**Genetic variation begets network complexity: empirical evidence from a plant-insect food web**

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**Abstract**

Predicting the eco-evolutionary dynamics of ecological networks requires a mechanistic understanding of how genetic variation scales to affect species interactions. To date though, we are lacking empirical tests of whether there is a genetic basis to species interactions in ecological networks, and if so, how changes in genetic variation will affect network structure. To address this knowledge gap, we used a common garden experiment to quantify the genetic basis to species interactions in a plant-insect food web. We found that genetic variation within a foundation plant species beget variability in the phenotypes, abundances, and composition of insect herbivores, which in turn, determined the composition and strength of interactions with a suite of insect parasitoids. After establishing the genetic basis to these multi-trophic interactions, we used a simulation to test the theoretical prediction that increasing genetic variation results in increased food web complexity. Concordantly, we found that food web complexity increased by 50% over the range of genetic variation in the plant population. Taken together, our results indicate that genetic variation in foundation plant species can play a key role in structuring ecological networks, which may in turn, affect network stability. Consequently, incorporating genetic variation into both theoretical and empirical studies of species interactions will be crucial for understanding the eco-evolutionary 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)). 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 the composition of species, thereby ignoring trophic links, or 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).

There are at least three avenues by which genetic variation may affect food web structure. Specifically, genetic variation in resource quality may alter the phenotypes (cite), abundance (Barbour et al. 2015), and composition (Whitham et al. 2012) of consumer species (Figure 1a). These direct effects of genetic variation on consumers may then have cascading effects on the strength and composition of trophic interactions between consumers and their predators. Regardless of the mechanism though, if there is a genetic basis to trophic interactions, then we would expect that increasing genetic variation in a basal resource would result in increased food web complexity (Bolnick et al. 2011; Moya-Larano 2012), or the number of links per species in a network (Figure 1b). Moreover, 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; McCann citation).

Here, we quantify the genetic basis to trophic interaction and 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; Figure 1c). We focused on this plant-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 ideal 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 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 gall size as well as the abundance and composition of galls and gall-parasitoid trophic links 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, resulting in differences in gall size, abundance, and composition. Second, we predict that genetic variation in resistance to galls will determine the abundance, composition, and strength of gall-parasitoid interactions 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 for how the gain/loss of genetic variation in a population will affect the 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).

*Quantifying 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: Willow genotypes vary in their resistance to galling insects, resulting in differences in gall size, abundance, and composition.*

To test for differences in gall size and abundance among willow genotypes, we used generalized linear models (GLMs) because they enabled us to flexibly model the error distributions of our data (O’Hara 2005). For gall size, we analyzed separate GLMs (error distribution = gaussian, link function = identity) with willow genotype as the predictor variable and gall diameter as the response variable. We analyzed separate GLMs since we did not always find all gall species on every willow. 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. We then calculated correlations (Pearson’s *r*) between gall size and abundance among willow individuals (phenotypic correlations) and genotypes (genetic correlations). To test whether variation in gall abundances among willow genotypes resulted in different gall community compositions, we used permutational MANOVA (PERMANOVA) with willow genotype as the predictor variable and a matrix of Bray-Curtis dissimilarities as the response variables. To identify the plant traits that were associated with resistance to galls, we used the same types of GLMs for gall abundances 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 size and gall abundances. 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 *(mariano recommends switching up how I start each subheading)*, we first examined whether there were differences in the abundance and composition of trophic links in the gall-parasitoid food web among willow genotypes. We used the same analytical approach as we did to test for differences in gall abundances (i.e. multivariate GLMs: error distribution = negative binomial, link function = logit) and composition (PERMANOVA, dissimilarity = Bray-Curtis). This time though (*maybe too colloquial)*, we had a matrix of the abundance (multivariate GLMs) or dissimilarity (PERMANOVA) of unique gall-parasitoid links as the response variables. To identify the extent to which gall size and gall abundances determined the abundance of gall-parasitoid links, we again used multivariate GLMs except that our predictor variables was now a matrix of gall abundances and gall sizes. We then used Aikaike information criteria (AIC) and likelihood ratio tests to identify which willow traits best predicted gall size and gall abundances. Further details of model analysis, model selection, and checking model assumptions are given in the supplementary material.

