Phenotypic evolution is less constrained in complex food webs or Food-web complexity alters the fitness landscape of an insect herbivore

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Abstract

Species-interaction networks provide a mechanistic link between community and population ecology, as they describe who interacts with whom in a community. Similarly, fitness landscapes provide a mechanistic link between population and evolutionary ecology, as they describe the influence of natural selection on phenotypic variation. It remains unclear, however, how the network structure of species interactions shapes the fitness landscape. Understanding this relationship is likely key for developing a predictive ecology across scales of biological organization. To examine the relationship between network structure and the fitness landscape, we conducted a field experiment that manipulated the network of trophic interactions (simple vs. complex) influencing the fitness of an insect herbivore. We then quantified the fitness landscape of herbivores in each treatment by measuring herbivore survival as a function of multiple phenotypic traits. We found that more traits were under selection in the simple vs. complex trophic network. This occurred because different natural enemies impose different selection pressures on herbivore traits, thereby minimizing relative fitness differences among herbivore phenotypes in the complex network. Our work suggests that more complex trophic networks allow phenotypic variation to persist, which could facilitate subsequent adaptive evolution of populations to environmental change.

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Introduction

The fitness landscape provides a unifying framework for linking the ecology and evolution of populations (Lande 2007; McPeek 2017). The average fitness of a population is a common currency in ecology and evolution, but usually goes by different names in each field. Ecologists refer to it as per-capita population growth rate (dN/Ndt), whereas evolutionary biologists call it the natural log of population mean fitness ($ln(\bar{W}_N)$. In addition to having different names, ecologists and evolutionary biologists have typically focused on different processes that shape the fitness landscape. For example, population ecologists have long studied the effect of a population's density on its per-capita growth rate (i.e. density-dependence, CITE Foundational and current work). In contrast, evolutionary biologists have focused on how the mean trait value of a population influences its average fitness, as this describes the direction and magnitude of natural selection (CITE foundational and current work). Therefore, the fitness landscape describes the joint ecological and evolutionary dynamics of a population in a given environment.

Community ecologists have extended the ecological side of the fitness landscape by incorporating network theory. Species-interaction networks, such as a food web describing who eats whom, provide an explicit representation of the biotic environment as they describe the interdependency of populations within an ecological community. This has provided an effective framework for predicting how changes in the biotic environment (e.g. density of directly and indirectly connected species) will impact population dynamics within species-rich communities. At the same time, evolutionary biologists have long recognized that changes in the biotic environment can alter the dynamics of natural selection. However, the biotic environment in which populations are evolving often remains a bit of a "black box" that's labelled by a general ecological process such as competition, predation, or mutualism. Because of this, it remains difficult to predict how changes in the biotic environment will affect the direction and magnitude of natural selection. Such predictions are urgently needed given the rapid changes in the biotic environment that most populations are currently experiencing throughout the world.

Here, we integrate species-interaction networks and the fitness landscape to empirically test how changes in the biotic environment – network of species interactions – affect the dynamics of natural selection. Specifically, we conducted a field experiment that manipulated the diversity of insect parasitoids that were able to impose selection on an abundant insect herbivore (*Iteomyia salicisverruca*)(Fig. 1). The larva of this herbivore species induce tooth-shaped galls when they feed on the developing leaves of willow trees (*Salix* sp., Russo (2006)). These galls provide protection from generalist predators (e.g. ants, spiders), thus the network of interacting parasitoids provides a realistic representation of the biotic environment this insect herbivore is experiencing. Therefore, our manipulation of parasitoid diversity alters the diversity of interactions, or food-web complexity, that this insect herbivore experiences.

Changes in food-web complexity could influence a resource population's

fitness landscape in at least two ways. First, if a more diverse community of consumers is more effective at suppressing resource densities (Ives, Cardinale, and Snyder (2005)), then this will result in lower mean fitness of the resource population. A reduction in mean fitness, all else equal, will intensify natural selection (Hunter et al. (2018)). On the other hand, if consumers impose different selection pressures on resource traits, then more diverse communities could dampen the strength of selection acting on a given trait. This is because a greater diversity in selection pressures is equivalent to greater uncertainty in the selective environment. Thus, a more diverse consumer community may relax the net selection pressures acting on resource traits. Here, we evaluate these hypothesized relationships through an experimental test of how changes in food-web complexity alters the fitness landscape of a resource population.

Materials & Methods

Study Site

We conducted our study within a four-year old common garden 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 in our garden 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).

Food-Web Manipulation

We setup our food-web manipulation across 128 plants soon after galls began developing on *S. hookeriana* in early June of 2013. These 128 plants came from eight different plant genotypes, spanning the range of trait variation observed in this willow population (Barbour et al. (2015)). On treatment plants (8 replicates per genotype), we enclosed 14 galled leaves with 10x15cm organza bags (ULINE, Pleasant Prairie, WI, USA) to exclude three parasitoid species that attack during larva development (hereafter larval parasitoids). This treatment did not exclude the egg parasitoid *Platygaster* sp. which attacks prior to gall initiation (note that in Cecidomyiid midges, larva initiate gall development CITE). On control plants (8 replicates per genotype), we used flagging tape to mark 14 galled leaves per plant (~30 larva), allowing the full suite of parasitoids to attack *Iteomyia*. Marking galls with flagging tape ensured that we compared control and treatment galls with similar phenology when we collected galls later in the season. Our food-web manipulation altered the average number of trophic interactions that *Iteomyia* was exposed to from BLANK on control plants to BLANK on treatment plants. Thus, we refer to galls on control plants as being

exposed to a 'complex' food web, whereas galls on treatment plants were exposed to a 'simple' food web. 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 under a dissecting scope and determined whether larva survived to pupation (our measure of fitness) or were parasitized. Since we were interested in selection imposed by interactions with parasitoids, we restricted our data to larva that either survived to pupation, was parasitized by an egg parasitoid (*Platygaster* sp.), or was parasitized by a larval parasitoid. For the food-web treatment that excluded parasitoids, we further restricted our data by removing any 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 of selection on those imposed by the egg parasitoid.
Together, we had survival estimates for 1,306 larva from 607 galls, 111 plants, and 8 plant genotypes.

