a function of gall midge oviposition preference. Transparent lines represent bootstrapped replicates to show the uncertainty in selection. For clarity, we only display 100 bootstraps even though inferences are based on 1,000 replicates. The decrease in the probability of observing egg parasitoids at high gall-midge densities indicate that larval parasitoids impose nonlinear selection on the extended phenotype of egg parasitoids.

- 396 de Mazancourt, C., E. Johnson, and T. G. Barraclough. 2008. Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* 11:380–388.

Gagné, R. J. 1989. The plant-feeding gall midges of North America. *agris.fao.org*.

399 Gripenberg, S., P. J. Mayhew, M. Parnell, and T. Roslin. 2010. A meta-analysis of preference–performance relationships in phytophagous insects. *Ecology Letters* 13:383–393.

Guimarães, P. R., Jr, M. M. Pires, P. Jordano, J. Bascompte, and J. N. Thompson. 2017. Indirect effects  
402 drive coevolution in mutualistic networks. *Nature* 550:511–514.

Hansen, T. F., and D. Houle. 2008. Measuring and comparing evolvability and constraint in multivariate characters. *J. Evol. Biol.* 21:1201–1219.

405 Hawkins, B. A., H. V. Cornell, and M. E. Hochberg. 1997. Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology* 78:2145–2152.

Heath, J. J., P. Abbot, and J. O. Stireman. 2018. Adaptive divergence in a defense symbiosis driven  
408 from the top down. *The American Naturalist* 192:E21–E36. PMID: 29897808.

Janzen, D. 1974. The deflowering of central america. *Natural History* 83:48–53.

Janzen, F. J., and H. S. Stern. 1998. Logistic regression for empirical studies of multivariate selection.  
411 *Evolution* 52:1564–1571.

Johansson, J. 2008. Evolutionary responses to environmental changes: how does competition affect adaptation? *Evolution* 62:421–435.

414 Johnson, M. T. J., and A. A. Agrawal. 2007. Covariation and composition of arthropod species across plant genotypes of evening primrose, *oenothera biennis*. *Oikos* 116:941–956.

Juenger, T., and J. Bergelson. 1998. PAIRWISE VERSUS DIFFUSE NATURAL SELECTION AND  
417 THE MULTIPLE HERBIVORES OF SCARLET GILIA, *IPOMOPSIS AGGREGATA*. *Evolution* 52:1583–1592.

- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size  
420 allometry. *Evolution* 33:402–416.
- Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution*  
37:1210–1226.
- 423 Lankau, R. A., and S. Y. Strauss. 2015. Community complexity drives patterns of natural selection  
on a chemical defense of *brassica nigra*. *Am. Nat.* .
- Lau, J. A. 2012. Evolutionary indirect effects of biological invasions. *Oecologia* 170:171–181.
- 426 Maddox, G. D., and R. B. Root. 1990. Structure of the encounter between goldenrod (*solidago*  
*altissima*) and its diverse insect fauna. *Ecology* 71:2115–2124.
- McCann, K. S. 2012. *Food Webs*. Princeton University Press.
- 429 McPeek, M. A. 2017. *Evolutionary Community Ecology*. Princeton University Press.
- Norberg, J., M. C. Urban, M. Vellend, C. A. Klausmeier, and N. Loeuille. 2012. Eco-evolutionary  
responses of biodiversity to climate change. *Nat. Clim. Chang.* 2:747–751.
- 432 Osmond, M. M., S. P. Otto, and C. A. Klausmeier. 2017. When predators help prey adapt and persist  
in a changing environment. *Am. Nat.* 190:83–98.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength.  
435 *Nature* 355:73.
- Preston, F. W. 1948. The commonness, and rarity, of species. *Ecology* 29:254–283.
- R Core Team. 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for  
438 Statistical Computing, Vienna, Austria.
- Rausher, M. D. 1992. The measurement of selection on quantitative traits: Biases due to environmental covariances between traits and fitness. *Evolution* 46:616–626.

