**Plant genetic variation drives dissimilarity in an insect food web**

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**Abstract**

Predicting the eco-evolutionary dynamics of ecological networks requires knowing the mechanisms by which heritable trait variation affects species interactions across multiple trophic levels. Using a common garden experiment, we show that genetic variation in a common plant species drives dissimilarity across multiple trophic levels in an insect food web. Specifically, we found that the susceptibility of insect herbivores (gall midges) to attack from particular parasitoid species and guilds depended on plant genotype. This variation in herbivore susceptibility was determined by both the density and size of herbivores, which in turn was affected by leaf quality and plant architecture traits. Taken together, our results indicate that genetic variation can play a key role in structuring ecological networks. Furthermore, our results highlight the potential for microevolutionary processes to shape both the structure and dynamics of ecological networks.

**Introduction**

The use of ecological networks to map out species interactions has resulted in a better understanding of the factors that govern the structure of food webs (Williams & Martinez 2000; Petchey et al. 2008; Eklof et al. 2013), as well as how this structure affects the persistence of ecological communities (Stouffer & Bascompte 2011; Theabault & Fontaine 2012; Roher et al. 2014). Within a network, key species play a fundamental role in the organization of species interactions and therefore the overall structure of a network. For example, INSERT EXAMPLE or elaborate on these keystone-type species.

However, these species-level networks implicitly assume that each species consists of a homogenous population of individuals, all of which interact equally (cite). Yet, virtually all populations are heterogenous mixtures of individuals that vary phenotypically and this phenotypic variation can have large effects on how individuals interact, as well as the the structure and dynamics of ecological communities (Woodward et al., 2010; Bolnick et al. 2011; Melian et al., 2014). To date, most network studies ignore these interactions

Consequently, if we continue to ignore how individual differences scale up to affect species interactions, we risk overlooking fundamental drivers of how ecological networks are organized (Araujo et al. 2011; Tur et al. 2014).

Genetic variation is a key driver of intraspecific variation and there are a range of examples demonstrating that heritable trait variation can have cascading effects on multitrophic interactions (Antonovics 1992; Whitham et al. 2003, 2012). For example, genetic variation within host-plant species can influence the richness, abundance, and size of associated herbivore species, which in turn can alter interactions with higher trophic levels of predator or parasitoids (Bailey et al., 2006; Johnson 2008; Abdala-Roberts and Mooney 2014).

Similarly, genetic variation within predators, such as fish and salamanders, has also been shown to mediate the strength of trophic cascades (Post et al. 2008; Harmon et al., 2009; Bassar et al., 2010). While it is clear that microevolutionary processes can influence pairwise species interactions and community composition at different trophic levels, these studies have neglected to quantify changes in the organization of the ecological network.

Understanding how genetic and phenotypic variation influences the organization of ecological networks will enhances our ability to predict the eco-evolutionary dynamics of multitrophic communities (Melian et al. 2011; Moya-Larano et al. 2012). For example, if trait variation in a plant species influences its susceptibility to different herbivore species, and this trait variation is heritable, then we have a mechanism by which genetic variation drives dissimilarity in the herbivore community (Agrawal 2005; Barbour et al. 2015). Moreover, if the genetic and phenotypic variation in the plant is large enough, then the resulting dissimilarity in the herbivore community may influence the foraging behaviour of upper trophic levels, providing a mechanism for how genetic variation could drive dissimilarity in an ecological network. From here, we can begin to predict how trait evolution will affect the eco-evolutionary dynamics of ecological networks (Guimeras et al., 20011; Nuismer et al., 2012). Despite this promising avenue for future research, we are currently lacking empirical tests of whether genetic variation drives dissimilarity in the structure of species interaction networks (but see Bukovinsky et al. 2008).