Measuring Gall Traits

We collected data on three different traits that we anticipated would experience selection based on our previous work (Barbour et al. (2016)) and others work with Cecidomyiid midges (Weis, Price, and Lynch (1983), Heath, Abbot, and Stireman (2018)). First, we measured gall diameter as the size of each gall chamber to the nearest 0.01 mm at its maximum diameter (perpendicular to the direction of plant tissue growth). Our previous work has shown that a larger gall diameter provides a refuge for larva from parasitoid attack (Barbour et al. (2016)). Second, we measured the clutch size of adult female midges by counting the number of chambers in each gall (Weis, Price, and Lynch (1983)). All larva collected from the same multi-chambered gall were scored with the same clutch size. Third, we measured female preference for oviposition (egg-laying) sites as the density of larva observed on a plant in an independent survey. Specifically, we randomly sampled five branches per tree and summed the number of individual gall chambers observed. We then converted these counts to a measure of gall density per 100 shoots by counting the number of shoots on the last branch we sampled. All larva collected from the same plant were scored with the same female preference. The measurement of larval densities on plants in the field is a commonly used index 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 preference (Singer (1986)). Fortunately, a couple of features of our study system suggest that larval density on a plant may be a good proxy for female preference. For example, since our data comes from a randomized placement of willow genotypes in a common garden, there is no consistent bias in which willow genotypes that females are exposed to while searching for oviposition sites. Also, egg predation is a minor source of mortality for galling insects in general (Hawkins, Cornell, and Hochberg (1997)), thus we do not expect any prior egg predation to bias our estimates of observed larval densities.

Quantifying the Fitness Landscape

To characterize the shape of the fitness landscape in simple and complex food webs, we first used a generalized linear mixed model to quantify selection surfaces on individual traits. We used a binomial error distribution (logit link function) since larval survival (0 or 1) was our response variable and measure of fitness. We specified linear and quadratic terms for each gall trait as well as linear interaction terms between each gall trait as fixed effects in the statistical models. To account for the correlated structure of clutch size (gall level) and female preference (plant level) as well as any independent effects of willow genotype on larval survival, we specified gall ID nested within plant ID nested within plant genotype as random effects. Since we were interested in characterizing the fitness landscape – the relationship between mean trait values and population mean fitness – we assumed the mean value of our random effects (i.e. setting them to zero) to estimate selection gradients. Also, the fitness landscape assumes that traits distributions are multivariate normal. To better meet this assumption, we log-transformed clutch size and added a small constant (1) to female preference before log transforming, since our surveys occassionaly estimated zero larval densities. We then scaled all phenotypic traits to mean=0 and SD=1 in order to calculate standardized selection gradients that were comparable across traits and with other studies of natural selection. We used the method of Frederic J Janzen and Hal S Stearn (1998) to calculate directional (β_{z_i}), quadratic (γ_{z_i,z_i}), and correlational (γ_{z_i,z_j}) selection gradients and used parametric bootstrapping (1000 replicates) to calculate their 95% confidence intervals (Bolker et al. (2009)). We estimated directional selection gradients by excluding quadratic terms and statistical interactions in the model. Note that for visualizing the fitness landscape we restrict trait axes to ± 1 SD of the mean trait value as this contains the majority of the trait distribution that selection is acting on.

Rather than imposing selection, parasitoids may themselves influence the expression of herbivore traits. Any influence on trait expression would bias selection gradients acting on those traits. In our system, it was plausible that parasitoids may influence chamber growth by promoting larval feeding (cite), speeding up larva development (cite), or killing larva before they complete their development (cite). Therefore, our estimates of selection on chamber diameter may be positively or negatively biased. To estimate this bias, we subset our data to only include galls where there was variation in larval survival ($1 >$ survival > 0) within the same gall. We then calculated "apparent" selection differentials for each gall by comparing the average chamber diameter of all larva (before "selection") to the average chamber diameter of surviving larva and analyzed separate one-sample t-tests for each food-web treatment. This analysis is based on the assumption that larva within each gall come from the same clutch and therefore should have similar chamber diameters regardless of whether they are parasitized. In general, we found that our estimates of directional selection on chamber diameter were positively biased (Appendix). In other words, our analyses were overestimating the magnitude of selection acting on gall diameter.

Therefore, we adjusted our estimates of directional selection on chamber diameter (β_{diam}) by subtracting the biased selection differentials. Note that selection gradients and selection differentials for chamber diameter were virtually the same (Appendix).

Quantifying Selective Constraints

The strength and pattern of selective constraints can be measured as the slope and curvature of the fitness landscape (Arnold 1992).

We can translate selection surfaces of individuals to the fitness landscape of a population

To characterize the net effects of food-web complexity on the slope and curvature of *Iteomyia*'s fitness landscape, we took advantage of existing theory that links selection surfaces of individuals to the fitness landscape of the population (Phillips & Arnold 1998, Arnold 2003). Specifically, the slope of the fitness landscape corresponds to the column vector of directional selection gradients:

Note that we ommitted the upper triangle of the matrix for clarity since it is simply the reflection of the lower triangle. Assuming that there is additive genetic variance and covariance between these traits under selection, then the slope and curvature of the fitness landscape give insight to how the population's mean trait value will change in the next generation as well as how additive genetic variance and covariance changes within a generation.

While making quantitative predictions about trait evolution requires knowledge of the additive genetic variance and covariance of these traits, the slope and curvature of the fitness landscape still give qualitative insight to the evolutionary trajectory of a population.

If we assume that there is additive genetic variance and covariance between these traits, then the matrix describing the curvature of the fitness landscape gives qualitative insight to the selective constraints acting on the population. For example, the diagonal of the curvature matrix dictates (qualitatively) whether the additive genetic variance in each trait will increase (+), decrease (−), or stay the same (0). Similarly, the off-diagonal of the curvature matrix dictates whether selection favors trait integration (positive covariance), a tradeoff (negative covariance), or no change in genetic covariance. In other words, we can get qualitative insight to how food-web complexity influences constraints on the fitness landscape by counting the number of negative sign values along the diagnoal (which imply a decrease in additive genetic variance) and the number of positive or negative signs along the off diagonal (which imply changes in additive genetic covariance that lead to either trait integration or tradeoffs).

All analyses and visualizations were conducted in R (R Core Team (2018)).

