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

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Abstract

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Introduction

Biological diversity – from genes, to phenotypes, to species – has fascinated evolutionary biologists for decades.

Much of this biological diversity has been shaped by natural selection via trophic interactions, such as resource competition (cite charater displacement), mutualistic exchanges of resource (cite?), and predation (cite recent Heath and Stireman paper).

NEED to recognize that evolutionary biologists have begun to explore how community context affects evolutionary change (work by Sharon Strauss, Casey terHorst, Lutz Becks, etc.). These results have begun to show interesting patterns whereby the composition of species in a community can alter the direction and strength of natural selection imposed on species embedded within these communities (cite).

Put another way, these results have begun to show biological diversity, in terms of differences between species, can drive evolutionary change.

While there is clear evidence for pairwise trophic interactions to drive evolution by natural selection, its unclear how biological diversity itself imposes natural selection and drives evolutionary change.

Exploring the effects of biological diversity requires an explicit examination of the network structure of trophic interactions between species in a community. Theoretical models have begun to examine how the network structure of species interactions drives evolutionary change (Nuismer paper; Guimeras paper; Ecology Letters paper from a spanish guy. . .); however, we are currently lacking experimental tests.

In contrast, ecologists have begun to embrace the complexity of the natural world, and seeking to identify the complex networks of interactions that underlie community structure and ecosystem function. However, these studies have not examined how evolutionary processes feedback to shape the structure and evolution of these interaction networks.

Food-web complexity may influence selection gradients in at least two ways. First, if more diverse predator communities are more efficient as suppressing prey densities (e.g. biodiversity-ecosystem fucntion; Ives 2005 Ecology Letters), then this will result in lower mean fitness. A reduction in mean fitness, all else equal, will intensify natural selection and thus could increase the rate of evolutionary change. Alternatively, if predators are functionally distinct, more diverse communities can reduce the strength of selection. This is because each predator has a different functional relationship between prey phenotype and the probability of an interaction.

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Here, we conducted a field experiment to test the effect of food-web complexity on the fitness landscape of a species embedded within this food web. To do this, we used a common garden experiment with a host plant (*Salix hooeriana*), an abundant herbivore (*Iteomyia salicisverruca*), and the diverse community of insect parasitoids that attack it. Prior work in this system has shown that there is directional selection for larger galls, likely because larger galls provide more of a refuge from parasitoid attack. However, there is also evidence that different parasitoid species impose differential selection on gall phenotypes.

Materials & Methods

We conducted our study within a four-year old common garden of *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. Clonal replicates (stem cuttings) of each genotype 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)).

We setup our food-web manipulation soon after galls began developing on *S. hookeriana* in early June of 2013. We manipulated gall exposure to parasitoids across 128 plants from 8 different plant genotypes that span 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 organza bags (MANUFACTORER DETAILS) 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, 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. In late August, we collected marked and bagged galls from each plant. We placed galls 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.

We collected data on three different phenotypes for each larva that have been shown to be important in our work (Barbour et al. (2016)) and in other work with Cecidomyiid midges (Weis, Price, and Lynch (1983), Heath, Abbot, and Stireman (2018)). First, we measured 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 counted the number of chambers in each gall, which is indicative of the clutch size of adult female midges (Weis, Price, and Lynch (1983)). All larva collected from the same multi-chambered gall were scored with the same clutch size. Third, we estimated gall density as the number of chambers per 100 shoots per plant. We did this by summing the number of chambers across all galls found on five randomly sampled branches per tree. To account for potential differences in the number of shoots per branch for each plant genotype (CITE other willow work), we then counted the number of shoots on the fifth branch to estimate the number of larva per 100 shoots for each plant. All larva collected from the same plant were scored with the same gall density phenotype. This phenotype is indicative of the preference of female midges for particular plant traits (hereafter 'female preference'). The measurement of insect densities on a plant 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 oviposition is a complex process and the number of individuals observed on plants in the field can be influenced by processes other than preference. While we recognize this, since our data comes from a randomized placement of genotypes and that we can still detect the presence of an individual even if it dies before development (empty chamber lacking an exit hole and without any evidence of larva or parasitoid). We cannot control for egg predation, although this likely plays a comparatively minor role in determining gall survival (Hawkins, Cornell, and Hochberg (1997)).

To identify the appropriate level of model complexity for testing the effects of food-web complexity on the fitness landscapes, we compared models using Aikaike Information Criteria. The maximal complexity we explored was

a generalized additive mixed model that fit cubic splines to each trait as well as linear interactions between a maximum of two traits as well as an interaction with food-web treatment. We then examined simpler models where

This analysis enabled us to explore the appropriate complexity of the model to include for our analyses (i.e. include non-linear and correlational selection gradients and whether they varied with food-web treatment).

We used generalized additive mixed models (GAMMs, cite Bolker et al. 2008) to test the effects of food-web complexity on the shape of fitness landscape. Larva survival (0 or 1) was our response variable and measure of fitness. We specified our food-web treatment, each gall trait, and all possible statistical interactions, as fixed effects to fully explore the effects of food-web complexity on the fitness landscape. This analysis implicitly assumes that selection is linear, which we felt was a necessary trade-off for exploring the shape of the fitness landscape. We specified plant genotype, plant individual nested within genotype, and multi-chambered gall nested within plant individual, as random effects.

To quantify selection gradients, we fit separate statistical models to data from each food-web treatment. We used the method of Frederic J Janzen and Hal S Stearn (1998) to calculate selection gradients and used parametric bootstrapping to calculate their 95% confidence intervals (Bolker et al. (2009)).

To account for the correlated structure of our gall phenotypes (oviposition preference at plant-level; clutch size at gall-level; gall diameter at chamber-level), we specified gall ID nested within plant ID nested within plant genotype as random intercepts in our statistical models.

From these GAMMs, we estimate selection gradients by assuming the mean value of our random effects (i.e. setting them to zero). This was appropriate for our analysis, since we were interested in estimating the fitness landscape, which is function of population mean fitness and mean trait values.

Results

We found that more phenotypic traits were under selection in the simple vs. complex 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 = ; simple Beta =)(Fig. 2A). In complex food webs, there was no evidence of selection on clutch size ($\beta_{clutch} =$) or female preference ($\beta_{preference} =$)(orange lines in Fig. 2B,C). In simple food webs, however, clutch size and female preference were under strong directional selection, with smaller clutch sizes and weaker preferences resulting in higher larval survival (blue lines in Fig. 2B,C). These different selection pressures resulted in different adaptive landscapes in complex vs. simple food webs, with evidence for more rugged landscapes in the simple rather than the complex food web (Fig. 3). Depending on the trait combinations used to create the landscape, we found that the ruggedness of the adaptive landscape ranged from 10% higher (Fig. 3A) to 274% higher (Fig. 3C) in the simple vs. complex food web. Our model comparison suggested that it was unnecessary to test for the effects of non-linear or correlational selection gradients (ref. supp. mat.).

Discussion

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