Here, we test the hypothesis that genetic and phenotypic variation drives dissimilarity in ecological networks using a subset of the insect food web associated with the coastal willow *Salix hookeriana*. This insect food web consists of four species of gall midges (Family: Cecidomyiidae) and the six species of natural enemies that attack them (Fig. 1A). This plant-insect food web was ideal for testing our hypothesis for two reasons. First, *S. hookeriana* displays considerable genetic and phenotypic variation that results in variation in the density of galling insects (Barbour et al. 2015 in press). *A priori*, we expect that variation in gall density would affect both the foraging behaviour of their natural enemies, thereby providing a mechanistic link for how plant genetic variation could affect this food web. Second, the closed nature of the galls restricts their parasitoid community to a small number of species that can successfully locate and parasitize galls. Consequently, it is easy to identify and quantify the sources of mortality, making this food web amenable to building quantitative interaction networks (van Veen et al. 2006).

If genetic and phenotypic variation drives dissimilarity in ecological networks, we would predict the following three things. Firstly, given prior evidence about genetic variation in resistance to herbivores, we predict that the structure of insect food webs will vary among willow genotypes. Secondly, we predict that variation in the insect food web will be explained by the functional and numerical responses of the natural enemies to genetic variation in gall density and gall size. Finally, we predict that variation in gall density and gall size will result from genetic variation in leaf quality and plant architectural traits. Taken together, our study seeks to understand how genetic variation shapes the structure of ecological networks. And since genetic variation provides the raw material for evolution, establishing a genetic basis to the organization of ecological networks will begin to inform the eco-evolutionary dynamics of multitrophic communities.

**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).

*Dissimilarity of the insect food web*

To build quantitative food webs, we collected galls from about 5 randomly chosen replicates of each genotype in September 2012 (N = 145 trees, range = 4-9 trees per genotype how many galls total?). For each replicate willow, we collected all galls occurring on one randomly selected basal branch. For each branch, we estimated the number of shoots based on an allometric equation using the stem diameter of the sampled branch (mean ± SD shoot count = 280 ± 124; details in supplementary materials). We then used these shoot estimates to quantify the density of gall-parasitoid interactions on each replicate willow. To quantify gall-parasitoid interactions, 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 (what percent of total number of galls?).

We measured the dissimilarity of insect food webs by analyzing both qualitative and quantitative differences in the composition of species interactions (Poisot et al. 2012). These differences in composition can then be partitioned into (i) species turnover and (ii) interaction components. Differences due to species turnover arise from the gain/loss of species altering the composition of species interactions, whereas differences due to interactions occur when species switch with whom they are interacting, despite the network maintaining the same species composition. To measure qualitative differences, we transformed the quantitative network into presence/absence data and calculated the pairwise Euclidean distances between sites. We used Euclidean distance because we considered the joint absence of the same interaction between sites as meaningful. We note though that we obtain the same qualitative results when we use other common dissimilarity indices for presence/absence (e.g. Jaccard index; details in supplementary materials). Since differences in species richness between sites will also affect dissimilarity, we used a probabilistic null model (Raup-Crick index) to control for these differences. The Raup-Crick index measures the probability that two sites will have different species composition and it does so by generating a null model where species occurrence probabilities are proportional to species site occupancies.

To measure quantitative differences, we used Euclidean distance. As the with presence/absence data, other common dissimilarity indices gave qualitatively the same results (e.g. Bray-Curtis index; details in supplementary materials). To get a better understanding of the processes driving the quantitative dissimilarity among genotypes, Since we were also interested in understanding which???