In addition, we examined whether there were differences in the strength of gall-parasitoid interactions among willow genotypes. Specifically, we used separate GLMs (error distribution = binomial, link function = logit) with willow genotype as the predictor variable and total parasitism rates on each gall species as our response variable. If we detected an effect on total parasitism rates we further explored which parasitoid species were driving this response. Finally, we examined whether parasitism rates were due to gall abundances, gall size, or their interaction.

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

To test this prediction, we estimated food web complexity at different levels of willow genotypic diversity (range = 1 to 26 genotype mixtures). To do this, we predicted the abundance of all trophic links in the network using multivariate GLMs. This enabled us to predict the structure of the average food web associated with each willow genotype. For a given level of genotypic diversity, we then randomly sampled genotypes from the pool of 26 genotypes, and took the average abundance of each trophic links for those sampled genotypes to calculate food web complexity, which was a quantitative index of linkage density (Bersier et al. 2002, Bersier 2009). 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). Mixtures from 3 to 24 genotypes received \_ unique simulations, whereas 2 and 25 had \_ unique simulations, and 1 and 26 were just the original numbers. We then ran a GLM with all of the data points (error distribution = gaussian, link function = identity) with the number of genotypes as the predictor variable and quantitative linkage density as the response variable.

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

**RESULTS**

*Prediction 1: Willow genotypes vary in their resistance to galling insects, resulting in differences in gall size, abundance, and composition.*

In concordance with our prediction (*Mariano wants me to take this out*), we found that willow genotype was a major determinant of resistance to galling insects (Fig. 2). For gall size, we found that only the diameter of leaf galls varied 2-fold among willow genotypes (*F*23,57 = 2.17, *P* = 0.009, Fig. 2c; Table S1). In contrast, three of the four gall species exhibited strong variation in abundance among willow genotypes (𝛘225,119 = 202.40, *P* = 0.001; Table S1). In particular, the abundance of leaf and bud galls varied 10- and 8-fold among willow genotypes, respectively (Fig. 2a,b). These differences in abundance resulted in the composition of gall communities on different willow genotypes being 69% dissimilar from each other on average (*F*22,89 = 1.96, *P* = 0.001).

*This entire section is cool, but buried in the methods and not at the end of the intro. Need to make it more clear that I’m examining the mechanisms at multiple levels.*

We found that genetic variation in resistance to galls was partially explained by willow size, leaf C:N ratios, and leaf secondary chemistry (Table S2). For example, leaf galls grew to smaller sizes on willows that had higher concentrations of condensed tannins and flavones in their leaves (*F*2,59 = 8.27, *P* < 0.001, Table S2). Leaf galls also tended to be less abundant on willows with lower C:N in their leaves (𝛘2 = 2.38, *P* = 0.067). Similar to leaf galls, bud galls tended to be less abundant on large willows (𝛘2 = 4.44, *P* = 0.045) with lower leaf C:N (𝛘2 = 2.46, *P* = 0.092). In contrast to leaf and bud galls, we found apical-stem galls at higher abundances on willows with higher concentrations of flavanones and flavanonols in their leaves (𝛘2 = 11.52, *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 the abundance (𝛘225,119 = 357.10, *P* = 0.001) and, in turn, composition (*F*12,45 = 1.57, *P* = 0.007) of trophic links in the gall-parasitoid network. In particular, parasitism from three parasitoids (*Platygaster* sp., *Mesopolobus* sp., and *Torymus* sp.) on leaf galls varied 270%, 30%, and 40% among willow genotypes, respectively, resulting in an average of 78% dissimilarity in gall-parasitoid link composition among willow genotypes.

