

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

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Abstract

Predicting the eco-evolutionary dynamics of ecological networks requires an understanding of how genetic variation affects 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 the gain or loss of 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 and phenotypic variation within a foundation plant species determined the phenotypes, abundances, and composition of insect herbivores, which in turn, mediated 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 genetic variation determines network complexity. Concordantly, we found that the complexity of the plant-insect food web 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 predicting the eco-evolutionary dynamics of ecological networks.

Introduction

Network theory has provided both a conceptual and quantitative approach for mapping interactions (links) between species (nodes) and making predictions for how the gain or loss of species affects the structure and dynamics of ecological networks (Dunne et al. 2002; Stouffer & Bascompte 2012; Rohr et al. 2014). Representing a network 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 in their phenotypes and there is growing 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 ecological networks (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). Nevertheless, there are two key components missing from these studies that are preventing us from scaling the genetic basis of pairwise interactions to ecological networks. First, these studies do not quantify how genetic variation affects the

composition of pairwise interactions that determine network structure. Instead, they either quantify the composition of species, thereby ignoring interactions, or quantify simple tritrophic interactions, thereby ignoring the complex network in which these interactions are embedded. As a result, the mechanisms by which genetic variation shapes network structure remain unclear. Second, these studies do not examine the effect of genetic variation *per se* on species interactions, rather these studies focus on testing whether different genotypes interact with particular species (Whitham et al. 2012). While demonstrating this genetic basis is a critical first step, we are currently ill-posed for predicting how the gain or loss of genetic variation will affect species interactions, and ultimately the structure of ecological networks (Bolnick et al. 2011).

Genetic variation may affect the structure of an ecological network through at least three different pathways. For a food web (network of trophic links), genetic variation in resource quality may alter the phenotypes (Abrahamson and Weis 1997), abundances (Barbour et al. 2015), and composition (Barbour et al. 2015; 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 greater food web complexity (number of links per species, Fig. 1b, Bolnick et al. 2011, Moya-Larano 2012). Moreover, greater complexity may in turn affect network dynamics, as more complex food webs are predicted to be more robust to species extinctions (MacArthur 1955, Dunne 2002,

McCann 2000).

In this study, we quantify the genetic basis to trophic interactions and test the hypothesis that genetic variation results in greater network complexity using a foundation plant species (Coastal willow, *Salix hookeriana*) and its associated insect gall-parasitoid food web (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 1997). 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. Taken together, our study seeks to test theoretical predictions for the patterns and mechanisms by which genetic variation influences the structure of ecological networks. In doing so, our study takes a crucial step toward a more predictive

understanding for how the gain or loss of genetic variation in a population will affect the dynamics of ecological networks.

Materials & Methods

Common garden and plant trait sampling

To isolate the effects of *Salix hookeriana* (hereafter ‘willow’) genetic variation on the plant-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).

To identify the plant traits that determine the phenotypes (size), abundance, and composition of galling insects, we measured 40 different traits associated with leaf quality (36 traits) and plant architecture (4 traits). 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 for all traits = 0.15 - 0.97; Barbour et al., 2015). Details on how these willow traits were sampled and quantified are given in

Barbour et al. (2015). We then reduced these 40 traits into 13 composite traits that had a negligible degree of multicollinearity using either principle components analysis (PCA), sequential regression (residuals of one trait after accounting for correlation between two traits), or removing one trait from a pair of highly correlated traits (details on methods in Barbour et al. 2015). The final set of leaf quality traits included salicylates/tannins PC1, flavones/flavonols PC1-2, phenolic acids PC1-2, flavanones/flavanonols PC1 (Table S3 of Barbour et al. 2015), Carbon : Nitrogen (C:N), water content, specific leaf area (residuals from water content), and trichome density. The final set of plant architecture traits included plant size, plant height (residuals from plant size), and foliage density (residuals from plant size).

Quantifying the genetic basis to plant-insect food web structure

Measurements—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 collected

from 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.

