

Adaptations of insect herbivores on different non-native host plants

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Introduction & background

General introduction

Introduced plant species may, and often will, have tremendous impacts on communities (Carroll & Dingle 1996)□. After a successful colonization indigenous plant species will engage competition and may ultimately even become extinct. Induced changes in species diversity and abundance of plants will in turn affect higher trophic levels such as insect herbivores. Newly arrived plant species often arrive without their natural enemies, creating an open niche for potential enemies. Due to the lack of coevolution, potential herbivores are likely to be poorly adapted, and therefore less effective. A phytophagous (herbivorous) insect on a plant is there, either through its own activities or because it was transported otherwise. It seems obvious that the insect either is able to feed and live or not, however, in order to acquire higher fitness on a specific host, adaptations may be advantageous. Evidence of adaptation of species to new hosts is observed in several cases (Strauss, Lau, & Carroll 2006)□. Sequential adaptations may cause species to diverge and ultimately become independent species. Thus the question whether and how adaptations occur is important to understanding host-shifting and even speciation. This paper will review some examples and mechanisms in literature in order to gain additional insight in adaptations of insect herbivores after host-shifting.

Colonization of native communities by non-native plant species

The occurrence of colonization of new areas is quite common throughout history. The colonization and inhabitation of land by former marine species is among the biggest events. A continuous process of small-scale colonizations of species is still in motion after spreading most taxonomic groups virtually all over the world. The impacts of a newly arrived species on the present ecosystem may be significant, and are therefore worth investigation. Where large-scale colonizations are presently rare, small-scale colonizations are quite common. The expansion to new areas and successful inhabitation, as well as the extinction of species will contribute to the local diversity, hence local species diversity is often variable.

For a plant species to be successful in a novel region, it must be transported from its native range to that area, colonize it, survive and reproduce, and then spread more widely. The success of establishment depends on many factors such as phylogenetic relatedness with the indigenous species and environmental factors. The predictive understanding of what controls variation in invader success among introduced populations is full of contradictions (Hierro, Maron, & Callaway 2005; Colautti et al. 2004)□. Non-indigenous species may gain a competitive advantage over residents due to the enemy release hypothesis (Mitchell et al. 2006)□. The enemy release hypothesis (further referred to as ERH) as reviewed by Keane (2002), states that non-indigenous species may escape natural enemies and gain a competitive advantage over residents. Supporting this idea there are indications that introduced plant populations are exposed to fewer species of pathogens and insect herbivores (reviewed by Hinz & Schwarzlaender 2004; Colautti et al. 2004)□. On the other hand, within-community comparisons indicate that introduced species do not consistently receive less damage from natural enemies compared to the resident species (Colautti et al. 2004). As I just briefly illustrated it is difficult to

understand the mechanisms influencing colonization, the prediction of impacts on native wildlife caused the newly arrived species may be even harder. (Mitchell et al. 2006) □ .

To complicate things even more not only natural causes influence colonization events. Due to the impacts on nature by people, colonization opportunities, and in some cases species behavior, have changed. Since the start of agriculture people started to spread many domesticated, as well as wild, animal and plant species. Many of this species managed to establish populations in nature and some eventually became a pest. Approximately 10% of all plant species are non-native, percentages up to 50% non-native species are documented in New Zealand (Heywood 1989). Although the intentional spreading of species continuous, plant introductions in gardens or ponds are common, unintentional introduced species proof to be abundant as well. Several introductions were caused by the use of ballast seawater in ships. This seawater taken in the boats is to be released virtually everywhere. Plankton sampling the ballast water from ships resulted in the finding of 367 different taxa (Carlton & Geller 1994). Not only the transportation of species is profited by humans, also the alternation of local environments creates conditions enhancing adaptation resulting from natural selection. Well-known examples include industrial melanism in peppered moths (Grant, Owen, & Clarke 1995) □ , host range expansion in the apple maggot fly (Feder et al. 2003) □ and soapberry bugs (Carroll et al. 2001) □ .

In general the successful establishment depends on several factors. Climate, soil composition, predation pressure, the degree of similarity between the original and invaded community and other differences may all play an important role in invader success. Also the number of individuals, seeds, eggs or spores imported, also known as the propagule pressure, is known to have tremendous impact on the chances of establishment (Green 1997) □ (Lockwood, Cassey, & Blackburn 2005) □ .