I need to go back to estimate a common alpha coefficient if the treatments do not differ from each other.

```
# In terms of the gammas, there was only evidence that food-web treatment altered nonlinear
summary(foodweb_glmer)
```

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
```

```
##   Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula:
## gall_survival ~ Foodweb * (sc.Diam + sc.log.Clutch + sc.log1p.Pref)^2 +
##     Foodweb * (I(sc.Diam^2) + I(sc.log.Clutch^2) + I(sc.log1p.Pref^2)) +
##     (1 | Genotype/Plant_Position/Gall_Number)
##    Data: gall_selection.df
## Control: glmerControl(optimizer = "bobyqa")
##
##      AIC      BIC   logLik deviance df.resid
##   1399.5   1518.1   -676.7   1353.5     1262
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -2.43637 -0.39448  0.08166  0.40662  2.61308
##
## Random effects:
##  Groups                                 Name        Variance Std.Dev.
##  Gall_Number:(Plant_Position:Genotype) (Intercept) 4.2727   2.0671
##  Plant_Position:Genotype               (Intercept) 0.6336   0.7960
##  Genotype                              (Intercept) 0.2006   0.4479
## Number of obs: 1285, groups:
## Gall_Number:(Plant_Position:Genotype), 613; Plant_Position:Genotype, 111; Genotype, 8
##
## Fixed effects:
##                                          Estimate Std. Error z value
## (Intercept)                              -0.69685    0.37782  -1.844
## FoodwebSimple                             1.75956    0.55810   3.153
## sc.Diam                                   1.65436    0.23584   7.015
## sc.log.Clutch                             0.06403    0.23937   0.267
## sc.log1p.Pref                            -0.54297    0.34148  -1.590
## I(sc.Diam^2)                              0.21368    0.14705   1.453
## I(sc.log.Clutch^2)                       -0.07400    0.17650  -0.419
## I(sc.log1p.Pref^2)                        0.70082    0.31013   2.260
## sc.Diam:sc.log.Clutch                    -0.15314    0.19274  -0.795
## sc.Diam:sc.log1p.Pref                    -0.53040    0.27222  -1.948
## sc.log.Clutch:sc.log1p.Pref               0.16936    0.27787   0.609
## FoodwebSimple:sc.Diam                    -0.11621    0.31148  -0.373
## FoodwebSimple:sc.log.Clutch              -0.88569    0.36150  -2.450
## FoodwebSimple:sc.log1p.Pref              -0.60782    0.47939  -1.268
## FoodwebSimple:I(sc.Diam^2)                0.05600    0.22934   0.244
## FoodwebSimple:I(sc.log.Clutch^2)         -0.21967    0.25755  -0.853
## FoodwebSimple:I(sc.log1p.Pref^2)         -0.88444    0.39493  -2.239
## FoodwebSimple:sc.Diam:sc.log.Clutch      -0.24383    0.28475  -0.856
## FoodwebSimple:sc.Diam:sc.log1p.Pref       0.38979    0.34340   1.135
## FoodwebSimple:sc.log.Clutch:sc.log1p.Pref -0.10381    0.33455  -0.310
```

```
##                                           Pr(>|z|)
## (Intercept)                                0.06513 .
## FoodwebSimple                              0.00162 **
## sc.Diam                                    2.3e-12 ***
## sc.log.Clutch                              0.78909
## sc.log1p.Pref                              0.11183
## I(sc.Diam^2)                               0.14618
## I(sc.log.Clutch^2)                         0.67503
## I(sc.log1p.Pref^2)                         0.02384 *
## sc.Diam:sc.log.Clutch                      0.42688
## sc.Diam:sc.log1p.Pref                      0.05136 .
## sc.log.Clutch:sc.log1p.Pref                0.54220
## FoodwebSimple:sc.Diam                      0.70909
## FoodwebSimple:sc.log.Clutch                0.01429 *
## FoodwebSimple:sc.log1p.Pref                0.20484
## FoodwebSimple:I(sc.Diam^2)                 0.80710
## FoodwebSimple:I(sc.log.Clutch^2)           0.39370
## FoodwebSimple:I(sc.log1p.Pref^2)           0.02513 *
## FoodwebSimple:sc.Diam:sc.log.Clutch        0.39184
## FoodwebSimple:sc.Diam:sc.log1p.Pref        0.25634
## FoodwebSimple:sc.log.Clutch:sc.log1p.Pref  0.75634
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##
## Correlation matrix not shown by default, as p = 20 > 12.
## Use print(x, correlation=TRUE)  or
##     vcov(x)        if you need it
```

```
# Therefore, we refit a model that only included this effect of food-web treatment on the g
foodweb_glmer_revised <- update(foodweb_glmer, .~. -Foodweb:I(sc.Diam^2) -Foodweb:I(sc.log.C

# Note that we still observe that food-web treatment alters nonlinear selection on female p
# There is also now marginal evidence for nonlinear selection on diameter as well as correl
summary(foodweb_glmer_revised)
```

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##   Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula:
## gall_survival ~ Foodweb + sc.Diam + sc.log.Clutch + sc.log1p.Pref +
##     I(sc.Diam^2) + I(sc.log.Clutch^2) + I(sc.log1p.Pref^2) +
##     (1 | Genotype/Plant_Position/Gall_Number) + sc.Diam:sc.log.Clutch +
##     sc.Diam:sc.log1p.Pref + sc.log.Clutch:sc.log1p.Pref + Foodweb:sc.Diam +
##     Foodweb:sc.log.Clutch + Foodweb:sc.log1p.Pref + Foodweb:I(sc.log1p.Pref^2)
##    Data: gall_selection.df
```

```
## Control: glmerControl(optimizer = "bobyqa")
##
##      AIC      BIC   logLik deviance df.resid
##   1392.6   1485.5   -678.3   1356.6     1267
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -2.56786 -0.39417  0.08248  0.40532  2.54775
##
## Random effects:
##  Groups                                  Name        Variance Std.Dev.
##  Gall_Number:(Plant_Position:Genotype) (Intercept) 4.2062   2.0509
##  Plant_Position:Genotype               (Intercept) 0.6052   0.7780
##  Genotype                              (Intercept) 0.2062   0.4541
## Number of obs: 1285, groups:
## Gall_Number:(Plant_Position:Genotype), 613; Plant_Position:Genotype, 111; Genotype, 8
##
## Fixed effects:
##                                  Estimate Std. Error z value Pr(>|z|)
## (Intercept)                     -0.588297   0.355456  -1.655   0.0979 .
## FoodwebSimple                    1.577451   0.479441   3.290   0.0010 **
## sc.Diam                          1.585657   0.217494   7.291 3.09e-13 ***
## sc.log.Clutch                    0.009263   0.208112   0.045   0.9645
## sc.log1p.Pref                   -0.524039   0.331334  -1.582   0.1137
## I(sc.Diam^2)                     0.211654   0.110801   1.910   0.0561 .
## I(sc.log.Clutch^2)              -0.167620   0.127219  -1.318   0.1876
## I(sc.log1p.Pref^2)               0.646133   0.296141   2.182   0.0291 *
## sc.Diam:sc.log.Clutch           -0.257952   0.140800  -1.832   0.0669 .
## sc.Diam:sc.log1p.Pref           -0.273306   0.160883  -1.699   0.0894 .
## sc.log.Clutch:sc.log1p.Pref      0.125058   0.151556   0.825   0.4093
## FoodwebSimple:sc.Diam           -0.050583   0.291165  -0.174   0.8621
## FoodwebSimple:sc.log.Clutch     -0.700008   0.295920  -2.366   0.0180 *
## FoodwebSimple:sc.log1p.Pref     -0.611523   0.461851  -1.324   0.1855
## FoodwebSimple:I(sc.log1p.Pref^2) -0.828557   0.382344  -2.167   0.0302 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##
## Correlation matrix not shown by default, as p = 15 > 12.
## Use print(x, correlation=TRUE)  or
##     vcov(x)        if you need it
```

```
summary(betas_glmer)
```

