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Plant sex alters Allee effects in aggregating plant parasites

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Species interactions are central to our understanding of population dynamics. While density typically strengthens competition, reducing absolute fitness, Allee effects can reverse this pattern, increasing fitness with density. Allee effects emerge in host–parasite systems when higher parasite densities dilute immune responses or increase resource-mobilization. The optimal density of individuals in these systems should be influenced by how host quality alters the rates at which facilitative and competitive effects change across densities. We tested these ideas using sumac *Rhus typhina* and a gall-forming parasite *Melaphis rhois* that attacks sumac leaves. Fitness peaked at intermediate densities, indicating an Allee effect, but the fitness peak depended on host sex. Patterns of abundance mirrored fitness patterns, with galls clustered on leaves and female hosts supporting greater numbers of galls. Within leaves, galls near the stem were more fit, and gall-makers preferentially oviposited near to the stem. The patterns of fitness and abundance are consistent with Allee effects caused by increased resource mobilization at higher gall-maker densities rather than diluted immune responses. Our results suggest that Allee effects in parasites can be described as the summative effects of competitive and facilitative processes and, because both are common, Allee effects are likely common in host–parasite systems.

Introduction

Interactions among individuals shape population dynamics and structure communities, forming the basis of our understanding of ecological and evolutionary dynamics. Ecologists are increasingly showing that interactions among individuals vary not only in magnitude, but also in type (Berlow 1999, McIntire and Fajardo 2011, He et al. 2013). Interestingly, an interaction between two individuals can not only change in strength, but can even change sign, switching between negative (e.g. competitive) and positive (e.g. facilitative) in different environments. These switches in the sign of an interaction often occur when the presence of the interacting species or individual causes the environment to become less stressful (He et al. 2013) or more nutritive for a focal species (Courchamp et al. 1999). For example, intraspecific interactions can switch from negative in benign seasons when resource competition is greatest to

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positive in stressful seasons when conspecifics can provide shelter (Biswas and Wagner 2014). Although most recent work on the variability of interactions has focused on interspecific interactions, there is an emerging consensus that shifts in the strength and direction of intraspecific interactions may play an important role in the dynamics of many populations (McIntire and Fajardo 2011, Biswas and Wagner 2014).

Density can increase, decrease, or change the sign of intraspecific interactions, as is explicitly modeled in population dynamic models, including those addressing changes in the per capita or total effect of competition. Allee effects occur when there is a positive relationship between a component of individual fitness and the number or density of conspecifics (Stephens et al. 1999, Courchamp and MacDonald 2001, Berec et al. 2007). These effects do not necessarily occur because low density confers reduced per capita competitive effects, but rather facilitative mechanisms outweigh competitive mechanisms at low densities (Courchamp et al. 1999). For example, Fajardo and McIntire (2011) showed tree seedlings planted at high density were more likely to survive than low density individuals, and suggested that seedlings planted at high density experienced increased resource competition, but the negative effects of increasing resource competition were more than offset by the facilitative effects of protection from high winds. In addition to reducing the impact of environmental stressors, density can alter the importance of facilitation via several mechanisms including cooperative defense (Stamps and Buechner 1985, Tobin et al. 2011), habitat alteration (Berec et al. 2007), and cooperative resource acquisition (Fordyce 2003, Karban and Agrawal 2002). The latter mechanism causes positive density dependence by increasing per capita resource availability, and is thought to be widespread in gregarious consumers (Courchamp and MacDonald 2001, Karban and Agrawal 2002).

Ecologists are often interested in the spatial distribution of parasites, with the clumped distribution of many parasites suggesting that Allee effects may be important (Anderson and May 1978). One group of parasites where cooperative resource acquisition may be common is gall forming insects (Larson and Whitham 1991). Many gall forming insects release chemicals to mobilize resources from their plant host, allowing gall formation, accelerating gall growth, and increasing gall-maker fitness (Fay et al. 1996). The concentration of resource-mobilizing chemicals typically increases with gall density (Fig. 1A; Sopow et al. 2003), but the effect of chemical concentration on resource availability is saturating (Fig. 1B; McCalla et al. 1962). While facilitative resource-acquisition is considered to be a saturating function of density, resource competition is often assumed to be linearly related to density (Lotka 1925, MacArthur 1970, Case and Taper 2000), or at least to saturate at relatively high densities (Fig. 1C; Gilpin and Ayala 1973, Abrams et al. 2008). If fitness increases with per capita resource availability (Johnson 1980, Abrams and Chen 2002), then we would predict that the resulting effect of density on fitness should be hump-shaped (Fig. 1D; Hughes et al. 2004), ultimately creating stabilizing selection on density (Lande and Arnold 1983). In this model, facilitation causes initial positive density dependence by increasing concentrations of a resource-mobilizing chemical and thus resource availability. Increasing levels of the chemical has little effect on resource availability at high densities, causing negative density dependence as per capita resource uptake exceeds per capita resource availability (Fig. 1C–D). The ascending and descending limbs of the curve can then be thought of as those densities at which facilitation is stronger than competition, and at which competition is stronger than facilitation respectively (Fig. 1C–D). Ultimately, hump-shaped density dependence can be measured as stabilizing selection on gall-maker density, with the detecting of such selection being indicative of Allee effects.