Plant herbivory

Natural enemies of plants generally consist of herbivores, fungal pathogens and bacterial and viral diseases. The role of these natural enemies is often studied and discussed numerous times (Burdon 1987) □ (Crawley 1986) □ . In order to understand the impacts of different plant species on herbivorous insects we must first understand some mechanisms involved in plant herbivory.

Flowering plants reputedly immune to attack by virtually all insects seem to be rarities. The chinaberry tree (*Melia azedarack Linnaeus*) is said to be such a curiosity (Thorsteinson 1959). In general however, for every plant species there is something evolved into eating it. Plants and herbivorous insects together contain up to ~50% of the known terrestrial species (Farrell, Mitter, & Futuyma 1992). Possibly this incredible species richness is partially caused by millions of years of co-adaptation, coevolution and speciation (Janz, Nylin, & Wahlberg 2006) □ . By feeding at the bottom of the food chain, herbivorous insects have access to a potentially enormous supply of resources; these are extensively subdivided among species, as most phytophagous insects are highly host specific (Ehrlich & Murphy 1988) □ (Dixon et al. 2009).

An early model by Ehrlich & Raven (1964) stated that plants evolving a new defense mechanism suffer less herbivory and as a result diversify in a new adaptive zone without their former herbivores. Counter-adaptations to the new defenses by the herbivores facilitate further radiation. The ongoing arms-race between herbivore and plant species has most likely resulted in a variety of insect- and plant-traits.

Herbivory generally has a negative influence the fitness of a plant. To reduce this fitness loss most plants have evolved defenses preventing herbivores from feeding freely. This defenses may include the production of detergent chemicals or other structures in the plant, also plants invest in herbivore toleration ability. Although the individual fitness may be stable even when under attack of specific enemies, for many species investing energy in resistance and tolerance, there is a fitness cost. In an environment without enemies an undefended genotype may outcompete the defended (Agrawal,

Strauss, & Stout 1999) (Redman, Jr., & Schultz 2001) . Again additional complexity is added when species are investing in specific defenses and therefore are vulnerable to other attackers (Rohner & Ward 1997) . Differences in plant phenology between species may often provide an additional barrier for insects, preventing them from performing host shifts and feeding freely.

Host shifting onto non-native plants

In order to perform a host shift a certain advantage must exist. Differences in species composition between novel and native environments may provide such an advantage. One way to benefit from living on a new host is when predation levels on the novel host-plant are reduced. Other mechanisms such as community disturbance may as well have significant effects on invasion behavior (Shea 2002). Non native organisms may become established in disturbed habitats by accessing resources left unused because resident taxa are reduced (Levine, Adler, & Yelenik 2004; Fargione & Tilman 2005) or because they are better adapted to disturbed habitats than are residents (Burke & Grime 1996).

Recently Gretten & Welter (2010) showed that enemy-free space can exist for an herbivorous fly (*Liriomyza helianthi*) utilizing a novel host plant, their enemies may even suffer fitness costs when attempting to develop in the novel host. Although this research, and many others, favor the enemy release hypothesis the hypothesis is not absolute. The potential for beneficial use of the ERH varies between species, this variation depends upon the three assumptions made in the hypothesis. First natural enemies ought to be important regulators of the population, second enemies should have a greater impact on native than on exotic species. Third species must be able to benefit from a reduced enemy pressure (Meijer 2008)(Keane 2002).

Three levels of specialization can be described: monophagy, oligophagy and polyphagy. These terms refer respectively to feeding on one plant genus, one plant family and to feeding on three or more plant families. In addition to these specialization levels, strict monophagy exists, here only one host species is accepted. As briefly mentioned before, most phytophagous insects are highly host specific as well as monophagous (Dixon et al. 2009; Ehrlich & Murphy 1988). Less than 10% of the herbivorous insects feed on more than three plant families (Bernays & Graham 1988).

The probability of a species shifting to a new host depends heavily on the level of adaptation to its original host(s) and the degree of specialization. Many insects have adapted to their host species, for example in resistance to (chemical) defenses, timing of reproduction and morphology. Due to the monophagous majority of the insects, a host shift onto a plant distant from the original host is less likely to occur (Thorsteinson 1959).

