**The genetic basis of food web structure: empirical evidence from a plant-insect food web**

Matthew A. Barbour1\*, Jordi Bascompte2, Joshua R. Nicholson1, Riitta Julkunen-Tiitto3, Erik S. Jules4, and Gregory M. Crutsinger1

1Department of Zoology, University of British Columbia, #4200-6270 University Blvd., Vancouver, B.C., V6T 1Z4, Canada

2Estación Biológica de Doñana, CSIC, C/ Américo Vespucio s/n, 41092 Sevilla. España

3Department of Biology, University of Eastern Finland, PO Box 111, FI-80101, Joensuu, Finland

4Department of Biological Sciences, Humboldt State University, 1 Harpst St., Arcata, California, 95521, USA

\*Author for correspondence, email: barbour@zoology.ubc.ca

**Abstract**

Predicting the eco-evolutionary dynamics of ecological networks requires understanding the mechanisms by which genetic variation scales to affect species interactions across multiple trophic levels. In this study, we used a common garden experiment to test predictions from network theory about the role of genetic variation in a dominant host plant in determining the composition and complexity of an insect food web. We observed extensive variability among host plant genotypes both in the abundance of galling by midges and the size of galls produced. Subsequently, variation in gall density and size predicted the composition of the gall-parasitoid food web for a given host plant clone. Overall, this predicts that plant genetic variation is a key determinant of food web complexity. Taken together, our results posit that there is a genetic basis to the organization of food webs. Furthermore, our results and that incorporating genetic variation will reveal how evolutionary processes can shape both the structure and dynamics of ecological networks.

**Introduction**

Food web ecologists seek to understand how the organization of trophic interactions affects the dynamics of ecological communities (Dunne 2006). In particular, network theory has provided both a conceptual and quantitative approach for mapping trophic interactions (links) between species (nodes) and making predictions for how the gain/loss of species affects food web structure and dynamics (Dunne et al. 2002; Stouffer & Bascompte 2012). Representing a food web at the species-level, however, makes the implicit assumption that each species consists of a homogenous population of individuals, all of which interact equally with individuals of different species. Yet, most populations are heterogenous mixtures of individuals that vary phenotypically and there is increasing evidence that this intraspecific variation is an important factor governing the assembly of ecological communities (Clark et al. 2010; Bolnick et al. 2011; Violle et al. 2012). Consequently, there is a clear need to account for the role of intraspecific variation in structuring food webs over space and time (Poisot et al. 2014).

Genetic variation is a key driver of intraspecific variation and many studies have now demonstrated direct and indirect genetic effects on species interactions (Bailey et al. 2006; Fritz 1995; Abdala-Roberts 2014) and the composition of communities across multiple trophic levels (Fritz 1988; Maddox and Root 1990; Harmon et al. 2009; Post et al. 2009)). Indeed, this empirical work has laid the foundation for understanding the eco-evolutionary dynamics of communities; however, there are two key components missing from these studies that are preventing us from scaling our understanding from pairwise trophic interactions to whole food webs. First, these studies do not quantify how genetic variation affects the composition of pairwise trophic links that determine food web structure. Instead, they quantify changes in either (1) the composition of species — thereby ignoring trophic links — or (2) simple tritrophic interactions — thereby ignoring the complex food web in which these interactions are embedded. As a result, the mechanisms by which genetic variation shapes trophic interactions, and in turn overall food web structure, remains unclear. Second, these studies do not examine the effect of genetic and phenotypic variation *per se* on trophic interactions*,* rather these studies focus on testing whether different genotypes are associated with particular communities (Whitham et al. 2012). While demonstrating this genetic basis is a critical first step, we have little empirical knowledge of how altering genetic and phenotypic variation will affect trophic interactions, and in turn the structure of whole food webs (Bolnick et al. 2011).

