



Predicting novel herbivore–plant interactions

Ian S. Pearse, David J. Harris, Richard Karban and Andrew Sih

I. S. Pearse (ispearse@ucdavis.edu), Cornell Lab of Ornithology, 159 Sapsucker Woods, Ithaca, NY 14850, USA. – D. J. Harris, R. Karban and A. Sih, Center for Population Biology, Univ. of California - Davis, 1 Shields Ave, Davis, CA 95616, USA. ISP and RK also at: Dept of Entomology, Univ. of California - Davis, 1 Shields Ave., Davis, CA 95616, USA. ISP, DJH and AS also at: Dept of Environmental Science and Policy, Univ. of California - Davis, 1 Shields Ave., Davis, CA 95616, USA.

As human-aided range expansions and climate change alter the distributions of plants and their herbivores, predicting and addressing novel species interactions will become increasingly pressing for community ecologists. In this context, a key, surprisingly understudied question is: when an exotic plant is introduced, which herbivores will adopt this new potential host? Whether the plant is a weed, an ornamental, or a crop, the development versus non-development of a novel plant–insect interaction can have profound effects for both economic and conservation applications. In this paper, we sketch mechanistic and statistical frameworks for predicting these interactions, based on how plant and herbivore traits as well as shared evolutionary history can influence detection, recognition, and digestion of novel plants. By emphasizing mechanisms at each of these steps, we hope to clarify different aspects of novel interactions and why they may or may not occur. We also emphasize prediction and forecasting, as a major goal is to know in advance which interactions will develop from the many plant or insect introductions that occur in natural and man-made systems.

Understanding the impacts of exotic species on ecosystems is one of the most important issues in modern ecology and evolution (Mack et al. 2000, Sih et al. 2010). Novel plants (including weeds, crop plants and ornamentals) are now a common, essentially ubiquitous feature of modern, human-dominated ecosystems. Moreover, as regional climates change, ranges of both plants and insects are predicted to change, which will often produce novel interactions between species that have not historically co-occurred (Parmesan 2006).

Predicting novel interactions between plants and herbivores is especially important, as herbivory is a key component of both natural and human-maintained ecosystems. Insect herbivores consume a tremendous proportion of the world's crops (which are introduced well outside of their native ranges), and agriculturists respond by using economically and environmentally costly insecticides. Novel herbivore associations must also be considered in conservation efforts surrounding invasive species, as they are the link between primary production and higher trophic levels, and herbivore abundance can limit both the abundance of some plant species as well as the abundance of higher trophic levels (Sih et al. 1985). Ecologists have accumulated a substantial storehouse of conventional wisdom in predicting novel herbivore–plant interactions, but there is a need to assemble this information into more rigorous predictive tools. For example, there has been a recent call to ecologists to make better quantitative predictions about the consequences of plant invasions for native communities (Mack et al.

2000, McEvoy 2002, NAS 2002, Simberloff et al. 2005). Prediction of novel herbivore–plant interactions may, in this case, increase the effectiveness of biological quarantines at ports of entry by identifying non-native plants that may escape their herbivores or non-native herbivores that may find suitable hosts in their novel range. Likewise, there is a current need to predict the non-target effects of herbivorous biological control agents on native plants (McEvoy and Coombs 1999, Louda et al. 2003). In this case, laboratory host-specificity trials are presently conducted between the introduced herbivore and a suite of potential hosts, but these laboratory trials do not always reflect what later happens in the field (Simberloff and Stiling 1996). This has prompted a call for better predictive methods that incorporate a more mechanistic understanding of novel plant–herbivore interactions (Louda et al. 2003).

In this paper, we discuss two approaches that can play a valuable role in forecasting herbivory in a changing world. One approach involves focusing on interactions between particular pairs of plants and insects under controlled conditions in the lab or field to make predictions for the same or similar pairs of species in the wild (Louda et al. 2003). Here, we develop a mechanistic framework for predicting the initial response of herbivores to novel plants based on information about plant and herbivore traits, their native host-associations, and their adaptive capacity. While many of the points that we discuss are familiar, we bring them together in one framework in a new way. Similar to native systems (Carmona et al. 2011), we conclude that factors

other than simple digestibility are likely crucial in driving novel herbivore–plant interactions. We then consider how adaptation between novel plants and herbivores might shape the ultimate outcome of their interaction. We find that both plant defenses and novel herbivore associations may be either gained or lost through evolution over relatively short times.

Alternatively, when the number of species to be considered is large, it may be useful to take a broader statistical approach to predict novel interactions using readily available databases of plant and insect traits and food web structure. Statistical methods like regression cannot provide a mechanistic understanding of specific interactions but they could help to narrow the field of potential interactions so that controlled studies and mechanistic models could be better targeted and therefore have more impact. This approach is analogous to analyses of non-mechanistic statistical relationships between organisms and their abiotic environments (i.e. ecological niche models) that have proven useful in predicting species distributions (Peterson et al. 2011). To date, these types of predictive statistics are unusual in herbivory studies. Thus we provide examples of techniques that might be useful to researchers interested in exotic plants and their native herbivores. Our suggested statistical framework incorporates traits and taxonomic information that are readily available for many plants and herbivores. We show that even relatively simple statistical techniques, common in fields such as consumer–product matching and niche modeling, have the potential to predict a large percentage of novel interactions using readily available data.

Initial responses of herbivores to novel plants: trait matching and mechanisms

The most influential hypothesis regarding herbivory on non-native plants is the enemy release hypothesis, which posits that non-native plants escape damage from herbivores and thereby achieve greater fitness in their novel range (Keane and Crawley 2002). Empirical studies often find support for the enemy release hypothesis, but also clearly show that there is large variation in the degree to which non-native plants actually escape native herbivores (Agrawal and Kotanen 2003, Agrawal et al. 2005), to the degree that in many cases, non-native plants are even better hosts for herbivores than natives (Morrison and Hay 2011, Nielsen et al. 2011). While enemy release is often thought to be due to the absence of enemies in the novel range, a key factor explaining variation in enemy release can be variation in tendency for other potential herbivores to actually adopt a novel plant (Maron and Vilá 2001, Colautti et al. 2004, Parker et al. 2006).