Adaptations/ evolution in response to host shifting

In order to discuss adaptation and evolution their existence should first be evaluated, the line between phenotypic plasticity and adaptation might be very thin. Straus et al.(Strauss, Lau, & Carroll 2006) provides a summary including thirty-three examples of native species that have evolved in response to newly arrived species in their communities. These responses can be found in several classes of traits, morphological and physiological (21 examples), behavioral (11 examples) and life history (3 examples). Although evidence supporting evolution was found in several types of ecological interactions (herbivory, competition, predation and disease), the most famous and well documented evidence was acquired through research on phytophagous insects. Host-shiftings in phytophagous insects prove to be excellent study objects, this because introduction of the host is often well documented and because the colonizing species can sometimes directly be compared to its congeners living on the original host-plant. Before a novel plant species can significantly impact selection in its new community, it is often ought to be abundant. Due to large population size's upon introduction, crop plants provide several examples of rapid evolution in insect herbivores (Malausa et al. 2005) . In the proximity of the native

hosts the introduced population size and ecological impact may be of even higher importance (Carroll 2007) □ . Although the extend of the impacts of invasions on selection is not fully understood, basic knowledge of evolutionary processes provides a possibility to predict when evolutionary responses to invasion are likely to occur (Fig. 1).

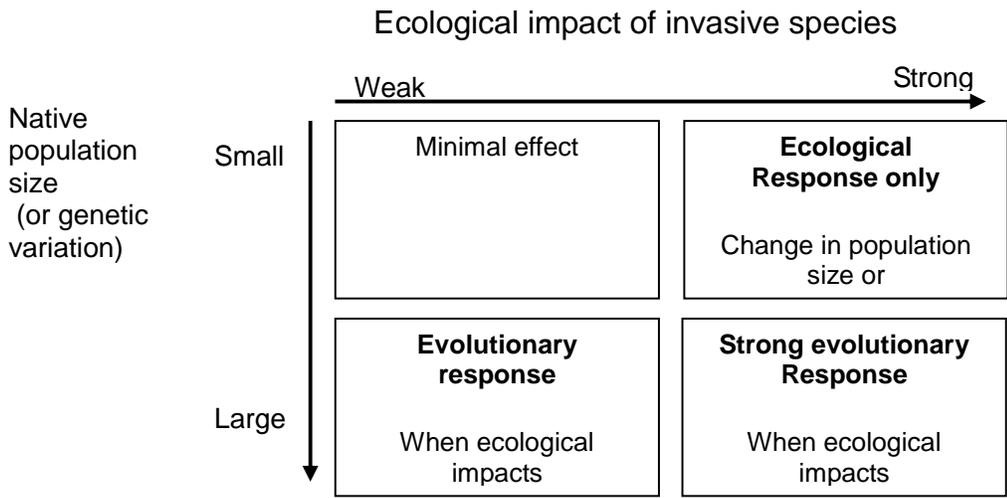


Figure 1. The likelihood of an evolutionary response depends on characteristics of both the invader and the affected native(s). If the invader’s impact is very weak, it may not be an important selective agent and will have minimal ecological and evolutionary effects on natives. If the invader’s impact is strong and if impacts do not differentially affect genotypes, then natives may experience population declines or exhibit plastic changes in habitat or resource use, but have no evolutionary response. When an invader has strong ecological effects, when these effects affect genotypes differentially, and when the native has a large enough population size to withstand these ecological impacts and to provide the genetic variability on which selection can act, then we expect an significant evolutionary response to occur (Strauss, Lau, & Carroll 2006) □ □

In order to review the adaptations of insect herbivores on different non-native host plants it is useful to summarize some examples found in literature.

The Hemipteran sub-family Serinethinae (*Rhopalidae*) is a worldwide group of medium-size seed predator bugs specializing on plants of the “soapberry” family (*Sapinadaceae*). In North America the soapberry tree (*Sapindus saponaria*) and the balloon vine (*Cardiaspermum coriundum*) are native hosts to the most studied soapberry bug, *J. haematoloma* (Carroll 2006). The introduction of three additional non-native *Sapindaceae* as *Koelreuteria elegans* (*Sp. formosana*), commonly planted in central Florida beginning five decades ago, resulted in colonization by *J. haemantoloma* within the 50 years after. Although the three introduced species differ from the native plants in fruit size, phenology, seed quality as well as chemical defense the bug was able to cope with, and even adapt to the differences. For example beak length varies with the size of the fruit predated on, a clear genetic basis was found and this tells us the phenomenon is not just plasticity but also evolutionary adaptation (Carroll, Dingle, & Klassen 1997) □ . Increased performance on the introduced host and decreased performance on the native host were observed in *J. haemotoloma* after 100 generations. Bugs living on the new host, compared with the native host, matured 25% more rapidly, were 20% more likely to

survive and laid twice as many eggs. Also the fecundity was doubled and egg mass was reduced by 20% (Carroll et al. 1997, 1998, 2001, 2003). The shifts visible in these traits indicate that performance has evolved, this may further reflect in host preference as well (Carroll, Dingle, & Famula 2003) □ .

