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The evolution of tolerance to deer herbivory: modifications caused by the abundance of insect herbivores

John R. Stinchcombe[*] **and Mark D. Rausher**

Ecology, Evolution and Organismal Biology Group, Biology Department, Duke University, Durham, NC 27708, USA (*mrausher@duke.edu*)

Although recent evidence indicates that coevolutionary interactions between species often vary on a biogeographical scale, little consideration has been given to the processes responsible for producing this pattern. One potential explanation is that changes in the community composition alter the coevolutionary interactions between species, but little evidence exists regarding the occurrence of such changes. Here we present evidence that the pattern of natural selection on plant defence traits, and the probable response to that selection, are critically dependent on the composition of the biotic community. The evolutionary trajectory of defence traits against mammalian herbivory in the Ivyleaf morning glory (*Ipomoea hederacea*), and which defence traits are likely to respond to selection, are both dependent on the presence or absence of insect herbivores. These results indicate that variation in community composition may be a driving force in generating geographical mosaics.

Keywords: geographical mosaic; coevolution; diffuse coevolution; herbivory; tolerance

1. INTRODUCTION

Coevolution is a fundamental evolutionary process that is believed to influence both the generation and maintenance of species diversity (Ehrlich & Raven 1964; Berenbaum 1983; Kearns *et al.* 1998), the evolution of infectious diseases (May & Anderson 1983), and the evolution of community structure and stability (Rummel & Roughgarden 1985). Moreover, accumulating evidence indicates that the outcome of coevolutionary interactions between a pair of species often varies on a biogeographical scale (the 'geographical mosaic' (Thompson 1994)). However, the causes of this geographical variation in coevolutionary outcomes remain unclear. One possibility is that geographical variation in abiotic factors, such as climate and nutrient availability, alter the balance between the costs and benefits of ecologically important traits such as resistance (or counter-resistance), and thereby cause different levels or types of resistance to evolve in different populations. Alternatively, it is possible that geographical differences in the coevolutionary trajectory of a focal pair of species are caused largely by differences in biotic conditions—that is, differences in the abundance of other, auxiliary species, that influence the interactions between the focal species.

Although some investigators have argued that variation in biotic conditions is responsible for much of the geographical mosaic (Thompson 1994), little definitive evidence exists to support this claim. The reports of geographical variation in ecologically important traits (Benkman 1999), or in the pattern of natural selection on such traits (Gómez & Zamora 2000), are consistent with both the biotic and the abiotic explanations.

One approach for distinguishing between these alternatives is to determine how frequently variation in biotic factors creates the conditions necessary for geographical mosaics to be generated. One such condition is that changes in the abundance of auxiliary species must alter either the patterns of selection imposed by a focal pair of species on each other or the response of those species to that selection, i.e. selection and response in coevolutionary interactions must be diffuse rather than pairwise (Iwao & Rausher 1997). Although one recent investigation provides evidence that patterns of selection imposed by herbivores are diffuse (Juenger & Bergelson 1998), it is unclear how general these results are. Even less well characterized is whether, and how frequently, the abundance of auxiliary herbivores influences the expected response to selection on resistance to a focal herbivore.

In this report we describe experimental evidence indicating that both the pattern of selection on tolerance to deer damage in the morning glory *Ipomoea hederacea*, as well as the probable response to that selection, are influenced by the presence of other natural enemies of this plant species. These results provide direct evidence that coevolutionary interactions are likely to be diffuse rather than pairwise, and thus indicate that variation in the composition of the biotic community may often contribute to the generation of the geographical mosaic.

2. MATERIAL AND METHODS

(a) *Study organism*

Ipomoea hederacea (L.) Jacquin (Convolvulaceae), the Ivyleaf morning glory, is a weedy annual vine common to roadsides and agricultural fields in the southeastern USA. Seeds typically germinate in June or July, and plants die with the first autumn frost, usually in late October or early November. In Durham and Orange Co., NC, *I. hederacea* is attacked by a variety of natural enemies—insects, mammals and fungi. Damage imposed by each of these natural enemies is distinctive, and each can be

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[*] Author and address for correspondence: Ecology and Evolutionary Biology, Brown University, Box G-W, Providence, RI 02912, USA (john_stinchcombe@brown.edu).