*Analysis*

To test whether willow genetic variation mediated dissimilarity of the insect food web, we used permutational ANOVA (PERMANOVA). Specifically, we modeled willow genotypes as a random effect and used the pairwise dissimilarities in species interaction composition as our multivariate response. We used Euclidean distance to calculate the pairwise dissimilarities for both the qualitative (i.e. presence/absence) and quantitative interaction data because we considered the joint absence of the same interaction between sites as meaningful. But since differences in species richness between sites will also affect dissimilarity, we used a probabilistic null model (Raup-Crick index) to control for these differences. The Raup-Crick index measures the probability that two sites will have different species composition and it does so by generating a null model where species occurrence probabilities are proportional to species site occupancies (Chase et al. 2010). We note though that we obtain the same qualitative results when we use other common dissimilarity indices for both presence/absence (e.g. Jaccard index) and quantitative (e.g. Bray-Curtis index) data (details in supplementary materials). In addition to looking at overall dissimilarity in network composition, we partitioned the relative contribution of species turnover and interaction components to understand the underlying processes (Poisot et al. 2012). To estimate the proportion of variance in network dissimilarity explained by willow genotype, we calculated broad-sense heritability (*H*2) using the equation: *H*2 = *V*G / *V*P, where *V*G is the total genotypic variance among clones, and *V*P is the total phenotypic variance, calculated as the sum of the residual (*VR*) and genetic variance (Lynch & Walsh 1998). Following Lynch and Walsh (1998), we used the Mean Sum of Squares in our PERMANOVA table and the average number of replicates per genotype to estimate *V*G and *V*P for calculating heritability. Heritability values range between 0-1, where values close to zero indicate low heritability (i.e. strongly influenced by the environment), and values close to 1 indicate high heritability (i.e. strongly controlled by underlying genetic variation).

In order to get a better understanding of the processes driving the dissimilarity in the food web, we analyzed whether the dominant gall-parasitoid species and guild interactions varied among willow genotypes. To do this, we analyzed random effect models, where willow genotype was specified as a random effect and the density of a particular gall-parasitoid species or guild interaction was the response variable. Since we had only one response variable in each model, we used restricted maximum likelihood (REML) to estimate the variance due to willow genotype (*VG*) and unexplained residuals (*VR*), which we used for calculating the broad-sense heritability of each interaction. We then performed restricted likelihood-ratio tests to examine whether willow genotype explained a significant proportion of the variance in each gall-parasitoid interaction.

*Genetic variation in gall density and size affects functional and numerical responses of natural enemies*

To test whether gall density (no. of galls per 100 shoots) and gall size (measured as the maximum diameter perpendicular to direction of plant tissue growth, to the nearest 0.01 mm) varied among willow genotypes, we used our gall collections from each replicate willow tree (N = 145). As with pairwise gall-parasitoid interactions, we analyzed separate random effect models for the density of each gall species. Since we had individual-level measurements for gall size, we analyzed a nested random effect model, where willow replicates were nested within willow genotype. We then used the variance due to willow replicate as another source of phenotypic variance (i.e. *VP* = *V*G + *V*willow + *VR*) for our estimates of broad-sense heritability. For both gall density and gall size, we restricted our analyses to gall species that were associated with genetic variation in gall-parasitoid interactions. Gall density and gall size were transformed as needed to make the distribution of random effects more normally distributed.

To test whether gall density and gall size influenced the numerical response of natural enemies, we used linear regression. Specifically, we modeled gall-parasitoid interaction density as our response variable with gall density, mean gall size (tree-level), and their interaction, as our predictor variables. To test whether gall density and gall size influence the functional response of natural enemies, we used generalized linear models (GLMs). GLMS were appropriate because they enabled us to model the probability of observing a gall-parasitoid interaction as our response variable (error distribution = binomial; link function = logit) with gall density, mean gall size, and their interaction, as predictor variables. We then used F tests (linear regression) and likelihood ratio tests (GLMs) to compare nested models. We started with the most complex model and removed non-significant predictors (P > 0.05) until we identified the most parsimonious model.

*Genetic variation in plant traits influences gall density and size*

To identify the plant traits influencing variation in gall density and gall size, 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 these traits included the following. 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 *in press*). We used scatterplots and Pearson correlation coefficients to identify a small number of traits for further model selection. Using multiple regression???, we then proceeded to drop non-significant (P < 0.05) traits from each model until we identified a final linear regression model for each gall response variable.