Other mechanisms, such as cooperative defense, can also produce hump-shaped density dependence or Allee effects. For example, plant defensive compounds may generate Allee effects in gall-makers (Cornelissen and Stiling 2005). In cases of induced plant defense, increasing gall density can dilute the immune response such that there is less defensive compound per gall-maker (Supplementary material Appendix 1 Fig. A1). However, at yet higher densities the benefits of immune dilution is likely to be outweighed by increasing resource competition (Supplementary material Appendix 1 Fig. A1). Ultimately, this tradeoff could be mediated by either changes in gall-maker fecundity or offspring survival, with the former being better characterized (Cornelissen and Stiling 2005). While it is often difficult to distinguish between cooperative resource acquisition and cooperative defense, we can use within- and among-host variation in host quality to better understand processes underlying Allee effects.

In systems where a parasite experiences hump-shaped density dependence, host quality is likely to alter the rates at which facilitation saturates and competition depresses fitness across densities (Harvey et al. 1994, Abrams et al. 2008). As a result, host quality should determine optimal parasite density. Insect galls are often formed on hosts differing in quality (Stiling and Moon 2005, Egan and Ott 2007), with high quality hosts either having greater resource availability or reduced defensive compounds (Ågren 1988, Cornelissen and Stiling 2005). However, changes to these two components of host quality are predicted to have different effects on optimal density. For example, classic population models that incorporate Allee effects (Liebhold and Bascompte 2003, Dennis 1989) predict that decreasing host defense results in a reduced optimal gall density as fewer individuals are needed to result in an equally diluted immune response (Fig. 1E), whereas increasing resource availability increases optimal density because resource competition is less severe (Fig. 1F; Supplementary material Appendix 1). Crucially, both mechanisms increase maximum fitness (Fig. 1E–F), so we can use the direction of change in optimal density to infer whether cooperative resource acquisition or cooperative defense is likely occurring. Such inferences should be broadly applicable, including between the sexes when

