

Food-web complexity alters the fitness landscape of an insect herbivore

Matthew A. Barbour^{*,a,b}, Christopher J. Greyson-Gaito^{a,c}, Arezoo Sootodeh^a, Brendan Locke^d, Jordi Bascompte^b

^a*University of British Columbia, Department of Zoology, 6270 University Blvd., Vancouver, BC, V6T 1Z4, Canada*

^b*University of Zurich, Department of Evolutionary Biology and Environmental Studies, Winterthurerstrasse 190, Zurich, 8057, Switzerland*

^c*University of Guelph, Department of Integrative Biology, 50 Stone Rd. East, Guelph, ONT, N1G 2W1, Canada*

^d*Humboldt State University, Department of Biological Sciences, 1 Harpst St., Arcata, CA, 95521, USA*

Abstract

Studies of natural selection and fitness landscapes usually treat the network of interacting species as a “black box”. Given that the loss of biodiversity is simplifying the structure of ecological networks, there is a pressing need to answer the question: how does network complexity affect natural selection and the fitness landscape of associated species? To answer this question, we conducted a field experiment that manipulated the complexity of a food web associated with a galling insect herbivore. To maintain complex food webs, we allowed the entire community of natural enemies to attack insect galls on 64 plants in a common garden setting. To create simple food webs, we excluded a guild of three larval parasitoids by bagging galls on 64 different plants; therefore, mortality in this treatment was primarily due to a single egg parasitoid that attacks prior to gall formation. We then measured herbivore survival as a function of three key gall traits in each treatment. We found that more traits were under selection in the simple vs. complex food web. This occurred because different parasitoid species impose different selection pressures on gall traits, thereby minimizing relative fitness differences among insect galls with different phenotypes. Our work suggests that more complex food webs allow phenotypic variation to persist, which could facilitate subsequent adaptive evolution to environmental change.

Introduction

Biological diversity – from genes, to phenotypes, to species – has and continues to be shaped by the interplay between ecological and evolutionary processes. Much of this biological diversity has been molded by natural selection arising from species interactions, such as resource competition (Schluter (2000)), mutualisms (Jordano (1987)), and predation (Abrams (2000)). While there is clear evidence that pairwise interactions can drive evolution, we also know that most species interact with multiple species in an ecological community. Understanding how evolutionary dynamics unfold in a community context is challenging and eminently theoretical (McPeck (2017), Mazancourt, Johnson, and Barraclough (2008), Guimarães et al. (2017), Nuismer, Jordano, and Bascompte (2013)). Given the rapid loss of species diversity we are experiencing throughout the world (cite), we are in urgent need of work that makes and tests predictions for how the loss of species will affect the evolutionary process in natural communities.

Predicting the evolutionary consequences of species loss first requires an understanding of the concomitant change in the species-interaction networks. Knowing the interaction network is crucial because the loss of biodiversity, in and of itself, will not alter evolution – it is the associated loss of ecological interactions that will affect evolutionary change (Janzen (1974)). For a network of directly connected species, we would expect that the loss of species to result in a loss of network complexity. Network complexity is a property that describes the diversity of interactions in an ecological community (Banasek-Richter et al. (2009)). Thus, all else equal, species loss will decrease the diversity of interactions, resulting in a more simple network.

*Corresponding Author

Email address: matthew.barbour@ieu.uzh.ch (Matthew A. Barbour)

Predicting how a change in network complexity will alter evolution also requires an understanding of the relationship between network structure and the adaptive landscape. The adaptive landscape (i.e. fitness landscape or selective surface) describes the relationship between the average trait value of a population and its average fitness (cite Arnold). For a trophic network, such as a food web, changes in network complexity can shape the adaptive landscape of constituent species in at least two ways. First, if a more diverse community of consumers is more efficient 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)) and thus could speed up the rate of evolutionary change. On the other hand, if consumers are functionally distinct, then more diverse communities can dampen the strength of selection. This is because each consumer has a different functional relationship with resource traits. In addition, there is a reduced probability in interacting with a specific consumer species in a more diverse community. Thus, a more diverse consumer community may impose more diffuse selection across the adaptive landscape.