**RESULTS**

*Genetic variation drives dissimilarity in insect food web*

We found that genetic variation within willows was a major driver of both qualitative (*H2* = 0.17, F25,118 = 2.12, P = 0.001) and quantitative (*H2* = 0.19, F25,118 = 2.27, P = 0.001) dissimilarity in the insect food web (Fig. 1b). This dissimilarity among willow genotypes was due primarily to species turnover (insert some sort of description in how much turnover there is). Importantly though, dissimilarity in the food web was not simply due to differences in interaction richness among genotypes (Raup-Crick, *H2* = 0.07, F25,118 = 1.40, P = 0.001), suggesting that the susceptibility of gall species to different parasitoid species depending on willow genotype (Fig. 1b). Indeed, their were three dominant types of interactions that varied among willow genotypes: egg and larval parasitism on the leaf galling midge, *Iteomyia salicisverruca* (hereafter *Iteomyia*), and larval parasitism on the bud galling midge, *Rabdophaga salicisbrassicoides* (hereafter *Rabdophaga*-bud) (Fig. 1a). Specifically, the density of egg (*H2* = 0.35, RLR test = 27.46, P < 0.001) and larval (*H2* = 0.28, RLR test = 17.00, P < 0.001) parasitism on *Iteomyia* varied 35- and 20-fold among willow genotypes, respectively. Similarly, the density of larval parasitism on *Rabdophaga*-bud varied 9-fold among willow genotypes (*H2* = 0.10, RLR test = 3.12, P = 0.029).

*Genetic variation in gall density and size affects functional and numerical responses of natural enemies*

We found that willows displayed heritable variation in resistance to galling insects in terms of both the density and size of galls. Specifically, the density of Iteomyia (*H2* = 0.32, RLR test = 23.11, P < 0.001) and *Rabdophaga*-bud (*H2* = 0.19, RLR test = 7.42, P = 0.002) galls varied 67- and 62-fold among willow genotypes, respectively. Gall density was best predicted by X traits, though weakly. Moreover, *Iteomyia* gall size varied 2-fold among willow genotypes (*H2* = 0.15, RLR test = 5.64, P = 0.007), whereas *Rabdophaga*-bud gall size did not vary significantly (*H2* = 0.04, RLR test = 0.55, P = 0.187) (Fig. 2b). Gall size is predicted by X phenotypes.

Genetic variation in resistance to galling insects mediated the observed shifts in the insect food web among willow genotypes. Overall parasitism rates (probability of attack for all gall species together, and maybe the 4 species). Differences in parasitism among plant genotypes. For example, rates of the key parasitoid on the key gall varied between 10 and 80% depending on clone. In contrast, a less important parasitoid varied between 0 10% depending on genotype. See supplements for each gall and each parasitoid.

In particular, the interaction between *Iteomyia* gall density and size as well as *Rabdophaga*-bud gall density explained 35% of the variance in the insect food web (*R*2 = 0.35, F4,76 = 10.30, P = 0.005). This effect was driven primarily high density of egg and larval parasitoids in *Iteomyia* galls and larval parasitoids to *Rabdophaga*-bud galls. Specifically, the density of *Iteomyia*-egg parasitism increased with higher *Iteomyia* gall density, ranging from X number of parasitioids when galls were at Y number to X number of parasitoids with galls were at Z number. In addition, the relationship between gall density and parasitoid density was particularly strong on individual willows with small galls (*R*2 = 0.47, F3,77 = 22.40, P < 0.001). For example, when a given genotype has galls less than 8 mm in diameter then the slope of the relationship was x. Anything larger, the slow was Y (plot A and B of the slopes).

Similarly, the density of *Iteomyia*-larva parasitiods increased with higher *Iteomyia* gall density, ranging from X% individuals when there were less than X galls per hundred shoots and X individuals when there were Y galls per hundred. Again, this relationship was contingent on gall size, with the relationship between parasitoid density and gall density being weaker for larger galls (*R*2 = 0.36, F2,78 = 21.50, P < 0.001). The density of *Rabdophaga*-bud-larval parasitism increased with higher *Rabdophaga*-bud gall densities (*R*2 = 0.49, F1,79 = 75.92, P < 0.001), but was not included in differences with gall size because gall size did not differ among willow clones. The influence of gall density and gall size varied for parasitism rate compared to parasitoid density. For example, the probability of an egg parasitoid attacking Iteomyia was higher when there were there were more galls and galls were smaller (𝝌23,77 = 32.77, P < 0.001)(Fig. 3a). In contrast, the rate of larval parasitism on Iteomyia was higher there were fewer galls (𝝌22,78 = 18.33, P < 0.001), but still preference for smaller galls (Fig. 3b), indicating that both egg and larval parasitoids prefer the same size galls larval parasitoids might be avoiding areas infested with egg parasitoids. In contrast to parasitism on Iteomyia, the probability of larval parasitoids attacking *Rabdophaga-*bud galls was independent of both gall density and gall size (𝝌21,66 = 0.25, P = 0.617) suggesting that preferences by larval parasitoids depends on the identity of the gall species..