Despite a lack of empirical evidence, network theory has proposed a clear hypothesis for how genetic and phenotypic variation should affect the structure of food webs (Bolnick et al. 2011; Moya-Larano 2012). In particular, we expect that genetic variation will increase food web complexity, or the number of links per species (Figure 1). For example, many plant species exhibit genetic variation in resistance to multiple insect herbivores, in terms of both herbivore abundance and growth, resulting in different herbivore communities on each plant genotype (Whitham et al. 2012). If herbivore communities vary among plant genotypes, then more genetic variation within the plant population will result in a more complex plant-herbivore network (Crutsinger et al. 2006). Furthermore, if variation in herbivore abundance and growth determines a herbivore’s vulnerability to being attacked by particular parasitoids (Citation needed), we would expect that more genetic variation within the plant population would result in a more complex herbivore-parasitoid network. Consequently, genetic variation within a single plant species may directly and indirectly increase the complexity of the whole food web. Greater complexity may in turn affect food web dynamics, as more complex food webs are predicted to be more robust to species extinctions (MacArthur 1955, Dunne 2002).

Here, we test the hypothesis that genetic variation results in greater food web complexity (number of links per species) using a common plant species (Coastal willow, *Salix hookeriana*) and its associated insect gall-parasitoid food web (four species of gall midges, six species of parasitoids). We focused on this insect food web for three reasons. First, we have demonstrated in previous work that *S. hookeriana* displays genetic variation in resistance to its galling insect community (Barbour et al. 2015). Second, the unique biology of galling insects makes them amenable for building quantitative food webs. In particular, galls provide a refuge for larva from attack by most predators, thereby restricting their natural enemy community to a small number of species. In our system, all of the natural enemies are insect parasitoids that complete their development within the gall after parasitizing gall larva, making it easy to identify and quantify the source of larval mortality by dissecting galls or rearing out the parasitoids. Third, the biology of galls is also ideal for identifying the mechanisms mediating trophic interactions (Abrahamson and Weis 1992). In particular, gall size is a key trait that affects the ability of parasitoids to successfully oviposit through the gall wall and into the larva within the gall (i.e. larger galls provide a refuge from parasitism). And since the gall phenotype is determined, in part, by the genotype of the plant (Abrahamson & Weis 1997), we have a clear mechanism by which plant genetic variation can affect the strength of trophic interactions.

To examine how genetic variation affects food web structure, we quantified differences in the composition of gall-parasitoid food webs among 26 locally-collected genotypes of *Salix hookeriana* in a common garden experiment. We then tested the following three predictions. First, we predict that willow genotypes would vary in their resistance to different galling herbivores (i.e. gall abundance and size). Second, we predict that genetic variation in resistance to galls will determine the abundance and composition of gall-parasitoid links on each willow genotype. Third, we predict that differences in the composition of gall-parasitoid links among willow genotypes will result in greater food web complexity with increased genetic variation. Taken together, our study seeks to test theoretical predictions for the patterns and mechanisms by which genetic variation influences food web structure and dynamics. In doing so, our study takes a crucial step toward a more predictive understanding of the eco-evolutionary dynamics of ecological networks as a whole.

**Materials & Methods**

*Common Garden*

To isolate the effects of genetic variation within *Salix hookeriana* (hereafter ‘willow’) on the insect food web, we used a common garden experiment consisting of 26 different willow genotypes (13 males; 13 females), located at Humboldt Bay National Wildlife Refuge (HBNWR) (40°40'53"N, 124°12'4"W) near Loleta, California, USA. Willow genotypes were collected from a single population of willows growing around Humboldt Bay. This common garden was planted in February 2009 with 25 clonal replicates (i.e. stem cuttings) of each willow genotype 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 2-4 m in height. Further details on the genotyping and planting of the common garden are available in Barbour et al. (2015, in press).

*Plant trait measurements*

To identify the plant traits that determine resistance to galling insects, we first measured 40 different traits associated with variation in leaf quality (36 traits) and plant architecture (4 traits). Details on how these willow traits were sampled and quantified are given in Barbour et al. (2015, in press), but we summarize which traits were sampled here. Leaf quality traits included: phenolic chemistry (7 classes of compounds, 31 individual metabolites), trichome density, specific leaf area (SLA), water content, and percent Carbon and Nitrogen (converted to C:N). Plant architecture traits included: plant size, fractal dimension (index of architectural complexity), height, and foliage density. Each of these 40 traits exhibited significant broad-sense heritable variation among willow genotypes (mean leaf quality *H*2 = 0.72; mean architecture *H*2 = 0.27; range of *H*2 = 0.15 - 0.97; Barbour et al., 2015).