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quantified independently (Bright 1998). In particular, deer remove entire leaves at once, thereby allowing deer damage to be scored by the presence of leaf scars on the stem or the existence of petioles without leaves.

(b) *Experimental design*

Our experimental approach was to alter the abundance of insect herbivores and fungal pathogens and determine whether these alterations affected patterns of genetic variation for, and selection on, tolerance to deer herbivory.

To generate our experimental seeds, we let 18 inbred lines self-fertilize in a greenhouse. Eighty self-fertilized (or selfed) seeds from each inbred line were planted into an agricultural field in a randomized block design consisting of 10 spatial blocks. The spacing between the rows and columns of the plants was 1.25 m and the plants were not staked.

Individual plants were randomly assigned to receive one of the following four treatments:

(i) natural levels of insect herbivores and fungal pathogens (sprayed with water);
(ii) natural levels of insect herbivores but reduced levels of fungal pathogens (sprayed with the fungicide Ridomil Gold Copper);
(iii) natural levels of fungal pathogens but reduced levels of insect herbivores (sprayed with a mixture of the insecticides Carbaryl and *Bt*); and
(iv) reduced levels of both insect herbivores and fungal pathogens (sprayed with both insecticide and fungicide).

Spraying treatments commenced when plants had four true leaves, and were imposed at approximately two week intervals such that only one pesticide was sprayed on each day. This pesticidal regime is highly effective at reducing insect herbivory and fungal damage, and has no adverse effects on the fitness of the plants of this species grown in the greenhouse (Stinchcombe & Rausher 2001). Furthermore, as described in the following paragraphs, this pesticidal regime has no effect on the amount of deer damage plants suffer.

Seven weeks after the emergence of the plants (prior to any leaf senescence), we recorded the total number of leaves and the number of leaves removed by deer (determined by leaf scars on stems or the presence of the petiole but no leaf) for the 1225 surviving plants. Mortality prior to the damage census was low (<5%). To measure the amount of deer damage for each plant, we counted the total number of leaves removed by deer and then divided that by the sum of the number of leaves removed by deer and the number of extant leaves. For example, if a plant had 20 leaf scars and 80 extant leaves, the proportion of deer damage was scored as 0.20 (proportion damaged equals $20/(20+80)$); measuring damage in this manner as a proportion thus accounts for any variations in plant size. As the average amount of deer damage suffered by plants did not differ between experimental treatments (mean deer damage varied between 0.25 and 0.27 in the four experimental treatments (Stinchcombe & Rausher 2001)), this procedure provides an accurate estimate of deer damage that is unbiased by the experimental treatments, and therefore, the presence or absence of insect herbivores and fungal pathogens.

All seeds produced by the experimental plants were gathered, stored and later counted. We calculated the relative fitness for each plant by dividing the number of viable seeds produced by the mean for all the plants. As *I. hederacea* has a selfing rate of 93% (Ennos 1981), calculating the fitness from the total seed set provides an estimate of the combined male and female fitness components. Individuals that survived up to the damage census but did not set any viable seed were assigned a fitness value of zero. Individuals that did not germinate or survive up to the damage census were excluded from the analyses.

(c) *Quantitative genetics of tolerance*

Due to the fact that all of the experimental seeds were the products of selfing a single individual per line, the between-inbred line variation reflects the total genetic variation (additive and nonadditive) and the maternal effects. Although the evolution of traits in outcrossing species depends specifically on additive genetic variation (Falconer & Mackay 1996), using the total genetic variation rate is appropriate for *I. hederacea* because of its high-selfing rate. In populations with such a high-selfing rate, natural selection acts primarily on the total genetic variation rather than just the additive genetic variation (Roughgarden 1979). Furthermore, the crosses necessary to discern the additive and nonadditive components of genetic variation would create an experimental population of seeds with artificially high levels of heterozygosity that would be of questionable relevance to natural populations of this species (Bright 1998; Mauricio 1998). Finally, our breeding design maximized our potential to detect variation between inbred lines in their degree of tolerance by minimizing the amount of variation present within an inbred line.