Another famous example of adaptation to a novel host is the host shift performed by the apple maggot fly (*Rhagoletis pomonella*). The species shifted from the hawthorn (*Crataegus* spp.) to the newly arrived apple (*Malus sylvestris*). Feder (1995) found that despite having higher egg-to-pupal mortality on the *Malus sylvestris*, the larvae suffered significantly less from parasite attacks compared with the original hawthorn host populations (Prokopy, Diehl, & Cooley 1988) □ . This escape from natural enemies facilitated performing host shift in the species.

In order to test whether the acquisition of enemy free space possibly influenced the host shift in the goldenrod ball gallmaker (*Eurosta solidaginis*), Brown et al. (1995) estimated levels of natural enemy attack in 25 host-race populations associated with *Solidago altissima* and *S. gigantea*. Although significantly higher mortality on the new host was found (17.1% versus 2.6%), mortality due to attack by the parasitoid wasp *Eurytoma obtusiventris* was dramatically reduced on the new host (30.5% versus 0.4%). Overall, the populations living on the new host benefited from significantly higher survivorship (36.6% versus 20.8%). Despite higher mortality associated with the new host plant, survivors experienced lower mortality from natural enemies, favouring the enemy release hypothesis. Preference-performance correlations have been observed for three races of *Eurosta solidaginis* and allochronic isolation seems to have resulted in reproductive isolation (Horner, Craig, & Itami 1999) □ .

The dynamics of the Colorado potato beetle (*Leptinotarsa decemlineata*) are particularly worth mentioning, this because the severity of the damage it caused and still causes to solanaceous plants (Hare 1980) □ , and therefore to crop yields and the economy. The Colorado potato beetle originated in Mexico and fed on wild relatives of potato species (Grapputo et al. 2005) □ . Present day the beetle expanded its diet to, and became a pest of, potato plants and other solanaceous plants such as tomato, aubergine and tobacco (this spread is documented by Johnson in 1967 □). After the first transition to the American Midwest, estimated in the 1860s, it took the beetle less than 20 years to reach the US East Coast. After accidental introduction in France in the 1920s within 30 years they spread throughout most of Europe. During all of these invasion events genetically distinct host races developed on different native and non-native host plants (Hsiao 1978) □ . Differences in offspring growth and survival, as well as differences in host preference were found (Horton, Capinera, & Chapman 1988) □ .

In the sulfur butterfly (*Colias philodice*) another host shift was documented. A host shift from native legume plants onto novel alfalfa (*Dedicago sativa*) was observed in North America at the end of the 18th century. Populations using the novel alfalfa host benefited and showed higher survival and faster growth (Tabashnik 1983) □ .

Singer (1993) found evidence for rapid evolution of host association independently in two populations of the host-specialist butterfly *Euphydryas editha*, each of which has recently added a novel host species into its diet. The reasons for these rapid evolutionary events lie in human land use practices: logging in one case and cattle ranching in the other. In contrast to other insects that have used tolerance of human activities to expand their ranges into disturbed habitats (Society 2010) □ , these rare butterflies have remained at their original sites and evolved adaptations to the changes occurring at those sites. In an eight year period the preference for the non-native host increased from 10% to 50%, not only the proportion of host preference has increased, in one case a clear genetic change was found. The population living on the non-native host is even starting to generate insects that refuse to accept their native host (Singer 1993).

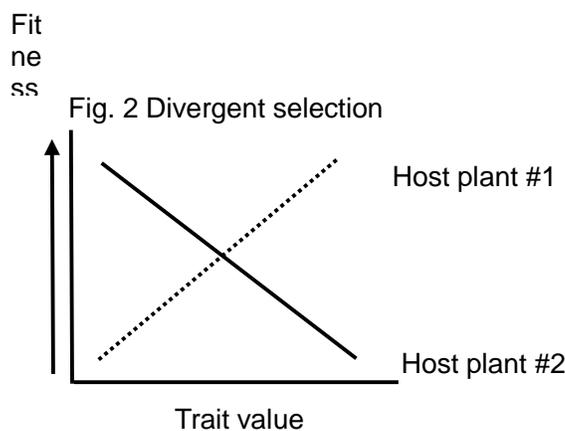
Now an interesting question arises; whether or not the evolution of particular traits is reversible (i.e the reacquisition of ancestral trait conditions). In nature reverse evolution is rare, only a few examples were found in natural populations (Teotónio & Rose 2001) □ . The best known, and perhaps

