

Consumer extinctions constrain phenotypic evolution in the resulting food web

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Abstract

Global change is altering the structure of ecological networks; however, we are currently in a poor position to predict how these altered 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 treats the community context of evolving populations as a “black box”. Here, we integrate ecological networks and adaptive landscapes to examine how changes in food-web structure shape evolutionary constraints. We conducted a field experiment that simulated the extinction of a guild of larval parasitoids 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 the number of traits under selection increased with the extinction of larval parasitoids. In contrast, the adaptive landscape was more neutral in the original food web because different parasitoid guilds impose different selection pressures, minimizing relative fitness differences among phenotypes. Our results suggest that the loss of trophic interactions due to consumer extinctions can impose greater constraints on phenotypic evolution. This indicates that the simplification of ecological communities may constrain the adaptive potential of remaining populations to future environmental change.

Introduction

18 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
21 genetic and phenotypic variation to evolution by natural selection (Lande, 1979; Arnold and
Wade, 1984*a,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
24 et al., 2006) interactions in driving evolutionary change. Although there is clear evidence that
pairwise interactions can shape the adaptive landscape, we still have a poor understanding of how
the adaptive landscape is shaped by the community context (McPeek, 2017; terHorst et al., 2018).
27 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).

Ecological networks, such as food webs describing who-eats-whom in ecological communities,
30 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 the
community context constrains evolutionary change. Different aspects of evolutionary constraints
33 can be inferred by quantifying the slope and curvature of the adaptive landscape (Arnold, 1992).
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). Selective
36 constraints on evolution increase with the number of traits under directional 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
39 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 general,
genetic constraints will increase with the number of traits under directional or stabilizing selection,
42 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 selection, as this type of selection decreases the evolutionary independence of traits (Hansen and Houle, 45). If we want to predict how the community context constrains phenotypic evolution, we must understand how ecological networks shape the adaptive landscape.

Global change is altering the structure of ecological networks, which may influence evolutionary 48 constraints in a number of ways. For example, in a food web, if different consumers impose directional selection on different traits of a shared resource, then a more diverse consumer community may constrain evolution by increasing the number of traits under selection. Alternatively, if 51 consumers impose selection on different values of a trait, then their selective effects would cancel each other out in more diverse communities. To examine these different possibilities, we conducted a field experiment that simulated the extinction of a consumer guild associated with an abundant 54 insect herbivore (*Iteomyia salicisverruca*, Family Cecidomyiidae; fig. 1). The larvae of this herbivore induce tooth-shaped 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 57 they suffer high mortality from egg and larval parasitoids (Barbour et al., 2016). We manipulated food-web structure by either excluding the guild of larval parasitoids (extinction food web) or allowing both egg and larval parasitoids to impose selection on gall midge traits (original food web, 60 fig. 1). We then applied modern statistical methods to quantify how changes in food-web structure altered the slope and curvature of the gall midge's adaptive landscape. Taken together, our study gives insight to how local extinctions may constrain the evolution of interacting populations.