(d) *Statistical analyses*

The statistical analysis proceeded in two stages. First, to determine whether tolerance to deer damage was genetically variable, we examined the relationship between deer damage and fitness using stepwise Analysis of Covariance (ANCOVA; Searle 1971) as implemented by the SAS Institute, Inc. (1990). For this and subsequent analyses, Type III sums of squares (type III ss) were used. The full model included block, deer damage and its square as covariates, inbred line as a random effect, and insect and pathogen treatments as fixed effects, as well as all two-, three- and four-way interactions. The full model was run first, any nonsignificant higher interaction terms were then eliminated, and the resulting reduced model containing only the main effects and significant interaction terms is reported herein.

The second stage of the analysis examined the pattern of selection on tolerance. As an individual plant cannot simultaneously exist in a damaged and undamaged state, it is impossible to measure a tolerance value for a single individual (Rausher 1992*b*; Strauss & Agrawal 1999). Instead, tolerance must be measured for a group of genetically related individuals—an inbred line in this case. We calculated tolerance values for individual inbred lines as the slope of a regression of relative fitness on damage for each inbred line (Simms & Triplett 1994; Mauricio *et al.* 1997; Tiffin & Rausher 1999). We elected to use naturally occurring deer herbivory for several reasons. First, it is simply not possible in this system to randomly impose natural herbivory by large mammals such as deer on individual experimental plants. Second, by using naturally occurring herbivory, plants experience the natural timing, pattern and distribution of herbivore damage (Tiffin & Inouye 2000). Third, using natural herbivory provides greater power in detecting natural selection on tolerance (Tiffin & Inouye 2000).

Estimating tolerance as the slope of a regression of fitness on damage measures tolerance as a reaction norm of plant fitness along a gradient of herbivory (Abrahamson & Weis 1997;

Table 1. An ANCOVA for relative fitness (log transformed) that demonstrates the existence of genetic variation for tolerance to deer herbivory.
(Significant effects are shown in bold. The results presented are for the reduced model, after the elimination of nonsignificant higher-order interactions from the full model.)

source	d.f.	type III ss	*F* value	*p*
block	**9**	**22.408015**	**12.54**	**<0.0001**
inbred line	**17**	**6.916007**	**2.05**	**0.0072**
insecticide	**1**	**3.431685**	**17.28**	**<0.0001**
fungicide	1	0.061743	0.31	0.5773
deer damage	**1**	**10.63562**	**53.55**	**<0.0001**
deer damage × inbred line	**17**	**5.611011**	**1.66**	**0.0441**
error	1023	203.173611		

Tiffin & Rausher 1999). We measured tolerance for each inbred line in each treatment separately. Only linear terms were included in the regressions for each inbred line because the first-stage analysis revealed no evidence of any nonlinear effects of damage on fitness. In these analyses we utilized the residuals of relative fitness (untransformed) after the effects of block had been removed to reduce the influence of spatial variation. Preliminary analyses also indicated no interactions between different types of damage on relative fitness, indicating that these estimates of deer tolerance are unaffected by other types of damage.

To measure selection on tolerance, an ANCOVA was performed in which fitness was the dependent variable and independent variables included tolerance and its square as covariates, inbred line as a random effect, and insect and pathogen treatments as fixed effects, as well as all interactions. There was no evidence of disruptive or stabilizing selection on tolerance in our experiment ($F_{1,60} \leqslant 0.34$, $p \geqslant 0.56$ for all quadratic regression coefficients), and as such we present only analyses on the pattern of directional selection and how it differed between experimental treatments.