Analyses—To quantify the genetic basis of the willow-gall interaction network, we tested for differences in gall sizes, abundances, and community composition among willow genotypes. For gall size, we analyzed separate linear models with willow genotype as the predictor variable and average gall size as the response variable, but we weighted the analysis by the number of galls used to calculate average gall size. We weighted the linear model by the number of galls because we expected that averages based on more galls reflect a more accurate estimate of gall size on a willow individual. For gall abundances, we analyzed multivariate generalized linear models (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 genotype averages (genetic correlations). For gall community composition, 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 gall sizes and abundances, we used the same types of models as used previously except that our predictor variables was now a matrix of willow traits. To select a final model of willow traits, we sequentially removed traits based on Akaike information criteria (AIC) to identify a nested set of candidate models. We then used likelihood ratio tests to identify the model of willow traits that best predicted gall size or gall abundances.

To quantify the genetic basis of the gall-parasitoid interaction network, we tested for differences in the abundance, composition, and strength of gall-parasitoid links among willow genotypes. For gall-parasitoid link abundance and composition, 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 index = Bray-Curtis). For these analyses though, 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 the same approach as we did to identify the willow traits that best predicted gall abundances (i.e. AIC and likelihood ratio tests), to identify which gall sizes and abundances best predicted the abundance of gall-parasitoid links. For the interaction strength of gall-parasitoid links, 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, then we analyzed separate GLMs for each parasitoid species to determine which parasitoids were driving total parasitism rates. Finally, we again used AIC and likelihood ratio tests to examine whether parasitism rates were due to gall abundances, gall size, or their interaction.

Genetic variation determines network complexity

To test this hypothesis, we estimated plant-insect food web complexity at different levels of willow genetic variation (range = 1 to 25 genotype polycultures). We omitted 1 of the 26 genotypes from this analysis (Genotype U) because we never collected any galls or gall-parasitoid links from the branches we sampled. To predict the structure of the average food web associated with each willow genotype, we analyzed a multivariate GLM (error distribution = negative binomial, link function = log) with willow genotype as the predictor variable and an abundance matrix of willow-gall and gall-parasitoid links as the response variables. Next, we randomly sampled genotypes from the pool of 25 genotypes (with replacement) for each level of genetic variation (1 to 25 genotype polycultures) and calculated quantitative weighted link density, LD_q , as an index of food web complexity (Bersier et al. 2002, Bersier 2009). LD_q is based on Shannon Entropy and is the average of the effective number of prey and predatory links for a given species. LD_q also weights the total prey and predatory links for each species to account for its energetic importance in the food web. LD_q is less sensitive to variation in sample size compared to other measures of food web complexity (Bersier 2009), making it an appropriate measure of complexity for our quantitative food web. We repeated this simulation 1000 times, resulting in 2,221 unique simulations (N = 100 for 4 - 20 genotype polycultures, N = 98 for 3, 21, and 22 polycultures, N = 89 for 2 and 23 polycultures, N = 1 for 25 polyculture, N = 25 for monocultures).

RESULTS

We found that willow genotypes varied in the size, abundance, and composition of galling herbivores, indicating that there is a genetic basis to the willow-gall interaction

network (Fig. 2). For gall size, only the diameter of leaf galls varied 2-fold among willow genotypes ($F_{23,57} = 2.17$, $P = 0.009$, Fig. 2c), with little variation observed for the other gall species (Table S1). In contrast, three of the four gall species exhibited strong variation in abundance among willow genotypes ($\chi^2_{25,119} = 202.40$, $P = 0.001$; 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 ($F_{22,89} = 1.96$, $P = 0.001$). Although we observed strong variation in leaf gall size and the abundance of multiple gall species among willow genotypes, only leaf and bud gall abundances exhibited a weak, positive correlation among willow individuals ($r = 0.19$, $n = 145$, $P = 0.02$) and genotypes ($r = 0.44$, $n = 26$, $P = 0.020$) (Table S2).

Genetic variation in leaf gall size and gall abundances was partially explained by willow size, leaf C:N ratios, and leaf phenolic chemistry (Table S3). For example, leaf galls grew to smaller sizes on willows that had higher concentrations of condensed tannins and flavones in their leaves ($F_{2,59} = 8.27$, $P < 0.001$). Leaf galls also tended to be less abundant on willows with lower C:N in their leaves ($\chi^2 = 2.38$, $P = 0.067$). Similar to leaf galls, bud galls tended to be less abundant on large willows ($\chi^2 = 4.44$, $P = 0.045$) with lower leaf C:N ($\chi^2 = 2.46$, $P = 0.092$). 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 ($\chi^2 = 11.52$, $P = 0.001$).