Differences in the abundance of trophic links among willow genotypes were determined by genetic variation in resistance to galling insects (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 (Table S2). Leaf gall size, however, was also an important determinant of the abundance of trophic links on both leaf and bud galls. Specifically, the abundance of *Platygaster* and *Mesopolobus* links to leaf galls decreases on willows that host larger leaf galls. In contrast, there was a tendency for *Torymus* to switch from parasitizing bud galls (coef. = -0.17, 𝛘2 = 3.99, *P* = 0.040) to leaf galls (coef. = 0.19, 𝛘2 = 2.92, *P* = 0.092) on willows that hosted larger leaf galls. The gall-parasitoid links that were unaffected by leaf gall diameter and did not increase with gall abundance were among the least abundant links and made up less than 13% of the total abundance of links in the gall-parasitoid network.

In addition to the abundance of trophic links, the probability of a gall being parasitized also depended on willow genotype, a pattern that was particularly strong for leaf galls (Fig. 3c; Table S1). Specifically, the proportion of leaf galls being parasitized varied between 0% and 100% among willow genotypes (𝛘223,58 = 75.79, *P* < 0.001; Fig. 2c) and this was primarily determined by leaf gall size (𝛘21,79 = 22.28, *P* < 0.001). Specifically, the odds of a leaf gall being parasitized decreased by 25% with every 1 mm increase in leaf gall diameter. Nevertheless, attack rates from individual parasitoid species depended on both leaf gall size and abundance (Fig. 3a,b). Specifically, parasitism from *Platygaster* and *Mesopolobus* both tended to decrease with larger leaf galls; however, *Platygaster* had disproportionately high attack rates at high gall abundances (𝛘21,77 = 8.71, *P* = 0.003), whereas *Mesopolobus* had disproportionately high attack rates at low gall abundances (𝛘21,77 = 4.21, *P* = 0.040)(Fig. 3a,b). In contrast, parasitism rates from *Torymus* slightly increased on larger leaf galls (𝛘21,78 = 3.8, *P* = 0.050), but similar to *Mesopolobus*, *Torymus* had its highest attack rates at low gall densities (𝛘21,78 = 5.2, *P* = 0.022)(Fig. 3a,b).

*Prediction 3: Increasing willow genotypic diversity increases food web complexity.*

Genetic variation in resistance to galling insects resulted in differences in the composition of trophic links for the entire plant-insect food web (*F*22,89 = 1.90, *P* = 0.001). Specifically, genotypes varied between 41% and 98% in the dissimilarity of their associated food webs (average = 73%), suggesting that many genotypes may have complimentary food web compositions. Indeed, in our simulated mixtures of different levels of willow genotypic diversity, we found that average food web complexity increased by 50%. The increase in food web complexity is not solely due to sampling effects, as food web complexity at the highest level of genotypic diversity was 8% greater than we would have expected from sampling effects alone.

**DISCUSSION**

We found that genetic variation in a foundation plant species had cascading effects on the composition of an insect food web, resulting in a positive relationship between genotypic diversity and overall food web complexity. These cascading effects occurred through the effects of different willow genotypes on galling herbivores, which in turn, determined the composition and strength of trophic interactions with a suite of parasitoid species. As a result, food web complexity increased by 50% over the range of genotypic diversity in the plant population.  Our study provides some of the first evidence of a genetic basis for food web structure and supports theoretical predictions for how changes in genotypic diversity may lead to the assembly or disassembly of food webs (cite Moya-Larano 2012 and Bolnick 2012). Taken together, our study presents a strong argument for understanding how evolution at key nodes in a network will shape the structure and stability of ecological networks.

