**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**

An ecological network provides a map of species interactions within a community. By accurately quantifying these species interactions, we can begin to understand the processes that organize these networks (Williams & Martinez 2000; Petchey et al. 2008; Eklof et al. 2013) as well as how network structure affects the persistence of ecological communities (Stouffer & Bascompte 2011; Theabault & Fontaine 2012; Roher et al. 2014). Typically though, studies quantifying the structure of ecological networks have been resolved to the species level (Ings et al., 2009). These species-level networks implicitly assume that each species consists of a homogenous population of individuals, all of which interact with individuals of different species in the same way. Yet, virtually all populations are heterogenous mixtures of individuals and this phenotypic variation can have large effects on the structure and dynamics of ecological networks (Woodward et al., 2010; Bolnick et al. 2011; Melian et al., 2014). 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 individual differences and there are a growing number of examples demonstrating its cascading effects on multitrophic interactions (Antonovics 1992; Whitham et al. 2003, 2012). For example, genetic variation within plant species can influence the density and size of herbivores, which in turn alters interactions with higher trophic levels (Bailey et al., 2006; Johnson 2008; Abdala-Roberts and Mooney 2014). Similarly, genetic variation within predators has been found 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 is important, as this 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, 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). 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**

**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.