We also found that willow genotype was a major determinant of the abundance ($\chi^2_{25,119} = 357.10$, $P = 0.001$) and, in turn, composition ($F_{12,45} = 1.57$, $P = 0.007$) of gall-parasitoid links, indicating a genetic basis to the gall-parasitoid interaction 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 (Fig. 3a,b).

Differences in the abundance of gall-parasitoid links were determined by genetic variation in leaf gall size and gall abundances ($\chi^2_{4,76} = 179.80$, $P = 0.001$). Specifically, the abundance of 67% (8 of 12) of the gall-parasitoid links increased with the abundance of their associated galls (Table S3). Leaf gall size, however, was also an important determinant of the abundance of trophic links on both leaf and bud galls. Specifically, willows with larger leaf galls had lower abundances of *Platygaster* and *Mesopolobus* links to leaf galls. In contrast, there was a tendency for *Torymus* to switch from parasitizing bud galls (coef. = -0.17, $\chi^2 = 3.99$, $P = 0.040$) to leaf galls (coef. = 0.19, $\chi^2 = 2.92$, $P = 0.092$) on willows with larger leaf galls. The gall-parasitoid links that were unaffected by leaf gall size and gall abundances 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 ($\chi^2_{23,58} = 75.79$, $P < 0.001$; Fig. 2c) and this was primarily determined by leaf gall size ($\chi^2_{1,79} = 22.28$, $P < 0.001$). For example, 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. 4; Table S4). For instance, parasitism from *Platygaster* and *Mesopolobus* both tended to decrease on willows with larger leaf galls; however, *Platygaster* had disproportionately high attack rates on willows with high gall abundances ($\chi^2_{1,77} = 8.71$, $P = 0.003$), whereas *Mesopolobus* had disproportionately high attack rates on willows with low gall abundances ($\chi^2_{1,77} = 4.21$, $P = 0.040$)(Fig. 4). In contrast, parasitism rates from *Torymus* slightly increased on willows with larger leaf galls ($\chi^2_{1,78} = 3.8$, $P = 0.050$), but similar to *Mesopolobus*, *Torymus* had its highest attack rates on willows with low gall abundances ($\chi^2_{1,78} = 5.2$, $P = 0.022$)(Fig. 4).

Genetic variation in willow-gall and gall-parasitoid interaction networks resulted in a 50% increase in average food web complexity over the simulated range of willow genetic variation (Fig. 5a). The increase in food web complexity was not solely due to sampling effects, as polycultures with six or more genotypes had greater average food web complexity than we would have expected from sampling effects alone (dashed line, Fig. 5a). Indeed, we found that the composition of plant-insect food webs on different willow genotypes were 73% dissimilar from each other on average ($F_{22,89} = 1.90$, $P = 0.001$, Fig. 5b), suggesting that many genotypes have complimentary food web compositions.

DISCUSSION

Our study provides some of the first empirical evidence of a genetic basis for the structure of ecological networks and supports theoretical predictions for how changes in genetic variation may lead to the assembly or disassembly of networks (Moya-Larano 2012, Bolnick et al. 2012). Within a large-scale common garden experiment, we observed cascading effects of genetic variation in a foundation plant species on the composition of a plant-insect food web, resulting in a positive relationship between plant genetic variation and food web complexity. Genetic effects occurred through the variation in resistance among willow genotypes to galling herbivores, which in turn, determined the composition and strength of trophic interactions with a suite of parasitoids. As a result, food web complexity increased by 50% over the range of genetic variation within the plant population. Taken together, our study presents a strong argument for understanding how the gain/lose of genetic variation 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 variation within primary producers leads to variability at the phenotypic, population, and community level of associated consumers (Whitham et al. 2012). In particular, we found that genetic variation in willow size and leaf chemistry (Barbour et al. 2015) resulted in differences in gall size (leaf galls: 2-fold variation among genotypes), abundances (3 of 4 species varied among genotypes), and community composition (mean dissimilarity = 69% among genotypes). This genetic specificity (i.e. differences among genotypes) corroborates