In this section, we outline the steps that occur when an insect colonizes a host, and we consider how some plant and herbivore traits may be important in the formation of any novel interaction, while other traits may be important in forming a match with a particular herbivore or host. We emphasize that the traits that mediate each step of colonization, not palatability alone, may be important in predicting novel herbivore–plant interactions. And we suggest that trait and phylogenetic similarity to local natives may be a good, but potentially limited, proxy for understanding the actual mechanisms of each novel interaction.

Steps in a novel herbivore–plant interaction

In order to predict which insects from a given community will effectively exploit a novel plant resource, it is necessary to understand the process by which an insect colonizes and successfully consumes a host. We briefly illustrate the steps that determine host-use by herbivores. The majority of research has focused on the performance/digestive ability of an insect to consume novel hosts, but each of the other steps in the process may also limit the interaction (Fig. 1).

Co-occurrence

For an interaction to occur between a plant and an insect, the two species must overlap in both space (geographic, habitat and microhabitat levels) and time (phenology - Fig. 1). By breaking down, traversing, or bypassing large-scale biogeographic barriers like mountain ranges and oceans, human activities such as trade allow for interactions that would not have been possible otherwise. While these introductions can be dramatic, they will not always produce successful interactions without co-occurrence in time and in space at a much finer scale.

Attraction (or preference)

If the herbivore encounters a plant, it will only consume it if the plant presents the appropriate blend of cues (attractants as opposed to deterrents - Fig. 1). While cues that attract herbivorous insects may also be visual or tactile, the most well-studied (and presumably most common) mechanisms of herbivore attraction to plants involve olfaction. Plant volatile profiles (i.e. scents) are often complex, and can be comprised of tens or even hundreds of individual metabolites which act in concert as attractants or deterrents of herbivores (Webster et al. 2010).

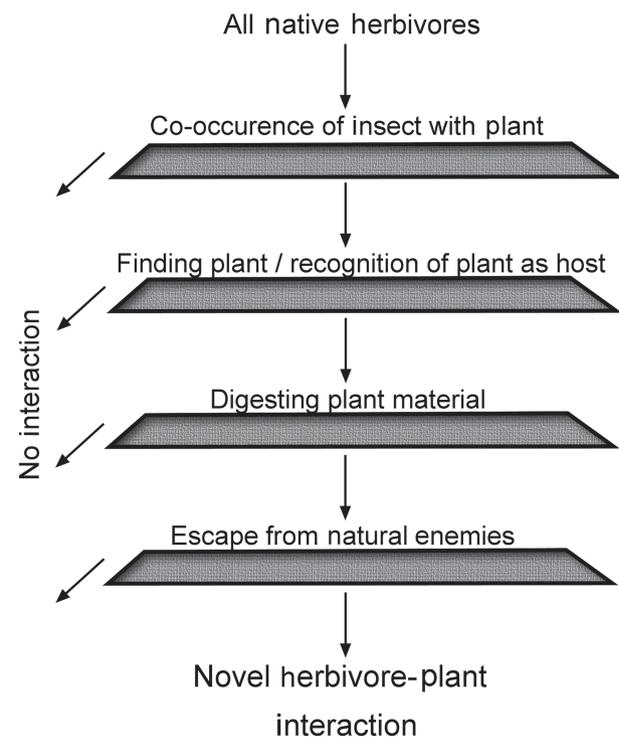


Figure 1. The steps involved in a novel herbivore–plant interaction.

Exploitation (or performance)

To successfully utilize the plant – and thereby increase its fitness at some cost to the plant – the herbivore must be able to access and digest the plant's resources and remain relatively safe from enemies (Fig. 1). This is the step that is most commonly examined in studies of herbivores on non-native plants, though it is unclear, whether it is necessarily the most important (Carmona et al. 2011). Plants produce a wide variety of defenses that inhibit herbivores' ability to exploit their tissues (Stamp 2003). At the same time, the herbivore must escape its own predators, which may be attracted to the host plant (Heil 2008).

Plant defense, herbivore diet breadth and trait matching

The previous section partitioned the components of a plant–insect interaction in time, but other ways of looking at the process can also be fruitful. The match or mismatch between specific plant and insect traits, regardless which process of the interaction these traits mediate, determines whether trophic interactions are realized (Agosta 2006). Trait matching has been proposed as a complementary hypothesis to co-evolution in describing the interactions (or matches) between particular plants and herbivores (Janzen 1985). This hypothesis posits that a discrete set of plant phenotypes may be exploited by an herbivore. Conversely, a discrete set of insect phenotypes predispose that herbivore to feeding on a particular plant. The likelihood of an interaction in this case is not then determined by the defensive investment of the plant per se, nor the host breadth of the herbivore per se, but rather the match between the two phenotypes. Ecological fitting is a particularly appealing framework for examining novel herbivore–plant interactions, as it does not assume that interactions between herbivores and plants are conserved over time (as does co-evolution), but instead that each interaction is a potentially labile match between phenotypes (Verhoeven et al. 2009, Harvey et al. 2010a).

We focus on two ways of predicting a match between herbivore and plant traits. First, we explore ordination and decomposition of traits as a method to reduce the complexity of all of the possible herbivore and plant phenotypes that may affect a potential interaction. Next, we explore the degree to which similarity or evolutionary relatedness to local natives allows a successful match between plant and herbivore.