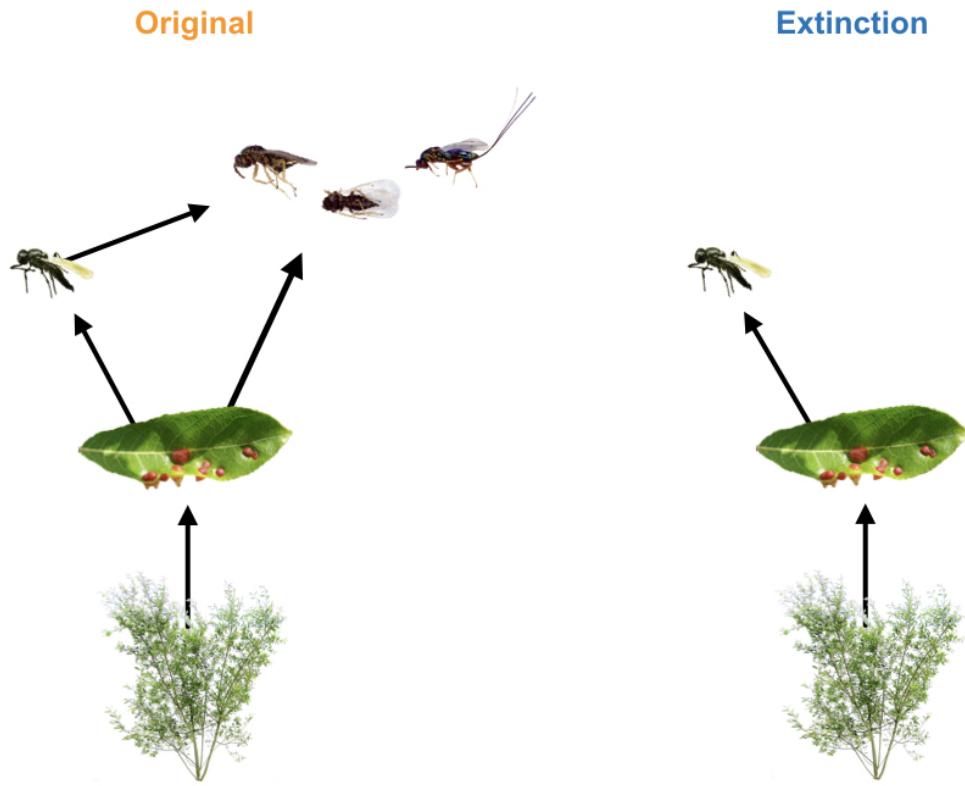


Figure 1: Experimental manipulation of food-web structure associated with a leaf-galling midge (*Iteomyia salicisverruca*) feeding on the willow *Salix hookeriana*. Black arrows denote the flow of energy in this network of trophic interactions. In the original food web, we allowed the full suite of egg and larval parasitoids to impose selection. To simulate consumer extinction, 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).

63 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 genotype) 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 Structure

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 original food web (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 all galls had similar phenology when we collected galls later in the season. To simulate consumer extinctions, 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 months at room temperature. We then opened galls

87 under a dissecting scope and determined whether larvae survived to pupation (our measure of
fitness) or were parasitized. We did not include other sources of mortality, such as early larval
death, as they could influence the expression of the gall phenotype and confound estimates of
90 selection. For the food-web treatment that excluded larval parasitoids, we further restricted our
data by removing any incidental instances of parasitism by a larval parasitoid. This represented
less than 3% of the observations in this food-web treatment and allowed us to focus our inferences
93 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

96 We collected data on three different traits that we expected to influence larval survival based on
previous work in this system (Barbour et al., 2016) and other 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
99 nearest 0.01 mm at its maximum diameter (perpendicular to the direction of plant tissue growth).
Previous work in this system has shown that larger galls are associated with higher survival
(Barbour et al., 2016). Second, we measured clutch size by counting the number of chambers in each
102 gall (Weis et al., 1983; Heath et al., 2018). All larvae collected from the same multi-chambered gall
were scored with the same 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
105 branches per tree and counting 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
108 the same oviposition preference. 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 larval densities can be influenced by processes other than
111 preference (Singer, 1986). Fortunately, a couple 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
114 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.

117 Quantifying the Adaptive Landscape

Inferring adaptive landscapes assumes that trait distributions are multivariate normal (Lande and Arnold, 1983). To approximate this assumption, we log-transformed clutch size and square-root
120 transformed oviposition preference. We then scaled all phenotypic traits (mean=0 and SD=1) prior to our analyses (detailed below) to ensure that our estimates of selection were comparable across traits and with other studies.

123 Our analysis 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 standardized phenotypic traits (i) of individuals —in each food-web treatment. Second, we
126 translated selection surfaces into the scale of relative fitness (w) in order to calculate standardized selection gradients. Third, we used our estimates of selection gradients to characterize the slope and curvature of the adaptive landscape, which we used to measure evolutionary constraints.

129 **Selection surfaces:** 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 (α_i),
132 quadratic (α_{ii}), and linear interactions (α_{ij}) between each trait. We also allowed these selection surfaces (α) to vary between food-web treatments. Note that to obtain valid estimates of linear selection surfaces, we removed nonlinear terms prior to estimating linear relationships (Lande
135 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
138 nonindependence of clutch size (measured at gall level) and oviposition preference (measured
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
141 statistical models with random effects are not common in analyses of natural selection, we think
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
144 relationship between mean trait values and mean fitness (adaptive landscape), we assumed the
mean value of our random effects (i.e., setting them to zero) when calculating selection surfaces. We
then used parametric bootstrapping (1,000 replicates) to estimate the effect of food-web treatment
147 on larval survival as well as selection surfaces in each food-web treatment.