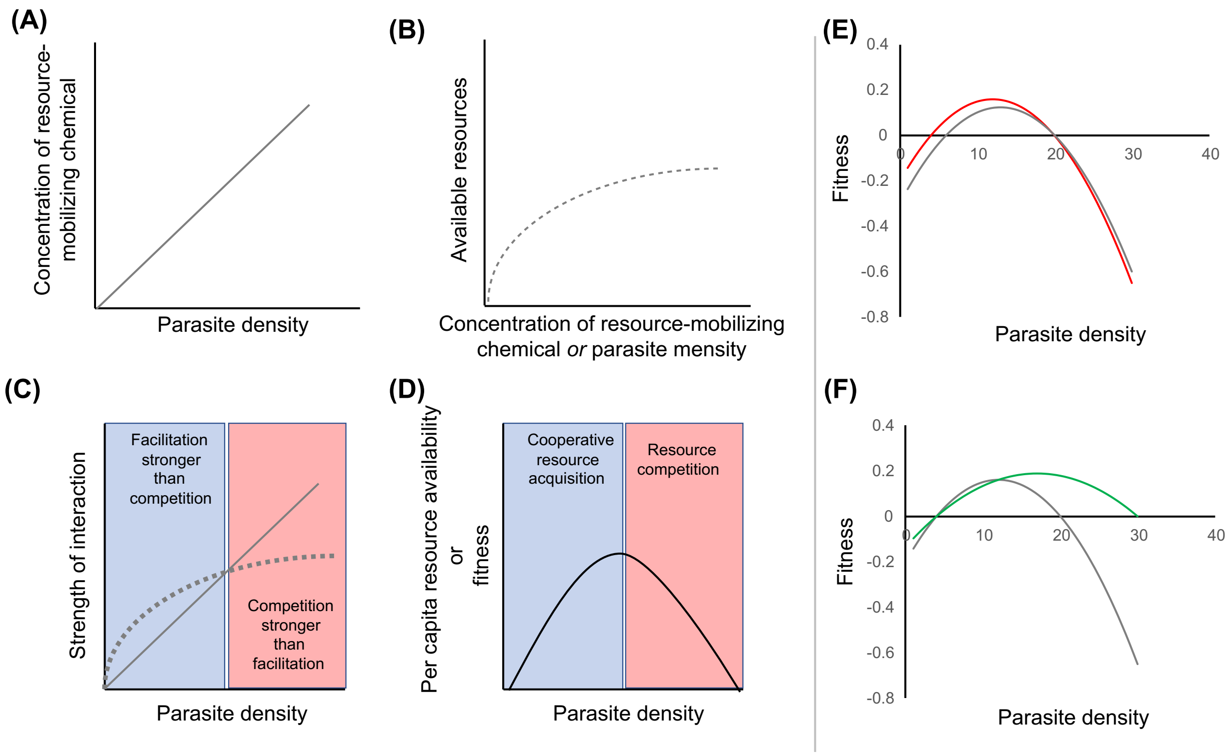

Figure 1. Hypothetical trends in density, resource-mobilization, and fitness of parasites that produce resource-mobilizing chemicals. (A) Each individual produces a similar amount of a resource-mobilizing chemical leading to a constant increase in the concentration of resource-mobilizing chemicals. (B) Despite a linear increase in the concentration of resource-mobilizing chemicals with parasite density, the effect on total resources is saturating as continuing to increase chemical concentration fails to appreciably increase the amount of resources available. (C) The strength of facilitation (dotted line) and competition (solid line) both increase with parasite density but facilitation initially increases more quickly whereas competition increases linearly. These relationships cause facilitation to be stronger than competition at low density (blue), but competition to outweigh facilitation as high density (pink). (D) Patterns of competition and facilitation create hump-shaped density–fitness relationships. Initially, increasing density increases the per capita resource availability and individual (clonal) fitness (blue). However, when the total amount of available resources saturates, per capita resource availability declines, increasing competition among individuals (pink). The optimal density occurs at the peak of the curve where the strength of facilitation and competition are equal. Using a simple population dynamics model (Supplementary material Appendix 1) we show that reducing host defenses (E) and increasing resource availability (F) both increase maximum fitness, but alter the optimal density in opposite ways. Reducing host defenses (red) reduces the optimal density (E), whereas increasing host resource availability (green) increases the optimal density (F).

individuals act as hosts. For example, the sexes often differ in both resource availability (Ågren 1988) and defenses (Cornelissen and Stiling 2005), making it difficult to infer the process underlying different levels of herbivory or parasitism. Females are likely to have greater resource availability owing to their use in making fruits (Ågren 1988), but may also have stronger defenses (Cornelissen and Stiling 2005). Distinguishing between these mechanisms may allow us to better understand the distribution of gall-makers and parasites generally.

Saturating cooperative resource acquisition causes individual fitness to peak at intermediate densities, ultimately causing stabilizing selection that favors mothers who oviposit gall-makers at intermediate densities (Fig. 1D; Lande and Arnold 1983). If adults searching for oviposition sites are able to distinguish among leaves with differing densities of galls (Whitham 1980), then we expect them to select habitat (oviposition sites) such that the density conferring maximum fitness is the modal density of gall-makers on leaves (Fretwell and Calver 1969), resulting in clumped distributions of an optimal size.

Spatially heterogeneous resource availability, as well as density effects, should select for individuals that recognize cues to optimize oviposition locations among and within hosts. Adult gall-makers that distinguish between high and low quality hosts (Egan and Ott 2007), and detect differences in density, should oviposit at higher densities on higher resource hosts (Fretwell 1972, Delph 1990). After oviposition, within hosts, the position of individual gall makers along a leaf can determines access to limiting nutrients (Larson and Whitham 1991). Gall makers nearer to the stem may have a greater ability to mobilize resources from adjacent leaves, and, because of the flow of nutrients from the stem outwards, should experience reduced competition relative to galls on distal leaves (Larson and Whitham 1991, Inbar et al. 1995). The behavioural corollary to the prediction of increased resource availability at proximal positions is that the free-living stage of the gall-maker should preferentially oviposit near to the stem. When combined with host quality and density effects, we expect that gall position, host quality, and gall density should contribute to differences in gall-maker fitness and patterns of habitat selection in nature.

We tested the above ideas using the gall-forming aphid *Melaphis rhois* (Order: Hemiptera, Family: Aphididae), an obligate parasite of staghorn sumac (*Rhus typhina*; Order: Sapindales, Family: Anacardiaceae). This system is ideal because sumac is dioecious, the galls can occur at high densities on some leaves but be completely absent from others, and because individual fitness is easily estimated by determining the number of clonal aphids within a gall (Supplementary material Appendix 1 Fig. A2). We use a sampling approach to test four hypotheses: 1) individual fitness of the gall-maker is a hump-shaped function of gall density (stabilizing selection on density; Fig. 1D), 2) the density of galls per leaf that confers the highest gall-maker fitness is greater on female trees owing to increased resource availability, 3) the adult free-living stage of aphids should select oviposition sites that maximize fitness, resulting in a unimodal distribution of gall densities that will be greater in female hosts, and 4) proximal galls have a fitness advantage relative to distal galls, causing preferential oviposition by the winged generation on proximal positions on the leaf.

Methods

Study system

Sumac aphid galls are formed by the aphid, *Melaphis rhois,* which has a complex life-cycle characterized by annual sexual reproduction followed by clonal generations (Supplementary material Appendix 1 Fig. A2). In spring, females mate and deposit a single egg on the leaf of a sumac (Moran 1989). While this winged generation is likely less dispersive than other aphids, dispersal ability in local areas where male and female sumac often co-occur in the same patch is likely (Hebert et al. 1991). Each egg hatches into a stem mother (the gall-making generation) which stimulates the production of a hollow gall before giving rise to a series of parthenogenetic generations which live inside the gall. Multiple galls are often found on a single leaf, even when many leaves on a tree remain unattacked. In fall, winged aphids are produced parthenogenetically; these winged individuals have the potential to lay eggs in the spring, after dispersing from the gall to moss patches where they overwinter (Hebert et al. 1991). Sumac are deciduous, so overwintering on live leaves is not possible.

Field methods

In Early September 2015, shortly before aphids dispersed to moss, we collected all sumac aphid galls, a plant parasite, from 56 leaves (173 galls) on fifteen male trees and 44 leaves (240 galls) on fifteen female trees at Koffler Scientific Reserve, King Township, Canada (44.02°N, 79.53°W). We selected widely distributed trees (>100 m) to reduce the likelihood of collecting galls from a single sumac clone, or from associating tree sex with particular environmental conditions. We collected from single trees separated by at least 100 m from an area of 1.6 km by 2.8 km. All trees were of a similar size and all female trees were fruiting.

