
Relationships between ecological interaction modifications and diffuse coevolution: similarities, differences, and causal links

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A major empirical approach in community ecology is to describe the dynamics of a community by examining small subsets of species. Unfortunately, interaction modifications, which cause pair-wise interaction coefficients to depend on the presence or absence of additional species, can make it difficult to predict the overall dynamics of species within a community from experiments with pairs of species. In a similar fashion, one of the major approaches in evolutionary ecology has been to describe the likely evolutionary dynamics of a single species by focusing on the selection imposed by a limited number of other species within the community. However, recent work on diffuse coevolution indicates that selection pressures due to one species can change in the presence of other species. The magnitude of the difficulty that interaction modifications and diffuse coevolution present for predicting ecological and evolutionary dynamics is an unresolved question. Here we outline the similarities and differences between the two topics, discuss experimental and statistical approaches to studying them, and make predictions about when ecological interaction modifications are likely to cause diffuse coevolution. Since the currencies for interaction modifications are usually fitness components such as growth, fecundity, or survival, it is likely that these will translate into corresponding differences in the relative fitness of individuals or genotypes, and thus in general these two phenomena will occur together. We argue that community ecologists and evolutionary ecologists will both benefit from experiments that test for the effects of interaction modifications, and that studies of the mechanisms driving interaction modifications and diffuse coevolution (e.g., changes in behavior, nonlinear effects on shared resources, genetic covariances) will aid our progress in understanding the ecological and evolutionary dynamics of communities.

One of the major empirical approaches in community ecology has been to describe the population dynamics of species in communities by examining subsets of the total community. The aim of this approach is to describe the community as the sum of interactions among these subsets, usually pairs, of species. However, the presence of interaction modifications (trait-mediated interactions, *sensu* Abrams et al. 1996) can make it

difficult to predict the overall dynamics of species within a community from simple experiments with pairs of species (Bender et al. 1984, Wootton 1994a). In a similar fashion, one of the major approaches in evolutionary ecology has been to describe coevolution – the evolutionary interactions between different species in response to each other – by evaluating a limited number of other species within the community. However, recent work on diffuse coevolution indicates that selection pressures due to one species can change in the presence of other species. For example, the strength and direction of selection on plant resistance traits by one herbivore species can depend on the presence or absence of other herbivores that feed on the same plant (Pilson 1996). The similarities between interaction modifications and diffuse coevolution point to similar central problems in community and evolutionary ecology – the difficulty in predicting ecological or evolutionary dynamics of species by examining subsets of natural communities. In this note, we outline the conceptual similarities between interaction modifications and diffuse coevolution, describe similarities between the experimental and statistical approaches taken to detecting interaction modifications and diffuse coevolution, and make predictions about when interaction modifications will result in diffuse coevolution or vice versa. We argue that the conceptual similarities and causal links between interaction modifications and diffuse coevolution illustrate the close relationship between community and evolutionary ecology, and point to several potentially fruitful and exciting areas of research.

Because most of the work on diffuse coevolution comes from studies on the evolution of plant resistance to insect herbivores, we have chosen to focus on plant-insect interactions in our real and hypothetical exam-

ples. In principle, the similarities between ecological interaction modifications and diffuse coevolution (or at least diffuse selection) hold across all taxonomic and trophic levels, and in some cases also apply to interactions among genotypes within a species.

Definitions and conceptual similarities

An interaction modification is a change in the sign or magnitude of a direct pairwise interaction mediated by the presence of one or more other species (Adler and Morris 1994, Wootton 1994a). This is distinct from so-called “interaction chains” (Wootton 1993), in which a series of direct effects involving other species can also link the two original species, changing the *net* sign or magnitude of the pairwise interactions between them (Wootton 1994a, b, Damiani 2000). Because interaction modifications involve changes in per capita interaction strengths, they cannot be predicted from a series of independent experiments involving pairs of species, but instead require experiments involving all of the species in the interaction. By contrast, because interaction chains are caused by numerical or density effects, they can be predicted from separate, independent experiments involving only pairs of species. Interaction modifications, indirect effects and nonlinear interactions have been lumped together under the terms “higher order interactions” and emergent properties, which include a collection of processes with the common feature that their effects are not always predictable using simple linear (first-order) models (Wilbur 1972, Billick and Case 1994, Sih et al. 1998). For the remainder of this note, we focus exclusively on interaction modifications because of their conceptual similarities to diffuse coevolution, which also cannot be predicted from a series of independent experiments involving pairs of species.