Selection gradients: Selection gradients cannot be estimated directly from GLMMs of selection
surfaces because the response is in terms of absolute fitness and the coefficients are on a nonlinear
150 scale. For example, the coefficients in the above model measure the change in the logarithm of
the odds of surviving (i.e., $\ln\{W(z)/[1 - W(z)]\}$) associated with 1 SD change in a trait with all
other traits held fixed at their mean. Therefore, we used the method developed by Janzen and
153 Stern (1998) to translate selection surfaces from the above model into the scale of relative fitness in
order to calculate directional (β_i), quadratic (γ_{ii}), and correlational (γ_{ij}) selection gradients. Briefly,
this method calculates the average gradient of selection surfaces by multiplying the average of
156 $W(z)[1 - W(z)]$ by each regression coefficient (e.g. α_i , α_{ii} , or α_{ij}). We then divided this average
gradient by the 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.
159 Note that we doubled all quadratic terms prior 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 measured evolutionary constraints by inspecting the slope and
162 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:

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

where each β_i corresponds to the directional selection gradient acting on each trait. By comparing

165 the number of directional selection gradients that show clear evidence of contributing to the slope
(i.e., 95% CI does not overlap zero) in our food-web treatments, we can infer the effect of food-web
structure on selective constraints.

168 The indirect effects of selection on the G-matrix ($\Delta G = G(\gamma - \beta\beta^T)G$) is governed by the curvature
of the adaptive landscape ($C = \gamma - \beta\beta^T$), which in our study corresponds to:

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

where each γ_{ii} (diagonal) corresponds to the quadratic selection gradient acting on a trait, and each

171 γ_{ij} (off-diagonal) corresponds to the correlational selection gradient acting on a particular trait
combination. Note that we omitted the upper triangle of each matrix for clarity since it is simply
the reflection of the lower triangle. Subtracting these two matrices results in the curvature matrix
174 of the adaptive landscape:

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

where each C_{ii} (diagonal) represents the effect of selection on the additive genetic variance in a
trait, and each C_{ij} (off-diagonal) represents the effect of selection on the additive genetic covariance

177 between a particular trait combination. In other words, 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, any nonzero covariance terms (off-diagonal) are indicative of
180 selection for trait integration (i.e., less independence). Therefore, we can infer the number of genetic
constraints by summing the 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
183 curvature matrix. For these analyses, we retained estimates for selection gradients that showed
clear evidence of being different from zero (i.e., 95% CI did not overlap zero) and set other gradients
to zero, prior to calculating the curvature matrix in each food-web treatment. This provides a
186 conservative estimate of the factors contributing to the curvature of the adaptive landscape.

Note that our metrics of selective and genetic constraints do not put much stock in differences in
the magnitude of selection between food-web treatments. This is because there is a high likelihood
189 that we are underestimating the magnitude of selection in our treatment that excludes larval
parasitoids. We expect this because larval parasitoids not only impose mortality on gall midges,
but egg parasitoids as well (fig. 1). Therefore, our short-term removal of larval parasitoids has
192 not allowed for an increase in egg parasitoid abundance after being released from intraguild
predation. An increase in the abundance of egg parasitoids would decrease mean survival of gall
midges, thus increasing the variance in relative fitness of midges, and consequently the magnitude
195 of selection estimates. A recent paper by Hunter et al. (2018) highlights this pervasive effect of
survival on the magnitude of selection estimates. This is why we use more qualitative metrics of
evolutionary constraints (i.e., selective constraints = number of traits under directional selection;
198 genetic constraints = number of decreasing variances + nonzero covariances).

Adjusting for biased measurements of selection

Rather than imposing selection, parasitoids may influence the expression of herbivore traits which
201 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
204 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
207 ID 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 modeled
210 only a linear relationship between chamber diameter and larval survival (α_{Diam}). We detected a positive bias in both food-web treatments (original $\alpha_{\text{Diam}} = 0.36$ [0.05, 0.67]; extinction $\alpha_{\text{Diam}} = 0.42$ [0.01, 0.82]), indicating that unadjusted relationships would overestimate the strength of selection
213 on chamber 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 selection surface and directional selection gradient.

216 Measuring selection on egg parasitoids

Once parasitized, the gall phenotype becomes the phenotype of the egg parasitoid. This phenotype may influence the egg parasitoid's survival in the face of larval parasitoids, and thus experiences
219 selection. Our food-web manipulation allows us to measure selection imposed by larval parasitoids on the phenotype of egg parasitoids. Using the same models as described above, we substituted egg parasitism as our response variable to quantify selection surfaces and selection gradients
222 acting on the egg parasitoid. Note that we cannot test the effect of food-web structure on the egg parasitoid's adaptive landscape—we can only estimate selection imposed by larval parasitoids. This comparison is still useful though in determining the extent to which the community context
225 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,

we report mean estimates of selection surfaces and selection gradients with 95% confidence intervals
228 in brackets. Note that for visualizing the adaptive landscape we restrict trait axes to ± 1 SD of
the mean trait value. This emphasizes the fact that we can only reliably estimate the shape of the
adaptive landscape near the mean phenotype of the population (Arnold et al., 2001). We also plot
231 mean larval survival on a natural log scale to accurately reflect the mathematical definition of the
adaptive landscape (Arnold, 2003). All data and code to reproduce the reported results are publicly
available on GitHub and have been archived on Zenodo (links are available from the journal office).