*Genetic variation in plant traits influences gall density and size*

We found that variation in both the density and size of galls was explained by both leaf quality and plant architecture traits. In particular, the density of both *Iteomyia* and *Rabdophaga-*bud galls was higher on shorter willows with higher leaf C:N content (*Iteomyia*: *R*2 = 0.17, F2,119 = 12.14, P < 0.001; *Rabdophaga-*bud: *R*2 = 0.15, F2,120 = 10.97, P < 0.001). Interestingly, the size of Iteomyia galls was not influenced by either willow height or leaf C:N. Instead, gall size was larger on willows with higher concentrations of salicylates and flavones in their leaves (*R*2 = 0.14, F2,75 = 5.88, P = 0.004).

**DISCUSSION**

**ACKNOWLEDGEMENTS**

**REFERENCES**

**(not complete)**

Abdala-Roberts, L., & Mooney, K. A. (2012). Environmental and plant genetic effects on tri-trophic interactions. *Oikos*, *122*(8), 1157–1166. doi:10.1111/j.1600-0706.2012.00159.x

Antonovics, J. (1992). Toward community genetics. In *Plant resistance to herbivores and pathogens: ecology, evolution, and genetics* (pp. 426–429). Chicago: University of Chicago Press.

Bailey, J. K., Wooley, S. C., Lindroth, R. L., & Whitham, T. G. (2006). Importance of species interactions to community heritability: a genetic basis to trophic-level interactions. *Ecology Letters*, *9*(1), 78–85. doi:10.1111/j.1461-0248.2005.00844.x

Bascompte, J., Jordano, P., Melián, C. J., & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. *Proceedings of the National Academy of Sciences of the United States of America*, *100*(16), 9383–7. doi:10.1073/pnas.1633576100

Bassar, R. D., Marshall, M. C., López-Sepulcre, A., Zandonà, E., Auer, S. K., Travis, J., … Reznick, D. N. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes. *Proceedings of the National Academy of Sciences of the United States of America*, *107Bassar,*(8), 3616–21. doi:10.1073/pnas.0908023107

Blanchet, F. G., Legendre, P., & Borcard, D. (2008). Forward selection of explanatory variables. *Ecology*, *89*(9), 2623–2632. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/18831183>

Craig, T. P., Itami, J. K., & Price, P. W. (1990). The window of vulnerability of a shoot-galling sawfly to attack by a parasitoid. *Ecology*, *71*(4), 1471–1482. Retrieved from <http://www.jstor.org/stable/10.2307/1938284>

Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C. C., & Sanders, N. J. (2006). Plant genotypic diversity predicts community structure and governs and ecosystem process. *Science*, *313*(5789), 966–968. Retrieved from <http://www.sciencemag.org/content/313/5789/966.short>

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *The Open Ecology Journal*, *2*, 7–24. Retrieved from <http://goedoc.uni-goettingen.de/goescholar/handle/1/5837>

Dormann, C. F., & Strauss, R. (2014). A method for detecting modules in quantitative bipartite networks. *Methods in Ecology and Evolution*, *5*(1), 90–98. doi:10.1111/2041-210X.12139

Guimarães, P. R., Jordano, P., & Thompson, J. N. (2011). Evolution and coevolution in mutualistic networks. *Ecology Letters*, *14*(9), 877–85. doi:10.1111/j.1461-0248.2011.01649.x

Guimera, R., & Amaral, L. (2005). Functional cartography of complex metabolic networks. *Nature*, *433*(February), 895–900. doi:10.1038/nature03286.1.