Decomposing novel herbivore–plant interactions into their major components

One particularly useful way to think about all the complexity of trait matching is with an ANOVA-like decomposition into main effects and interaction terms. For example, some plants might be more heavily defended than others across the board (main effect of plant trait). These plants are unlikely to be attacked by most members of the herbivore community, all else equal. Likewise, some insects have traits that allow them to consume a broader range of plants (main effect of insect trait). Again, holding all else equal, these are the species that are most likely to attack a novel plant. Finally, some plant species may only be available to insects with particular phenotypes (interaction between plant and insect traits).

Identifying these interaction terms allows us to make predictions about specific plant–insect pairs, which would be difficult or impossible to do accurately with only the main effects.

Such a model may be impractical when a large number of traits govern the trophic interaction or when the effects of traits are not additive. This is almost certainly the case for herbivore–plant interactions, but decomposition of herbivore and plant traits still serves two important purposes. First, decomposition of trait matching provides the basis for the more tractable ordination methods described later. Second, the three major components of the decomposition of trait matching – the two kinds of main effects and the interaction terms – provide useful heuristics for thinking about herbivory. In the following sections, we discuss these three components from both mechanistic and statistical perspectives.

Herbivore host breadth

As one might expect, generalist herbivores are more likely than specialists to include novel hosts in their diets (Bertheau et al. 2010). As a broad pattern, herbivore host breadth is evolutionarily labile, where even closely related herbivores may consume vastly different numbers of plant host species (Janz et al. 2001).

Host-breadth traditionally is closely linked to digestive physiology (and thus performance aspects of the herbivore–plant interaction), however, diet breadth may also incorporate all other steps in the herbivore–plant interaction. Herbivores that have a broad distribution or broad phenology (such as multivoltine insects) can encounter more potential hosts (Altermatt 2010). Likewise, insects that have more catholic tastes for hosts (broad preference) may include a broader range of hosts in their diet than insects with narrow preferences. The most-studied aspect of diet breadth is digestive physiology of the herbivore. In several examples, herbivores with more generalized diet breadth had higher survival rates when reared on novel brassicate hosts than did specialist herbivores (Keeler and Chew 2008, Harvey et al. 2010a). However, when a novel plant is very similar to a local native, even fairly specialized herbivores might be able to consume it (Bertheau et al. 2010).

General plant defenses

Some plants have traits that make them susceptible to a broad range of herbivores, while others are well-defended against all but a few. If one knows where a novel plant falls on this spectrum, one can make rough predictions about its likely interactions with every herbivore in the native community. While most of the literature focuses on plant defenses that limit herbivore digestion, 'defenses' can operate at the other steps we outlined above as well: plants can also vary in how broadly available they are in space and time, how chemically attractive or repulsive they are to insects, or in how much enemy-free space they provide for herbivores (Carmona et al. 2011).

Plants that are rare or ephemeral may encounter fewer herbivores than plants that are common, have long-lived leaves, and are generally attractive to herbivores. For example leaves present at times of the year when few herbivores are present (such as during dry seasons) may be highly palatable, but experience little damage as they encounter few herbivores

(Aide 1992). Likewise unapparent plants, or plants that have deterrent odors may avoid herbivores irrespective of the actual nutritional quality of their tissues (Feeny 1976).

If herbivores successfully encounter a particular plant, then herbivore performance is most commonly thought to be limited by plant defenses. Defensive traits are found in all groups of plants and tend to limit the herbivory experienced by the plant (Stamp 2003). So, novel plants that invest heavily in defensive traits may be more difficult for most herbivores to consume. Defensive investment is often associated with slow-growing plants with persistent leaves, which occur in areas with high herbivore density or low resource abundance (Fine et al. 2006, Pearse and Hipp 2012), so non-native plants from these habitats may experience less herbivory than plants from regions with lower herbivore densities or mesic environments. Some of the most 'general' plant defenses involve the attraction of higher trophic levels, 'natural enemies', in order to suppress herbivores. Numerous examples of plant-mediated tri-trophic interactions exist (Heil 2008). Several examples have been shown in which tritrophic indirect defenses have developed as novel interactions. For example, non-native argentine ants are commonly attracted to extrafloral nectaries (Lach et al. 2010), non-native maize volatiles attract both parasitoid hymenoptera and entomopathogenic nematodes (Turlings et al. 1990, Rasmann et al. 2005), and agricultural cotton suppresses herbivore populations with predatory mites housed in its domatia (Agrawal and Karban 1997). Unfortunately, the general importance of top-down limitation of herbivores on non-native plants is far from clear, and much work remains in determining how much non-native plants rely on or actively recruit natural enemies to suppress their novel herbivores (Harvey et al. 2010b).

Traits that matter in the context of specific interactions

Although one can get a baseline prediction of the likelihood of a novel interaction from knowing a plant's overall vulnerability and an herbivore's level of generalism, the efficacy of most plant 'defenses' depends on the herbivore they are defending against. There is a high degree of specificity in most herbivore-plant interactions, and specialization of herbivores to host-plants occurs over many different axes of plant traits (Barrett and Heil 2012). As such, the ability of an herbivore to adopt a novel plant will usually be determined by the match of a multitude of plant traits with herbivore habits and feeding mechanisms (Agrawal 2006, Barrett and Heil 2012).

Co-occurrence, as the term suggests, requires matching between herbivore and host in both space and time; otherwise compatible species that are mismatched in this way might never interact. For example, the host-range of the introduced biocontrol agent *R. conicus* on non-target thistle hosts is largely determined by its phenological match with those thistles (Louda et al. 2003). Likewise, the effects of plant cues, such as volatile emissions, are also contingent on the herbivore involved. While some compounds may be broadly attractive or broadly repellent, the same volatile blend can still have opposite effects on different herbivore species (Campbell and Borden 2009). Finally, an herbivore's 'offensive' digestive traits must match a plant's defenses in order for it to digest a novel plant's tissues (Fig. 1). For example,

variation in the composition of cytochrome P450 enzymes in the gut of parsnip webworms determine the caterpillar's ability to feed on populations of parsnip with varying furanocoumarin defenses (Zangerl and Berenbaum 2003).

