**Intraspecific genetic variation increases network complexity: empirical evidence from a plant-insect food web**

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**Abstract**

I might start with a general sentence about what Eco-evolutionary dynamics is and why its cool. Predicting the eco-evolutionary dynamics of ecological networks requires a comprehensive understanding of how population-level genetic variation affects community-level species interactions. To date though, we are lacking empirical knowledge of the extent to which genetic variation determines the assembly of ecological networks, as well as 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 extent to which heritable trait variation within a dominant host plant determines the assembly of associated food webs, and drives overall network complexity. We found that heritable variation in a susceptibility to antagonistic interactions with galling insects, which, in turn, indirectly affected trophic interactions between with insect parasitoids. Direct and indirect genetic effects increased food web complexity by 50% over the range of genetic variation in the experimental host-plant population. Taken together, our results indicate that genetic variation structures ecological networks and may affect network persistence over time, thereby …..link back to eco-evolutionary dynamics so you start and end with it.

**Significance**

We know that the gain or loss of species can have cascading effects on the complexity and persistence of a food web; however, it is less clear whether similar fluctuations in population-level genetic variation, an often over-looked component of biodiversity, will similarly affect food webs. In this study, we document the host-plant genotypes vary in their direct and indirect effects on associated insect food webs resulting in unique networks of species among clones. Moreover, the gain or loss of particular genotypes would fundamentally alter total food web complexity. Taken together, our results suggest that preserving genetic variation within dominant species may be a critical for maintaining complex and robust food webs under future environmental change.

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**Introduction**

Network theory has provided both a conceptual and quantitative approach for mapping interactions between species and making predictions about how the gain or loss of species affects the structure and dynamics of ecological networks(1–3). 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 (4–6). Consequently, there is a clear need to account for the role of intraspecific variation in structuring ecological networks (7).

Genetic variation is a key driver of intraspecific variation and many studies have now demonstrated direct and indirect genetic effects on species interactions(8–10) and the composition of communities across multiple trophic levels (11–14). Nevertheless, there are two key components missing from these studies that are preventing us from scaling effects of genetic variation on pairwise interactions to the network level. 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 (11–14), thereby ignoring interactions, or quantify simple tritrophic interactions (8–10), 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, studies have not examined the effect of genetic variation *per se* on species interactions*,* rather prior work has focused on whether different genotypes support particular species(15). Demonstrating the genetic specificity of interactions (i.e. differences among genotypes) are only the first step in predicting how the gain or loss of genetic variation will affect species interactions, and ultimately the structure of ecological networks (6).

The structure of an ecological network could be affected by intraspecific genetic variation through at least two different mechanisms. For a food web (network of trophic interactions), genetic variation in resource quality may alter both the abundances (16) and/or phenotypes (17) of consumer species. These direct genetic effects on consumers may then have cascading effects on the strength of trophic interactions between consumers and their associated predators; resulting in distinct compositions of trophic interactions associated with different genotypes of the basal resource (Fig. 1). Regardless of the mechanism, if such genetic specificity in the composition of trophic interactions occurs, we would predict that increasing genetic variation will result in greater food web complexity (number of interactions per species; (6, 18) (Fig. 2). Moreover, greater complexity may in turn affect network dynamics, as more complex food webs are predicted to be more robust to species extinctions(1, 19).

In this study, we quantify the genetic specificity of trophic interactions and test the hypothesis that increasing genetic variation results in greater network complexity using a common garden experiment of 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* (hereafter, willow) displays genetic variation in resistance to its galling insect herbivore community(16). 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. 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) (20). Since the gall phenotype (size and shape) is determined, in part, by the genotype of the plant (20), 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 how 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.