234 Results

Consumer extinctions increase selective constraints

We found that the extinction of larval parasitoids increased the number of gall midge traits under
237 directional selection (3 of 3) relative to the original food web (1 of 3)(table 1). For example, we
observed directional selection for smaller clutch sizes when we excluded larval parasitoids, but
there was no evidence of selection acting on this trait in the original food web (table 1; fig. 2C). This
240 absence of selection appeared to be a result of conflicting selection pressures imposed by each guild
of parasitoids. 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
243 ($\beta_{\text{Clutch}} = 0.13 [0.04, 0.24]$). We also observed clear evidence of directional selection for midges to
avoid ovipositing on plants with high densities of conspecifics when we excluded larval parasitoids
(table 1; fig. 2B); however, there was no clear relationship in the original food web (table 1). This
246 was likely a result of larval parasitoids imposing greater mortality on egg parasitoids at high gall
midge densities (see Selection on egg parasitoids section), and thus a less than additive effect on gall
midges. Chamber diameter experienced positive directional selection in both food-web treatments
249 (fig. 2A). Although the magnitude of selection on chamber diameter was relatively higher in the
original food web (table 1), this was not due to any difference in the relationship between chamber

diameter and survival (selection surfaces: original $\alpha_{\text{Diam}} = 1.15$ [0.75, 1.61]; extinction $\alpha_{\text{Diam}} = 1.1$
252 [0.64, 1.65]), but was simply a consequence of the (expected) lower survival in the original food web (original $\bar{W} = 0.42$ [0.28, 0.56]; extinction $\bar{W} = 0.68$ [0.54, 0.81]).

Table 1: Standardized selection gradients acting on gall midges in the original food web and with the extinction of larval parasitoids.

Selection gradient	Original	Extinction
β_{Diam}	0.34 [0.22, 0.48]	0.21 [0.12, 0.31]
β_{Clutch}	0.06 [-0.05, 0.17]	-0.09 [-0.17, -0.01]
β_{Pref}	-0.13 [-0.29, 0.05]	-0.16 [-0.26, -0.06]
$\gamma_{\text{Diam:Diam}}$	0.13 [-0.06, 0.33]	0.1 [-0.02, 0.23]
$\gamma_{\text{Clutch:Clutch}}$	-0.05 [-0.27, 0.18]	-0.11 [-0.28, 0.03]
$\gamma_{\text{Pref:Pref}}$	0.34 [0.07, 0.63]	0.02 [-0.15, 0.18]
$\gamma_{\text{Diam:Clutch}}$	-0.04 [-0.16, 0.08]	-0.07 [-0.15, 0.02]
$\gamma_{\text{Diam:Pref}}$	-0.13 [-0.29, 0.02]	-0.02 [-0.1, 0.07]
$\gamma_{\text{Clutch:Pref}}$	0.03 [-0.1, 0.18]	0 [-0.07, 0.07]

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

β_{Diam} has been adjusted for bias.

Consumer extinctions increase genetic constraints

255 The curvature of the adaptive landscape indirectly affects genetic constraints and is influenced by directional, quadratic, and correlational selection gradients. There was no clear evidence of correlational selection for any combination of traits in either food-web treatment (table 1). Similarly,
258 there was no clear evidence of quadratic selection on chamber diameter or clutch size in either food-web treatment (table 1; fig. 2A,C). In contrast, our food-web treatment did alter quadratic

selection acting on oviposition preference (table 1). The negative relationship between oviposition
261 preference and larval survival damped at high densities in the original food web, but not with
the exclusion of larval parasitoids (fig. 2B). This damped relationship was partly due to a trend
for nonlinear selection imposed by larval parasitoids ($\gamma_{\text{Pref:Pref}} = 0.18 [-0.02, 0.42]$), but was also
264 magnified by the lower average survival in complex food webs.