Because density dependence – whether through facilitated resource acquisition or diluted immune response – is expected to occur during the process of gall formation, we focus on the effects of the density of gall-makers (as represented by gall density) on gall-maker fitness (as represented by number of aphids per gall). However, our measure of fitness is also an indication of fitness of the adult (after one generation), hence selection may equally act to modify patterns of oviposition (Supplementary material Appendix 1 Fig. A2). As such, we counted the number of galls on each leaf and recorded the distance between the first gall and the stem, then weighed each gall. To relate gall mass to the number of aphids produced by the gall, we dissected and counted individuals from 30 galls divided equally between male and female trees. Note that differences in aphid production among galls are likely caused primarily by changes in fecundity (Whitham 1980, Hebert et al. 1991), but that mortality of aphids within the gall may also play a role. The number of aphids in a gall represents the number of offspring produced by the gall-maker that stimulated gall formation and is therefore a reliable estimate of fitness assuming that the number of clonal aphids corresponds to the number of dispersing winged aphids (Whitham 1980). We opened all galls but found no sign of attack from natural enemies.

Statistical methods

We used a series of linear models to test for the effects of tree sex, gall density, and gall position on fitness and patterns of distribution. To relate mass to the number of aphids produced (clonal fitness) we regressed log-transformed gall mass against number of aphids, then used the regression equation to estimate the abundance of aphids for all remaining galls (Supplementary material Appendix 1 Fig A2; $R^2 = 0.75$, $p < 0.001$). Tree sex had no effect on the relationship between the number of aphids and gall mass when included as a fixed effect in our model ($p = 0.41$). We continued our analysis by standardizing all independent variables by subtracting the mean and dividing by the standard deviation. We then calculated relative fitness across all galls by dividing the number of aphids in a gall by the mean number of aphids produced by all galls (Lande and Arnold 1983). Our measure of fitness therefore assumes that all *Melaphis rhois* at our field site form a single population and are under hard selection (de Lisle and Svensson 2017).

We then tested for the effects of tree sex and density on gall fitness by calculating selection coefficients (β; the slope of the relationship between a trait and relative fitness). We first used a linear mixed effects model (LMM) to estimate selection coefficients, predicting relative fitness using density, position, and tree sex as main effects (predictors), and including leaf nested in tree as a random effect. We then partitioned the data and separately analyzed data from male and female trees, employing regression analyses to both describe the shape of the fitness function, and estimate the strength of selection (Lande and Arnold 1983). We estimated gall fitness using a linear model (LM) with first and second order terms for density and position, as well as the interaction of both traits, then repeated the analyses for galls on male and female trees. Significant effects of squared trait values and the interaction between position and density represent non-linear and correlational selection respectively (Lande and Arnold 1983). We doubled non-linear selection coefficients to calculate their true magnitude (Stinchcombe et al. 2008). We then re-ran the LMs without the quadratic or interaction terms to estimate the coefficients of directional selection (Lande and Arnold 1983). These analyses allowed us to estimate the true value of non-linear and directional selection for each sex, rather than simply determine if those differences were significant.

We then tested for differences in host quality between tree sexes in two ways. First, we tested for differences in the height of fitness optima from our selection analysis. We centered the fitness peak about zero by subtracting the second coefficient from the non-linear selection analysis from each gall density. We then used an LMM to regress gall density against relative fitness, including leaf nested in tree as a random effect, and repeating the analyses separately for male and female trees. To test for differences in the height of the fitness peak we then compared the intercepts from the separate models using a t-test. The second way we compared the quality of male and female host trees was by testing for differences in aphid abundance size across gall densities. We used a GLMM with a Poisson error distribution to estimate the number of aphids per leaf, including tree sex and gall density and squared gall density as main effects, and tree as a random effect. A significant interaction term (tree sex by either gall density term) or tree sex term would indicate that one sex of tree could support more individuals on a single leaf, in effect demonstrating that it is a higher quality host.

We next aimed to determine if patterns of abundance and oviposition were consistent with patterns of selection across densities and positions. We first tested whether between-host-sex differences in fitness functions across densities corresponded to patterns of abundance. In particular, we tested whether the mean density of galls per leaf (leaf is the unit of replication) differed between sexes by using a GLMM with a Poisson link function that included tree sex as a main effect. To control for other host differences we also included individual tree as a random effect. We further tested this possibility by using a GLM with a Poisson error distribution to predict the number of galls found at each density (habitat selection) using the average number of aphids found in a gall at each density (fitness). We next aimed to relate fitness differences among positions on a leaf to patterns of oviposition, inferred from the distribution of galls. Specifically, we tested if *Melaphis* was preferentially selecting positions near the trunk, by using a linear model to estimate the distance of the first gall from the trunk across a range of densities, and comparing our results to a null distribution generated by simulating random oviposition, as follows. If aphids select positions near the trunk, we expect no relationship between density and distance, whereas a random placement of galls would generate a negative relationship, as greater densities of galls increases the chance that at least one gall will be closer than average to the trunk. A more negative slope in the simulated (random oviposition) data then the real data would indicate preferential oviposition near to the stem. Data was simulated by drawing random numbers from a list of distances taken from leaves containing greater than six galls. We simulated an equivalent number of leaves as there were for each density in the real data then selected the lowest number (the distance nearest to the trunk) as the first gall for that branch. To test for differences in the slopes between real and simulated data we repeated the simulation one thousand times, then fit a linear model with distance to the first gall as the response variable and density as a fixed effect. We repeated this model independently for each simulated data set. We then compared the coefficient from the linear model for each simulation to the coefficient generated from the real data using the same model. By counting the number of simulated data sets which had a lower or higher coefficients than the real data we generated an estimate of the significance of the difference in slope between real and simulated data. Because we counted mature galls rather than eggs we are assuming the gall abortion is not biased by position or host sex (Whitham 1980). Statistical analyses were conducted in R (ver. 3.1.1, 2014) using the base package and the 'lme4' package (Bates et al. 2015).