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##   Approximation) [glmerMod]
```

```
##  Family: binomial  ( logit )
## Formula:
## gall_survival ~ Foodweb * (sc.Diam + sc.log.Clutch + sc.log1p.Pref) +
##     (1 | Genotype/Plant_Position/Gall_Number)
##    Data: gall_selection.df
## Control: glmerControl(optimizer = "bobyqa")
##
##      AIC      BIC   logLik deviance df.resid
##   1394.0   1450.7   -686.0   1372.0     1274
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -2.2378 -0.3985  0.1132  0.3910  2.7651
##
## Random effects:
##  Groups                                 Name        Variance Std.Dev.
##  Gall_Number:(Plant_Position:Genotype) (Intercept) 4.4523   2.1100
##  Plant_Position:Genotype               (Intercept) 0.6350   0.7969
##  Genotype                              (Intercept) 0.2966   0.5446
## Number of obs: 1285, groups:
## Gall_Number:(Plant_Position:Genotype), 613; Plant_Position:Genotype, 111; Genotype, 8
##
## Fixed effects:
##                              Estimate Std. Error z value Pr(>|z|)
## (Intercept)                 -0.26211    0.30437  -0.861  0.38915
## FoodwebSimple                1.07015    0.35648   3.002  0.00268 **
## sc.Diam                      1.53362    0.20976   7.311 2.64e-13 ***
## sc.log.Clutch                0.20562    0.19224   1.070  0.28480
## sc.log1p.Pref               -0.67099    0.33534  -2.001  0.04540 *
## FoodwebSimple:sc.Diam        0.02185    0.28368   0.077  0.93861
## FoodwebSimple:sc.log.Clutch -0.70280    0.28710  -2.448  0.01437 *
## FoodwebSimple:sc.log1p.Pref -0.15620    0.37677  -0.415  0.67845
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##             (Intr) FdwbSm sc.Dim sc.l.C sc.1.P FdS:.D FS:..C
## FoodwebSmpl -0.505
## sc.Diam     -0.002  0.100
## sc.lg.Cltch  0.138 -0.088 -0.140
## sc.lg1p.Prf -0.215  0.181 -0.117 -0.081
## FdwbSmpl:.D -0.035  0.121 -0.525  0.167  0.061
## FdwbSmp:..C -0.080  0.195  0.051 -0.682  0.069 -0.206
## FdwbSm:.1.P  0.191 -0.119  0.042  0.020 -0.772 -0.092  0.025
```

```r
betas_glmer_revised <- update(betas_glmer, .~. -Foodweb:sc.Diam -Foodweb:sc.log1p.Pref)
summary(betas_glmer_revised)
```

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##   Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula:
## gall_survival ~ Foodweb + sc.Diam + sc.log.Clutch + sc.log1p.Pref +
##     (1 | Genotype/Plant_Position/Gall_Number) + Foodweb:sc.log.Clutch
##    Data: gall_selection.df
## Control: glmerControl(optimizer = "bobyqa")
##
##      AIC      BIC   logLik deviance df.resid
##   1390.1   1436.6   -686.1   1372.1     1276
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -2.2674 -0.3980  0.1138  0.3907  2.7868
##
## Random effects:
##  Groups                                 Name        Variance Std.Dev.
##  Gall_Number:(Plant_Position:Genotype) (Intercept) 4.4391   2.1069
##  Plant_Position:Genotype               (Intercept) 0.6320   0.7950
##  Genotype                              (Intercept) 0.2961   0.5441
## Number of obs: 1285, groups:
## Gall_Number:(Plant_Position:Genotype), 613; Plant_Position:Genotype, 111; Genotype, 8
##
## Fixed effects:
##                             Estimate Std. Error z value Pr(>|z|)
## (Intercept)                  -0.2381     0.2984  -0.798 0.425022
## FoodwebSimple                 1.0519     0.3512   2.995 0.002744 **
## sc.Diam                       1.5430     0.1782   8.657  < 2e-16 ***
## sc.log.Clutch                 0.2062     0.1892   1.090 0.275618
## sc.log1p.Pref                -0.7793     0.2120  -3.676 0.000237 ***
## FoodwebSimple:sc.log.Clutch  -0.6983     0.2805  -2.490 0.012792 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##             (Intr) FdwbSm sc.Dim sc.l.C sc.1.P
## FoodwebSmpl -0.496
## sc.Diam     -0.023  0.193
## sc.lg.Cltch  0.142 -0.107 -0.061
## sc.lg1p.Prf -0.109  0.143 -0.169 -0.100
## FdwbSmp:..C -0.093  0.228 -0.070 -0.671  0.138
```

```r
foodweb_glmer_revised_again <- update(foodweb_glmer_revised, .~. -Foodweb:sc.Diam -Foodweb:s
summary(foodweb_glmer_revised_again)
```