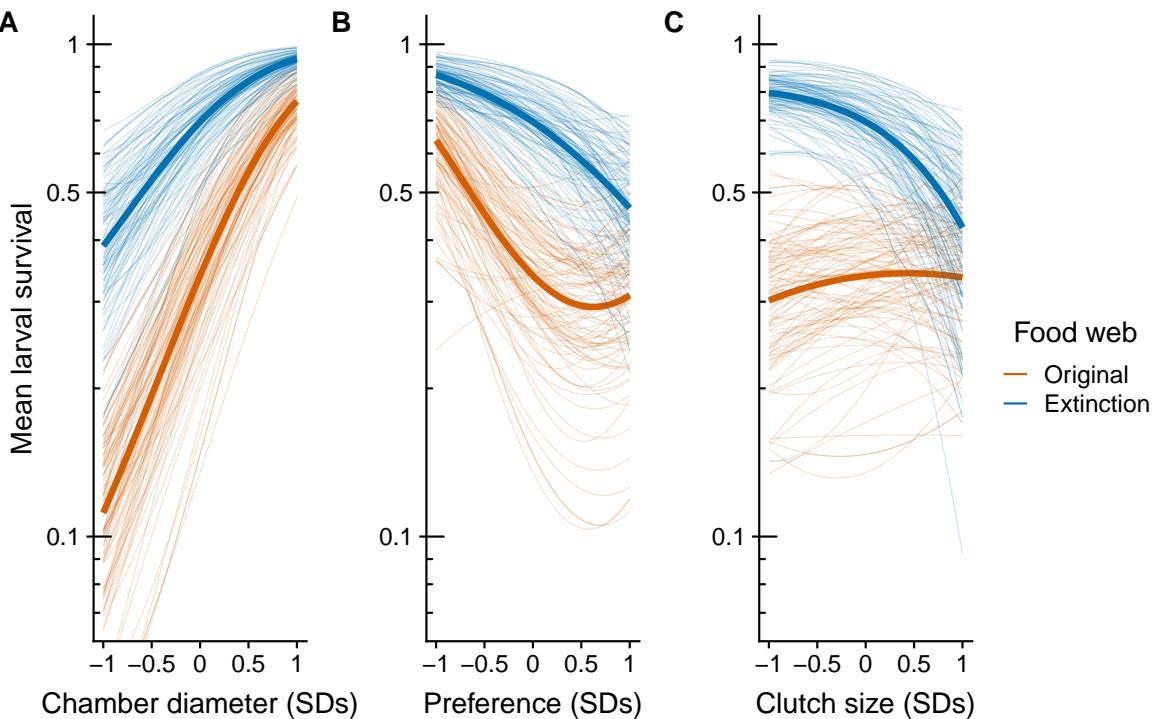


Figure 2: Adaptive landscape of gall midge phenotypes in the original food web and with the extinction of larval parasitoids. Each panel corresponds to a different phenotypic trait: chamber diameter (A); oviposition preference (B); and clutch size (C). Bold lines represent selection experienced in the original food web (orange) and with consumer extinctions (blue). Thin 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.

Using our estimates of directional (β_i), quadratic (γ_{ii}), and correlation selection (γ_{ij}), we calculated the curvature ($C = \gamma - \beta\beta^T$) of the adaptive landscape in each food-web treatment. In our study,
 267 this corresponds to:

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

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

where each C_{ii} (diagonal) represents the effect of selection on the additive genetic variance in a
 270 trait, and each C_{ij} (off-diagonal) represents the effect of selection on the additive genetic covariance
 between a particular trait combination. In order to obtain a conservative estimate of the factors
 contributing to the curvature, we only used estimates of selection that clearly differed from zero
 273 (bold values in table 1), otherwise we set estimates of selection to zero (non-bold values in table
 1) prior to our calculation. We found that the curvatures of the adaptive landscape exhibited the
 following structures:

$$\text{Curvature}_{\text{original}} = \begin{pmatrix} 0 & & \\ 0 & 0 & \\ 0 & 0 & 0.34 \end{pmatrix} - \begin{pmatrix} 0.34 \cdot 0.34 & & \\ 0 \cdot 0.34 & 0 \cdot 0 & \\ 0 \cdot 0.34 & 0 \cdot 0 & 0 \cdot 0 \end{pmatrix}$$

$$\text{Curvature}_{\text{original}} = \begin{pmatrix} -0.12 & & \\ 0 & 0 & \\ 0 & 0 & 0.34 \end{pmatrix}$$

$$\mathbf{Curvature}_{\text{extinction}} = \begin{pmatrix} 0 & & \\ 0 & 0 & \\ 0 & 0 & 0 \end{pmatrix} - \begin{pmatrix} 0.21 \cdot 0.21 & & \\ -0.09 \cdot 0.21 & -0.09 \cdot -0.09 & \\ -0.16 \cdot 0.21 & -0.16 \cdot -0.09 & -0.16 \cdot -0.16 \end{pmatrix}$$