Here, we provide a quantitative test of how the loss of species diversity – and concomitant loss of network complexity – shapes the adaptive landscape of a constituent species in a natural community. We conducted a field experiment that manipulated the diversity of insect parasitoids that were able to impose selection on the insect herbivore, *Iteomyia salicisverruca*. The larva of this herbivore species induces tooth-shaped galls when they feed on the developing leaves of willow trees (*Salix* sp., Russo (2006)). Prior work with this study system has shown that there is directional selection for larger galls, likely because larger galls provide a refuge from parasitoid attack (Barbour et al. (2016)). However, there is also evidence that each parasitoid species imposes differential selection on gall traits (Barbour et al. (2016)). Taken together, our aim is to provide evidence for how the simplification of natural communities affects the adaptive potential of constituent species.

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, 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.

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. The measurement of larval densities on plants in the field is a commonly used index for measuring oviposition preference (Gripenberg et al. (2010)), although caution must be taken in inferring ‘preference’ (Singer (1986)). This is because larval densities can be influenced by processes other than preference. For example, if an ovipositing female is not exposed to the full spectrum of plant types (in this case genotypes), then it is difficult to infer whether patterns of larval densities are actually due to preference. Also, observed larval densities could be influenced by egg predation.

While we recognize these limitations, a couple of aspects of our study system likely alleviate these limitations. 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. Although we cannot control for egg predation, this source of mortality appears to play comparatively minor role in determining the mortality of galling insects (Hawkins, Cornell, and Hochberg (1997)). To quantify female preference (gall density), we randomly sampled five branches per tree and summed the number of individual gall chambers observed. We 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.

Statistical Analyses

To characterize the shape of the fitness landscape in simple and complex food webs, we fit separate statistical models to quantify individual selection surfaces acting on each trait. We used generalized linear mixed models (GLMMs, Bolker et al. (2009)) with larval survival (0 or 1) as our response variable and measure of fitness. In our full model, 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 other independent effects of willow genotype on larval survival, we specified gall ID nested within plant ID nested within plant genotype as random intercepts in our statistical models. 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. We then used the method of Frederic J Janzen and Hal S Stearn (1998) to calculate directional (β_{z_i}), quadratic (γ_{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. To test whether selection gradients differed between treatments, we used our bootstrapped estimates to calculate the probability that selection gradients in the simple food web were larger/smaller than in the complex food web (i.e. the p-value). Together, we had survival estimates for 1,306 larva, 607 galls, 111 plants, and 8 plant genotypes. We report estimated selection gradients and the 95% confidence intervals in parentheses. All analyses and visualizations were conducted in R (R Core Team (2018)).

```
## Summarize Control Selection Gradients ----
summary_beta_control <- data.frame(
  Phenotype = c("Gall diameter", "Clutch size", "Female preference"),
  Food_Web = "Complex",
  Model = "GLMM",
  Type = "Beta",
  Estimate = round(Beta_avg_grad(beta_control), 3),
```

```

lower_2.5 = round(apply(boot_beta_control$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.025))
upper_97.5 = round(apply(boot_beta_control$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.975))

# doubled quadratic estimates to make comparable to directional selection gradients (Stinchcombe et al. 2008)
summary_quad_control <- data.frame(
  Phenotype = c("Gall diameter", "Clutch size", "Female preference"),
  Food_Web = "Complex",
  Model = "GLMM",
  Type = "Quadratic",
  Estimate = 2*round(Beta_avg_grad(quad_control),3)[-c(1:3)],
  lower_2.5 = 2*round(apply(boot_quad_control$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.025))
  upper_97.5 = 2*round(apply(boot_quad_control$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.975))

summary_corr_control <- data.frame(
  Phenotype = c("Diam,Clutch", "Diam,Pref", "Clutch,Pref"),
  Food_Web = "Complex",
  Model = "GLMM",
  Type = "Correlational",
  Estimate = round(Beta_avg_grad(corr_control),3)[-c(1:6)],
  lower_2.5 = round(apply(boot_corr_control$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.025))
  upper_97.5 = round(apply(boot_corr_control$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.975))

## Summarize Treatment Selection Gradients ----
summary_beta_treatment <- data.frame(
  Phenotype = c("Gall diameter", "Clutch size", "Female preference"),
  Food_Web = "Simple",
  Model = "GLMM",
  Type = "Beta",
  Estimate = round(Beta_avg_grad(beta_treatment),3),
  lower_2.5 = round(apply(boot_beta_treatment$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.025))
  upper_97.5 = round(apply(boot_beta_treatment$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.975))

# doubled quadratic estimates to make comparable to directional selection gradients (Stinchcombe et al. 2008)
summary_quad_treatment <- data.frame(
  Phenotype = c("Gall diameter", "Clutch size", "Female preference"),
  Food_Web = "Simple",
  Model = "GLMM",
  Type = "Quadratic",
  Estimate = 2*round(Beta_avg_grad(quad_treatment),3)[-c(1:3)],
  lower_2.5 = 2*round(apply(boot_quad_treatment$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.025))
  upper_97.5 = 2*round(apply(boot_quad_treatment$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.975))

summary_corr_treatment <- data.frame(
  Phenotype = c("Diam,Clutch", "Diam,Pref", "Clutch,Pref"),
  Food_Web = "Simple",
  Model = "GLMM",
  Type = "Correlational",
  Estimate = round(Beta_avg_grad(corr_treatment),3)[-c(1:6)],
  lower_2.5 = round(apply(boot_corr_treatment$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.025))
  upper_97.5 = round(apply(boot_corr_treatment$t, 2, FUN = function(bootstraps) quantile(bootstraps, 0.975))

bind_rows(summary_beta_control, summary_beta_treatment) %>% arrange(Phenotype)