Harmon, L. J., Matthews, B., Des Roches, S., Chase, J. M., Shurin, J. B., & Schluter, D. (2009). Evolutionary diversification in stickleback affects ecosystem functioning. *Nature*, *458*(7242), 1167–70. doi:10.1038/nature07974Graham, M. H. (2003). Confronting multicollinearity in ecological multiple regression. *Ecology*, *84*(11), 2809–2815. Retrieved from <http://www.esajournals.org/doi/abs/10.1890/02-3114>

Hezewijk, B. Van, & Roland, J. (2003). Gall size determines the structure of the Rabdophaga strobiloides host–parasitoid community. *Ecological Entomology*, *28*, 593–603. doi:10.1046/j.1365-2311.2003.00553.x

Ings, T. C., Montoya, J. M., Bascompte, J., Blüthgen, N., Brown, L., Dormann, C. F., … Woodward, G. (2009). Ecological networks--beyond food webs. *The Journal of Animal Ecology*, *78*(1), 253–69. doi:10.1111/j.1365-2656.2008.01460.x

Johnson, M. T. J. (2008). Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology*, *89*(1), 145–154. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/18376556>

Krause, A. E., Frank, K. a, Mason, D. M., Ulanowicz, R. E., & Taylor, W. W. (2003). Compartments revealed in food-web structure. *Nature*, *426*(6964), 282–5. doi:10.1038/nature02115

Nuismer, S. L., Jordano, P., & Bascompte, J. (2012). Coevolution and the architecture of mutualistic networks, 338–354. doi:10.5061/dryad.tk400

Olesen, J. M., Bascompte, J., Dupont, Y. L., & Jordano, P. (2007). The modularity of pollination networks. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(50), 19891–6. doi:10.1073/pnas.0706375104

R Core Team (2013). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Rezende, E. L., Albert, E. M., Fortuna, M. a, & Bascompte, J. (2009). Compartments in a marine food web associated with phylogeny, body mass, and habitat structure. *Ecology Letters*, *12*(8), 779–88. doi:10.1111/j.1461-0248.2009.01327.x

Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems. *Science*, *345*(6195), 1253497–1253497. doi:10.1126/science.1253497Thébault, E. (2012). Identifying compartments in presence-absence matrices and bipartite networks: insights into modularity measures. *Journal of Biogeography*, n/a–n/a. doi:10.1111/jbi.12015

Stouffer, D. B., & Bascompte, J. (2011). Compartmentalization increases food-web persistence. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(9), 3648–52. doi:10.1073/pnas.1014353108

Thébault, E., & Fontaine, C. (2010). Stability of ecological communities and the architecture of mutualistic and trophic networks. *Science (New York, N.Y.)*, *329*(5993), 853–6. doi:10.1126/science.1188321

Van Veen, F. J. F., Morris, R. J., & Godfray, H. C. J. (2006). Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. *Annual Review of Entomology*, *51*(107), 187–208. doi:10.1146/annurev.ento.51.110104.151120

Whitham, T. G., Young, W. P., Martinsen, G. D., Gehring, C. A., Schweitzer, J. A., Shuster, S. M., … Kuske, C. R. (2003). Community and Ecosystem Genetics: a Consequence of the Extended Phenotype. *Ecology*, *84*(3), 559–573. doi:10.1890/0012-9658(2003)084[0559:CAEGAC]2.0.CO;2

Whitham, T. G., Gehring, C. A., Lamit, L. J., Wojtowicz, T., Evans, L. M., Keith, A. R., & Smith, D. S. (2012). Community specificity: life and afterlife effects of genes. *Trends in Plant Science*, *17*(5), 271–281. doi:10.1016/j.tplants.2012.01.005

**Figure Legends**

**Figure 1.** (A) Metaweb of interactions among four species of galling insects (circles) and their six natural enemies (inverted triangles) found on the willow, *Salix hookeriana*,in a common garden experiment. The width of each link is proportional to the observed frequency of each interaction. Each colour corresponds to a different species in the metaweb. (B) Hierarchical clustering of dissimilarity in insect food web among 26 willow genotypes.