Our findings provide strong support for the notion that genetic and phenotypic variation within primary producers begets variability in the phenotypes, abundances, and community composition of consumers (Whitham et al. 2012). In particular, we found that genetic variation in willow size and leaf chemistry (Barbour et al. 2015) mediated resistance to galling herbivores, resulting in differences in leaf gall size (phenotype), gall abundances (3 of 4 species), and community composition (mean dissimilarity = 69%). These findings correspond to a diverse array of plant-gall (Abrahamson, Price, other’s work) and other plant-herbivore systems (Whitham et al. 2012; cite other studies). Interestingly, functional traits other than body size are rarely included in mechanistic models of food web structure (Petchey et al. 2008). Consequently, current food web models are ill suited for predicting interactions between herbivorous insects and plants and other host-parasite interactions in general (Petchey et al. 2008, others). Given that plants, insect herbivores, and their natural enemies make up as much as 70% of terrestrial biodiversity (cite), incorporating functional trait variation other than body size, as well as intraspecific trait variation, is an important future direction for food web models.

Our results demonstrate that the effects of genetic and phenotypic variation within a key node may extend beyond pairwise interactions and simple food chains to determine the assembly of whole food webs. Specifically, we found that genetic variation in willow resistance to galling herbivores indirectly affected the foraging behavior of a suite of parasitoid species. These findings resonate with previous work that has demonstrated that genetic variation within plants may indirectly affect the strength of trophic interactions in simple food chains (Fritz 1995, Abrahamson’s work, Bailey et al. 2006, Abdala-Roberts 2014). Importantly though, our network approach enabled us to track the multiple pathways (i.e. multiple galling herbivores) by which genetic variation affected upper trophic levels (i.e. multiple parastoid species). Intriguingly, we found that these pathways were uncorrelated with each other, suggesting that their coevolutionary interactions with the plant may be independent of one another (Fritz and Simms 1992). Although the mechanisms determine trophic interactions may be on different evolutionary pathways, our results suggest that the attack rates of multiple parasitoid species can depend on the interaction between the two (Fig. 4). For example, if there is selection for increased leaf gall resistance through both pathways (i.e. smaller galls and lower abundance), then we would expect to see both higher overall parasitism rates and a shift from a Platygaster dominated interaction to a Mesopolobus dominated one, which has its highest attack rates on small galls at low abundances. In contrast, if there was independent selection for smaller but more abundant galls, then we would likely continue to see the interaction being dominated by Platygaster. Although there has been some theoretical attention given to understanding how G-matrices and O-matrices affect the eco-evolutionary dynamics of species interactions, there is virtually no empirical work (Moya-Larano et al. 2012, Moya-Larano 2012). An important future direction will be to understand how the strength and direction of genetic correlations will affect the eco-evolutionary dynamics of food webs.

Our simulations support the hypothesis that genetic variation begets food web complexity (Moya-Larano 2012; Bolnick 2012). In part, this positive relationship is due to random draws of genotypes with complex food webs (sampling effects, Huston 1992). However, even the genotype that supported the most complex food web was never above the average complexity of simulated mixtures of genotypes above ~ 6 clones in a population. Moreover, we observed strong differences in food web composition among willow genotypes (Fig. 4), indicating that willow genotypes exhibit complimentarity in the species and links they support. It is important to note though, that our simulation is limited to examining the potential additive effects of genotypic diversity on food web structure. We do know that plant genotypic diversity can have non-additive effects on the diversity of upper trophic levels (Crutsinger et al. 2006; Johnson et al. 2006); however, whether there are non-additive effects on the strength and composition of species interactions will require additional experimental work. Still, our simulation supports the notion that that increasing plant genotypic diversity results in greater food web complexity, which may also increase food web stability. While we are currently lacking empirical tests of this, it has been shown that higher plant species diversity results in more stable herbivore and predator communities (Haddad et al. 2011).