```

```
## Warning in bind_rows(x, .id): Unequal factor levels: coercing to character
```

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

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

```
##           Phenotype Food_Web Model Type Estimate lower_2.5 upper_97.5  
## 1      Clutch size  Complex  GLMM Beta    0.043   -0.044    0.106  
## 2      Clutch size   Simple  GLMM Beta   -0.091   -0.243   -0.012  
## 3 Female preference Complex  GLMM Beta   -0.093   -0.246    0.051  
## 4 Female preference Simple  GLMM Beta   -0.232   -0.906   -0.362  
## 5      Gall diameter Complex  GLMM Beta    0.442    0.418    0.604  
## 6      Gall diameter Simple  GLMM Beta    0.328    0.191    0.319
```

```
bind_rows(summary_quad_control, summary_quad_treatment) %>% arrange(Phenotype)
```

```
## Warning in bind_rows(x, .id): Unequal factor levels: coercing to character
```

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

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

```
##           Phenotype Food_Web Model      Type Estimate lower_2.5 upper_97.5  
## 1      Clutch size  Complex  GLMM Quadratic  -0.056   -0.228    0.118  
## 2      Clutch size   Simple  GLMM Quadratic  -0.110   -0.440    0.094  
## 3 Female preference Complex  GLMM Quadratic    0.180    0.028    0.276  
## 4 Female preference Simple  GLMM Quadratic  -0.076   -0.548    0.266  
## 5      Gall diameter Complex  GLMM Quadratic    0.066   -0.070    0.188  
## 6      Gall diameter Simple  GLMM Quadratic    0.064   -0.122    0.232
```

```
bind_rows(summary_corr_control, summary_corr_treatment) %>% arrange(Phenotype)
```

```
## Warning in bind_rows(x, .id): Unequal factor levels: coercing to character
```

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

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

```
##           Phenotype Food_Web Model      Type Estimate lower_2.5 upper_97.5  
## 1 Clutch,Pref  Complex  GLMM Correlational    0.041   -0.054    0.142  
## 2 Clutch,Pref   Simple  GLMM Correlational    0.006   -0.110    0.119  
## 3 Diam,Clutch  Complex  GLMM Correlational  -0.044   -0.144    0.060  
## 4 Diam,Clutch   Simple  GLMM Correlational  -0.093   -0.278    0.009  
## 5  Diam,Pref  Complex  GLMM Correlational  -0.105   -0.245    0.008  
## 6  Diam,Pref   Simple  GLMM Correlational  -0.012   -0.114    0.114
```