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

²⁷⁶ Remember that we can infer the indirect effects of selection on genetic constraints by summing
 the 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
²⁷⁹ structure of these matrices indicates that the extinction of larval parasitoids increased the number
 of genetic constraints on gall midges (6 of 6) relative to the original food web (1 of 6). For example,
 directional selection resulting from the exclusion of larval parasitoids acted to decrease genetic
²⁸² variance for all three phenotypic traits (negative diagonal terms), whereas only one trait (chamber
 diameter) experienced a decrease in additive genetic variance in the original food web. For genetic
 covariances, the combined effects of directional selection resulting from consumer extinctions
²⁸⁵ favored integration among all three phenotypic traits (nonzero off-diagonal terms), and thus
 constraints along all three axes of covariance (fig. 3). In contrast, the absence of directional selection
 in clutch size and oviposition preference did not promote trait integration along any axis in the
²⁸⁸ original food web (fig. 3).

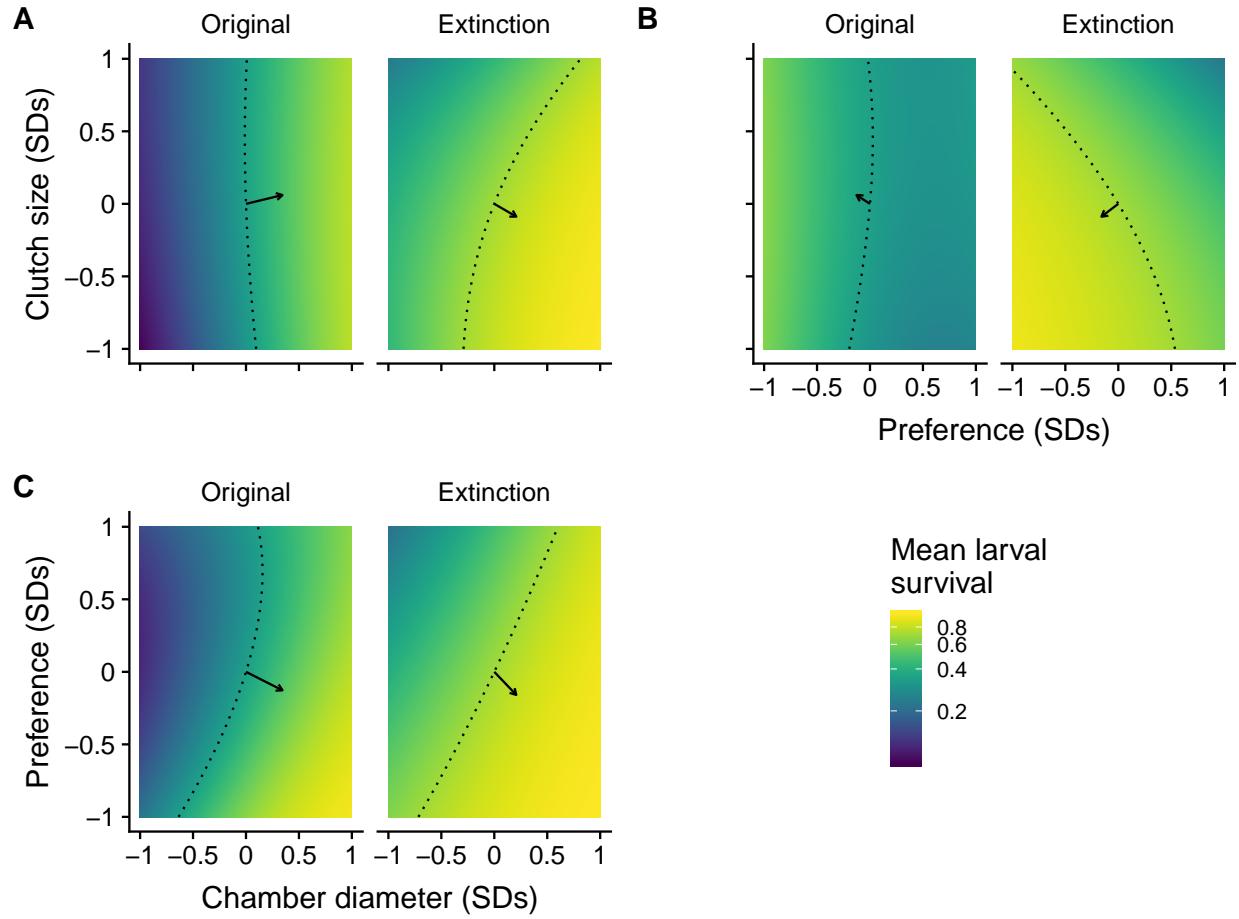


Figure 3: Two dimensional view of adaptive landscapes of gall midge phenotypes in the original food web and with the extinction of larval parasitoids. Each panel corresponds to a different combination of phenotypic traits: clutch size and chamber diameter (A); clutch size and oviposition preference (B);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