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##   Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula:
## gall_survival ~ Foodweb + sc.Diam + sc.log.Clutch + sc.log1p.Pref +
##     I(sc.Diam^2) + I(sc.log.Clutch^2) + I(sc.log1p.Pref^2) +
##     (1 | Genotype/Plant_Position/Gall_Number) + sc.Diam:sc.log.Clutch +
##     sc.Diam:sc.log1p.Pref + sc.log.Clutch:sc.log1p.Pref + Foodweb:sc.log.Clutch +
##     Foodweb:I(sc.log1p.Pref^2)
##    Data: gall_selection.df
## Control: glmerControl(optimizer = "bobyqa")
##
##      AIC      BIC   logLik deviance df.resid
##   1390.5   1473.0   -679.2   1358.5     1269
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -2.54938 -0.39242  0.08266  0.39760  2.57612
##
## Random effects:
##  Groups                                 Name        Variance Std.Dev.
##  Gall_Number:(Plant_Position:Genotype) (Intercept) 4.2426   2.0598
##  Plant_Position:Genotype               (Intercept) 0.6433   0.8021
##  Genotype                              (Intercept) 0.2027   0.4502
## Number of obs: 1285, groups:
## Gall_Number:(Plant_Position:Genotype), 613; Plant_Position:Genotype, 111; Genotype, 8
##
## Fixed effects:
##                                  Estimate Std. Error z value Pr(>|z|)
## (Intercept)                      -0.50735    0.34880  -1.455  0.14579
## FoodwebSimple                     1.31940    0.43004   3.068  0.00215 **
## sc.Diam                           1.57197    0.18409   8.539  < 2e-16 ***
## sc.log.Clutch                     0.02541    0.20704   0.123  0.90232
## sc.log1p.Pref                    -0.81032    0.25766  -3.145  0.00166 **
## I(sc.Diam^2)                      0.21338    0.11085   1.925  0.05424 .
## I(sc.log.Clutch^2)               -0.16136    0.12748  -1.266  0.20561
## I(sc.log1p.Pref^2)                0.60114    0.29750   2.021  0.04332 *
## sc.Diam:sc.log.Clutch            -0.24864    0.14046  -1.770  0.07669 .
## sc.Diam:sc.log1p.Pref            -0.25261    0.15951  -1.584  0.11326
## sc.log.Clutch:sc.log1p.Pref       0.12585    0.15240   0.826  0.40892
## FoodwebSimple:sc.log.Clutch      -0.72888    0.29353  -2.483  0.01302 *
## FoodwebSimple:I(sc.log1p.Pref^2) -0.59758    0.34290  -1.743  0.08138 .
```

```
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

##
## Correlation matrix not shown by default, as p = 13 > 12.
## Use print(x, correlation=TRUE)  or
##     vcov(x)        if you need it
```

```
## METHOD OF JANZEN AND STERN 1998 ----

# Estimate mean fitness and mean "brackets" for each food-web treatment (see Janzen and Ste
complex_predict <- predict(foodweb_glmer, newdata=filter(gall_selection.df, Foodweb=="Comple
complex_mean_brackets <- mean(complex_predict * (1 - complex_predict))
complex_mean_fitness <- mean(complex_predict)

simple_predict <- predict(foodweb_glmer, newdata=filter(gall_selection.df, Foodweb=="Simple'
simple_mean_brackets <- mean(simple_predict * (1 - simple_predict))
simple_mean_fitness <- mean(simple_predict)

# Double-check that using the Beta-only model doesn't influence estimes of mean "brackets" a
alt_predict <- predict(betas_glmer, newdata=filter(gall_selection.df, Foodweb=="Complex"), t
alt_mean_brackets <- mean(alt_predict * (1 - alt_predict))
alt_mean_fitness <- mean(alt_predict)
test_mean_brackets <- complex_mean_brackets
test_mean_fitness <- complex_mean_fitness
test_mean_brackets - alt_mean_brackets # virtually the same
```

```
## [1] 8.652519e-05
```

```
test_mean_fitness - alt_mean_fitness # virtually the same
```

```
## [1] 0.0001767182
```

```
# Tidy data for beta terms
foodweb_tidy_betas <- tidy(betas_glmer, conf.int=T) %>%
  filter(term %in% c("(Intercept)","FoodwebSimple","sc.Diam","sc.log.Clutch","sc.log1p.Pref'
                     "FoodwebSimple:sc.Diam","FoodwebSimple:sc.log.Clutch","FoodwebSimple:sc
  mutate(Foodweb = c("Complex","Simple",rep("Complex",3),rep("Simple",3)),
         Selection_form = c(NA,NA,rep("Directional",6)),
         Multiplier = rep(1,8))
```

```
## Warning in bind_rows_(x, .id): binding factor and character vector,
## coercing into character vector

## Warning in bind_rows_(x, .id): binding character and factor vector,
## coercing into character vector
```

```r
# Tidy data for gamma terms. Note that we multiply quadratic (nonlinear) selection coefficie
foodweb_tidy_gammas <- tidy(foodweb_glmer, conf.int=T) %>%
  filter(term %in% c("I(sc.Diam^2)","I(sc.log.Clutch^2)","I(sc.log1p.Pref^2)",
                     "sc.Diam:sc.log.Clutch","sc.Diam:sc.log1p.Pref","sc.log.Clutch:sc.log1p
                     "FoodwebSimple:I(sc.Diam^2)","FoodwebSimple:I(sc.log.Clutch^2)","Foodwe
                     "FoodwebSimple:sc.Diam:sc.log.Clutch","FoodwebSimple:sc.Diam:sc.log1p.P
  mutate(Foodweb = c(rep("Complex",6),rep("Simple",6)),
         Selection_form = c(rep("Nonlinear",3),rep("Correlational",3),rep("Nonlinear",3),rep
         Multiplier = c(rep(2,3),rep(1,3),rep(2,3),rep(1,3)))
```

```
## Warning in bind_rows_(x, .id): binding factor and character vector,
## coercing into character vector
```

```
## Warning in bind_rows_(x, .id): binding character and factor vector,
## coercing into character vector
```