Data deposition

Data available from the Dryad Digital Repository: < http://dx.doi.org/10.5061/dryad.c6f97 > (Start and Gilbert 2017).

Results

Tree sex, gall density, and position all affected individual fitness of *Melaphis rhois*. Particularly, female trees were able to support a higher gall load than males without large declines in gall fitness (Fig. 2A; tree sex × density, $p < 0.001$), but on average conferred lower gall fitness (Fig. 2B; tree sex, $p < 0.001$). However, female trees provided the highest fitness peak (comparison of centered intercept, $p = 0.02$), and, except for at very low gall densities (tree sex × density, $p < 0.001$), supported a greater number of aphids per leaf (tree sex, $p < 0.001$) suggesting they were a higher quality host (Fig. 2B). Regardless, aphid abundance declined in both hosts at particularly high gall densities (tree sex^2, $p < 0.001$).

Position nearer to the trunk conferred higher fitness ($p < 0.001$), but this effect was unaffected by host sex

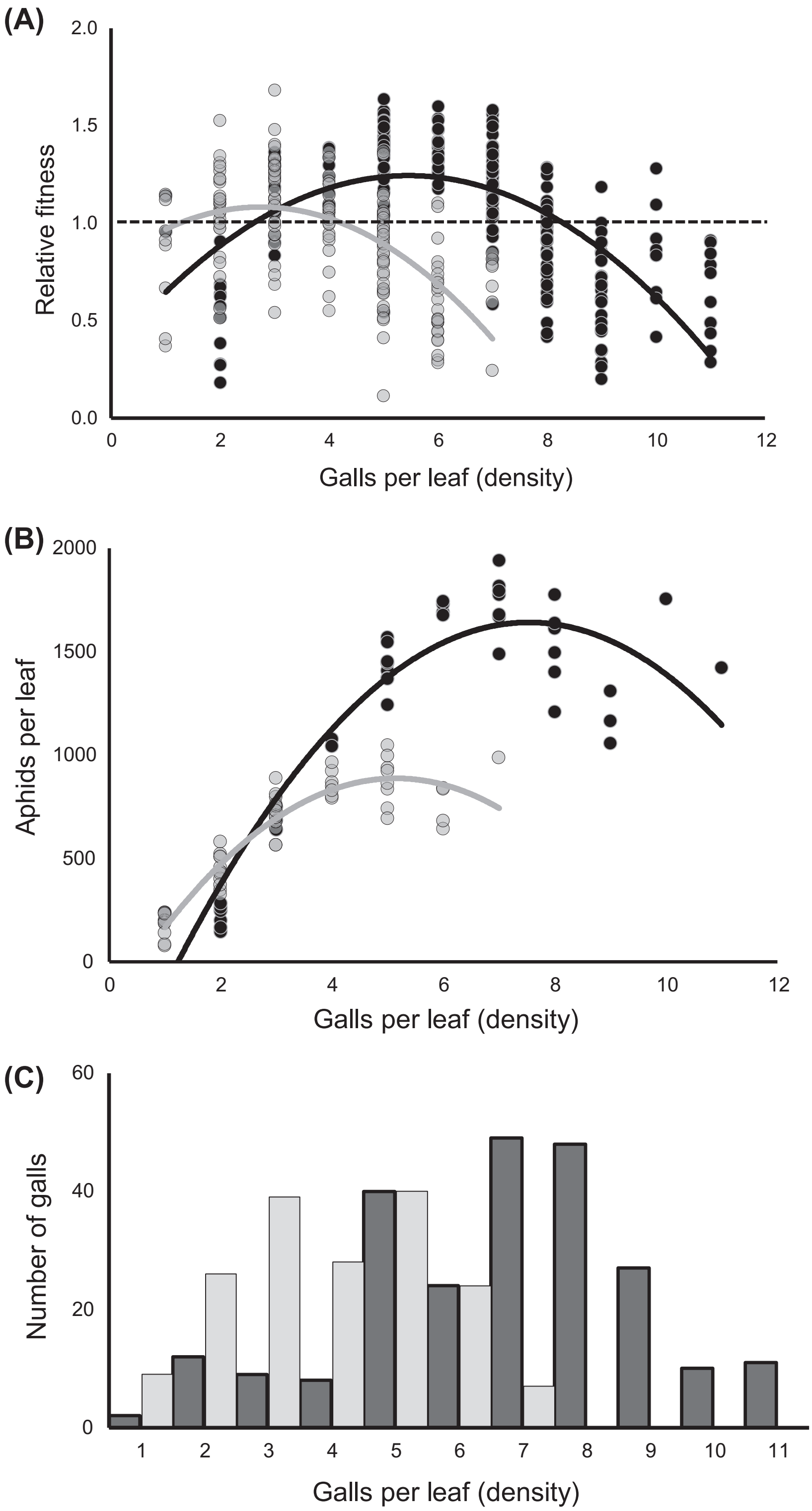

Figure 2. The effects of gall density and tree sex on the fitness and abundance of *Melaphis rhois*. (A) Aphid fitness is a hump-shaped function of density on both male (grey) and female (black) trees. Best fit lines were estimated from a LM including the quadratic density term (non-linear selection), and were fit separately for galls on male and female trees. The dash lines shows a relative fitness of one, or the level at which an individual on average replaces itself; (B) The number of aphids on a leaf peaks then declines across gall densities. There were more aphids on female trees and their numbers peaked at higher gall densities. Best fit lines were estimated from an LMM and were fit separately for male and female trees; (C) A histogram showing counts of galls at different densities on male (grey) and female (black) trees. Patterns of abundance mirrored patterns of fitness with mean density being greater on female trees.

Table 1. Coefficients and significance values for models estimating gall-maker fitness on male and female trees. Models were fit separately for galls on male and female trees using linear models, with non-linear and linear selection coefficients being calculated independently. All terms were significant except for non-linear selection on position.

	Male		Female	
Term	Coefficient	p-value	Coefficient	p-value
Density^2	–0.38	0.008	–0.38	<0.001
Density	–0.061	0.004	–0.073	0.0016
Position^2	0.15	0.453	0.013	0.729
Position	–0.14	<0.001	–0.10	<0.001
Density × Position	–0.1	<0.001	–0.15	<0.001