3. RESULTS

(a) *Genetic variation for tolerance*

Inbred lines differed in tolerance to deer damage, as revealed by a significant inbred-line × deer damage interaction in an ANCOVA (Simms & Triplett 1994), with fitness as the response variable (table 1). This interaction indicates that the slopes of the relationship between fitness and deer damage, the definition of tolerance, differ among the inbred lines. For this analysis we log-transformed fitness to improve the normality of the residuals (Mitchell-Olds & Shaw 1987), although the results were similar for an analysis with untransformed fitness.

We have demonstrated elsewhere that in our experimental population, resistance to deer damage is genetically variable (Stinchcombe & Rausher 2001). Such variation could have resulted in apparent genetic variation for tolerance in the analyses presented here if the relationship between damage and fitness is nonlinear, for example if there is relatively little fitness reduction per unit increase in damage when damage is small, but a large fitness reduction when damage is high. However, our analyses yield no evidence that the relationship between damage and fitness deviates from linearity either within or among the lines ($p > 0.45$ for all terms involving the square of damage in the full model), indicating that the genetic variation for tolerance we detected is not an artefact of variation in resistance.

A similar problem could arise if there is a genetic correlation between tolerance to deer damage and resistance to deer, insect or pathogen damage. In this situation, lines would appear to have different tolerance to deer damage, not because of intrinsic differences in tolerance, but because of differences in resistance. This possibility also seems improbable in our experiment for two reasons. First, there is no evidence that there is genetic variation for resistance to pathogen damage in our experimental population (Stinchcombe & Rausher 2001). Second, all genetic (line mean) correlations between deer tolerance and either insect or deer resistance in the experimental population (data pooled across treatments) are weak and nonsignificant (all $r_{16} \leqslant 0.22$, $p \geqslant 0.39$ (Stinchcombe 2001)). Furthermore, none of these patterns differed when we examined the significance of these genetic correlations within individual experimental treatments.

(b) *Genetic correlations across treatments*

A pairwise response to selection imposed by a focal herbivore requires that the same plant traits evolve in both the presence and the absence of auxiliary natural enemies. For tolerance to deer damage in *I. hederacea*, this requirement does not appear to be met. Despite the existence of genetic variation for tolerance, genetic correlations for tolerance to deer damage between all pairs of treatments ranged from −0.32 to 0.29, and none were significantly different from 0 (d.f. = 16, $p > 0.20$ for all correlations). Calculations using standard jack-knifing techniques (Sokal & Rohlf 1995) indicated that none of the 95% confidence limits for any of the correlations approached 1. As genetic correlations substantially less than 1 indicate substantial independence of the genes controlling a trait in two environments (Lynch & Walsh 1998), these results indicate that the actual tolerance characters that are likely to respond to selection imposed by deer will differ depending on whether insect herbivores and fungal pathogens are present.

(c) *Patterns of selection*

To assess whether the pattern of selection on tolerance to deer herbivory depended on the presence of auxiliary enemies, we estimated the coefficient of a standardized regression of fitness on tolerance using inbred-line means, following standard methods (e.g. Lande & Arnold 1983; Rausher 1992*a*; Mauricio *et al.* 1997; Tiffin & Rausher

Table 2. An ANCOVA for relative fitness that shows that the pattern of selection on tolerance to deer herbivory differs depending on the presence of insects.
(Significant effects are shown in bold.)

source	d.f.	type III ss	*F* value	$p > F$
deer tolerance	**1**	**2.712**	**35.58**	**<0.0001**
insecticide	1	0.000008	<0.001	0.9921
fungicide	1	0.00003	<0.001	0.9853
insecticide × fungicide	1	0.0012	0.02	0.9001
deer tolerance × insecticide	**1**	**0.4813**	**6.31**	**0.0145**
deer tolerance × fungicide	1	0.0094	0.12	0.7602
tolerance × insecticide × fungicide	1	0.1069	1.40	0.2408
error	64	4.8789		