```r
# Combine and tidy the regression (alpha) coefficients
get_alphas <- bind_rows(foodweb_tidy_betas, foodweb_tidy_gammas) %>%
  mutate(alpha = estimate, alpha_2.5 = conf.low, alpha_97.5 = conf.high, P = p.value) %>%
  select(term, Foodweb, alpha, alpha_2.5, alpha_97.5, P, Selection_form, Multiplier)

complex_alphas <- filter(get_alphas, Foodweb == "Complex"); complex_alphas
```

```
## # A tibble: 10 x 8
##    term  Foodweb   alpha alpha_2.5 alpha_97.5        P Selection_form
##    <chr> <chr>     <dbl>     <dbl>      <dbl>    <dbl> <chr>
##  1 (Int~ Complex -0.262    -0.859     0.334   3.89e- 1 <NA>
##  2 sc.D~ Complex  1.53      1.12      1.94    2.64e-13 Directional
##  3 sc.l~ Complex  0.206    -0.171     0.582   2.85e- 1 Directional
##  4 sc.l~ Complex -0.671    -1.33     -0.0137  4.54e- 2 Directional
##  5 I(sc~ Complex  0.214    -0.0745    0.502   1.46e- 1 Nonlinear
##  6 I(sc~ Complex -0.0740   -0.420     0.272   6.75e- 1 Nonlinear
##  7 I(sc~ Complex  0.701     0.0930    1.31    2.38e- 2 Nonlinear
##  8 sc.D~ Complex -0.153    -0.531     0.225   4.27e- 1 Correlational
##  9 sc.D~ Complex -0.530    -1.06      0.00314 5.14e- 2 Correlational
## 10 sc.l~ Complex  0.169    -0.375     0.714   5.42e- 1 Correlational
## # ... with 1 more variable: Multiplier <dbl>
```

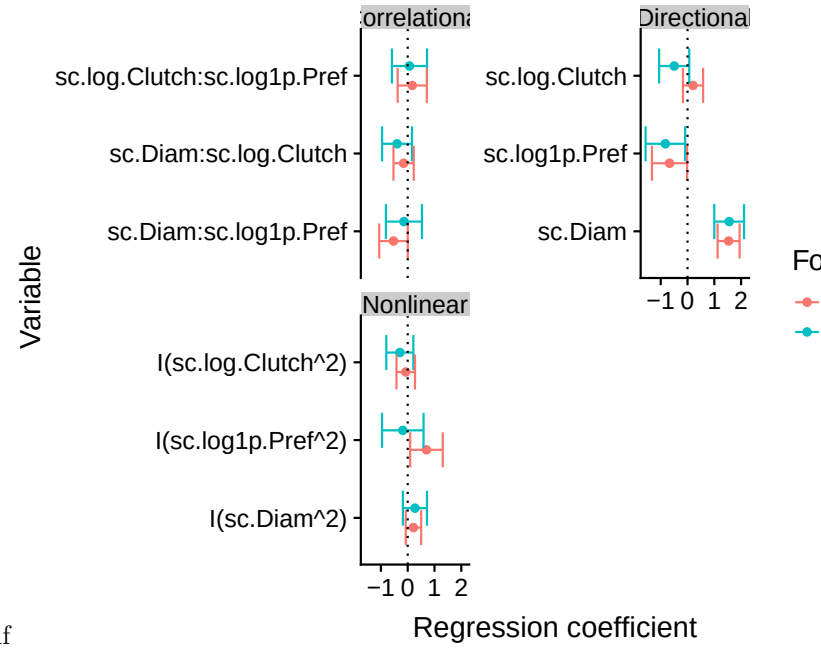
```r
simple_alphas <- filter(get_alphas, Foodweb == "Simple"); simple_alphas
```

```
## # A tibble: 10 x 8
##    term  Foodweb   alpha alpha_2.5 alpha_97.5       P Selection_form
##    <chr> <chr>     <dbl>     <dbl>      <dbl>   <dbl> <chr>
##  1 Food~ Simple   1.07       0.371      1.77  0.00268 <NA>
##  2 Food~ Simple   0.0218    -0.534      0.578 0.939   Directional
```

```
##  3 Food~ Simple  -0.703     -1.27      -0.140 0.0144  Directional
##  4 Food~ Simple  -0.156     -0.895      0.582 0.678   Directional
##  5 Food~ Simple   0.0560    -0.393      0.505 0.807   Nonlinear
##  6 Food~ Simple  -0.220     -0.724      0.285 0.394   Nonlinear
##  7 Food~ Simple  -0.884     -1.66      -0.110 0.0251  Nonlinear
##  8 Food~ Simple  -0.244     -0.802      0.314 0.392   Correlational
##  9 Food~ Simple   0.390     -0.283      1.06  0.256   Correlational
## 10 Food~ Simple  -0.104     -0.760      0.552 0.756   Correlational
## # ... with 1 more variable: Multiplier <dbl>
```

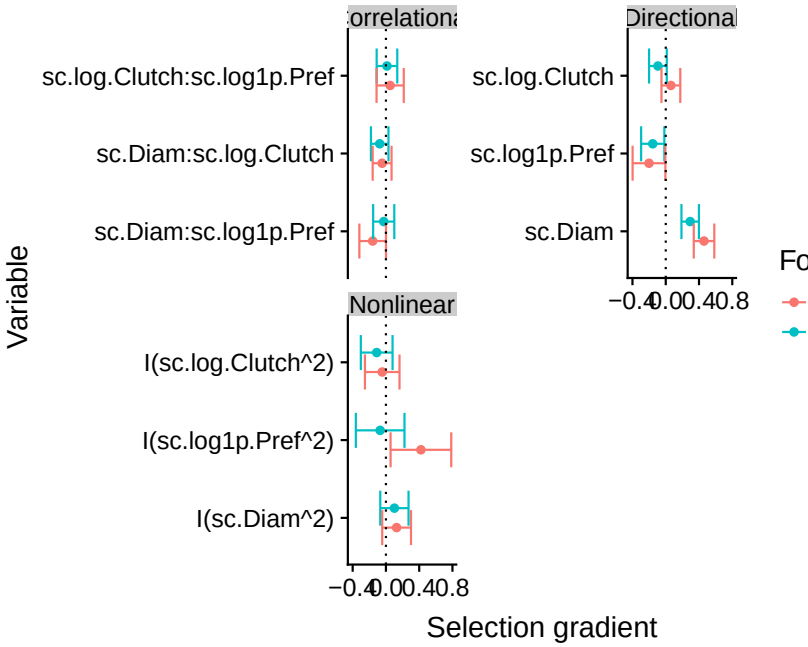
```
coefs_gradients <- data.frame(Variable = complex_alphas$term,
           a_complex = complex_alphas$alpha,
           a_complex_2.5 = complex_alphas$alpha_2.5,
           a_complex_97.5 = complex_alphas$alpha_97.5,
           a_simple = complex_alphas$alpha + simple_alphas$alpha,        # the baseline is
           a_simple_2.5 = complex_alphas$alpha + simple_alphas$alpha_2.5, # same addition pr
           a_simple_97.5 = complex_alphas$alpha + simple_alphas$alpha_97.5,
           Selection_form = complex_alphas$Selection_form,                # doesn't matter
           Multiplier = complex_alphas$Multiplier) %>%
  mutate(b_complex = complex_mean_brackets * a_complex / complex_mean_fitness * Multiplier,
         b_complex_2.5 = complex_mean_brackets * a_complex_2.5 / complex_mean_fitness * Mult
         b_complex_97.5 = complex_mean_brackets * a_complex_97.5 / complex_mean_fitness * Mu
         b_simple = simple_mean_brackets * a_simple / simple_mean_fitness * Multiplier,
         b_simple_2.5 = simple_mean_brackets * a_simple_2.5 / simple_mean_fitness * Multipli
         b_simple_97.5 = simple_mean_brackets * a_simple_97.5 / simple_mean_fitness * Multip