($p = 0.48$). When analyzed separately, galls on both male ($\gamma = -0.38$, $p = 0.008$) and female ($\gamma = -0.38$, $p < 0.001$) trees showed stabilizing selection (a hump-shaped fitness function) with respect to density (Fig. 2A), but not position (Table 1, both $p > 0.453$). Directional selection favored low densities for galls on both male ($\beta = -0.061$, $p = 0.004$) and female ($\beta = -0.073$, $p = 0.0016$) hosts. Directional selection also favored gall positions nearest to the tree for those galls on both male (Fig. 3B; $\beta = -0.1$, $p < 0.001$) and female (Fig. 3A; $\beta = -0.15$, $p < 0.001$). Correlational selection weakened overall selection on density and position for galls on female and male trees (Fig. 3A–B; both negative coefficients, $p < 0.001$). When we visually inspected the fitness surfaces, we found that fitness on female trees was maximized by being in a near position at high density (Fig. 3A). In contrast, fitness on male trees was maximized at the nearest position for all densities, but positions further from the stem showed decreasing fitness at higher densities (Fig. 3B). This indicates that, the way in which position and density interact to determine fitness differs between male and female trees.

The distribution of galls per leaf matched selection on gall density on male and female trees. Gall density was higher on female than male leaves (slope = 0.50632, $p < 0.001$), suggesting a correspondence between fitness and distribution (Fig. 2C), although the distribution is determined by the winged adult stage (oviposition differences), while we measured fitness for their offspring (the gall-inducing stem mother). In an additional test, average gall maker fitness at a particular density positively predicted the number of galls found at that density ($p < 0.001$), further suggesting adaptive habitat selection by the winged adults. Patterns of oviposition matched those expected from fitness differences,

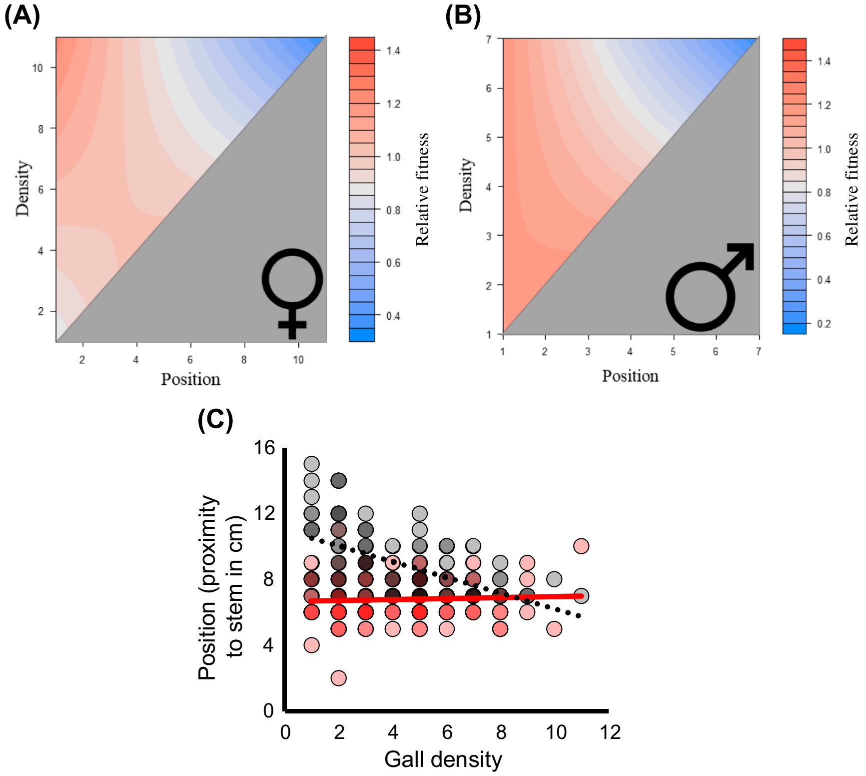

Figure 3. Patterns of fitness and oviposition depend on tree sex, density, and gall position. Effects of gall density and position interact to influence the fitness of *Melaphis rhois,* but the effects differed between female (A) and male (B) trees. Fitness was optimized at low density and closer to the stem on male trees, but at high density and a closer to the stem on female trees. In both sexes, the effect of position was magnified at high density. (C) Aphid galls were positioned near the stem, where fitness is greatest. Actual data (red) showed no trend in distance from the first gall to the stem whereas simulated data (black) with the same structure showed the expected negative relationship. The difference between actual and simulated data is indicative of female aphids preferentially ovipositing near to the stem.