**Results and Discussion**

**Testing the genetic specificity of the willow-gall interaction network.** We observed clear differences in the abundance of 3 of the 4 galling insects among willow genotypes (multivariate GLM, 𝛘225,119 = 202.40, *P* = 0.001). Specifically, we found that the average abundance of leaf, bud, and apical-stem galls varied 10-, 8-, and 1.4-fold among willow genotypes, respectively (Fig. 2A-C), resulting in 69% dissimilarity in the average composition of gall communities (*F*22,89 = 1.96, *P* = 0.001). Moreover, we found that the average diameter of leaf galls varied 2-fold among willow genotypes (Fig. 2D). This observed genetic specificity in the abundance and phenotypes of insect herbivores is in concordance with previous work in this system (16), corroborates decades of work in other plant-gall(8, 11, 20) and plant-herbivore systems(12, 15).

Importantly though, our extensive screening of willow phenotypes (*Materials and Methods*) enabled us to determine the mechanisms underlying the genetic specificity of the willow-gall interaction network. In particular, we found that leaf C:N, certain leaf secondary metabolites (flavanones/flavanonols PC1), and plant size were associated with changes in the abundance of galling insects (multivariate GLM, 𝛘23,104 = 28.44, *P* = 0.004; Table S3), whereas leaf gall diameter was determined by variation in a different suite of leaf secondary metabolites (salicylates/tannins PC1 and flavones/flavonols PC1)(weighted linear model, *F*2,59 = 8.27, *P* < 0.001; Table S3). These results highlight that accounting for intraspecific variation in multiple plant traits is important for predicting antagonistic interactions between plants and insect herbivores (16), and should therefore be incorporated into mechanistic models of food web structure.

**Testing the genetic specificity of the gall-parasitoid interaction network.** We found that the effects of willow genetic variation extended beyond pairwise interactions with herbivores (11, 12, 15) and simple food chains (8–10, 20) to determine the assembly of the gall-parasitoid interaction network (multivariate GLM, 𝛘225,119 = 357.10, *P* = 0.001; Table S1). Specifically, the frequency of parasitism from three parasitoids (*Platygaster* sp., *Mesopolobus* sp., and *Torymus* sp.) on leaf galls varied 270%, 30%, and 40% among willow genotypes, respectively (Fig. 3A-C), resulting in 78% dissimilarity in the average composition of gall-parasitoid interactions (*F*12,45 = 1.57, *P* = 0.007). In addition to the abundance of trophic interactions, the probability of a gall being parasitized also depended on willow genotype (Table S1), a pattern that was particularly strong for leaf galls (Fig. 3D).

The genetic specificity of the gall-parasitoid interaction network was determined by variation in both the abundance and size of galling insects. Specifically, we found that the abundance of 67% (8 of 12) of the gall-parasitoid interactions increased with the abundance of their associated galls, and that leaf gall size affected the abundance of trophic interactions with both leaf and bud galls (multivariate GLM, 𝛘24,76 = 179.80, *P* = 0.001; Table S3). In terms of interaction strength, we found that parasitism rate decreased by 25% with every 1 mm increase in leaf gall diameter (GLM, 𝛘21,79 = 22.28, *P* < 0.001). Nevertheless, the strength of trophic interactions with individual parasitoid species depended on both leaf gall size and abundance (Fig. 5A-B; Table S4), suggesting that natural selection has the potential to shape food web structure. For example, if there were selection on willows for increased resistance to leaf galls through smaller galls and lower gall abundances, then we would expect to see more parasitism overall and a shift in dominance from *Platygaster* to *Mesopolobus*; *Mesopolobus* had its highest attack rates on small galls at low abundances (Fig. 5A). While our results are limited to the effects of standing genetic variation on a tri-trophic food web over a single season, there is growing evidence that eco-evolutionary dynamics play an important role in determining pairwise, consumer-resource interactions (24, 25). Taken together, understanding how evolutionary processes affect the structure of ecological networks, and vice versa (26, 27), is likely a fruitful topic for future research.

**Genetic variation determines network complexity.** To test the hypothesis that increasing genetic variation results in greater network complexity, we used our empirical data to predict how the complexity of the plant-insect food web would change across different levels of genetic variation (no. of genotypes) in the plant population (*Materials and Methods*). We found that the genetic specificity of the willow-gall and gall-parasitoid interaction networks resulted in a 50% increase in average food web complexity over the range of willow genetic variation (Fig. 5A). In part, this positive relationship is due to random draws of genotypes with complex food webs (i.e. sampling effects, (28). 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). Indeed, we found that willow genotypes differed by 73% in the average composition of their trophic interactions (Fig. 5B), suggesting that complementarity was an important contributor to the positive relationship between genetic variation and food web complexity. 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 (29, 30), but partitioning non-additive effects on the strength and composition of species interactions in ecological networks will require additional experimental work.