Results

Two key patterns emerged from our analyses. First, fewer phenotypic traits were under selection in the complex vs. simple food web. In both complex and simple food webs, gall diameter was under strong directional selection, with larger galls resulting in higher larval survival (complex $\beta_{diam} = 0.442$ [0.418,0.604] ; simple $\beta_{diam} = 0.328$ [0.191,0.319])(Fig. 2A). In simple food webs, both clutch size and female preference experience directional selection, with smaller clutch sizes ($\beta_{clutch} = -0.091$ [-0.243,-0.012] and weaker preferences ($\beta_{pref} = -0.232$ [-0.906,-0.362]) resulting in higher larval survival (blue lines in Fig. 2B,C). In contrast, there was no evidence of selection on clutch size ($\beta_{clutch} = 0.043$ [-0.044,0.106]) or female preference ($\beta_{pref} = -0.093$ [-0.246,0.051]) in complex food webs (orange lines in Fig. 2B,C). The absence of selection on clutch size and female preference was likely a result of conflicting selection pressures imposed by each guild of parasitoids due to their different functional relationships with gall traits. Together, these different patterns of selection resulted in an ideal combination of traits having higher fitness in the simple food web (large diameter, smaller clutches, weaker preference), whereas there was a larger combination of trait values that had equal fitness in the complex food web (Fig. 3). We did not find any strong evidence for nonlinear or correlational selection gradients acting on gall traits in either food-web treatment. The second major pattern was that the overall intensity of selection was stronger in the complex vs. simple food web. This result appeared to be driven by selection on gall diameter in the complex food web, which was more than $1.3 \times$ larger than any other selection gradient in our analyses.

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 constraints 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 (Abrahamson’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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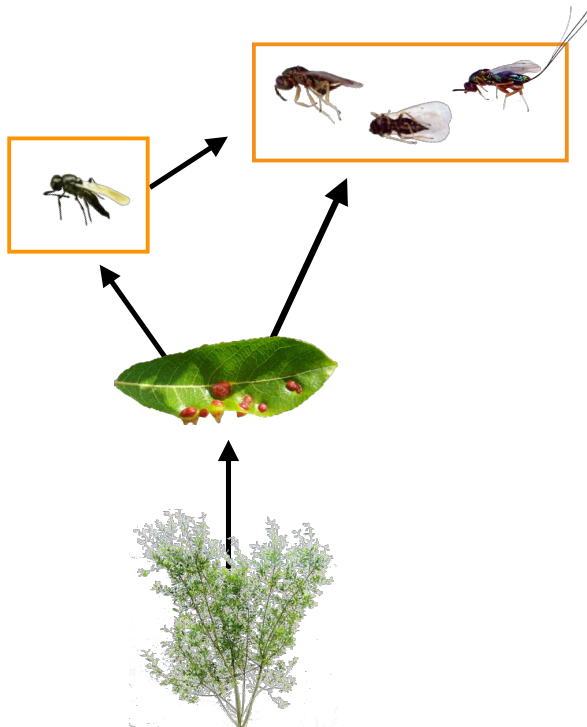
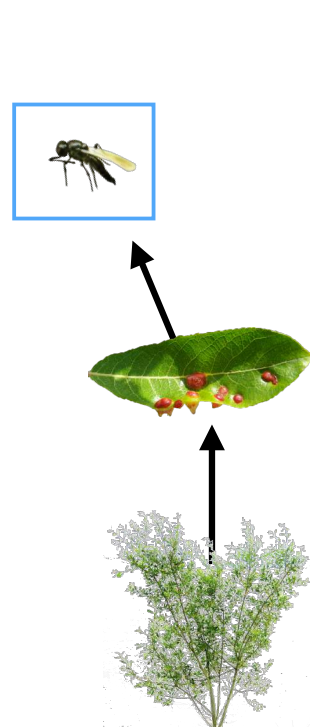
A**B**

Figure 1: Illustrations of complex (A) and simple (B) food webs associated with the insect herbivore, *Iteomyia salicisverruca*. Black arrows denote 'who-eats-whom' in this network of trophic interactions.