*Insect food web composition and gall size*

To quantify the abundance of galls and gall-parasitoid links associated with each willow genotype, we collected galls from about 5 randomly chosen replicates of each genotype in September 2012 (N = 145 trees, range = 4-9 trees per genotype). For each replicate willow, we collected all galls occurring on one randomly selected basal branch. To quantify the abundance of gall-parasitoid links, we placed collected galls into 30 mL plastic transport vials (loosely capped at the end), which we maintained at room temperature in the lab for four months. We then opened galls under a dissecting scope and determined whether the gall survived or was parasitized, and if parasitized, the identity of the parasitoid species. We omitted from analyses those galls for which we could not reliably determine the cause of mortality. We quantified gall abundance by counting the number of surviving and parasitized larva for each gall species on each branch. For gall size, we measured galls at their maximum diameter perpendicular to the direction of plant tissue growth, to the nearest 0.01 mm.

*Prediction 1: Genetic variation in resistance to galling insects*

To test this prediction, we first examined whether there were differences in gall abundance and gall size among willow genotypes. To do this, we used generalized linear models (GLMs) because they enabled us to flexibly model the error distributions of our data (O’Hara 2005). For gall abundances, we modelled multivariate GLMs (error distribution = negative binomial, link function = log) with willow genotype as the predictor variable and an abundance matrix of galls as the response variables. To describe differences in gall community composition among willow genotypes, we calculated Bray-Curtis dissimilarities between each genotype’s average gall community. For gall size, we analyzed separate GLMs (error distribution = gaussian, link function = identity) since we did not always find all gall species on every willow. We then calculated correlations (Pearson’s *r*) between gall density and gall size among willow individuals (phenotypic correlations) and genotypes (genetic correlations). To identify the plant traits that were associated with resistance to galls, we used the same types of GLMs for gall community composition and gall size except that our predictor variables was now a matrix of willow traits. We then used Aikaike information criteria (AIC) and likelihood ratio tests to identify which willow traits best predicted gall community composition and gall size. Further details of model analysis, model selection, and checking model assumptions are given in the supplementary material.

*Prediction 2: Insect food web composition is determined by variation in resistance to galling insects.*

To test this prediction, we first examined whether there were differences in insect food web composition among willow genotypes. To do this, we used the same analytical approach as we did to test for differences in gall community composition (i.e. multivariate GLMs: error distribution = negative binomial, link function = logit). This time though, we had a matrix of the abundance of unique gall-parasitoid links as the response variables. To describe differences in food web composition, we first partitioned differences into species turnover and switching components (Poisot et al. 2012). Differences due to species turnover arise from the gain/loss of species (i.e. either gall or parasitoid), whereas differences due to switching occur when species switch the partners with which they are interacting, despite having the same species composition (Figure in supplement). We then calculated differences in each composition component using Bray-Curtis dissimilarities between each genotype’s average food web.

*Prediction 3: Loss of willow genetic variation decreases food web complexity*

To test this prediction, we simulated the successive extinction of willow genotypes and estimated its impact on food web complexity. To do this we would randomly remove a genotype, calculate a quantitative index of linkage density (Bersier et al. 2002, Bersier 2009) for the food web, and then repeat this process until only one genotype was left. The quantitative index of linkage density is an appropriate measure of food web complexity in that it is less sensitive to variation in sample size (Bersier 2009). In addition, we calculated food web complexity for both the plant-gall and gall-parasitoid networks to partition the direct and indirect effects of genetic variation on food web complexity. We repeated this simulation 1000 times and for each simulation we ran a GLM (error distribution = gaussian, link function = identity) with the number of genotypes as the predictor variable and quantitative linkage density as the response variable. We then used a t-test to examine whether the average slope from our simulated extinctions was different than zero. We predicted that the average slope would be less than zero indicating, that the loss of genetic variation decreases food web complexity.