1999). For this analysis, we utilized the residuals of relative fitness after block effects were removed to minimize the effects of spatial variation. Tolerance was included as a continuous variable in an ANCOVA that also included insecticidal and fungicidal treatments as categorical variables, with all possible interactions. As tolerances in different treatments were statistically and genetically independent (see § 3(b)), we considered the estimates of tolerance in each treatment to be independent. Three important features are indicated by this selection analysis. First, neither the insecticidal nor the fungicidal treatment, nor their interaction, affected mean relative fitness ($p > 0.89$ for each, table 2). Second, the pattern of directional selection on deer tolerance did not differ depending on the fungicidal treatment, either when applied alone or in concert with the insecticidal treatment (cf. deer tolerance × fungicide and deer tolerance × insecticide × fungicide interaction terms, table 2). Third, the significant interaction between insecticidal treatment and tolerance (deer tolerance × insecticide term, table 2) indicated that the relationship between fitness and tolerance differed between insecticidal treatments, i.e. the magnitude of selection on deer tolerance depended on whether insects were present. Directional selection acted to reduce tolerance in both treatments, presumably because of the costs of tolerance (Abrahamson & Weis 1997). Nevertheless, the strength of selection was greater when insects were present (figure 1).

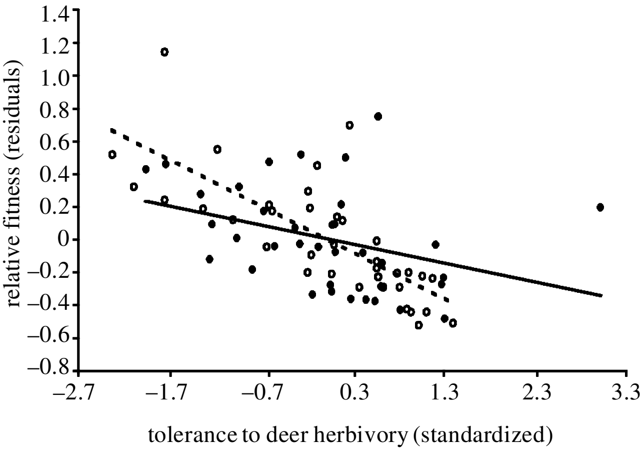

Figure 1. A graphical portrayal of selection acting on tolerance to deer herbivory in the presence and absence of insects. The y-axis depicts the residuals of relative fitness after the effects of the block had been removed, and the x-axis depicts the tolerance to deer herbivory, standardized to a mean of 0 and standard deviation of 1. Data from plants with insects present are indicated by open circles and the dashed line and data from plants without insects are indicated by closed circles and the solid line. The slopes of the two regressions are significantly different from each other (ANCOVA: $F_{1, 64} = 6.31$, $p = 0.0145$).

4. DISCUSSION

For a system consisting of a single plant species and multiple natural enemies, coevolution is pairwise if the trajectory of coevolution between the plant and each enemy, as predicted by the pattern of natural selection and the probable response, is independent of whether the other enemies are present. Otherwise, coevolution is considered diffuse (Hougen-Eitzman & Rausher 1994; Rausher 1996). Previously, two criteria have been proposed for determining whether interactions in such a system will lead to diffuse or pairwise coevolution:

(i) resistances (or tolerances) to different natural enemies are genetically uncorrelated and as such will lead to a pairwise response to selection; and
(ii) the pattern of selection imposed by one natural enemy is independent of whether other enemies are present (Rausher 1996; Iwao & Rausher 1997).

If both criteria are satisfied, then coevolution is likely to be pairwise; otherwise, it is probably diffuse. Our finding that tolerance to the same herbivore in the presence and absence of other natural enemies are genetically uncorrelated indicates a third criterion that must be met for coevolution to be pairwise:

(iii) the genes contributing to variation in resistance (or tolerance) to each enemy must be the same in the presence and absence of other enemies.