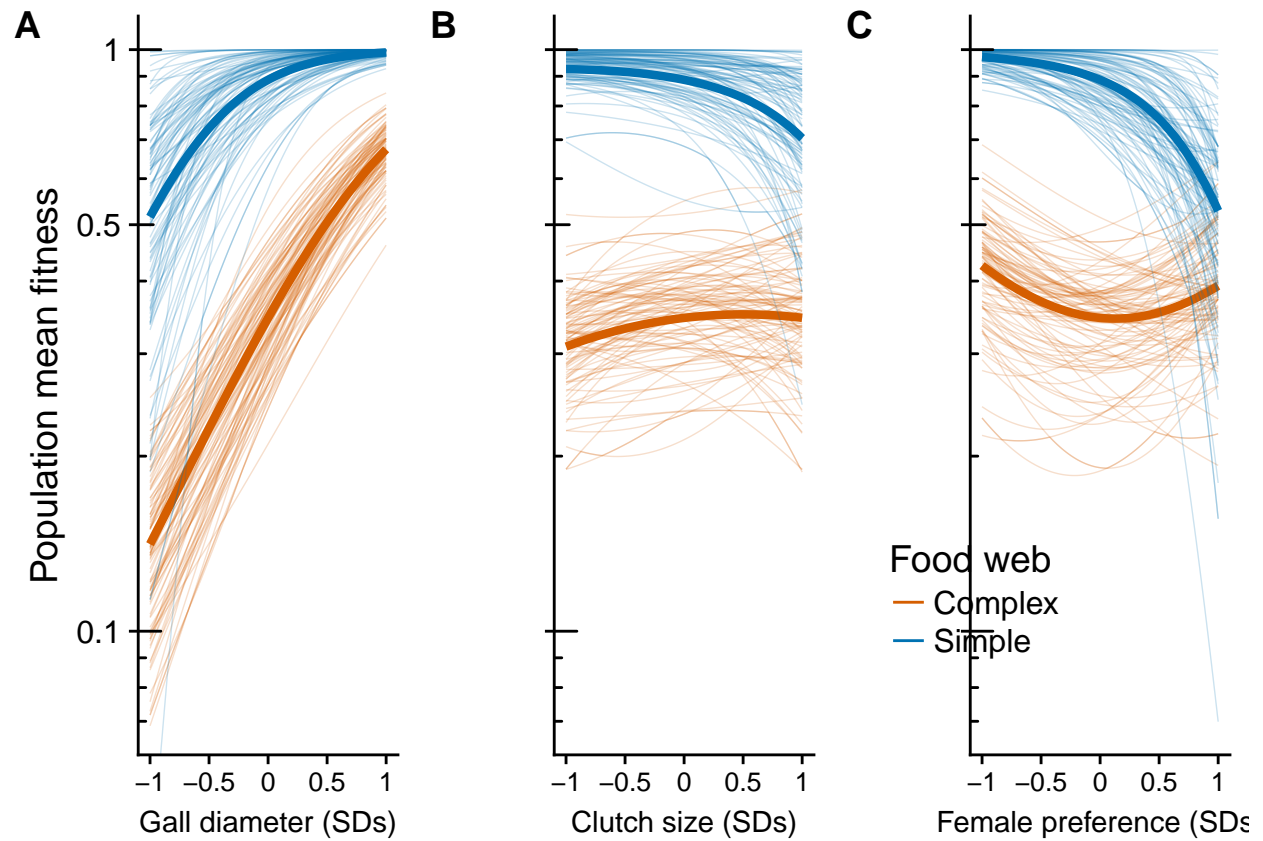


Figure 2: Selection gradients acting on gall traits in complex vs. simple food webs. Each panel corresponds to a different gall trait: gall diameter (A); clutch size (B); and female preference (C). Solid lines represent the estimated gradients in complex (orange) and simple (blue) food webs. Transparent lines represent bootstrapped replicates ($n=100$) to show the uncertainty in estimated gradients. Note that only 100 bootstraps are displayed here, but that inferences are based on 1,000 bootstrapped samples.