Ordination methods to predict novel herbivore plant interactions

In the absence of a detailed mechanistic model for trait matching, which would be hard to build for all of the thousands of pairs of species in a moderately sized food web, researchers can fall back on statistical methods. One might want to model trait matching using the ANOVA-type decomposition described above, with one interaction term describing each possible pair of plant traits and insect traits. Unfortunately, this approach is impractical when we lack data on all the important traits, the number of parameters in the model becomes too large, or the measured traits are highly correlated – all of which seem likely in real-world scenarios. However, there is some evidence that since much of the information will tend to be either redundant or irrelevant, knowledge of a few key factors can be sufficient to explain outcomes. For instance, while species can vary in an indefinite number of ecologically important ways, Ricklefs (2008) suggests that one can represent each species with a small number of coefficients and still capture much of the variance in who-eats-whom. Compressing data down to a few important axes of variation, commonly called 'ordination' in ecology and known as 'dimensionality reduction' or 'matrix factorization' in other fields, can help make problems more tractable by greatly reducing the number of parameters and overall size of the data set; these techniques have been enormously successful across scientific domains, from dealing with large genomic data sets (Brunet et al. 2004) to modeling the preferences of a large group of customers for a large class of products (Koren et al. 2009).

Trait ordination is no new phenomenon when explaining interactions between herbivores and native plants. For example, numerous studies have found significant covariation between plant defensive phenotypes (Agrawal and Fishbein 2006, Pearse and Hipp 2012), which have even been described as 'plant defense syndromes' (Kursar and Coley 2003, Agrawal and Fishbein 2006). Likewise, there is covariation in host use by various herbivore at some scales but not others. At a large scale, 50% of the variation in the occurrence of 24 caterpillar species on Canadian trees could be described in only three principal components, suggesting that many caterpillars utilized a similar set of hosts (Ricklefs 2008). Conversely, at a smaller scale, there was little covariation in the occurrence of herbivores on different primrose genotypes, suggesting that each herbivore species utilized a unique set of genotypes (Johnson and Agrawal 2007). The scale- and context-dependence of how herbivores interact with plants and plant traits implies that typical linear approaches to dimensionality reduction (like principal components analysis) might struggle with this type of data. Current neural network – based dimensionality reduction techniques are less susceptible to non-linearities in data (Hinton and Salakhutdinov 2006) and may prove useful in condensing information in herbivore-plant interactions. Applied to the problem of predicting interactions with novel plants, trait ordination could identify the most important

ways in which phenotypes and evolutionary history help determine the structure of food webs, and could also be used for prediction whenever these broad patterns are important.

Similarity to natives and evolutionary conservatism of host use as a proxies for trait matching

The previous section largely assumed that species interactions are primarily driven by very general patterns – that we can make the most progress by focusing on relatively few plant and insect traits that usually affect the food web structure in particular ways. While there is evidence that this kind of broad approach can work at least on a broad scale (Ricklefs 2008), there can also be more variable, idiosyncratic, or local patterns that are best seen from the perspective of individual species.

Figure 2 sketches one way of thinking about this local perspective, by plotting the fitness of an individual herbivore species as a function its native hosts' possible trait values. Different herbivores will have different fitness functions, which will typically consist of one or more optimal combinations of host traits (Fig. 2a), with much lower fitness when plants are very different from these optima (Fig. 2b). If individual traits are too numerous or complex to put on a single plot, then the x-axis may instead measure distance or dissimilarity between a novel host and the species' optimum, with more catholic species having broader fitness functions (Fig. 2c). But how can we estimate these functions (or something like them) for each herbivore? How can we know what 'dissimilarity' means from the perspective of an insect or what its optimal plant would look like, given that this optimum may not be represented at all in the native plant community?

These are questions with well-studied analogues in other fields, especially marketing. For example, many statistical

techniques that predict customer preference for products are also built to make predictions based on similarity, with similar products defined as those that receive similar ratings from different users, or with similar users defined as those that give similar ratings to products (Schein et al. 2002, Ahn 2008). This approach is the source of the familiar, 'if you liked X, you'll love Y' and 'users with similar tastes liked Z' suggestions on e-commerce sites. These methods require very little mechanistic understanding before modeling can begin. Unfortunately, a problem arises if we wish to make predictions for a new plant in its introduced range: we often don't know anything about who consumes it, so similarity has to be defined in some other way. For instance, a novel plant's similarity to existing plants in the introduced range has been estimated as phylogenetic similarity (Connor et al. 1980, Hill and Kotanen 2009, Pearse and Hipp 2009, Gilbert et al. 2012) or trait similarity (Pearse and Hipp 2009).

Shared evolutionary history can be a good proxy for similarity of phenotypes in many organisms (Pagel and Harvey 1991), and phylogenetic constraint, as applied to native herbivore–plant interactions, is a central tenet of theories of herbivore–plant coevolution (Ehrlich and Raven 1964). At a broad scale, related plant species have similar defensive phenotypes, and many herbivores use a single phylogenetically clustered group of plants (Odegaard et al. 2005, Weiblen et al. 2006). In the case of novel interactions, the relative similarity between the novel plant and other local plants may predict how novel its defenses are. Phylogenetic similarity to a native plant has been a strong predictor of many novel plant–herbivore interactions, but it will only be useful when there is a high phylogenetic signal in the plant traits that govern herbivore interactions. Of course, when key plant traits have a low phylogenetic signal and evolve rapidly (so that taxonomically related species have different