The mechanisms by which interaction modifications work are typically thought to be through changes in behavior, rather than through changes in a species density, although the distinction can be difficult to make in the field. A large majority of the examples of interaction modifications involve changes in a rate of consumption: the presence or absence of a predator or competitor (or both) alters a behavior that affects the rate of predation or herbivory (Werner and Anholt 1996, Sih et al. 1998). Several mechanisms can cause interaction modifications in plant-insect interactions and change rates of herbivory. Plant tissue consumption rates by insect herbivores have been shown to change in response to the (non-lethal) presence of predators (e.g., Schmitz et al. 1997, Peckarsky and McIntosh 1998, Gastreich 1999), and in response to other herbivores with which they never interact directly, via changes in the quality, phenology, or architecture of the shared host plant (e.g., Shultz and Baldwin 1982, Harrison and Karban 1986, Strauss 1991, Preus and

Morrow 1999, Denno et al. 2000). In addition, herbivory rates can also change in response to other plant species growing nearby that affect herbivore behavior (e.g., Karban 1997, Hambäck et al. 2000). While many of the studies involving plant-herbivore interactions have focused on effects on the herbivores, differing amounts of herbivory can also affect the relative fitness of the plants, and thus potentially the pattern of selection imposed on the plants (Mauricio and Rausher 1997, Parmesan 2000).

Coevolution has been defined as the successive evolutionary change in each of two species in response to selection imposed by the other species (Janzen 1980). Janzen (1980) and Fox (1981) noted that coevolution in multispecies interactions was likely to be qualitatively different than coevolution between single pairs of species, and described coevolution in multispecies interactions as “diffuse coevolution”. Under their view of diffuse coevolution, it is only possible to understand coevolution in an interaction by considering the interactions among multiple species.

Recently, Rausher and colleagues (Rausher 1992a, Hougen-Eitzman and Rausher 1994, Iwao and Rausher 1997, Stinchcombe and Rausher 2001) have proposed criteria for experimentally quantifying diffuse coevolution. Their approach has been to use quantitative and evolutionary genetics to understand the likely evolutionary dynamics of ecologically important traits, concentrating on aspects of plant-herbivore interactions such as resistance to herbivores. In their view, diffuse coevolution is a likely product of either of two phenomena (or both): first, genetic correlations between resistances to different natural enemies or herbivores, and second, changes in the pattern of natural selection on resistance to one herbivore depending on the presence or absence of other herbivores. If there are genetic correlations between resistances to different herbivores, it would be impossible for a plant to have an independent evolutionary relationship with each of its herbivores or natural enemies: selection on resistance to one herbivore would likely produce a correlated response to selection in resistance to another herbivore. In like fashion, if the pattern of natural selection on resistance to one herbivore differs depending on the presence or absence of other herbivores, then the evolutionary dynamics of traits that confer resistance to one herbivore will be dependent on the presence or absence of other herbivores in the community. In essence, this approach characterizes diffuse coevolution as the likely product of either a diffuse response to selection or a diffuse pattern of natural selection.

It appears likely that the nature of selection imposed by a single herbivore species often changes when in the presence or absence of other herbivore species – that is, selection is often diffuse in nature (Rausher 1996). For example, Pilson (1996) found that the pattern of selection for resistance to flea beetle (*Phyllotreta crucifera*)

damage was not independent of the amount of damage imposed by diamondback moths (*Plutella xylostella*) in wild mustard (*Brassica rapa*). In particular when diamondback moth damage is high, lower levels of resistance are favored, but when diamondback moth damage is low, higher levels of resistance are favored. Juenger and Bergelson (1998) also detected diffuse components to selection imposed on flowering phenology by herbivores of scarlet gilia (*Ipomopsis aggregata*). In scarlet gilia, the effects of seed fly attack on selection on flowering phenology differed depending on the presence or absence of Lepidoptera larvae.