If this criterion is violated, then different resistance (or tolerance) characters will evolve depending on which other enemies are present—in other words, the trajectory of evolution will differ.

A number of investigations in a variety of plant–enemy systems have assessed whether criterion (i) is satisfied. In general, resistances to different natural enemies are genetically uncorrelated (Rausher 1996), indicating that in most cases criteria (ii) and (iii) will determine whether coevolution is pairwise or diffuse. The results of this study indi-

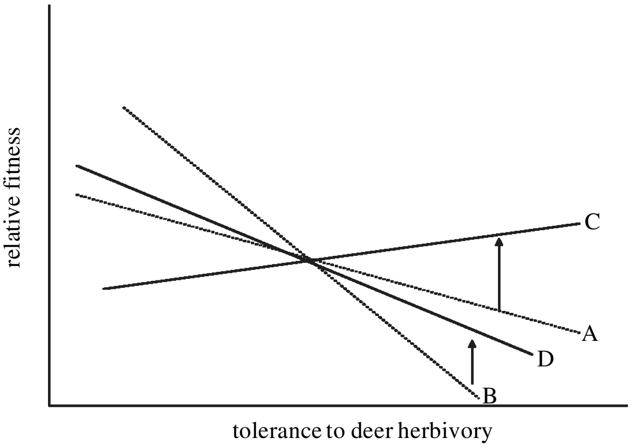

Figure 2. A graphical presentation showing how changes in the costs of tolerance in different environments could alter the direction of selection on tolerance to deer herbivory. In this example, lines A and B represent the pattern of selection observed on tolerance to deer herbivory in the presence and absence of insect herbivores, respectively. In an environment where the costs of tolerance are reduced, lines C and D represent the pattern of selection on tolerance in the presence and absence of insects, resulting in different directions in the pattern of selection.

cate that both of these criteria are violated in our system with respect to tolerance to deer herbivory.

In our experiment, criterion (ii) is violated because the magnitude of selection on tolerance to deer damage, presumably imposed by deer herbivory, depended on whether insect herbivores were present or absent. Although the direction of selection, and thus the ultimate level of tolerance that is favoured, was not altered in our experiment, it is not difficult to imagine that similar effects of auxiliary enemies could alter the direction of selection in other populations. For example, tolerance to deer herbivory in *I. hederacea* is costly (Stinchcombe 2001). In general, the magnitude of the costs of tolerance and resistance are believed to depend on environmental factors such as the intensity of competition plants' experience and the availability of nutrients (Bergelson 1994). In an environment in which tolerance was less costly than in our experiment, net selection in the absence of insects might well be absent or favour increased tolerance, while still favouring decreased tolerance in the presence of insects (figure 2). We note, however, that this scenario is only speculative.

We also found criterion (iii) to be violated in our experiment because tolerances to deer herbivory in the presence and in the absence of insects were genetically uncorrelated. Although little is known about the physiological basis of tolerance in *I. hederacea*, or in any other plant species, it is well known that damage by insects leads to substantial physiological changes, including induced resistance, in many plant species (Karban & Baldwin 1997). Moreover, such induced changes are known to occur in the closely related *I. purpurea* (Rausher *et al.* 1993). It is not difficult to imagine that these changes could alter whether variation at a specific locus contributes to genetic variation for tolerance. An analogous phenomenon is exhibited by resistance to aphids in the goldenrod *Solidago altissima*, in which the existence of genetic variation for aphid resistance requires the presence of other insects that damage the plant meristem (Pilson 1992). More generally, our result is also consistent with recent reports indicating the environmental dependence of the contribution of specific quantitative trait loci to a quantitative character (Xia *et al.* 1999; Vieira *et al.* 2000). Regardless of the physiological and genetic details, our results indicate that different characters conferring tolerance to deer damage are expected to evolve in the presence and in the absence of insects.