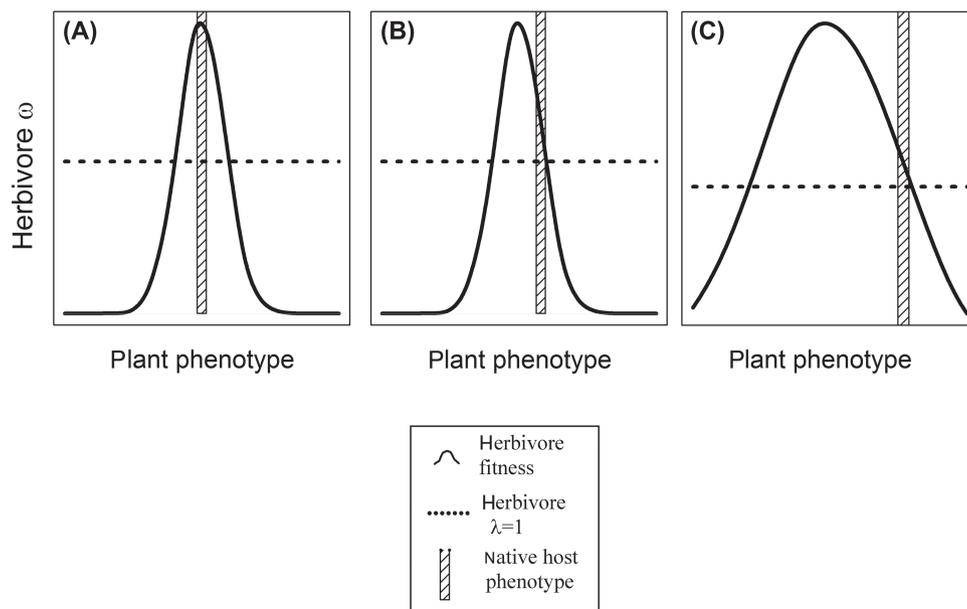


Figure 2. Fitness landscapes of herbivores over some multivariate group of plant traits that differ among plant species. If host-use is under selection for the herbivore, the native host (the dashed bar) may be near an adaptive optimum for its herbivores (A). If plant defenses are also under selection by the herbivore, the native host may not actually be an optimal phenotype for the herbivore (B–C). If a herbivore is a generalist, it may be able to tolerate a broader range of plant phenotypes (C) than a more specialized herbivore (A–B). A novel plant's phenotype may fall anywhere along this graph, and in reality the axis of plant phenotype must be vast and multidimensional.

traits) or when evolutionary convergence occurs in plant phenotypes (so taxonomically unrelated species have similar traits), phylogenetic relatedness will not work as a proxy for phenotypic similarity, and researchers will need a mechanistic understanding of the traits that mediate the interaction (Becerra 1997).

One application of phylogenetic similarity between native and non-native plants is in the extrapolation of native herbivore–plant food webs to predict herbivore interactions with non-native plants (Fig. 3). With this approach, researchers can construct a host-use model of a native herbivore–plant food network (Odegaard et al. 2005, Weiblen et al. 2006, Gilbert et al. 2012) that describes the host-affiliations of each herbivore based on the phylogenetic similarity of their native hosts (Fig. 3 - step 1). By knowing the phylogenetic relationships between a given non-native plant and each of the native hosts of each herbivore, predictions can be made to describe the likelihood of each potential novel interaction between native herbivores and non-native plants (Fig. 3 - step 2). For screening purposes, these predictions may be the goal of the model. However, when information on actual novel herbivore–plant interactions is available, the transferability of the predictive model to novel interactions can be assessed (Fig. 3 - step 3). The goal of such models would be to distinguish those interactions that will occur from those that will not. A preliminary test of extrapolation of native herbivore–plant food networks onto non-native plants shows that a simple model incorporating rough phylogenetic relationships among plants predicts 83% of all actual novel interactions between moths and non-native plants in central Europe with only a 10% false positive rate.

Another application of phylogenetic similarity between native and non-native plants is the prediction of herbivore damage to non-native plants, without necessarily knowing the herbivore causing the damage. This might be especially important, as the damage to a non-native plant caused by native herbivores may explain whether the loss of its herbivores from its native range affects the plant's success. A handful of studies have begun to study this relationship in detail. In an early observational study, Connor et al. (1980) found that leaf mining herbivores tended to colonize non-native trees that were taxonomically related to native hosts. Using a common garden setup, non-native oak trees that were more distant relatives to a single, local native oak experienced less herbivory than more closely related non-native oaks (Pearse and Hipp 2009). Likewise, several broad surveys of herbivore damage to non-native plant species have shown that phylogenetic dissimilarity reduces herbivory experienced by non-native plants (Brandle et al. 2008, Dawson et al. 2009, Hill and Kotanen 2009, 2010, Ness et al. 2011, Gilbert et al. 2012, Harvey et al. 2012). On the other hand, other studies have found that phylogenetic similarity to a native is a poorer predictor of herbivore damage to non-native plants than conserved plant traits (Hill and Kotanen 2011), and that phylogenetic isolation does not drive escape from generalist herbivores (Pearse 2011, Parker et al. 2012). The general patterns that emerge from these few studies suggest that herbivores do often exploit non-native plants that are phylogenetically similar to a local native, but this trend is both

herbivore dependent and scale-dependent (considering all plants or looking within a single genus).

One expectation might be that phylogenetic similarity to a native matters less for herbivores that impose a high fitness cost for the plant. The observation that similarity to a native predicts the chance of a novel interaction implies an asymmetry in selection imposed by host onto herbivore versus selection imposed by herbivore onto host. Plant phenotype exerts a strong selection pressure for herbivores, and herbivores often adapt quickly to plant defenses (Carroll et al. 1997). So, local herbivores are often locally adapted to their native hosts and not to novel plants (Van Zandt and Mopper 1998). Herbivory also exerts strong selection pressure on native plants, and defensive traits of native plants may actually be particularly effective against local herbivores as compared to novel herbivores (Verhoeven et al. 2009, Morrison and Hay 2011). In such cases, the novel plant could actually be a better host for a novel herbivore than its normal hosts. Interestingly, in many of the cases in which novel (native) herbivores thrive on hosts that are more distant from their co-evolved host, the herbivore has a large negative impact on its native host plant. For example, the bronze birch borer (a potentially lethal North American herbivore on native birches) performs better on non-native, Eurasian birch species than on North American birch species (Nielsen et al. 2011). In contrast, most studies of sub-lethal leaf-feeding herbivores find that native hosts and their close relatives are favored by local herbivores (Dawson et al. 2009, Hill and Kotanen 2009, Pearse and Hipp 2009).