Selection on egg parasitoids

The extinction of larval parasitoids only altered the relationship between gall midge preference and
 291 the probability of observing egg parasitoids (table 2). Specifically, the impact of larval parasitoids increased nonlinearly with higher gall midge densities (fig. 4).

Table 2: Standardized selection gradients acting on egg parasitoids (*Platygaster* sp.)

Selection gradient	Contrast = Original - Extinction
β_{Diam}	0.03 [0.3, -0.25]
β_{Clutch}	-0.07 [0.26, -0.39]
β_{Pref}	0.25 [0.64, -0.09]
$\gamma_{\text{Diam:Diam}}$	0.05 [0.43, -0.33]
$\gamma_{\text{Clutch:Clutch}}$	0.21 [0.68, -0.26]
$\gamma_{\text{Pref:Pref}}$	0.46 [1.07, 0.02]
$\gamma_{\text{Diam:Clutch}}$	0 [0.29, -0.27]
$\gamma_{\text{Diam:Pref}}$	-0.25 [0.04, -0.6]
$\gamma_{\text{Clutch:Pref}}$	0.18 [0.52, -0.12]

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

β_{Diam} has been adjusted for bias.

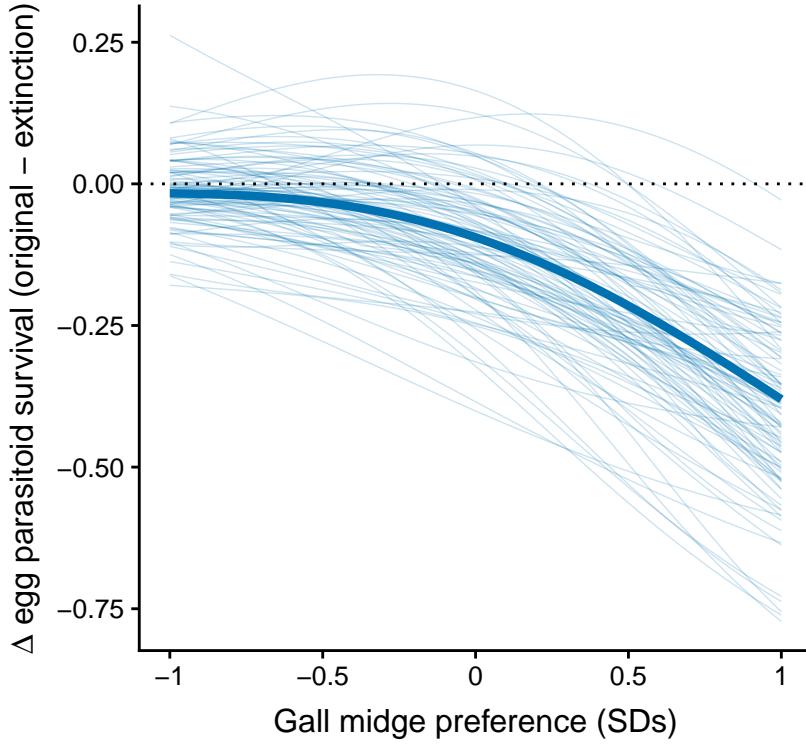


Figure 4: Selection imposed by larval parasitoids on egg parasitoids (*Platygaster* sp.). The bold line represents the average difference in the probability of observing the egg parasitoid (original - extinction of larval parastiods) as a function of gall midge oviposition preference. Thin lines represent 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 egg parasitoids.

Discussion

- 294 We found that the extinction of larval parasitoids constrained phenotypic evolution in gall midges in two key ways. First, more traits contributed to the slope of the adaptive landscape in the absence of larval parasitoids, suggesting greater constraints on the trajectory of phenotypic evolution.

