**Heritability of ecological network structure: a field experiment with a plant-gall-parasitoid food web**

**Genetic basis to ecological network structure: a field experiment with a plant-gall-parasitoid network**

**Genetic basis to food web structure: a field experiment with a plant-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**

Species interactions are dominant drivers of population dynamics and energy flow in ecological communities (Thompson et al. 2012). Likely for this reason more than any, communities have been described as species interaction networks for over a century (Camerano 1880, Dunne 2006). Indeed, the conceptual and mathematical representation of species as nodes and interactions as links between nodes has enabled us to make predictions for how the loss/gain of species alters network structure and subsequently affects community dynamics (cite). The implicit assumption of species interaction networks, however, is that each species consists of a homogenous population of individuals, all of which interact with individuals of different species equally. Yet, virtually all populations are heterogenous mixtures of individuals that vary phenotypically and we are just beginning to seriously consider the consequences of this intraspecific variation for pairwise species interactions and the composition of entire communities (Clark et al. 2010; Bolnick et al. 2011; Violle et al. 2012). Consequently, our current representation of ecological networks may be ill-suited for a mechanistic understanding of how communities are structured.

Genetic variation is a key driver of intraspecific variation and there are a growing number of examples demonstrating its effects on pairwise species interactions and community composition (Antonovics 1992; Whitham et al. 2003, 2012). For example, we have known for decades that plants exhibit genetic variation in traits that confer resistance to insect herbivores (e.g. toxic secondary metabolites), thereby affecting the strength of pairwise plant-insect interactions (cite). The strength of these plant-insect interactions can then cascade up to affect pairwise interactions between insect herbivores and upper trophic levels (Bailey et al. 2006; Abdala-Roberts \_\_\_). Similarly, fish predators exhibit genetic variation in traits that influence their ability to capture zooplankton (e.g. gill raker depth), which can mediate the strength of trophic cascades on phytoplankton communities (Post et al. 2008; Harmon et al., 2009; Bassar et al., 2010). What these studies are missing though is a mechanistic understanding of the direct and indirect effects of genetic variation on the composition of trophic links within the food web. Identifying the genetic basis to multitrophic links is crucial, as this enhances our ability to predict the structure of food webs. Moreover, because genetic variation is the raw material for evolution, incorporating the genetic basis of networks should enable us to begin to predict the effects of microevolutionary processes (e.g. natural selection, genetic drift) on the structure of food webs through time. Yet, no study to date has tested whether there is a genetic basis to multitrophic links and so the eco-evolutionary dynamics of ecological networks remain poorly understood (Melian et al. 2011; Moya-Larano et al. 2012).

Here, we test the hypothesis that genetic and phenotypic variation drives variation in ecological networks using a plant-gall-parasitoid food web. This insect food web is ideal for examining the genetic basis to food web structure for several reasons. First, the closed morphology of most insect galls restricts their natural enemy community to a small number of specialists that can successfully locate and parasitize galls, making it easy to identify the quantify the source of mortality. Second, many plant species are attacked by multiple, closely related gall species that share the same parasitoid community, making this system amenable to building quantitative species interaction networks (van Veen et al. 2006). Third, there is a plethora of evidence from the plant-insect literature demonstrating plant genetic variation in resistance to galling insects (cite). Variation in gall resistance may then indirectly affect food web structure through both gall density- and gall trait-mediated pathways. For example, differences in gall density among plant genotypes could affect the foraging behavior of upper trophic levels (e.g. density-dependent or density-independent attack). In addition, the phenotype of a gall results from an interaction between the insect and plant phenotypes (Abrahamson and Weis Monograph). 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). Consequently, plant-gall-parasitoid food webs enable us to identify the different mechanisms by which plant genetic variation affects food web structure.

To test our hypothesis that genetic and phenotypic variation affects ecological network structure, we used a common garden field experiment. This common garden consisted of 26 genotypes of a common plant species (Coastal willow, *Salix hookeriana*) from a single population, and we quantified differences in the structure of its gall-parasitoid food web (four species of gall midges, six species of parasitoids) among the different genotypes. Prior work in this system has found substantial phenotypic variation among different *S. hookeriana* genotypes, which has also been linked to variation in the density of one of its common gall species (*Iteomyia salicisverruca*) (Barbour et al. 2015). If genetic and phenotypic variation affects ecological network structure, we have several testable predictions. First, we predict that the composition of gall-parasitoid links will vary among willow genotypes. Second, we predict that gall community composition will vary among willow genotypes. Third, we predict that the size of galls will vary among willow genotypes. Fourth, we predict that gall community composition and gall size will drive variation in the composition of gall-parasitoid links. Fifth, we predict that gall community composition will be determined by variation in leaf quality and plant architecture traits. Sixth, we predict that variation in gall size will be determined by variation in leaf quality and plant architecture traits. Taken together, our study seeks to understand the mechanisms by which intraspecific variation scales up to affect the assembly of ecological networks. Furthermore, this empirical test of whether genetic variation influences ecological network structure, is a crucial step toward a predictive science of the eco-evolutionary dynamics of ecological networks.

**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). 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.

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 having 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 modelled 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 only had 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 (count 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 modelled 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 always 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 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 in press). We used scatterplots and Pearson correlation coefficients to identify a small number of traits for further model selection. 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*

In concordance with our prediction, we found that willow genotype 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. 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 gall species varied in their susceptibility 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. 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 significantly vary (*H2* = 0.04, RLR test = 0.55, P = 0.187) (Fig. 2b).

Genetic variation in resistance to galling insects mediated the observed shifts in the insect food web among willow genotypes. 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 by the numerical response of egg and larval parasitoids to *Iteomyia* galls as well as larval parasitoids to *Rabdophaga*-bud galls. Specifically, the density of *Iteomyia*-egg parasitism increased with higher *Iteomyia* gall density, but was especially pronounced on willows with small galls (*R*2 = 0.47, F3,77 = 22.40, P < 0.001). Similarly, the density of *Iteomyia*-larva parasitism increased with higher *Iteomyia* gall density, but decreased on willows with 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).

Interestingly, numerical responses of the different parasitoid guilds did not always correspond to a similar functional response. For example, the probability of an egg parasitoid attacking Iteomyia increased with higher gall density, but its attack rate also depended on gall size (𝝌23,77 = 32.77, P < 0.001)(Fig. 3a). In contrast, he probability of a larval parasitoid attacking Iteomyia actually decreased with increasing gall density (𝝌22,78 = 18.33, P < 0.001), although it also had higher attack rates on small galls (Fig. 3b). 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).

*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 (*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**

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**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.