decades of work in plant-gall (Fritz 1986, Abrahamson and Weis 1992, Bailey et al. 2006) and other plant-herbivore systems (Maddox and Root 1987, Whitham et al. 2012). Moreover, these results highlight that multiple plant traits are important in predicting herbivore community responses (Barbour et al. 2015). Interestingly, intraspecific trait variation and traits other than body size are rarely included in mechanistic models of food web structure (Petchey et al. 2008, Woodward et al. 2011). Consequently, current food web models are generally ill suited for predicting interactions between plants and insect herbivores or other host-parasite interactions (Petchey et al. 2008, Lafferty et al. 2008). Given that plants, insect herbivores and parasitoids comprise over half of all known species of metazoans (Price 1980, Strong 1984), incorporating intraspecific trait variation in a wide range of traits in addition to body size (Henri and van Veen 2011) is an important future direction for food web models.

The effects of genetic variation within a key node may extend beyond pairwise interactions and simple food chains to determine the assembly of entire ecological networks. Specifically, we found that genetic variation in the size, abundances, and composition of galling herbivores indirectly affected the composition and strength of interactions with a suite of parasitoid species. These findings resonate with previous work demonstrating that genetic variation within plants may indirectly affect the strength of trophic interactions in simple food chains (Fritz 1995, Abrahamson and Weis 1992, Bailey et al. 2006, Abdala-Roberts 2014). Importantly though, a network approach enabled us to track the multiple pathways (e.g. size and abundance of several gall species) by which genetic variation affected upper trophic levels. Intriguingly, we found

weak genetic correlations among the size of leaf galls and the abundances of multiple gall species, suggesting that their coevolutionary interactions with the plant are mostly independent of one another (Fritz and Simms 1992). In addition, we found that the attack rates of multiple parasitoid species can depend on the interaction between gall size and abundance (leaf galls, Fig. 4), suggesting that the composition of the parasitoid community will depend on how selection acts on gall size and abundance. For example, if there was selection for increased resistance of willows to leaf galls through smaller galls and lower gall abundances, then we would expect to see both higher overall parasitism rates and a shift in dominance from *Platygaster* to *Mesopolobus*, because *Mesopolobus* had its highest attack rates on small galls at low abundances (Fig. 4a). In contrast, if there was independent selection for smaller but more abundant leaf galls, then we would expect to see the interaction continue to be dominated by *Platygaster* (Fig. 4b). Although there has been some theoretical attention given to understanding how genetic correlations and natural selection affect the eco-evolutionary dynamics of ecological networks (Moya-Larano et al. 2012, Moya-Larano 2012), there has been virtually no empirical work. An important future direction will be to test theoretical predictions from these models in the field, with plant-gall-parasitoid food webs being ideal candidate systems for doing so.

Our simulation supports the hypothesis that increased genetic variation results in greater network complexity (Fig. 5a, Moya-Larano 2012, Bolnick 2012). In part, this positive relationship is due to random draws of genotypes with complex food webs (i.e. sampling effects, Huston 1992). However, the average complexity of food webs in simulated polycultures with six or more genotypes was always greater than our expectation from

sampling effects alone (dashed line, Fig. 5a). Moreover, we observed strong differences in food web composition among willow genotypes (Fig. 5b), indicating that willow genotypes show varying degrees of complementarity in their trophic links. It is important to note though, that our simulation is limited to estimating the potential additive effects of genetic variation 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). Whether there are non-additive genetic effects on the strength and composition of species interactions will require additional experimental work. Still, our simulation supports the notion that increasing plant genetic variation results in greater food web complexity, which may also enhance the stability of a food web. While we are currently lacking empirical tests of this, it is worth noting that higher plant species diversity has been linked to 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 (Post et al. 2008, Bassar et al. 2010, Harmon et al. 2009) in a variety of taxa may also affect community dynamics and ecosystem processes. For example, we know that high levels of genetic variation 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, Ruff et al. 2011). 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 compared to nodes of less structural importance (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 on its associated food web over a short time scale; however, we know that natural selection can have rapid effects on phenotypic variation that affects the strength of trophic interactions on ecological time scales (Hairston et al. 2003, Agrawal et al. 2012). Therefore, our results suggest that evolutionary processes that alter genetic variation may also 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 variation and leads to stick insects with maladapted camouflage on their host plants (Farkas et al. 2013). This maladapted camouflage attracts birds, which increases predation pressure and results in decreased abundance and diversity of arthropods on the host plant (Farkas et al. 2013), and likely a less complex food web. In contrast, local adaptation, which increases genetic variation, in trinidadian guppies has been shown to lead to divergent community and ecosystem processes in their aquatic habitats (Bassar et al. 2010). Divergence in community composition and ecosystem processes is the recipe for increased food web complexity via complementarity. We advocate using a network approach and 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.