Our study focused solely on how genetic variation within a foundation plant species affected food web structure; however, there is a growing literature that genetic variation within herbivores (Farkas et al. 2013) and predators (Palkovacs & Post , Bassar et al. , Harmon et al. ) in a variety of taxa may also affect community dynamics and ecosystem processes. For example, we know that high levels of genetic diversity in sockeye salmon, a keystone species, reduces inter- and intra-annual variability in salmon populations, which provides stable and extended access to a diverse community of mobile predators (including humans) and scavengers in terrestrial and aquatic ecosystems (Schindler et al. 2010). An important future direction of network theory will be to examine whether genetic variation at certain key nodes, such as foundation or keystone species, enhances the robustness of ecological networks (Hughes et al. 2008). This will lend insight to a pressing question in community genetics research: what is the relative importance of genetic variation for predicting and maintaining community and ecosystem processes (Morin 2003, Ricklefs 2003, Hersch-Green et al. 2011)?

This common garden experiment targeted the effects of standing genetic variation within a single population on its associated food web over a short time scale. However, eco-evolutionary dynamics research over the past decade has shown that natural selection can have strong and rapid effects on phenotypic variation that affects the strength of trophic interactions on ecological time scales (Hairston et al. 2003; Bassar et al. , Agrawal et al. 2012 Science). Our results suggest that evolutionary processes that alter genetic diversity may affect food web structure and dynamics, and evidence from other systems tentatively supports this hypothesis. For example, gene flow between locally adapted populations of the stick insect, *Timema cristinae*, results in lower genetic diversity and stick insects with maladapted camouflage (Farkas et al. 2013). This maladapted camouflage attracts birds, which increases arthropod predation and results in decreased abundance and diversity of arthropods on the host plant (Farkas et al. 2013). In contrast, local adaptation, which increases genetic diversity, in trinidadian guppies has been shown to lead to divergent community and ecosystem processes in their aquatic habitats (Bassar et al. ). Divergence in community composition and ecosystem processes is the recipe for increased food web complexity via complementarity on a landscape scale. Future work should take a network approach by quantifying the genetic basis to trophic interactions throughout the food web, as we have done here, as this permits predictions for how evolutionary processes will affect the structure and dynamics of food webs.

Our study has taken a network approach to disentangle the mechanisms by which genetic variation within a foundation species affects food web complexity. Moreover, our results highlight how changes in population genotypic diversity at a key node in a network can fundamentally alter food web complexity and therefore the persistence of food webs. There are two take-home messages from this study. First, intraspecific trait variation is an important driver of network structure, therefore mechanistic models of food web structure should incorporate such variability (Poisot et al. 2014) instead of relying solely on average trait values of species to predict trophic links (Petchey et al. 2008; Kefi et al. 2014). Second, understanding the genetic basis to food web structure, as we have done here, is essential for predicting how evolutionary processes will affect the structure and stability of food webs. Indeed, our simulation suggests that processes that erode genetic diversity result in less complex and less robust food webs. Moreover, genetic diversity provides the raw material for evolution by natural selection; therefore, losing genetic diversity at key nodes in a network may hinder the adaptive capacity of both the node and the network under future environmental change. Given that the current rate of population extinction is probably three orders of magnitude higher than the rate of species extinction (Hughes et al. 1997), our study highlights the pressing need for both theoretical and empirical work to further test how the loss of genetic diversity within and among populations will affect food webs and the ecosystem services they provide (cite).

Extra:

* Indeed, while previous models of food webs have considered how population extinctions alter food web structure (cite), our results suggest that changes in the genetic diversity and composition of a population for a key node may have profound effects on food web structure.
* Genetic diversity also provides the raw material for evolution by natural selection (cite). Consequently, the loss of genetic variation at key nodes in the network may hinder the adaptive capacity of this node under future environmental change. This may then affect the food web because loss of genetic variation makes a population more susceptible to extinction resulting in a loss of a node from a network. Moreover, the loss of genetic variation may reduce food web complexity which may compromise food web structure and dynamics before the population goes extinct.