with aphids selecting to oviposit near to the trunk. We found that the distance between the branch and first gall did not vary among leaves, whereas a negative relationship would occur if oviposition were random with respect to distance from the branch (the observed pattern showed no trend whereas the simulated data showed a negative slope; Fig. 3C, real data had the 11/1000th highest coefficient, $p = 0.011$). In other words, the significant difference in slope between real and simulated data along with real data having a near-zero slope (slope = 0.03) indicates that female aphids preferentially oviposited in the position nearest to the trunk.

Discussion

Our study demonstrates that the fitness of a gall-forming parasite has hump-shaped density dependence (Fig. 2A; stabilizing selection), indicative of an Allee effect at low densities and self-limitation at high densities. The non-linear effect of density on fitness is modified by host sex, or among-host differences, and position relative to other galls within hosts. These fitness functions were closely matched to the actual density of galls observed on sumac leaves, as well as biased positioning of galls close to tree stems on parasitized leaves (Whitham 1980). Together, these patterns help discriminate among mechanisms predicted to cause hump-shaped density dependence (Fig. 1E–F), furthering our understanding of causes of spatial aggregation, and providing insights into the generality of within- and among-host effects on parasite performance.

The fitness of *Melaphis* gall-makers across density and gall positions suggests that resource mobilization, rather than other mechanisms, are responsible for the switch from positive density dependence at low densities (an Allee effect) to negative density dependence at higher densities. Although stabilizing selection is predicted by theory on parasite resource mobilization (Fig. 1; McCalla et al. 1962) and parasite saturation of host defenses (Supplementary material Appendix 1 Fig. A1; Metcalf et al. 2011, Greischar et al. 2014), distinguishing between these hypotheses is often difficult (Fig. 1E–F; Handel et al. 2009). In our system, galls found at low density experienced reduced fitness (Fig. 2A), a pattern consistent with both hypotheses (Fig. 1, Supplementary material Appendix 1 Fig. A1). Similarly, both hypotheses are consistent with a decrease in fitness at very high densities (Fig. 2A) as a result of competitive dynamics overwhelming the benefits of greater numbers of aphids, whether these benefits arise from resource mobilization (Fig. 1, Whitham 1980) or defense saturation (Supplementary material Appendix 1 Fig. A1). However, we saw that higher quality hosts (female trees) supported a higher optimal gall density and higher absolute fitness at that density, consistent with cooperative resource acquisition but not cooperative defense (Fig. 1E–F). Our system also revealed higher fitness in proximal galls relative to distal galls (Fig. 3A–B), a result that is consistent with a resource-limitation hypothesis but not an immune–saturation hypothesis. A negative correlation between proximity to the stem and fitness suggests that proximal galls are able to monopolize the collective pool of resources because of their relative proximity to the source of resources (Fig. 3C; Larson and Whitham 1991). Conversely, immune functioning should produce no pattern if innate defense compounds were found in leaves, or would harm proximate galls if defenses were induced and mobilized from the stem of the tree (i.e. opposite of the observed pattern). Crucially, immune mechanisms may be rare among gall-makers, largely because they manipulate host-plant physiology making immune responses more difficult (Mattson et al. 1988). The negative correlation between proximity and fitness also precludes the possibility that gall densities are simply tracking host quality among trees. In other words, while multiple mechanisms could create Allee effects in host–parasite systems, sumac galls seem to experience an Allee effect mediated by resource-mobilization. Given that many parasites chemically induce resource-mobilization, including human parasites (Charron and Sibley 2002) and plant pathogens (Matyssek et al. 2005), the mechanism we describe here may be relatively common in host–parasite systems.