All R code for analyses are given in the supplementary info.

**RESULTS**

*Prediction 1: Genetic variation in resistance to galling insects*

In concordance with our prediction, we found that willow genotype was a major determinant of both gall community composition and gall size (𝛘225,119 = 202.4, *P* = 0.001; Fig. 2). In particular, the abundance of leaf (mean range = 0 - 10) and bud (mean range = 0 - 8) galls and to a lesser extent apical-stem galls (mean range = 0 - 1.4 galls) varied among willow genotypes (Fig. 2a,b; supplement figure, supplement table). These differences in abundance resulted in an average dissimilarity of 52% (SD = 19%) in gall community composition among willow genotypes. For gall size, we found that leaf galls varied 2-fold in diameter among willow genotypes (*F*23,57 = 2.1, *P* = 0.012, Fig. 2c), but none of the other gall species responded to willow genotype.

We found that variation in both the abundance and size of galls was partially explained by willow size, leaf C:N ratios, and leaf flavonoid chemistry (Table Supplement). In particular, the abundance of leaf and bud galls increased by 3- and 8-fold over the range of leaf C:N ratios, although these relationships were only marginally significant (leaf galls: 𝛘2 = 2.38, P = 0.067; bud galls: 𝛘2 = 2.46, P = 0.092). Bud gall abundance also decreased by 9% with every 10% increase in willow size (𝛘2 = 4.44, P = 0.045). The abundance of apical-stem galls increased 15-fold over the range in leaf flavonoid chemistry (𝛘2 = 11.52, P = 0.001), while the abundance of mid-stem galls decreased by 37% with every 10% increase in willow size, although this effect was only marginal (𝛘2 = 3.92, P = 0.053). The size of leaf galls though decreased by 21% and 23% over the range in salicylate/tannin and flavonoid chemistry, respectively (F2,59 = 8.27, P < 0.001).

*Prediction 2: Insect food web composition is determined by variation in resistance to galling insects.*

In concordance with our prediction, we found that willow genotype was a major determinant of insect food web composition (𝛘225,119 = 357.10, *P* = 0.001). In particular, parasitism from three parasitoids (*Platygaster* sp., *Mesopolobus* sp., and *Torymus* sp.) on leaf galls varied X, Y, and Z among willow genotypes, resulting in an average of 77% dissimilarity (SD = 20%) in gall-parasitoid link composition among willow genotypes. Difference in link composition among willow genotypes were due to variation in both gall abundance and leaf gall size (𝛘24,76 = 179.80, *P* = 0.001). Specifically, the abundance of 67% (8 of 12) of the gall-parasitoid links increased with the abundance of their associated galls (Fig. 3a,b; supplement table). On the other hand, every one mm increase in the diameter of leaf galls resulted in a 19% to 24% decrease in the frequency of *Platygaster* sp. and *Mesopolobus* sp. links, respectively. Leaf gall diameter also appeared to cause *Torymus* sp. to switch which gall species it attacked. Specifically, as leaf gall diameter increased, there was a trend for *Torymus* to switch from parasitizing bud galls (coef. = -0.17, 𝛘225,119 = 3.99, *P* = 0.040) to leaf galls (coef. = 0.19, 𝛘225,119 = 2.92, *P* = 0.092). The gall-parasitoid links that did not increase with gall abundance and were unaffected by leaf gall diameter were among the least abundant links and made up less than 13% of the total abundance of links in the food web.