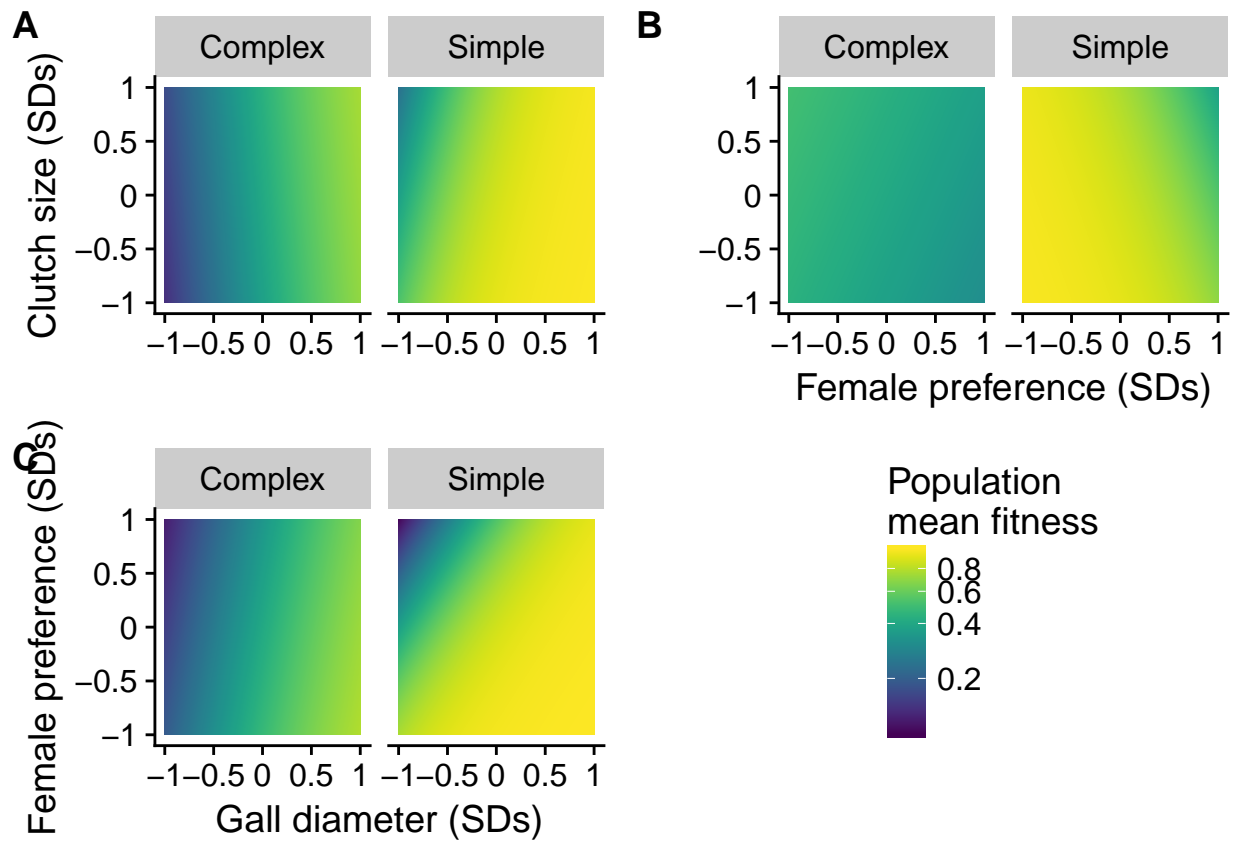


Figure 3: Fitness landscapes of gall traits in complex vs. simple food webs. Each panel corresponds to a different combination of traits: clutch size and gall diameter (A); clutch size and female preference (B); female preference and gall diameter (C). Note that traits for all plots range 1 SD below and above the mean ($=0$).