- <sup>441</sup> Roche, B. M., and R. S. Fritz. 1997. Genetics of resistance of *salix sericea* to a diverse community of herbivores. *Evolution* 51:1490–1498.
- Russo, R. 2006. Field Guide to Plant Galls of California and Other Western States. 1st ed. University of California Press.
- <sup>444</sup>
- Sahli, H. F., and J. K. Conner. 2011. Testing for conflicting and nonadditive selection: floral adaptation to multiple pollinators through male and female fitness. *Evolution* 65:1457–1473.
- <sup>447</sup> Scheffers, B. R., L. De Meester, T. C. L. Bridge, A. A. Hoffmann, J. M. Pandolfi, R. T. Corlett, S. H. M. Butchart, P. Pearce-Kelly, K. M. Kovacs, D. Dudgeon, M. Pacifici, C. Rondinini, W. B. Foden, T. G. Martin, C. Mora, D. Bickford, and J. E. M. Watson. 2016. The broad footprint of climate change from genes to biomes to people. *Science* 354.
- <sup>450</sup>
- Schiestl, F. P., A. Balmer, and D. D. Gervasi. 2018. Real-time evolution supports a unique trajectory for generalized pollination. *Evolution* 72:2653–2668.
- <sup>453</sup> Schluter, D. 1988. Estimating the form of natural selection on a quantitative trait. *Evolution* 42:849–861.
- . 1996. ADAPTIVE RADIATION ALONG GENETIC LINES OF LEAST RESISTANCE.
- <sup>456</sup> Evolution 50:1766–1774.
- . 2000. Ecological character displacement in adaptive radiation. *The American Naturalist* 156:S4–S16.
- <sup>459</sup> Simpson, G. G. 1944. *Tempo and Mode in Evolution*. Columbia University Press.
- Singer, M. C. 1986. The Definition and Measurement of Oviposition Preference in Plant-Feeding Insects, pages 65–94. Springer New York, New York, NY.
- <sup>462</sup> Start, D., C. Bonner, A. E. Weis, and B. Gilbert. 2018. Consumer-resource interactions along urbanization gradients drive natural selection. *Evolution* 72:1863–1873.

- Start, D., and B. Gilbert. 2016. Host-parasitoid evolution in a metacommunity. *Proc. Biol. Sci.* 283.
- 465 Stinchcombe, J. R., A. F. Agrawal, P. A. Hohenlohe, S. J. Arnold, and M. W. Blows. 2008. Estimating nonlinear selection gradients using quadratic regression coefficients: double or nothing? *Evolution* 62:2435–2440.
- 468 Stinchcombe, J. R., and M. D. Rausher. 2001. Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *ipomoea hederacea*. *Am. Nat.* 158:376–388.
- terHorst, C. P. 2010. Evolution in response to direct and indirect ecological effects in pitcher plant inquiline communities. *Am. Nat.* .
- 471
- 474 TerHorst, C. P., J. A. Lau, I. A. Cooper, K. R. Keller, R. J. La Rosa, A. M. Royer, E. H. Schultheis, T. Suwa, and J. K. Conner. 2015. Quantifying nonadditive selection caused by indirect ecological effects. *Ecology* 96:2360–2369.
- terHorst, C. P., P. C. Zee, K. D. Heath, T. E. Miller, A. I. Pastore, S. Patel, S. J. Schreiber, M. J. Wade, and M. R. Walsh. 2018. Evolution in a community context: Trait responses to multiple species interactions\*. *Am. Nat.* .
- 477
- Walsh, M. R. 2013. The evolutionary consequences of indirect effects. *Trends Ecol. Evol.* 28:23–29.
- Walsh, M. R., and D. N. Reznick. 2008. Interactions between the direct and indirect effects of
- 480 predators determine life history evolution in a killifish. *Proc. Natl. Acad. Sci. U. S. A.* 105:594–599.
- . 2010. Influence of the indirect effects of guppies on life-history evolution in *rivulus hartii*. *Evolution* 64:1583–1593.
- 483 Weis, A. E., and W. G. Abrahamson. 1985. Potential selective pressures by parasitoids on a Plant-Herbivore interaction. *Ecology* 66:1261–1269.
- Weis, A. E., P. W. Price, and M. Lynch. 1983. Selective pressures on clutch size in the gall maker
- 486 asteromyia carbonifera. *Ecology* 64:688–695.

Wise, M. J. 2007. Evolutionary ecology of resistance to herbivory: an investigation of potential genetic constraints in the multiple-herbivore community of *solanum carolinense*. *New Phytol.*  
489 175:773–784.

Wise, M. J., and M. D. Rausher. 2013. Evolution of resistance to a multiple-herbivore community: genetic correlations, diffuse coevolution, and constraints on the plant's response to selection.  
492 *Evolution* 67:1767–1779.

Wright, S. 1931. Evolution in mendelian populations. *Genetics* 16:97–159.