bind_rows(mutate(select(coefs_gradients, Variable, a=a_complex, a_2.5=a_complex_2.5, a_97.5=
          mutate(select(coefs_gradients, Variable, a=a_simple, a_2.5=a_simple_2.5, a_97.5=a_
  filter(Variable != "(Intercept)") %>%
  ggplot(., aes(x = Variable, fill=Foodweb, color=Foodweb)) +
  geom_point(aes(y=a), position = position_dodge(width=0.5)) +
  geom_errorbar(aes(ymax = a_97.5, ymin = a_2.5), position = position_dodge(width=0.5)) +
  coord_flip() +
  geom_hline(yintercept=0, linetype="dotted") +
  facet_wrap(~Selection_form, nrow=2, scales = "free_y") +
  ylab("Regression coefficient")
```



Selection Gradients for GLMER-1.pdf

```
## Modify to be directional, nonlinear, then correlational with legend in 4th area.
## Modify so that axes have gamma and beta with the trait as a subscript
bind_rows(mutate(select(coefs_gradients, Variable, b=b_complex, b_2.5=b_complex_2.5, b_97.5=
          mutate(select(coefs_gradients, Variable, b=b_simple, b_2.5=b_simple_2.5, b_97.5=b_
  filter(Variable != "(Intercept)") %>%
  ggplot(., aes(x = Variable, fill=Foodweb, color=Foodweb)) +
  geom_point(aes(y=b), position = position_dodge(width=0.5)) +
  geom_errorbar(aes(ymax = b_97.5, ymin = b_2.5), position = position_dodge(width=0.5)) +
  coord_flip() +
  geom_hline(yintercept=0, linetype="dotted") +
  facet_wrap(~Selection_form, nrow=2, scales = "free_y") +
  ylab("Selection gradient")
```



Selection Gradients for GLMER-2.pdf

What's the rationale for this test? First, we focus on galls where there is evidence of both survival and parasitism within the gall. The idea is that galls from the same clutch should be similar in size, therefore, any selection on diameter would be apparent. If we assume that this is all due to the effect of parasitism on larval development, truncating gall diameter, then we can consider this new selection gradient to be the result of confounding factors. Note that this is likely overestimates the effect of the confounding factor, since we are assuming that any heterogeneity in gall size (for this dataset) is due to a confounding effect of parasitism on gall diameter. Then, we can just subtract this value from the observed covariance between gall diameter and larval survival to adjust for the confounding effects of parasitism. This analysis should be relegated to the supplement.

Would we expect any confounding effects on nonlinear selection?

Appears to be selection for Platygaster to attack larva at high densities in more complex food webs (and a decrease in the variance). This may be a result of the poorer searching ability of parasitoids at very high gall densities, potentially due to saturation. This suggests that the fitness landscape may be dynamic because these selective effects (assuming there is heritable variation in the egg parasitoid) will change the following year. This could be an important discussion point to take into account for future work. This is different from simply altering the strength of selection, which will occur as species move along the fitness landscape, but this result suggests that the nature of the fitness landscape may actually be changing. For example, larval parasitoids could be driving selection on Platygaster to be very efficient at foraging, which will dampen once this pressure is removed, and then could also dampen the selection acting on the

	Food web (Estimate [95% CI])	
Coefficient	**Complex**	**Simple**
$Diam$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Clutch$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Pref$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Diam^2$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Clutch^2$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Pref^2$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Diam : Clutch$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Diam : Pref$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$Clutch : Pref$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]

	Food web (Estimate [95% CI])	
Selection gradient	**Complex**	**Simple**
β_{Diam}	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
β_{Clutch}	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
β_{Pref}	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$\gamma_{Diam,Diam}$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$\gamma_{Clutch,Clutch}$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$\gamma_{Pref,Pref}$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$\gamma_{Diam,Clutch}$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$\gamma_{Diam,Pref}$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]
$\gamma_{Clutch,Pref}$	‘r ‘ [‘r ‘-‘r ‘]	‘r ‘ [‘r ‘-‘r ‘]

galling herbivore.

Table for Alpha regression coefficients

Table for Iteomyia selection gradients

Table for bias

Table for Platygaster selection

Note that equation 3 in Phillips and Arnold 1998 is good justification for why quadratic selection cofficients should be multiplied by two (but not correlational ones?)

The G-matrix is essentially a scalar. For my data, since there is no correlational selection, it doesn't matter if there is genetic covariance between the

Type	**Bias s_{Diam}**
Complex (All)	‘r ‘ [‘r ‘-‘r ‘]
Complex (Larval guild)	‘r ‘ [‘r ‘-‘r ‘]
Simple (*Platygaster*)	‘r ‘ [‘r ‘-‘r ‘]

Selection differential	Estimate [95% CI]
s_{Diam}	‘r ‘ [‘r ‘-‘r ‘]
s_{Clutch}	‘r ‘ [‘r ‘-‘r ‘]
s_{Pref}	‘r ‘ [‘r ‘-‘r ‘]
$s_{Diam,Diam}$	‘r ‘ [‘r ‘-‘r ‘]
$s_{Clutch,Clutch}$	‘r ‘ [‘r ‘-‘r ‘]
$s_{Pref,Pref}$	‘r ‘ [‘r ‘-‘r ‘]

traits, as this will not effect the change in genetic covariances within a generation (because there is no selection). Also, the G_matrix does not qualitatively alter the conclusions that there will be a decrease in additive genetic variance in gall diameter due to the strong directional selection; however, there will be an increase in the additive genetic variance in female preference. Since this is an experiment, we can assume that the G-matrix is the same between treatments

Remember that the diagonals refer to additive genetic CO-variances. Thus, positive or negative values for delta_G give insight to whether selection will act to integrate traits (positive covariance) or create trade-offs (negative covariance).

Assuming that there is positive additive genetic variance and co-variance in these traits (i.e. all values of G-matrix are positive), then the curvature of the fitness landscape can give insight to qualitative changes in the G matrix. This is because the G-matrix acts as a scalar of changes in the fitness landscape.