*HOW DOES THIS STUDY FUNDAMENTALLY CHANGE HOW PEOPLE THINK ABOUT FOOD WEBS.*

*Take-home messages*

* by quantifying the genetic basis to food web structure, our results enable us to make predictions for how the gain/loss of population genetic diversity will affect the structure and dynamics of multi-trophic communities. While previous work supports the notion that population-level genotypic diversity promotes higher diversity at multiple trophic levels (Crutsinger et al. 2006; Johnson et al. 2006), and therefore increased food web complexity, it is unclear whether the structural effects of population genetic diversity are sufficient to actually affect food web dynamics. This is whether network theory can step in, to identify whether genetic variation will have particularly important impacts at certain nodes in the network. Then we need empirical studies to test theoretical predictions by tracking the dynamics of systems whether genetic variation has been manipulated at different nodes. While this is definitely a tall order, an important first step might be to tackle this problem in protist microcosms where it may be more tangible to manipulate genetic variation at different nodes within a network.
* Our results provide a number of important questions that need theoretical attention.
* For plant-insect food webs specifically, our results highlight 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.* Our results also point to the fact that multiple traits are important in determining food web structure, including leaf quality traits.
* need to understand how the loss of genetic diversity will affect food webs.
* Previous work in food web research has focused on the consequences of species extinctions for food web structure and dynamics. Our results suggest that the loss of genetic variation may compromise the structural integrity of a food web, even before a species is completely lost from a food web.
* The loss of genetic diversity appears to be a non-linear processes (tipping point?)
* *Interpretation of biology of foraging patterns. Should consider mentioning this in the results section.* both Platygaster and *Mesopolobus* had higher attack rates on smaller galls, whereas Torymus preferred larger galls. However, Mesopolobus and Torymus had disproportionately llower attack rates at high gall densities, where Platygaster had its highest attack rate. , suggesting their may be a behavioral priority effect of Platygaster since it attacks leaf galls at the egg stage before other these larval parasitoids. Alternatively, this which may possibly be due to the long handling times often associated with parasitizing galling insects (cite Abrahamsson’s work). In addition though, parasitoids were differentially sensitive to the size of galls, which may reflect their preferences for different sized gall larva. Moreover, because certain parasitoid species specialized on particular gall species (e.g. *Platygaster* and *Mesopolobus* on leaf gall), difference in gall composition resulted in differences in gall-parasitoid link composition. By identifying the mechanisms determining food web assembly, our study permits us to make predictions for how evolution of plant resistance to herbivores will shape the rest of the insect food web. *Something about how novel this work is compared to all the studies to come before*

MINOR POINTS LIST:

In many ecosystems, foundation species are a critical determinant of food web structure (Ellison et al. 2005). Our results suggest that the loss of genetic variation in foundation species may compromise the structural integrity of their associated food webs. The loss of genetic variation in keystone species may have similar effects on food web structure.

Previous work in food web research has focused on the consequences of species extinctions for food web structure and dynamics. Our results suggest that the loss of genetic variation may compromise the structural integrity of a food web, even before a species is completely lost from a food web. Our work illustrates that the loss of genetic variation may also affect the structural complexity of food webs, thereby altering their persistence. Indeed, our simulation found that … There are a number of ways in which genetic variation can be lost from a system (e.g. gene flow between locally adapted populations, inbreeding depression, recombination, mutation). Although our study is unique in that we actually quantified the effects of genetic variation, and its loss, on food web structure, work in other systems point to the same results (cite trinidadian guppy system). 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). The loss of genetic variation may even affect ecosystem services, as has been demonstrated for salmon populations in Bristol bay is a critical component that maintains the stability of this system (Schindler et al. 2010). Future work needs to explicitly measure food web structure, as we have done here, but also experimentally manipulate genetic variation (which has been done a bit) (cite Johnson et al. 2006 and Crutsinger et al. 2006).

**ACKNOWLEDGEMENTS**

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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.