The overarching goal of our study was to disentangle the mechanisms by which genetic variation within a foundation species affects food web complexity. Moreover, our results highlight how changes in population genetic variation at a key node in a network can fundamentally alter food web complexity and therefore the persistence of food webs. There are two main conclusions from our work. 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 over time. Indeed, our simulation suggests that the loss of genetic variation will result in less complex and less robust food webs. Moreover, genetic variation provides the raw material for evolution by natural selection; therefore, losing genetic variation at key nodes in a network may hinder the adaptive capacity of both the node and the network under future environmental change (Alsos et al. 2012, Carroll et al. 2014). Given that the current rate of population extinction is 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 variation within and among populations will affect food webs and the ecosystem services

they provide (Luck et al. 2003, Schindler et al. 2010).

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Figure Legends

Figure 1. Conceptual model of how genetic variation determines network complexity in a plant-insect food web. (A) Genetic variation in a basal resource (green circles) results in variability in the phenotypes, abundances, and composition of consumer species (blue shapes). (B) Hypothetical example of how increasing genetic variation (number of green circles) will result in greater network complexity (number of links per species). (C) Plant-insect food web aggregated among all willow genotypes examined in this study, where the width of each grey link is proportional to the number of individuals associated with the trophic link. This food web consists of a foundation plant species (Coastal willow, *Salix hookeriana*), four herbivorous galling insects (Family: Cecidomyiidae), and six insect parasitoids. The four species of galls include, from left to right, the apical-Stem gall (Cecidomyiid sp. A), bud gall (*Rabdophaga salicisbrassicoides*), leaf gall (*Iteomyia salicisverruca*), and mid-Stem gall (*Rabdophaga salicisbattatus*). The six species of parasitoids include, from left to right, *Torymus* sp. (Family: Torymidae), Eulophid sp. A (Family: Eulophidae), *Lestodiplosis* sp. (Family: Cecidomyiidae), *Mesopolobus* sp. (Family: Pteromalidae), *Platygaster* sp. (Family: Platygastriidae), and Mymarid sp. A (Family: Mymaridae).

Figure 2. Genetic basis to the willow-gall interaction network. (A-B) Box plots of variation in (A) leaf and (B) bud gall abundance among willow genotypes. (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. Genetic basis to the gall-parasitoid interaction network. (A-C) 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. Genetic variation in leaf gall size and abundance determines the composition and strength of parasitoid interactions. (A) Proportion of leaf galls parasitized by *Platygaster*, *Mesopolobus*, and *Torymus* as a function of gall size, but at low gall abundances (1 - 4 leaf galls per branch). (B) Proportion of leaf galls parasitized by the same three parasitoid species as a function of gall size, but at high gall abundances (5 - 22 leaf galls per branch). Lines correspond to slopes estimated from generalized linear models. Each line type and colour corresponds to a different parasitoid species (solid blue = *Platygaster*; short, dashed green = *Mesopolobus*; long, dashed orange = *Torymus*).

Figure 5. Genetic variation begets network complexity. (A) Simulation of how plant-

insect food web complexity (LD_q) changes with increasing genetic variation (no. of genotypes) in the willow population. Open, grey circles correspond to individual simulations, whereas solid, blue circles correspond to averages at each level of genetic variation. The dashed line is the highest food web complexity observed on a single willow genotype and represents the expected magnitude of food web complexity under sampling effects alone. (B) Ordination of Bray-Curtis dissimilarities in plant-insect food web compositions among willow genotypes using a constrained analysis of principle coordinates (CAP). Black letters and grey ovals correspond to the centroid and standard error of the centroid for each willow genotype.