Galls also varied in their susceptibility to being parasitized depending on willow genotype, but only for leaf galls. Specifically, the percentage of leaf galls being parasitized varied between 0% and 100% among willow genotypes (F23,58 = 2.4, *P* = 0.004; Fig. 2c). As expected from our link composition analysis, the odds of a leaf gall being parasitized decreased by 25% with every 1 mm increase in gall diameter (𝛘21,79 = 10.7, *P* = 0.001). This pattern was primarily driven by the decreases in percent parasitism from *Platygaster* (𝛘21,79 = 16.9, P < 0.001) and *Mesopolobus* (𝛘21,79 = 7.8, P = 0.005)(Fig. 3b). In contrast, percent parasitism from *Torymus* slightly increased on larger leaf galls (𝛘21,79 = 4.0, P = 0.045)(Fig. 3b).

*Prediction 3: Loss of willow genetic variation decreases food web complexity.*

Fig. 5. Note that I need to get the code running for the way I’ve decided to modify this analysis.

**DISCUSSION**

Our results demonstrate that genetically distinct plants can host distinct insect food webs, resulting in a positive relationship between plant genetic variation and insect food web complexity. Moreover, we identified the density- and trait-mediated mechanisms by which plant genetic variation scales up to affect pairwise gall-parasitoid interactions. In doing so, we can begin to predict how evolutionary processes will alter food web structure and dynamics.

*Scaling individual-level interactions to whole food webs - a trait-based approach*

1. Our results highlight several points for understanding the mechanisms by which food webs are structured, especially for plant-insect interactions.

I would start out with the major point being that there is a genetic basis to understanding food web structure and therefore integrating population and community level patterns together will lead to a better and more predictable understanding of how networks are assembled. This is the major point.

* 1. Multiple traits are important in predicting food web structure (more minor point, I wouldn’t focus too much on this but its worth mentioning). Rather, I would focus on flushing out the patterns and mechanisms related to the gall-parasitoid relationships first, then go into the plant traits that might influence gall abundance (since you can just cite your Functional ecology paper and point readers to that work, rather than repeating yourself in this paper)
     1. For example, we found that multiple plant traits were important in determining resistance to galling insects, a result that is well supported by our previous work in this system and the rest of the plant-herbivore literature.
     2. However, mechanistic models of food web structure currently focus on body size as the key determinant of food web structure, neglecting quality-related traits that may be just as important in determining trophic interactions, especially in regard to plant-insect herbivory (e.g. leaf secondary chemistry). (again….minor point, certainly you shouldn’t lead the discussion with these. Focus on the big ideas, the major findings of how and why the food webs vary among clones, which species are driving it, and why and then where to go next.
  2. Traits that predict the presence/absence of an interaction in a food web may not necessarily be the same traits that predict the strength of an interaction in a food web. I might rephrase this as both trait-based and abundance or density based mechanisms were fundamental to understanding the role of genetic variation in shaping networks. In this case plant and gall size versus gall abundance and parasitism.
     1. For example, body size is a poor predictor of who-eats-whom in plant-insect food webs that are resolved at the species-level (Petchey et al. 2008; van Veen et al. 2012). Yet, our individual-level data showed that plant size and gall size were important predictors of gall density and parasitoid attack rates, respectively. *Elaborate on how our findings are well supported by the literature* (Price 1991; Abrhamson & Weis 1992; Murdoch et al. 2003; Carmona et al. 2011; Barbour et al. 2015). This discrepancy between species-level and individual-level trait responses is likely quite common for other specialized trophic interactions.

*Eco-evolutionary dynamics of food webs*

* 1. Our results suggest that processes affecting the amount of genetic variation within a population can alter the structure of its associated food web. All the next bit is about food web complexity. Why not lead with what your results mean for the loss and gain of genetic diversity for food web complexity. Remember, community and network structure are not well defined terms. So its better to be more specific.
  2. Processes that promote genetic variation within populations may increase food web complexity. For example, local adaptation in Trinidadian guppies results in divergence in biomass of algae and invertebrate communities as well as the flux rates
  3. In contrast, evolutionary processes that reduce genetic variation within populations may decrease food web complexity. For example, decreased genetic variation in the stick insect, *Timema cristinae*, via gene flow causing maladapted camouflage on their host plants, resulted in decreased abundance and diversity of other arthropods on the host plant via increased bird predation, due to the maladapted stick insects attracting birds (Farkas et al. 2013).