The obvious conceptual similarity between interaction modifications and diffuse coevolution (selection) is that the actions of each imply that it may be impossible to predict community and evolutionary dynamics by examining a small subset of species in a community. Interaction modifications, which can be measured by changes in a population growth rate or in species' densities, are typically driven by changes in individual behavior. Diffuse coevolution is caused by genetic correlations or changes in the pattern of natural selection depending on community composition. While these responses are measured at the population level, they are caused by individuals having unique suites of traits that covary genetically, or changes in the relative fitness of individual phenotypes depending on the presence or absence of other species.

Experimental and statistical methods

To detect an interaction modification or diffuse coevolution it is necessary to record the interaction between two focal species, while also manipulating or recording the density of a third (or fourth, etc.) species. As an example, consider a plant and two herbivore species (A and B). At its most basic, an experiment to detect an interaction modification can consist of a factorial design with only three treatments: the plant with species A only, the plant with species B only, and all three species together. For simple factorial designs the data are usually analyzed using a generalized linear model (typically ANOVA) with the presence of appropriate significant interaction terms indicating an interaction modification or diffuse coevolution. This simplest design confounds the effects of total herbivore density and herbivore identity. Thus it is strongly preferable to use multiple densities of both herbivore species, so that nonlinear interaction strengths or selection gradients can be detected and true interaction modifications more reliably inferred (Adler and Morris 1994, Sih et al. 1998). When using multiple densities of both species A and B one can still use a factorial design, and analyze the data with ANOVA or multiple regression. As an alternative that offers greater statistical power for investigating nonlinear effects, one could use a response surface

design and use a likelihood-based method for model fitting, comparing the fit of models with or without appropriate interaction terms (Burnham and Anderson 1998, Inouye 2002). This alternative approach of model selection holds promise for greater contact between theory and empirical work, because it allows empiricists to estimate and evaluate the functional relationships between species using the same terms that theoretical studies normally require.

An experiment designed to test for the presence of a likely diffuse response to selection or a diffuse pattern of selection is similar to an experiment designed to look for an ecological interaction modification, with a few important differences. First, these experiments typically involve a quantitative genetic approach, and use a number of different families that have been generated by appropriate crossing (Falconer and Mackay 1996, Lynch and Walsh 1998). Second, these experiments require an estimate of the relative fitness of the focal species (often viable seed set for plants), whereas ecological interaction modifications are usually measured in terms of effects on short-term growth, survival, or reproduction – fitness components rather than relative fitness of individuals or genotypes. Third, in ecological experiments data are often log-transformed before analysis, so that the interaction terms in the ANOVA use a multiplicative null-model as opposed to an additive model (Billick and Case 1994), and to make model residuals more approximately normal. In genetic analyses it is often questionable whether to log-transform data before analysis, because selection analyses utilizing relative fitness values that have been log-transformed can be very different from analyses using relative fitness values that have not been log-transformed.

To evaluate the potential cause of diffuse coevolution, one can test for genetic correlations between the ecologically important traits using standard quantitative genetic techniques to estimate genetic variances and covariances (e.g., Falconer and Mackay 1996, Lynch and Walsh 1998). To evaluate the potential cause of diffuse selection, one has to estimate the pattern of natural selection on the trait of interest in the presence or absence of candidate species. This can be accomplished by evaluating the regression of relative fitness on phenotypic values (Lande and Arnold 1983) or estimates of breeding values or genotypic means (Rausher 1992b). The crossing designs necessary to evaluate the first potential cause of diffuse coevolution (genetic correlations) typically yield the necessary data for the breeding values/genotypic means approach described by Rausher (1992b), which also has the benefit of being unbiased by environmental covariances between traits and fitness (Mitchell-Olds and Shaw 1987, Rausher 1992b). To determine whether the pattern of natural selection on the trait of interest differs depending on the presence or absence of other species, one can compare the selection gradients using standard ANOVA and ANCOVA tech-

niques (Iwao and Rausher 1997). As above, a significant interaction term between the focal trait and the presence or absence of a third species indicates that the pattern of natural selection on the trait differed depending on the presence or absence of other species, and thus selection (coevolution) was diffuse.