The utility of phylogenetic similarity in predicting novel interaction is almost certainly dependent on the phylogenetic scale in question. In general phylogenetic similarity to native hosts will be useful at a large scale in predicting the novel host associations between plants and herbivores. Often host-ranges of herbivores are confined to plants at the genus or family level, so deep phylogenetic history of host-plants will help explain the associations of all but the most polyphagous herbivores (Odegaard et al. 2005, Weiblen et al. 2006). Indeed, using the previous example, even though the bronze birch borer may capitalize on non-coevolved birch species, its novel interactions are still confined to birches and not other trees (Nielsen et al. 2011). At a smaller phylogenetic scale, we do see numerous examples of convergence in defensive phenotypes. In oaks, for example, evolutionary transitions between tough, tannin-rich leaves and softer, tannin-poor leaves have occurred multiple times (Pearse and Hipp 2012). In *Bursera* (a semi-tropical tree genus), the composition of terpenoid compounds, which affect the affiliation of herbivorous beetles, has undergone strong convergence in multiple lineages (Becerra 1997). In milkweeds, defensive phenotype has also undergone such convergence that led researchers to consider milkweeds from different lineages as conforming to particular 'defensive syndromes' (Agrawal and Fishbein 2006). So, at small phylogenetic scales, a more mechanistic understanding of novel interactions may be necessary. As previously discussed with dimensionality reduction techniques, modern non-linear similarity-based methods using neural networks (Salakhutdinov and Hinton 2007) can overcome the problem of scale dependence and also define similarity based on both shared evolutionary history and shared traits.