1. *Incorporating the environment (i.e. GxE interactions) into future work.*
   1. *This will be especially important for understanding how food webs will change under future environmental conditions. WHY?*
2. Our results suggest that genetic variation in parasitism rates may feedback to affect plant fitness. *I recognize this is a stretch, but I feel like I should at least talk about the potential for their to be an eco-eco feedback (or why we wouldn’t expect one). Seems like a stretch but ok.*
   1. Abdala-Robert’s and Mooney study, where parasitoids altered fitness function of plants at different levels of genotypic diversity.
   2. Moreira and Mooney’s work showing that plant species diversity can alter plant fitness by affecting foraging behavior of ants.

*Conclusions*

1. Understanding how individual traits scale up to affect populations, communities, and whole food webs is critical for predicting how food webs will respond to environmental change. Why? Your study is about genetic variation, not climate change.
   1. Foundation and keystone species may be especially important in structuring communities and genetic variation may be especially important in these species. Yet, we need future work to incorporate environmental variation for understanding how changing environments will alter food web structure and dynamics in these systems. *Also weave in a discussion of eco-evo dynamics and natural selection could affect these food webs.*
   2. Current mechanistic models of food webs are ill suited for predicting the structure of host-parasite food webs, such as those of plants and insect herbivores and insect herbivores and parasitoids. Plants, insect herbivores, and their natural enemies make up as much as 70% of terrestrial biodiversity, *so we need to get on it in figuring out how these food webs are structured.* Out of anything, there is the most meat here. I would say its better to focus on this out of anything you have mentioned.

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**Figure Legends**

**Figure 1.** Conceptual model of how decreasing genetic variation results in decreased food web complexity in a plant-insect food web. Here, the number of plant genotypes corresponds to the amount of genetic variation, while the number of links per species corresponds to the degree of food web complexity. If plant genotypes vary in which links they support in the food web, then decreasing genetic variation may decrease food web complexity through two different mechanisms. (A) Decreasing genetic variation results in the loss of plant phenotypes that are preferred by certain herbivore species, which directly (plant-herbivore) and indirectly (herbivore-parasitoid) decreases food web complexity. (B) Decreasing genetic variation results in the loss of herbivore phenotypes that are preferred by different parasitoid species, which indirectly decreases food web complexity.

**Figure 2.** Willow genotypes vary in both gall community composition and gall size. (A, B) Box plots of variation in leaf and bud gall abundance among willow genotypes, respectively. (C) Plot of variation in leaf gall diameter among willow genotypes. Each circle corresponds to an individual willow and the size of the circle is proportional to the number of galls used to estimate mean gall diameter (diamond). Colours correspond to different gall species. For all plots, we ordered willow genotypes based on mean leaf gall abundance (low to high). We did this to illustrate the differences in relative abundance of leaf and bud galls among willow genotypes as well as the lack of genetic correlations in gall abundance and gall size.

**Figure 3.** Willow genotypes vary in both gall-parasitoid link composition and parasitoid attack rates on galls. Box plots of variation in parasitism from (A) *Platygaster*, (B) *Mesopolobus*, and (C) *Torymus* on leaf galls among willow genotypes. (D) Plot of variation in proportion of leaf galls parasitized among willow genotypes. Each circle corresponds to an individual willow and the size of the circle is proportional to the abundance of galls used to estimate mean percent parasitism (diamond). Colours correspond to different gall or parasitoid species. As with Fig. 2, we ordered willow genotypes based on mean leaf gall abundance (low to high).

**Figure 4.** Variation in resistance to leaf galls determines gall-parasitoid link composition. (A) Abundance of Platygaster, Mesopolobus, and Torymus parasitism on leaf galls in response to variation in leaf gall abundance. (B) Proportion of leaf galls parasitized by Platygaster, Mesopolobus, and Torymus in response to variation in leaf gall diameter. Lines correspond to slopes estimated from generalized linear models. Each line type and colour corresponds to a different parasitoid species.

**Figure 5**. Simulation of how insect food web complexity will increase with greater genetic variation.