The effects of hump-shaped density dependence on patterns of spatial aggregation may be complex, but gall-makers in our study were distributed in ways consistent with stabilizing selection between host sexes. In the short-term, a unimodal response of fitness to density should cause patchy spatial distributions of parasites, as the winged adult selects moderately dense habitats to optimize offspring (gall-maker) fitness (Fretwell 1972, Amarasekare 1998, Stephens and Sutherland 1999). While differential egg abortion could theoretically cause observed distribution, this is unlikely in our system for at least two reasons. First, previous studies in related organisms have shown no effect of gall (egg) density on abortion rates (Whitham 1980). Moreover, most leaves on a tree were not attacked, yet most leaves that were attacked supported many galls (Fig. 2C), strongly suggesting that winged adults can select among leaves differing in egg density. This distribution of gall densities reflected stabilizing selection and differences in optimal fitness between male and female trees, with fitness peaking at a higher density in females (Fig. 2A) and female trees supporting greater gall densities per leaf (Fig. 2C). This type of density-dependent habitat selection has previously been demonstrated among the free-living stages of gall makers. For example Whitham (1980) found that *Pemphigus* aphids could detect differences in leaf quality and conspecific density, and matched patterns of oviposition with those predicted by an ideal free distribution. Conversely, patchy distributions can also be driven by other mechanisms, including differences in fitness across several generations in the absence of habitat selection (Amarasekare 1998), or through passive dispersal from parent habitats (Hubbell 1979). However because *Melaphis* recolonizes sumac every year, and uses moss patches to overwinter, these mechanisms cannot produce the patchy distributions observed in our system. Patchy distributions might equally be caused by variation in leaf quality, but this mechanism would not cause Allee effects, produce the effect of position on fitness, or result in the concordance between observed densities and fitness peaks. Because our findings do not match predictions of other mechanisms and because habitat selection has been demonstrated in several other parasite systems (Read et al. 1970, Whitham 1980, Fernandes and Price 1992), we suggest that adaptive density-dependent habitat selection drives the patchy distribution of individuals in our study.

The optimal density of parasites frequently depends on host quality (Anderson and May 1978), suggesting that physiological differences between males and females may commonly lead to different parasite loads. In our study, we found a higher optimal density of galls on female than male sumac (Fig. 2). Increased nutrient content of female trees, particularly during fruiting (Ågren 1988, Delph 1990), appears to increase the concentration of resources available to *Melaphis* gall-makers, reducing competition and allowing for high gall densities without reducing mean fitness. The ability of female trees to support larger numbers of aphids per leaf (Fig. 2B), and the shift of the fitness peak to higher gall densities (Fig. 2A) further supports females being the higher quality host. This difference in optimal parasite density per leaf and parasite load between sexes is likely a common pattern due to the prevalence of dioecy in both plants and animals, and the sometimes large differences in male and female physiology (Ågren 1988, Delph 1990, Zuk and McKean 1996). However, increased parasite load or increased herbivory on males is often observed (Cornelissen and Stiling 2005), suggesting that differences between sexes can have variable effects on parasites. For example, Larson and Whitham (1991) found that rather than increasing available resources, fruit competed with galls for resources and thus reduced fitness. Increased male parasitism can also be driven by behavioural, physiological, or hormonal differences (Zuk and McKean 1996). In these cases the optimal density depends not only on the resource availability within a host, but also on resistance to parasites and differences in the behaviour of males and females (Zuk and McKean 1996, Moore and Wilson 2002). In animals, males typically allocate fewer resources to immune functioning to the benefit of reproductive effort (McNamara et al. 2013), improving male quality for parasites and reversing our observed relationship. A similar pattern is possible in plants if males allocate fewer resources to defensive compounds, allowing greater attack rates (Cornelissen and Stiling 2005). However, this pattern depends on the sensitivity of parasites to plant defensive compounds, which may be minimal for many gall-makers (Hartley 1998). Overall, resource availability and parasite defense often depend on host sex, but the specific outcome of these differences between sexes may be unpredictable a priori because multiple differences between sexes can influence parasite fitness in opposite ways.

The advantage of intermediate gall densities and more proximate gall positions highlights a potential tradeoff in habitat selection for gall makers. Female trees had the highest mean fitness at optimal densities, indicating that ovipositing by the adult winged stage at these densities on female trees would optimize gall-maker fitness (Fig. 2A). However, proximal galls had higher fitness than distal galls, and this effect was amplified at high density (Fig. 3A–B). Proximal galls are better able to access resources mobilized from adjacent leaves or roots as they flow into the leaf, prior to removal by conspecifics (Larson and Whitham 1991). Essentially, proximal galls are ‘upstream’ of distal galls, and thus gain priority in resource acquisition. However, optimal fitness is only attained by being in both a proximal position and at a high density. Assuming adaptive habitat selection, proximal positions are likely the first to be exploited (Fig. 3C), with those adult winged aphids then unable to select across a range of densities but instead getting their choice of oviposition sites. This dynamic should cause a tradeoff, where early laying winged aphids are able to preferentially oviposit in a proximal position, but late emerging aphids are able to select among leaves differing in density. Such a tradeoff may be common when delaying emergence increases an individual’s ability to accurately perceive the quality of an environment (Eitam et al. 2005), but decreases the potential competitive advantages of early arrival (Lawler and Morin 1993).

In summary, our study highlights the importance of Allee effects for fitness and the distribution of parasites, and suggests a potentially widespread mechanism mediating Allee effects in host–parasite systems. We have shown that density-dependent shifts from net-positive to net-negative interactions are expected when per capita facilitative and competitive effects have specific non-linearities, and that these non-linearities are likely to be found when host resource mobilization is a saturating function of parasite density. Our study further demonstrates that host quality changes the optimum parasite density. These types of dynamics are likely common in host-parasite dynamics, given the numerous mechanisms that can mediate Allee effects in these systems (Hilker et al. 2009), and the strong coevolutionary dynamics between hosts and parasites (Brooks 1979, Legendre et al. 2002, Gandon and Michalakis 2002). We suggest that Allee effects be considered in studies of host–parasite dynamics, particularly when studying temporally and spatially variable parasite abundance.

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Supplementary material (available online as Appendix oik-04405 at < www.oikosjournal.org/appendix/oik-04405 >). Appendix 1.