Compared to the GLM, the GLMM gives the same inferences about the effect of food-web treatment. The main difference was that there was stronger evidence of correlational selection, but no evidence that this correlational selection varied among food-web treatments. Still, this stronger evidence for correlational selection should be interpreted with caution since the GLM does not account for the non-indepedence of these fitness estimates.

Results

We found that changes in food-web complexity altered the shape of *Iteomyia*'s fitness landscape ().

For example, there was directional selection for larger gall diameter in both complex and simple food webs, but the magnitude of the selection gradient was X-fold higher in the complex food web. The steeper selection gradient in the complex food web was not a result of stronger covariance between gall diameter and larval survival, but a result of average larval survival being X-fold lower in the complex food web.

We observed directional selection for smaller clutch sizes in the simple food web, but no evidence of selection on this trait in the complex food web. The absence of selection in the complex food web appeared to be a result of conflicting selection pressures imposed by the egg parasitoid *Platygaster* and the guild of larval parasitoids (statistical test focus on egg vs. larval parasitoids). Specifically, larval parasitoids actually impose directional selection for larger clutch sizes

(selection gradient), but the net effect is no selection when both parasitoid guilds are present.

We found evidence of disruptive selection acting on female preference in the complex food web, but no evidence of nonlinear selection on this trait in the simple food web. Similar to clutch size, these differences in nonlinear selection appeared to be due to different selection pressures imposed by egg and larval parasitoids.

Characterizing the slope and curvature of the fitness landscape Old

Discussion

Our key finding was that the adaptive landscape was less constrained in the complex vs. simple food web. These fewer constraints arise from conflicting selection pressures imposed by different parasitoid guilds, resulting in fewer traits under selection in the complex food web. At the same time, we observed an overall greater intensity of selection in the complex food web, suggesting that trait evolution can be faster in complex vs. simple food webs. Our observation that natural selection was more constrained and less intense in simple vs. complex food webs suggests that the loss of biodiversity could constrain the adaptive potential of interacting species by reducing genetic and phenotypic variation in multiple traits.

Current theory suggests that when the number of selective constrains is less than the number of genetic constraints (i.e. some genetically variable traits are selective neutral), there are multiple positions on the landscape that confer equal fitness (Lande 1981; Lande and Arnold 1985). In this scenario, trait differences between populations may simply be due to neutral processes (e.g. genetic drift and mutation) moving trait values of the population. For our system, we currently lack quantitative estimates of genetic variation in our traits, although work with other species of galling insects has shown that gall diameter (Abramhson, Heath's work), clutch size (look to Weiss' work), and oviposition preference (Abrahmson's work?) are genetically variable. We encourage others to examine how changes in community context will alter selection on multiple traits.

One interesting result of our work was that the overall intensity of selection appeared to be larger in complex food webs. This result was driven by the large selection gradient acting on gall diameter in complex vs. simple food webs. This difference in selection intensity is likely not driven by a difference in the ecological relationship between gall diameter and parasitoid attack (i.e. slope), but actually a result of the lower mean fitness of *Iteomyia* in the complex food web. This lower mean fitness is not surprising —we excluded an entire guild of parasitoids from attacking the insect. But this more intense selection pressure may simply represent a transient dynamic. This is because we would expect the egg-parasitoid *Platygaster* to increase in abundance over time once its intraguild predator has been removed. While our results suggest that this wouldn't affect the slope of the relationship, the higher abundance of the egg parasitoid would

likely reduce the mean fitness of *Iteomyia*, thus increasing the selection gradient acting on gall diameter closer to what we observed in the complex food web. We don't expect it to fully compensate, given that the larval parasitoids exhibit a different functional relationship with gall traits, and thus we expect a more diverse community of primary parasitoids to generally impose greater parasitism pressure, a factor that appears to be a general trend in parasitoid community (Hawkins citation) and likely for other consumers (Ives and Cardinale Ecology Letters).

Our study focused on quantifying the direct effects of changes in network complexity on the fitness landscape; however, changes in network complexity may have pervasive indirect effects via coevolution or by initiating evolutionary cascades. In our system, we observed that excluding the guild of larval parasitoids altered selection on both the basal resource (*Iteomyia*) and the intraguild prey (*Platygaster*). GIVE DETAILS AND SUGGEST A POTENTIAL EVOLUTIONARY CASCADE.

Our study manipulated food-web complexity and examined changes in the fitness landscape of species embedded within this network. However, other studies have also examined, at least theoretically, how changes in the diversity of competitive communities affects evolution. These studies have generally suggested that the diversity of competitors may actually constrain the adaptive landscape, a finding that stands in contrast to our results. NEED TO REVIEW THESE PAPERS TO SEE HOW ITS DIFFERENT.

We suggest that by explicitly focusing on network structure, we can predict how changes in biodiversity will affect the adaptive potential of constituent species. A network allows a powerful representation of the 'community context', lending predictive power to how changes in network structure (either due to loss of species or links), will alter natural selection and consequently evolutionary change. Our results also suggest that losing biodiversity may not just have consequences at the community level, but also population-level consequences that may actually constrain adaptation to changing environments. This argues that changes in network complexity may not only affect the robustness of communities, but also that of constituent populations to future environmental change.

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