**Figure 2.** Probability of two common parasitoid guilds parasitizing the leaf galling midge *Iteomyia* as a function of gall density and gall size. (A) The probability of egg parasitism increases with higher gall density, but only for small galls. (B) The probability of larval parasitism decreases with both higher gall densities and larger galls.

Figures

1a) Genotype against your 4 different gall species and leaf gall size.

2.) Parasitism rates and density against genotype.

3) The slopes of the relationships for big and small galls.

**Paragraph 1**

1. Network theory does a way to characterize foodwebs and are typically characterizes as species in their trophic position and their interactions as connecting links, provides an intuitive visualization of the interaction web of a community.
2. By understanding the importance of a given species or their ineractions to the overall network, you can predict the structure of the network, as well as what might happen if they are gained or lost.
3. However, the overall assumption is that species are the same, when we know that populations are heterogeneous.
4. Consequently, we are only beginning to understand the role of individual variation for how networks function and therefore have no overarching understanding of its important.

**Paragraph 2**

Genetic variation is a key component of phenotypic variation among individuals within a food web.

Incorporating the genetic basis of phenotypic variation has increases our understanding of how individuals and species interact, at least in a pairwise context. For example, there is a long history in the plants- herbivores literature. Genetic resistance to herbivores has been known for decades

These interactions can even ripple through the foodweb. For example, extend to higher tophic levels (predators).

We also know that genetic variation can result in differences in overall community-level patterns. For example different genotypes of plants can support different herbivore and predator assemblages.

However, we missing the in-betweens from the pairwise interaction to the entire community, and a detailed understanding of all the linkages.

These links are fundamental to understanding a variety if things, including who are the key players, what happens if species/genotypes are lost or gained, etc….and ultimately how communities are structured and assembled.

Moreover, because genetic variation is the raw material for natural selection, incorporating the genetic basis of networks will result in a better understanding the effects of evolution on the structure of networks through time.

**Paragraph**

Why plants, galls and parasitoids are **THE** system to begin to incorporate genetic variation.

We have a good background on genetic resistance to herbivores

Galls represent both an interaction AND an extended phenotype…really the phenotypes of both the plant and the herbivore. In fact some of our best understanding of evolution and tritrophic interactions come from these systems. For example, gall size…thereby providing a direct link of traits between the plants, the herbivore, and susceptibility to predators/parasitoids.

Both the performance of the herbivore and the predator-prey interaactions are contained.

They are small, abundant, and ubiquous across X number of families, species, orders, and many trophic levels…

Relate back to previous….you can characterize the genetic and phenotypic variation, you can look at pairwise interactions, and the contained community allows an easier characterize of the interactions within a network which is difficult to do in open systems.

Taken together, this system is ideal to test these ideas

**Paragraph**

Here we use a common garden field experiment to address the role of intraspecific genetic variation in X, Y, and Z about network theory using 26 different genotypes of a dominant willow species, Salix Hookeriana and its associated galls (4 species) and parasitoids (6 species). We test the hypothesis that genetic variation will lead to dissimilarity in the structure of networks. This might occur through a variety of correlated pathways. First, genetic variation might influence the identity of the interactions within the network, either through different species identities or different links between the same species. For example, in the plant-gall-parasitoid system, prior evidence some galling species might prefer one host plant genotype over another or some parasitoids as well as gall size that might result in differences in parasitism. Genetic variation might also mediate the strength of interactions (i.e. the magnitude of a given linkage…or whatever) between species within network. For example, differences

thereby increasing the dissimilarity within the ecological networks

Given prior evidence from the plant-herbivore literature, we predict there will be genetic variation in resistance to insect galling, thereby influence both the density of galls, as well as gall size. In this study, we explore how this variation expands through the plant-gall-parisitoid network.