For some systems it will not be feasible to measure or manipulate the population density of one of the focal species, though it still might be desirable to look for the presence of an interaction modification. For these situations it might be possible to measure a proxy or surrogate for density and then use that covariate for analyses to test for nonlinearities. For example, for plant-insect systems it might be possible to record the amount of a certain kind of damage imposed on plants as a surrogate for herbivore density. The diversity of induced and compensatory responses that plants exhibit following herbivore damage, however, makes it likely that using damage as a proxy for herbivore density will only be valid over very short time frames. We encourage community and evolutionary ecologists to pursue alternative methods for manipulating the density of focal species.

When can interaction modifications result in diffuse coevolution?

Below, we consider the four cases in which interaction modifications are present or absent and either cause or do not cause diffuse coevolution. Our focus is on the first case, when ecological interaction modifications cause diffuse coevolution, as we believe that in general these two phenomena will occur together. Since the currencies for interaction modifications are usually fitness components such as growth, fecundity, or survival, it is likely that differences in these fitness components will translate into corresponding differences in relative fitness of individuals or genotypes, and thus changes in patterns of selection (but see Juenger and Bergelson 1998). Therefore, to the extent that interaction modifications are common in nature, coevolutionary interactions should be diffuse as opposed to strictly pair-wise. While we have illustrated the cases described below using plant-herbivore examples, in principle these arguments apply equally to any other sets of potentially coevolving species, such as competitors (Roughgarden 1983), predators and prey (Vermeij 1987), or parasites and their hosts (Hafner et al. 1994, Rothstein and Robinson 1998, Morand et al. 2000).

Case I – interaction modification present, diffuse coevolution present

The first possibility is that ecological interactions change selection gradients and result in diffuse coevolu-

tion. For example, it is possible that a second herbivore species changes the amount or kind of damage imposed by a focal herbivore species (Hougen-Eitzman and Rausher 1994). If the focal herbivore changes feeding behavior, for instance switching from feeding on flowers to eating less preferred leaves, then the presence of the second herbivore can alter the kind of selection imposed by the focal herbivore on the plant. Changes in the amount of damage done by the focal herbivore can alter the pattern of selection imposed on a plant if there is a nonlinear relationship between damage and plant fitness (e.g., Fig. 1). For example, on the right side of the curve, there will be selection for increased resistance – that is, decreased amounts of damage. However, the presence of a second herbivore or a behavioral response to a predator that shifts the amount of damage caused by the focal herbivore below a threshold value will result in no selection on resistance. For instance, on the left side of the curve there is no selection for increased resistance (i.e., decreased amounts of damage) because in this region the covariance between resistance and fitness is zero.

There are numerous potential mechanisms that might underlie these changes. It is possible that the two herbivores are in direct competition for preferred plant tissues (e.g., Denno et al. 1995, Karban 1986). Similarly, apparent competition between the two herbivores acting through a shared generalist predator might produce similar effects if the presence of the second species, and the attendant recruitment of predators, decreases the abundance and subsequent damage imposed by the

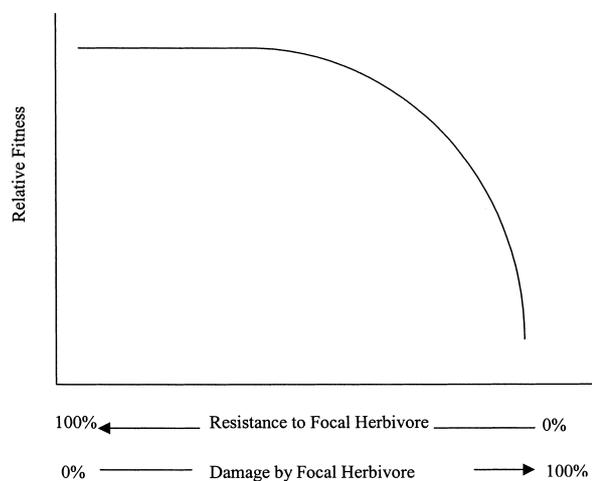


Fig. 1. Diagram that shows how changes in the amount of damage imposed by a focal herbivore in the presence of a second herbivore can alter the pattern of selection on resistance traits when there is a non-linear relationship between damage and fitness. On the left side of the figure, when low levels of damage exist there is no selection for increased resistance. On the right side of the figure, where the amount of damage imposed by the focal herbivore is greater, there will be selection for increased resistance.

first herbivore species. Qualitatively similar patterns could also be produced if one of the additional species is an omnivore that in addition to eating plant tissue also consumes the first herbivore.