- 297 Second, excluding larval parasitoids indirectly increased the number of genetic constraints, which
could act to constrain the gall midge's adaptive potential in the face of novel selection pressures.
Our experiment also revealed evidence of indirect selection pressures, suggesting that the loss of
300 consumers may have complex effects on the trajectories of phenotypic evolution. Taken together,
our study provides experimental evidence from the field that consumer extinctions may constrain
the adaptive potential of remaining populations.
- 303 All three phenotypic traits we examined experienced directional selection when we excluded larval
parasitoids, 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
306 clear evidence of selective constraints on clutch size and oviposition preference in the original food
web. This suggests 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
309 traits. This also implies that as selective constraints dampen in more complex food webs, then
the trajectory of evolution becomes more determined by how genetic constraints interact with
other evolutionary processes (e.g. genetic drift, gene flow, and mutation). Interestingly, this aligns
312 with Schlüter (1996)'s hypothesis that phenotypic evolution often follows 'genetic lines of least
resistance'. Schlüter (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
315 from the 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.
- 318 We also found evidence for more genetic constraints when we excluded larval parasitoids 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
321 and Houle, 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
324 that consumer extinctions 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
327 dynamically changing 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
330 context.

The generality of our results likely depends on the relative abundance and functional differences between consumers in a community. For example, if consumers do not differ from each other,
333 then we do not expect changes in food-web structure to modify evolutionary constraints. 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
336 communities (Paine, 1992) support this notion. When consumers are abundant though, the effect of food-web structure will depend on whether different species impose conflicting selection pressures or select for distinct traits. For example, parasitoids and birds impose conflicting selection pressures
339 on the size of galls induced by the fly *Eurosta solidaginis* (Weis and Abrahamson, 1985; Abrahamson and Weis, 1997). 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
342 (Start et al., 2018) causes a shift from neutral to directional 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
345 resistance to different insect herbivores (Maddox and Root, 1990; Wise, 2007; 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
348 gaining predictive insight to the evolutionary consequences of food-web disassembly requires an understanding of the mechanisms governing the assembly of trophic interactions.

Our results suggest that the loss of consumers may not only directly affect connected species,
351 but also result in indirect evolutionary effects. In our study, this indirect effect arises from egg
parasitoids being released from intraguild predation when we excluded larval parasitoids. This
release occurs more on trees with high larval densities, which could intensify selection on gall
354 midge oviposition preference. A growing number of experiments over the past two decades have
demonstrated the presence and potential importance of indirect evolutionary effects that emerge
in a community context (Pilson, 1996; Juenger and Bergelson, 1998; Stinchcombe and Rausher,
357 2001; Lankau and Strauss, 2007; Walsh and Reznick, 2008, 2010; terHorst, 2010; Sahli and Conner,
2011; Lau, 2012; terHorst et al., 2015; Schiestl et al., 2018; Start et al., 2019). If indirect evolutionary
360 effects are common (Miller and Travis, 1996; Walsh, 2013), then predicting evolutionary trajectories
resulting from consumer extinctions will require evolutionary studies to explicitly account for the
ecological networks that species are embedded in.

There is a growing number of theoretical studies on adaptation to directional environmental
363 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
which pairwise interactions modify the adaptive potential of species. Our study hints at a novel
366 mechanism, whereby more complex food webs flatten the adaptive landscape, thus facilitating
future adaptation by allowing genetic and phenotypic variation to persist. This mechanism only
emerges once we move beyond pairwise interactions to consider selection on multiple traits in a
369 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 species diversity on adaptation occurs because there is a greater chance that
372 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 species-rich communities.

375 Our study has some limitations to consider when relating our findings to the effect of consumer

extinctions on evolutionary constraints more generally. First, we removed other sources of mortality prior to our analyses. While this was necessary to avoid confounding estimates of selection
378 with effects on phenotypic expression, we may be overestimating the effects of selection due to consumers. Second, our metrics of evolutionary constraints do not account for variation in the magnitude of selection pressures. While metrics that incorporate the magnitude of selection are
381 possible (Hansen and Houle, 2008), they were not appropriate for our study as our experimental removal of larval parasitoids artificially increased the mean fitness of gall midges (in the short term), which dampens the magnitude of selection gradients in this treatment (Hunter et al., 2018).
384 This is why we used more qualitative metrics of evolutionary constraints, which are robust to this artificial effect and simply require sufficient sample sizes to detect evidence of selection.

Our study gives insight to how consumer extinctions alter evolutionary constraints on remaining
387 populations. In particular, it hints at a potential insidious effect of local extinctions that 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
390 simplification of ecological communities may actually reduce the predictability 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
393 eco-evolutionary dynamics focus on phenotypic change in a single trait, yet our results highlight that the number of traits under selection may change with the community context. Importantly, we found that different species/guilds imposed different selection pressures. Knowing these
396 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
399 consequences of changes in ecological communities.

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