Our results are consistent with those of the only two other studies that have explicitly examined criteria (ii) and (iii). As described earlier, Pilson (1992) found that criterion (iii) was violated in goldenrod, while Juenger & Bergelson (1998) demonstrated that criterion (ii) was violated because the pattern of selection on flowering phenology in scarlet gilia (*Ipomopsis aggregata*) imposed by lepidoptera depended on whether seed flies were present. Along with these studies, our results indicate that interactions producing a diffuse pattern of selection and response to selection, and therefore potentially diffuse coevolution, may frequently characterize plant–natural enemy associations.

This conclusion in turn indicates that geographical variation in the outcome of coevolutionary interactions may often result from geographical variation in the community of natural enemies associated with a plant species. The geographical-mosaic pattern of coevolutionary interactions appears to be ubiquitous in nature (e.g. Thompson 1999), and the mosaic perspective has been advocated as a replacement for the notion of diffuse coevolution (Thompson 1997, 1999). However, even if the existence of a geographical-mosaic pattern is accepted, elucidation of the processes that create that pattern is still necessary. Diffuse selection and coevolution, coupled with geographical variation in community composition, is one process that may generate a geographical mosaic. The evidence accumulated to date indicates that diffuse selection is common and thus indicates that this process may contribute substantially to creating the geographical mosaic.

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REFERENCES

Abrahamson, W. G. & Weis, A. E. 1997 *Evolutionary ecology across three trophic levels: goldenrods, gallmakers, and natural enemies*. Princeton University Press.

Benkman, C. W. 1999 Coevolution between crossbills and pine. *Am. Nat.* **153**, S75–S91.

Berenbaum, M. 1983 Coumarins and caterpillars: a case for coevolution. *Evolution* **37**, 163–179.

Bergelson, J. 1994 The effects of genotype and environment on costs of resistance in lettuce. *Am. Nat.* **143**, 349–359.

Bright, K. 1998 Geographic variation and natural selection on a leaf shape polymorphism in the Ivyleaf morning glory (*Ipomoea hederacea*). PhD dissertation. Duke University, Durham, NC, USA.

Ehrlich, P. R. & Raven, P. H. 1964 Butterflies and plants: a study in coevolution. *Evolution* **18**, 586–608.

Ennos, R. A. 1981 Quantitative studies of the mating system in two sympatric species of *Ipomoea* (Convolvulaceae). *Genetica* **57**, 93–98.

Falconer, D. S. & Mackay, T. F. C. 1996 *Introduction to quantitative genetics*. Harlow: Longman.

Gómez, J. M. & Zamora, R. 2000 Spatial variation in selection. *Am. Nat.* **155**, 657–668.

Hougen-Eitzman, D. & Rausher, M. D. 1994 Interactions between herbivorous insects and plant–insect coevolution. *Am. Nat.* **143**, 677–697.

Iwao, K. & Rausher, M. D. 1997 Evolution of plant resistance to multiple herbivores: quantifying diffuse coevolution. *Am. Nat.* **149**, 316–335.

Juenger, T. & Bergelson, J. 1998 Pairwise versus diffuse natural selection and the multiple herbivores of scarlet gilia, *Ipomopsis aggregata*. *Evolution* **52**, 1583–1592.

Karban, R. & Baldwin, I. T. 1997 *Induced responses to herbivory*. University of Chicago Press.

Kearns, C. A., Inouye, D. W. & Waser, N. M. 1998 Endangered mutualisms: the conservation of plant–pollinator interactions. *A. Rev. Ecol. Syst.* **29**, 83–112.

Lande, R. & Arnold, S. J. 1983 The measurement of selection on correlated characters. *Evolution* **37**, 1210–1226.

Lynch, M. & Walsh, B. 1998 *Genetics and analysis of quantitative traits*. Sunderland, MA: Sinauer.

Mauricio, R. 1998 Costs of resistance to natural enemies in field populations of the annual plant *Arabidopsis thaliana*. *Am. Nat.* **151**, 20–28.