Likewise, it is possible that induced changes in plant quality might lead to indirect competition or an indirect mutualism between herbivores. Insect herbivore responses to damage imposed by earlier feeding herbivores or the presence of a second herbivore species can be either positive (e.g., Williams and Myers 1984) or negative (Karban and Baldwin 1997). If the induced changes caused by the second herbivore substantially alter the abundance or the amount of damage imposed by the first herbivore, then these changes could also alter the pattern of natural selection imposed on resistance traits.

Case II – interaction modification present, diffuse coevolution absent

As described above, there are numerous potential ecological interactions that *could* lead to diffuse coevolution. Simply because there are significant ecological interactions, however, does not imply that coevolution will always be diffuse (Iwao and Rausher 1997, Juenger and Bergelson 1998). To gain an intuitive understanding of how this could be the case, consider the following examples. First, it is possible that the presence or absence of another herbivore species alters the mean level of damage imposed by the focal species, but not the actual slope of the selection gradient, so that coevolution is not diffuse. In statistical terms, this is equivalent to a “common slope model” (Litell et al. 1996) where the slopes of lines are not different, but the means or elevations are (e.g., Fig. 2a and b). Second, it is also possible that the likely response to selection will not be altered by the presence of an additional herbivore species. For example, if there is no genetic variation present for the relevant phenotypic traits under selection ecological interactions might alter the amount of damage imposed by one herbivore, or the ecological relationship between the plant and the herbivore, but still not lead to evolutionary change. Other possible reasons that ecological interactions might not lead to diffuse coevolution include the presence of significant costs associated with the traits under selection (e.g., costs of resistance) or significant genetic correlations between the trait(s) under selection by herbivores and other life history or morphological traits.

Case III – interaction modification absent, diffuse coevolution present

At least two possible mechanisms might lead to diffuse coevolution but not an interaction modification. First,

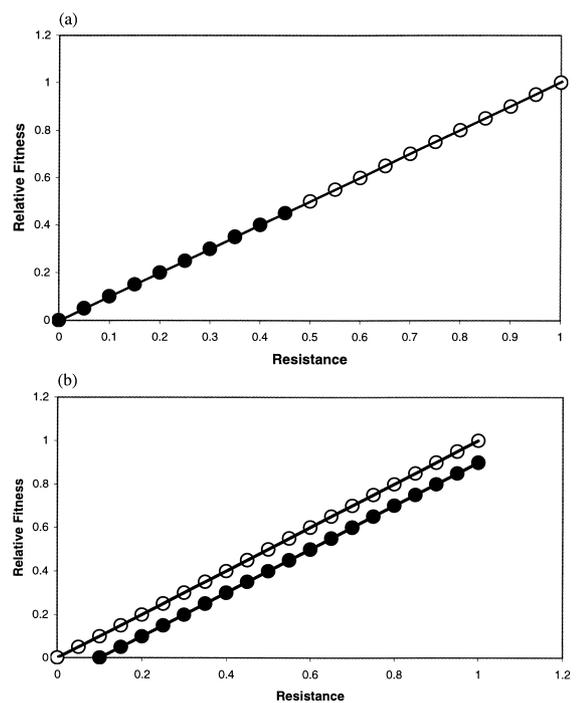


Fig. 2. A graphical portrayal of a common slope model illustrating how the pattern of selection on resistance to damage by a focal herbivore (open circles) is not altered if the presence of a second herbivore simply alters either the mean amount of damage (a) or the mean fitness or elevation (b) (filled circles).

it is possible that there are no ecological interactions between herbivores, but that there is a genetic correlation between resistance to each herbivore. Thus, the evolutionary response of resistance to one herbivore would lead to a correlated response to selection in resistance to the other herbivore, even in the absence of direct ecological interactions. Second, it is possible that non-additive fitness effects of damage might lead to diffuse coevolution in the absence of ecological interactions (Hougen-Eitzman and Rausher 1994, Wise and Sacchi 1996). If this is the case, it is possible that the amount of damage imposed by each herbivore is not altered by the presence or absence of the other herbivore, but the *fitness consequences* of this herbivore damage are altered by the presence or absence of the other herbivore. Stinchcombe and Rausher (2001) describe a case in which the fitness consequences of deer damage, but not the absolute amount of deer damage, are greater in the presence of insect herbivores than in the absence of insect herbivores.