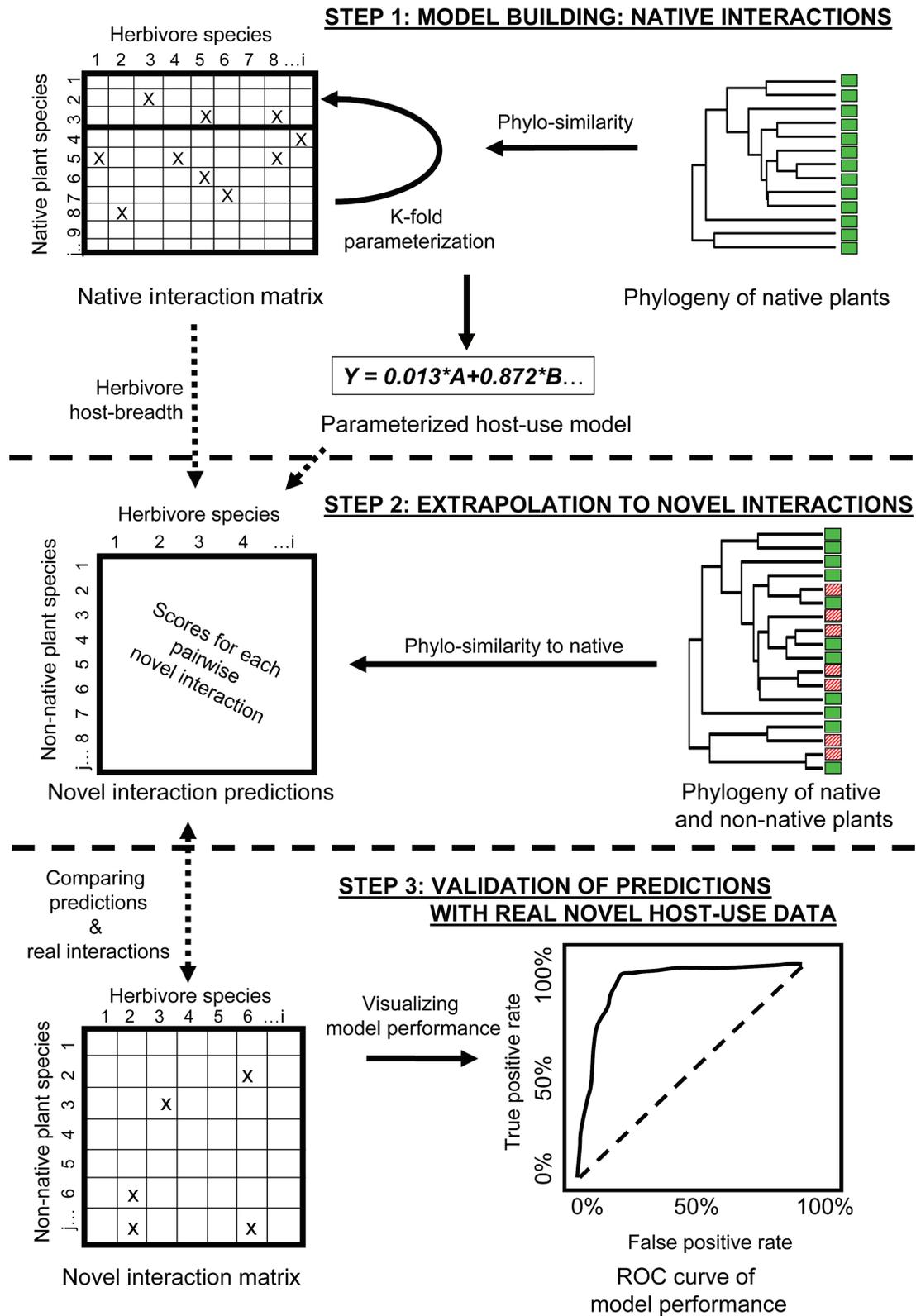


Figure 3. A schematic of a proposed method to extrapolate herbivore interactions with non-native plants from a native herbivore–plant food network. First (step 1), using only information from a native herbivore–plant food network, a model is built by splitting the native food network (using techniques such as K-fold), and using phylogenetic similarity between the plants in each partition to create a model that estimates the importance of phylogenetic similarity and herbivore host breadth in determining host-affiliations within that food web. Next (step 2), based on the phylogenetic similarity between native and non-native plants, this model is extrapolated to herbivore interactions with non-native plants. Finally (step 3), if information on actual herbivore interactions with non-native plants is available, the success of the model may be estimated. The model success can be visualized in the form of a receiver operating characteristic (ROC) curve, that maps the rate of true predictions against the rate of false predictions.

Conclusion: traits and mechanisms of novel interactions

While past studies have focused primarily on palatability trials (i.e. demonstrating digestibility) to explore the potential novel interactions between introduced plants and herbivores, it is clear that other parts of host colonization (i.e. attraction, phenological co-occurrence and avoidance of predators) play a large role in determining novel herbivore–plant interactions. Programs that screen the potential host-breadth of herbivores on novel plants often focus on a few plant traits and insect behaviors that relate to palatability (Louda et al. 2003). While palatability and no-choice feeding trials are powerful tools in screening the potential herbivore–plant interactions that may follow an interaction, it may also be useful to consider more broadly the steps of host colonization by herbivores and the type of traits that drive a successful colonization.

Trait matching between plants and herbivores is likely more important than either plant defense or herbivore host breadth alone. Similarity to native plants can be a robust predictor of rates of herbivory to non-natives, but there are limitations to this. Phylogenetic similarity to a native accounts for 13–18% of the variation in herbivory to non-natives in several systems (Hill and Kotanen 2009, Pearse and Hipp 2009, Ness et al. 2011). But at small phylogenetic scales, this may be misleading, as an herbivore may be able to capitalize on plants that are within its diet-breadth, but lack co-evolved defenses (Verhoeven et al. 2009).

Predictive modeling approaches can incorporate current information about how herbivore plant interactions work and can forecast which herbivores will use which novel host-plants. Dimensionality reduction, and similarity-based predictive methods seem to offer unique advantages although these techniques are only beginning to be rigorously applied to explain novel plant–herbivore interactions. At present, our best inferences still come from the phylogenetic similarity between introduced plants and natives. Future modeling efforts will be more interpretable and gain more predictive power by including a mechanistic understanding of herbivore–plant interactions. Even with current techniques and data, a large portion of novel herbivore–plant interactions can be predicted using quantitative methods.

Contemporary evolution in novel herbivore–plant interactions

In the previous section, we discussed conditions that make it more likely that herbivores will immediately prefer and perform well on a novel plant. This scenario is only one possible outcome of an encounter between a novel plant and herbivore (Fig. 4 - region C). Even species that are not initially compatible can later evolve a robust trophic interaction. Suppose herbivores tend not to detect the novel plant as a potential host and perform poorly on it in the rare cases when they do attack it (Fig. 4 - region A); in such a situation, there will be little selection pressure for the herbivore to adapt either its preference or digestive physiology, because the plant would still make a poor host. In contrast, regions B and D are cases in which preference and performance are not

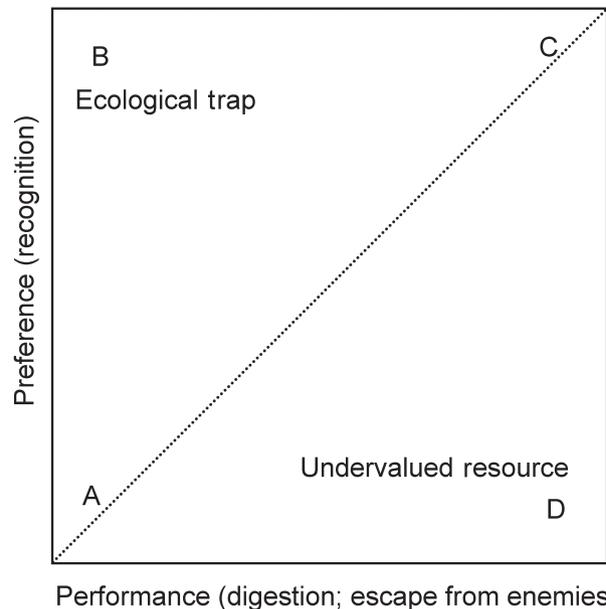


Figure 4. In novel herbivore–plant interactions, there may or may not be a good link between preference (recognition and ability to locate) and performance of an herbivore for a novel host. In region A, the herbivore has an exaptation to use the novel host, and can immediately persist on it. Region B of this chart is an ecological trap; the herbivore recognizes the plant as a host but cannot actually digest it. In region C, the herbivore correctly recognizes the plant as a non-host. In region D, the herbivore sub-optimally rejects the novel plant: it can digest the novel plant but does not recognize it as a host.

well matched, and the plant would make a fine host if either of the two barriers (weak preference or weak performance) were removed. This situation is very common (Gripengberg et al. 2010), and provides more opportunities for host shifts, as discussed below.

In region B, the herbivore perceives and prefers the novel plant as a host, but performs poorly on it. At the outset, this is an ecological trap for the herbivore (Schlaepfer et al. 2005). There are many reasons why naïve herbivores may prefer plant species that they have not experienced over their evolutionary history. For example, females of the butterfly *Lycaeides melissa* were apparently attracted to the abundant floral resources that introduced alfalfa provides, and preferred to oviposit on it despite the fact that this plant is a poor host for developing caterpillars (Forister et al. 2009).