Mauricio, R., Rausher, M. D. & Burdick, D. S. 1997 Variation in the defense strategies of plants: are resistance and tolerance mutually exclusive? *Ecology* **78**, 1301–1311.

May, R. M. & Anderson, R. M. 1983 Epidemiology and genetics in the coevolution of parasites and hosts. *Proc. R. Soc. Lond.* B **219**, 281–313.

Mitchell-Olds, T. & Shaw, R. G. 1987 Regression analysis of natural selection: statistical inference and biological interpretation. *Evolution* **41**, 1149–1161.

Pilson, D. 1992 Aphid distribution and the evolution of goldenrod resistance. *Evolution* **46**, 1358–1372.

Rausher, M. D. 1992*a* The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution* **46**, 616–620.

Rausher, M. D. 1992*b* Natural selection and the evolution of plant–insect interactions. In *Insect chemical ecology: an evolutionary approach* (ed. B. D. Roitberg & M. B. Isman), pp. 20–88. New York: Chapman & Hall.

Rausher, M. D. 1996 Genetic analysis of coevolution between plants and their natural enemies. *Trends Genet.* **12**, 212–217.

Rausher, M. D., Iwao, K., Simms, E. L., Ohsaki, N. & Hall, D. 1993 Induced resistance in *Ipomoea purpurea*. *Ecology* **74**, 20–29.

Roughgarden, J. 1979 *Theory of population genetics and evolutionary ecology: an introduction*. New York: MacMillan.

Rummel, J. D. & Roughgarden, J. 1985 A theory of faunal buildup for competition communities. *Evolution* **39**, 1009–1033.

SAS Institute, Inc. 1990 *Sas/Stat user's guide*, v. 6. Cary, NC: SAS Institute, Inc.

Searle, S. R. 1971 *Linear models*. New York: Wiley.

Simms, E. L. & Triplett, J. 1994 Costs and benefits of plant responses to disease: resistance and tolerance. *Evolution* **48**, 1973–1985.

Sokal, R. R. & Rohlf, F. J. 1995 *Biometry: the principles and practice of statistics in biological research*. New York: Freeman.

Stinchcombe, J. R. 2001 Evolutionary ecology of deer resistance and tolerance in the ivyleaf morning glory, *Ipomoea hederacea*. PhD dissertation. Duke University, Durham, NC, USA.

Stinchcombe, J. R. & Rausher, M. D. 2001 Diffuse selection on resistance to deer herbivory in the Ivyleaf morning glory, *Ipomoea hederacea*. *Am. Nat.* **158**, 376–388.

Strauss, S. Y. & Agrawal, A. A. 1999 The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* **14**, 179–185.

Thompson, J. N. 1994 *The coevolutionary process*. University of Chicago Press.

Thompson, J. N. 1997 Evaluating the dynamics of coevolution among geographically structured populations. *Ecology* **78**, 1619–1623.

Thompson, J. N. 1999 Specific hypotheses on the geographic mosaic of coevolution. *Am. Nat.* **153**, S1–S14.

Tiffin, P. & Inouye, B. 2000 Measuring tolerance to herbivory: accuracy and precision of estimates made using natural versus imposed damage. *Evolution* **54**, 1024–1029.

Tiffin, P. & Rausher, M. D. 1999 Genetic constraints and selection acting on tolerance to herbivory in the common morning glory, *Ipomoea purpurea*. *Am. Nat.* **154**, 700–716.

Vieira, C., Pasyukova, E. G., Zeng, Z. B., Hackett, J. B., Lyman, R. F. & Mackay, T. F. C. 2000 Genotype–environment interaction for quantitative trait loci affecting life span in *Drosophila melanogaster*. *Genetics* **154**, 213–227.

Xia, X. C., Melchinger, A. E., Kuntze, L. & Luebberstedt, T. 1999 Quantitative trait loci mapping of resistance to sugarcane mosaic virus in maize. *Phytopathology* **89**, 660–667.