Our results clearly suggest that genetic variation in a foundation plant species affects food web structure; however, there is a growing literature documenting the effects of genetic variation in herbivores and predators from a variety of taxa on community dynamics and ecosystem processes (14, 31–33). An important future direction for network theory will be to examine whether genetic variation at certain key nodes, such as foundation or keystone species or top predators???, enhances the robustness of ecological networks compared to nodes of less structural importance. This direction would 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(34–36)?

**Conclusions**

Our results demonstrate that changes in genetic variation of a foundation plant species can fundamentally alter food web complexity and therefore the persistence of food webs. There are two main conclusions from our work. First, intraspecific variation in multiple traits is an important driver of network structure; therefore, mechanistic models of food web structure should incorporate such variability within species (7) as this can enhance the power of these models to predict what??? (37). Given that plants, insect herbivores, and their parasitoids comprise over half of all known species of metazoans (38, 39), accounting for intraspecific variation in a wide range of functional traits should be a priority for future food web models (40). Second, understanding the direct and indirect effects of genetic variation on trophic interactions is essential for predicting how evolutionary processes will affect the structure and persistence of food webs over time. Indeed, our simulation suggests that the loss of genetic variation will result in less complex food webs. Moreover, genetic variation provides the raw material for evolution by natural selection; therefore, losing genetic variation in foundation or keystone species may hinder the adaptive capacity of both the species and the food web under future environmental change (41, 42). Given that the current rate of population extinction is orders of magnitude higher than the rate of species extinction (43), 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 (33, 44).

**Materials & Methods**

**Common garden and plant trait sampling.** To isolate the effects of coastal willow (*Salix hookeriana*) 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(16).

To identify the plant traits that determine resistance to 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 (i.e. proportion of variance due to willow genotype) [mean leaf quality *H*2 = 0.72; mean architecture *H*2 = 0.27; range of *H*2 for all traits = 0.15 - 0.97; (16)). For further details on how these willow traits were sampled and quantified, see methods in (16). 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(16). 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(16), 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.** To quantify the abundance of galls and gall-parasitoid interactions associated with each willow genotype, we collected galls from about 5 randomly chosen replicates of each genotype in September 2012 (N = 145 willows, range = 4 - 9 replicates per genotype). For each replicate willow, we collected all galls occurring on one randomly selected basal branch. We restricted our gall collections to those induced by midges in the insect family Cecidomyiidae. These species included a leaf galler, *Iteomyia salicisverruca*, bud galler, *Rabdophaga salicisbrassicoides*, apical-stem galler (unknown midge species), and mid-stem galler, *Rabdophaga salicisbattatus*. To quantify the abundance of 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. In total, we identified one predatory midge (Lestodiplosis sp., Family: Cecidomyiidae) and five species of hymenopteran parasitoids, including *Platygaster* sp. (Family: Platygastridae), *Mesopolobus* sp. (Family: Pteromalidae), *Torymus* sp. (Family: Torymidae), *Tetrastichus* sp. (Family: Eulophidae), and an unknown species of Mymaridae (hereafter, Mymarid sp. A). 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 to the nearest 0.01 mm at their maximum diameter (perpendicular to the direction of plant tissue growth).

To test the genetic specificity of the willow-gall interaction network, we analyzed variation 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 because we expected that averages based on more galls reflect a more accurate estimate of the average size of galls found on a willow individual. For gall abundances, we analyzed multivariate generalized linear models (multivariate GLMs, error distribution = negative binomial, link function = log) with willow genotype as the predictor variable and a matrix of gall abundances as the response variables. For gall community composition, we used permutational MANOVA (PERMANOVA) with willow genotype as the predictor variable and a matrix of Bray-Curtis dissimilarities in gall abundances as the response variable. To identify the plant traits mediating resistance to galling insects, we used the same, previous analyses for gall sizes (weighted linear models) and abundances (multivariate GLMs) 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 Aikaike information criteria (AIC) to identify a nested set of candidate statistical models. We then used likelihood ratio tests to identify the statistical model of willow traits that best predicted gall abundances or gall sizes.