When herbivores are attracted to hosts on which they perform poorly, selection should favor individuals that either do not recognize the novel plant as a host and do not consume it (Fig. 4: a shift from outcome B to A), or selection should favor individuals that are able to better exploit the novel host thus allowing a host-expansion (Fig. 4: a shift from outcome B to C). Following plant introductions, both of these outcomes of selection have been recorded. Populations of checkerspot butterflies *Euphydryas editha* colonized introduced host plants that supported lower larval survival than the native host species (Singer et al. 1993). In two separate cases, those individuals that preferred the novel hosts were strongly selected against and preferences shifted towards favoring the longstanding resident hosts (Fig. 4: B

to A) (McBride and Singer 2010, Singer and McBride 2010; M. C. Singer pers. comm.).

There are also many well documented examples of herbivores that colonize a new host on which they initially perform poorly and they subsequently evolve traits that increase their fitness on these new hosts (Fig. 4: B to C). When garlic mustard was introduced to North America, the vast majority of individuals of the native butterfly *Pieris oleracea* were unable to survive on this new host (Courant et al. 1994). Now that this plant has become abundant in eastern North America, there are butterfly populations that are able to perform well on it (Keeler and Chew 2008). While this change has been dramatic, we know little about the adaptations that have allowed *P. oleracea* individuals to utilize garlic mustard. Soapberry bugs which feed on seeds enclosed in pods of their sapindaceous hosts provide an example in which some of the morphological and life history changes associated with rapid evolution on new hosts are better resolved. Populations that feed on host species with smaller pods have evolved smaller mouthparts, shorter juvenile periods, and greater fecundity – traits that allow them to more effectively use the new hosts (Carroll and Boyd 1992, Carroll et al. 1997, 1998).

There have been other cases where an exotic plant could have presented a valuable new resource for native herbivores, but it was not initially used (Fig. 4 region D). This is an example of what Gilroy and Sutherland (2006) called an ‘undervalued resource’. For example, sulfur butterflies co-occur with crown vetch, an introduced plant in Michigan, but do not tend to oviposit on it, despite the increased fecundity they could achieve by doing so (Karowe 1990). Although behavioral constraints such as these are often assumed to limit acquisition of new hosts (Egan and Funk 2006), changes in preference have received less attention than changes in performance.

Of course, herbivores are not the only ones evolving. There will also be selection on plants to be less attractive to herbivores even if they are actually palatable (Fig. 4 shifting from C to D), or less palatable even if they are recognizable (Fig. 4 shifting from C to B). In particular, plants that colonize new locations that lack herbivores are expected to lose their (presumably expensive) defensive traits that reduce herbivore performance when herbivores are removed as selective agents, the evolution of increased competitive ability (EICA) hypothesis (Fig. 3 from A to D; Blossey and Notzold 1995). For example, the current North American populations of several invasive plants introduced over the last century have lower levels of constitutively expressed defenses than ancestral populations (Siemann and Rogers 2003, Beaton et al. 2011). When the non-native plant re-encounters herbivores, its defenses may increase. For example, introduced parsnip plants collected in North America before the introduction of herbivores were unlikely to be recognized as hosts and had low concentrations of defenses (Fig. 4 close to A) (Zangerl and Berenbaum 2005). Since the introduction of a major herbivore from the native range (moving them to C), the plants have evolved higher levels of furanocoumarin defenses (moving them from C towards B). Similarly, populations of western red cedar from islands that had historically lacked herbivores had low levels of terpenes and were highly preferred by recently introduced deer; introductions of deer to

some of these islands has led to increases in defenses (Fig. 4: A to C to B) (Vourc’h et al. 2002).

Conclusion: contemporary evolution

Given these opposing selective forces, what can we say about where future coevolution will take a novel plant-herbivore relationship? First, the strength of selection will likely be asymmetric between plants and herbivores (c.f. Dawkins and Krebs 1979 ‘life-dinner principle’ of unequal selection pressures). An inedible, or dangerous host-plant can reduce an insect’s fitness to zero, but relatively few plants can be killed or sterilized by a single insect (but see Raffa and Berryman 1983). This may help explain why soapberry bugs quickly evolved shorter proboscis length as a response to the thinner seeds of a novel tree, while the host appears not to have changed its seed morphology (Carroll et al. 1997). Selection could also be asymmetrical because of species’ relative abundances. Thus, rare novel plants might have several generations to adapt their defenses to the local herbivore community before they become abundant enough for the herbivores to evolve countermeasures. On the other hand, the more abundant species might have an evolutionary advantage simply because of their larger effective population sizes and all the benefits that go with them – e.g. buffers against genetic drift, higher equilibrium genetic variation, a greater influx of beneficial mutations, and a greater ability to respond to small selective events (Templeton 2006). With respect to plant invasions, the details of the plant invasion history can influence the adaptability of the plant to herbivores, as genetic variance differs greatly among invasions (Lee 2002). In sum, predicting future evolution is difficult, but progress along this front will be important, since evolution post-introduction will almost certainly influence the ultimate outcome of novel plant-herbivore interactions (Strauss et al. 2006, Orians and Ward 2010, Forister and Wilson 2013).

Overall conclusion

Currently, most consequences of biotic introductions are very difficult to predict, however, because there are many predictable properties of the association of herbivorous insects with host plants, it may be possible to estimate which novel herbivore-plant interactions will arise after an introduction or range expansion. Insect herbivores often have specialized host-associations which are delimited by plant traits and evolutionary affiliations. Large datasets of native herbivore-plant interactions provide a basis for quantitatively assessing these herbivore-plant associations and extrapolating them to novel interactions. Quantitative predictions of novel herbivore-plant interactions will be useful in the management of introduced plants and herbivores. Still, caution should be taken when interpreting predictions of novel herbivore-plant interactions; these interactions represent a dynamic evolutionary relationship.

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