Case IV – interaction modification absent, diffuse coevolution absent

In this case, there are neither ecological interactions, nor genetic correlations that lead to diffuse coevolution.

This is the ideal case for predicting community ecological and evolutionary dynamics from simple experiments, since simple linear models should produce accurate predictions of the (short term) responses to perturbations. In essence, this case represents the null hypothesis against which the other cases are tested.

Future directions and conclusions

Given the potential links between interaction modifications and diffuse coevolution, there are several promising areas of research that deserve greater attention. Foremost among them, more experiments are needed that integrate the ecological and evolutionary processes in multispecies interactions. These experiments, ideally carried out in the field or semi-natural habitats, should incorporate both genetics and ecological approaches, by incorporating multiple genotypes of the focal species and multiple densities of its interacting partners.

It may turn out that most community and evolutionary dynamics can be predicted from pairwise interactions, but we believe that this is still an open empirical issue. Although the necessary experiments may be logistically challenging, the accumulating evidence from both community ecology and evolutionary ecology indicates that the patterns that emerge from multispecies investigations can be quite different than the patterns that emerge from investigations of pairs of species (e.g., Messina 1981, Damiani 2000). As such, rather than trying to minimize the variation in ecological and evolutionary interactions by considering only tightly controlled pairs of species, we should attempt to assess the magnitude of this variation directly and determine how it informs our understanding of these processes in multispecies communities.

Furthermore, more experimental work on diffuse coevolution is also needed. Though some have advocated abandoning the distinction between diffuse and pair-wise coevolution (e.g., Thompson 1997), quantifying diffuse coevolution gives direct information about the balance of ecological and genetic forces governing the evolution of ecologically important traits. Moreover, diffuse coevolution explicitly puts evolution into an ecological context. While the majority of work on diffuse coevolution has focused on plants and herbivores (see Rausher 1996 and Mitchell-Olds and Bergelson 2000 for reviews), studies of coevolution are also called for in pollination biology (e.g., Iwao 1995), host-pathogen and host-parasitoid interactions, predation, and competition.

The inclusion of the 'co' in coevolution has to date, largely been on the basis of assumptions rather than demonstration – there have been few true demonstrations of reciprocal selection in the field (for exceptions see Davies and Brooke 1989a, b, Clayton et al. 1999).

Given the evidence that plants of different varieties or quality can alter insect characters such as pupal mass (Morris 1997), feeding rate (Slansky and Feeny 1977), and population dynamics (Underwood and Rausher 2000), it seems probable that plants are imposing selection on insects. Whether selection is being imposed in this direction and whether selection in this direction is diffuse as well have been virtually unexplored. Though difficult, more work needs to be done to determine if the selection hosts or host plants impose on their pathogens and herbivores differs depending on the presence or absence of other species.

The connection between interaction modifications and diffuse coevolution represents an example of how ecology, evolution, and genetics can be mutually informative. Studying the interplay of ecology, evolution, and genetics in species interactions will inform us of when ecological interactions cause or limit evolutionary interactions, and when evolutionary or genetic factors can cause, limit, or alter ecological interactions. For ecologists studying interaction modifications, a first step towards examining diffuse coevolution is to consider links between the response variables that they measure, such as short term individual or population growth rates, and relative fitness, the ultimate currency of selection. For evolutionary biologists interested in coevolution, it seems worthwhile to keep in mind the likelihood that ecological interaction modifications will lead to diffuse selection pressures, and to design experiments that include multiple species as either covariates or treatments. We are optimistic that utilizing a diversity of experimental, analytical, and conceptual approaches will facilitate our understanding of ecological and evolutionary dynamics in multispecies interactions.

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