To quantify the genetic basis of the gall-parasitoid interaction network, we tested for differences in the abundance, composition, and strength of gall-parasitoid interactions among willow genotypes. For gall-parasitoid interaction 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 interactions as the response variables. To identify the extent to which gall size and gall abundances determined the abundance of gall-parasitoid interactions, 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 interactions. For the interaction strength of gall-parasitoid interactions, we used separate GLMs (error distribution = binomial, link function = logit) with willow genotype as the predictor variable and proportion of galls parasitized as our response variable for each gall species. 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 used our empirical data to predict the complexity of the plant-insect food web 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 interactions 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 interactions 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, , as an index of food web complexity(45, 46). is based on Shannon Entropy and is the average of the effective number of prey and predatory interactions for a given species, weighted by their energetic importance (i.e. total number of prey and predatory interactions). Specifically, is calculated using the following equations. Given an *s*-by-*s* food web matrix **b** = , with corresponding to the number of individuals of species j (galls or parasitoids) emerging from species i (willow or galls) per willow branch over a single growing season, the sum of row *i*, the sum of column *j*, and the total sum, the Shannon indices for the prey and predator interaction is

with the effective number of prey and predatory interactions and respectively; quantitative weighted link density,

(hereafter, food web complexity) is less sensitive to variation in sample size compared to other measures of food web complexity (46), 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 polycultures of 4 - 20 genotypes; N = 98 for polycultures of 3, 21, and 22; N = 89 for polycultures of 2 and 23; N = 1 for the polyculture of 25; and N = 25 for monocultures).

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**Figure Legends**

**Fig. 1.** Genetic specificity of trophic interactions in a plant-insect food web. This food web represents the trophic interactions aggregated from all plant individuals sampled in this common garden experiment, whereas each genotype subweb represents the trophic interactions aggregated from all plant individuals of the corresponding genotype. The species comprising this food web include 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), *Tetrastichus* sp. (Family: Eulophidae), *Lestodiplosis* sp. (Family: Cecidomyiidae), *Mesopolobus* sp. (Family: Pteromalidae), *Platygaster* sp. (Family: Platygastridae), and Mymarid sp. A (Family: Mymaridae). The width of each grey link is proportional to the number of individuals associated with each trophic interaction. Note: the width of trophic interactions was scaled to be comparable among genotype subwebs, but not between subwebs and the metaweb, in order to emphasize the differences among genotype subwebs.

**Fig. 2.** Conceptual model of how increasing genetic variation (number of shades of green circles) results in greater food web complexity (number of interactions per species). If different genotypes of a basal resource are associated with distinct compositions of trophic interactions (i.e. genetic specificity of trophic interactions), then increasing genetic variation in the resource will result in a more complex food web because of the increase in the number of interactions per species at all three trophic levels. Colors correspond to different trophic levels (green = basal resource, blue = primary consumer, orange = secondary consumer), while different shapes within each trophic level correspond to different species.

**Fig. 3.** Coastal willow (*Salix hookeriana*) exhibits genetic variation in resistance to galling herbivores. Among the 26 willow genotypes we surveyed in our common garden experiment, we found that: (A) average abundance of leaf galls varied 10-fold (GLM, 𝛘225,119 = 74.60, *P* = 0.001); (B) average abundance of bud galls varied 8-fold (GLM, 𝛘225,119 = 55.02, *P* = 0.006); (C) average abundance of apical-stem galls varied 1.4-fold (GLM, 𝛘225,119 = 44.47, *P* = 0.042); and (D) average diameter of leaf galls varied 2-fold (weighted linear model, *F*23,57 = 2.17, *P* = 0.009). Plots (*A – C*) display the median (bar within box), interquartile range (IQR = 25th to 75th percentiles, box edges), 1.5 \* IQR (whiskers), and outliers (points) for gall abundances (no. per branch) found on each willow genotype. For plot (*D*), each circle corresponds to the average gall diameter for an individual willow and the size of the circle is scaled according to the number of galls used to calculate the weighted average for each willow genotype (diamond). Colors correspond to different gall species (orange = leaf gall, blue = bud gall). For all plots, we ordered willow genotypes based on mean leaf gall abundance (low to high).

**Fig. 4.** Coastal willow (*Salix hookeriana*) exhibits genetic variation in the abundance and strength of gall-parasitoid interactions. Among the 26 willow genotypes we surveyed in our common garden experiment, we found that: (*A*) leaf gall parasitism by *Platygaster* sp. varied 270% (GLM, 𝛘225,119 = 79.51, *P* = 0.001); (*B*) leaf gall parasitism by *Mesopolobus* sp. varied 30% (GLM, 𝛘225,119 = 50.00, *P* = 0.009); (*C*) leaf gall parasitism by *Torymus* sp. varied 40% (GLM, 𝛘225,119 = 60.11, *P* = 0.001); and (*D*) the proportion of leaf galls parasitized varied between 0.0 and 1.0 (GLM, 𝛘223,58 = 75.79, *P* < 0.001). Plots (*A – C*) display the median (bar within box), interquartile range (IQR = 25th to 75th percentiles, box edges), 1.5 \* IQR (whiskers), and outliers (points) for the abundance of gall-parasitoid interactions (no. per branch) associated with each willow genotype. For plot (*D*), each circle corresponds to the proportion of galls parasitized on each replicate willow and the size of the circle is scaled according to the number of galls used to calculate the weighted average for each willow genotype (diamond). Colors correspond to different gall-parasitoid interactions. As with Fig. 3, we ordered willow genotypes based on mean leaf gall abundance (low to high).

**Fig. 5.** Variation in the size and abundance of leaf galls on willows determines the strength and composition of gall-parasitoid interactions. (*A – B*) In general, the proportion of leaf galls parasitized by both *Platygaster* and *Mesopolobus* decreases as gall size increases, while *Torymus* exhibits the opposite pattern. On willows with small leaf galls though (< 8 mm), *Mesopolobus* had the highest attack rate at low gall abundances (1 – 4 leaf galls per branch, N = 46 per parasitoid species), whereas *Platygaster* was the dominant parasitoid at high gall abundances (5 – 22 leaf galls per branch, N = 35 per parasitoid species). Lines correspond to slopes estimated from generalized linear models (GLMs), while each line type and color corresponds to a different parasitoid species (solid blue = *Platygaster*; short, dashed green = *Mesopolobus*; long, dashed orange = *Torymus*). Points were jittered slightly to avoid overlapping values.

**Fig. 6**. Increasing genetic variation in coastal willow (*Salix hookeriana*) results in a more complex plant-insect food web due to complementarity in trophic interactions. (*A*) The average complexity (*LDq*) of the plant-insect food web increased by 50% over the range of genetic variation (no. of genotypes) in the willow population. (*B*) The average composition of trophic interactions (willow-gall and gall-parasitoid) differs by 73% among willow genotypes [constrained analysis of principal coordinates (CAP) on Bray-Curtis dissimilarities, *F*22,89 = 1.90, *P* = 0.001]. For plot (*A*), open, grey circles correspond to food web complexity of individual simulations (N = 100 for polycultures of 4 - 20 genotypes; N = 98 for polycultures of 3, 21, and 22; N = 89 for polycultures of 2 and 23; N = 1 for the polyculture of 25; and N = 25 for monocultures), whereas solid, blue circles correspond to the average complexity of food webs at each level of genetic variation. The dashed line is the highest level of complexity observed on a single willow genotype and represents the expected magnitude of food web complexity under sampling effects alone. For ordination diagram (*B*), black letters and grey ovals correspond to the centroid and standard error of the centroid for each willow genotype, respectively.