the best characterized, example is the adaptation of the peppered moth (*Biston betularia*) to variable air pollution in industrialized environments. Industrial fallout darkens resting surfaces, favoring darker, better camouflaged, moths. With the rise of air pollution levels in the second half of the 19th century, populations in central Europe, the Netherlands, the United States and England (Teotónio & Rose 2001) □ changed from being mainly pale typica forms to primarily darkcarbonaria forms. In recent years, in response to improved air quality, the frequency of dark moths has been dropping (Grant, Owen, & Clarke 1995) □ . Teotónio & Rose (2001) stated that reverse evolution could occur because sufficient genetic variability was maintained, the change in melanism was merely a reflection of a change in allele frequency. This gives rise to the idea that all adaptations might be reversible, as long as sufficient genetic variability remains. Severe population bottlenecks and other variation reducing processes may cause adaptations to become irreversible. It is shown that irreversibility can occur rapidly, for example after the evolution of polyploidy in one generation (Bull & Charnov 1985) □.

Speciation

The idea speciation can be promoted by adaptation and divergence was already documented by Darwin in 1859. Research on phytophagous insects has contributed strongly to the development of the hypothesis of 'ecological speciation' (Matsubayashi, Ohshima, & Nosil 2010) □ . This hypothesis can be defined as the process by which barriers preventing gene-flow between populations evolve caused by divergent selection (i.e., reproductive isolation) (Schluter 2009).

Three main forms of selection are commonly recognized: sexual selection, differences between environments and interactions between populations, such as competition and predation. Selection may cause populations to diverge. The term 'divergent selection' can alternatively be defined by crossing fitness functions as illustrated in fig. 2 (Matsubayashi, Ohshima, & Nosil 2010). Different host plant species might differ in their chemistry and morphological structure. Thus, selection might act in contrasting directions between populations of insects feeding on different host species, favoring opposing trait values on different hosts. The extremely rapid genetic divergence (and even speciation) that can occur with invasion of new habitats has been documented for several biological systems recently (Schluter 1994; Schluter & Rambaut 1996; Rieseberg & Burke 2001) □.



Matsubayashi et al. (2010) found evidence that preference and performance can be under control of few loci, potentially facilitating divergence and contributing to the likelihood of sympatric speciation (Berlocher & Jiggins 2002) .

In addition to ecological speciation there are several non-ecological factors entangled in the process of speciation. Phytophagous insects are particularly susceptible to 'non-ecological speciation'. Due to patchy distribution, small local population sizes, and population bottlenecks caused by host-plant shifts, the likelihood of speciation through random genetic drift is increased (Knowles et al. 1999).

Discussion

It is evident that invasion events may dramatically influence and alter resident ecosystems, this alteration is likely to negatively influence one and often more species. The change in species composition in a specific environment may in turn result in the creation of a disturbed habitat, thereby creating an opportunity for even more change in species composition. A cascade of events may lead to damage to biodiversity and may even influence public health, the economy and safety (Meijer 2008) . Although the term 'invasive species' usually refers to introduced species that have a negative effect, the examination of invasion events and its effects has the potential to provide insight in evolution itself and therefore may be a valuable source of information.

A variety of ecological entries for the evolution of natives adapting to invaders and vice versa can be observed. This includes new host and resource availability, the presence of new competitors, predators, parasites and pathogens. Adaptations have the ability to reduce impacts of the changing environment and may improve survivability (Teotónio & Rose 2001) . On the other hand, failure to adapt sufficiently, either plastically or genetically, may result in long term attrition and declines in population size (Strauss, Lau, & Carroll 2006) . Even short-term ecological effects on a community vary from near or total extinction to increased population sizes, weak population divergence, rapid coevolution and even complete speciation (Singer 1993). The possible ecological responses mediated by an invasion event are numerous and hard to predict.

By adapting genetically to rapid-induced changes in habitat, populations risk becoming dependent on the induced changes. Especially human induced changes, such as cultural evolution, can act faster than the genetic adaptation (Singer 1993), this may in turn result in extinction and in the rise of a new problem in conservation biology. Not only speed may be insufficient when genetic adaptation is needed, reduced genetic variation, caused by selection after adaptation on the new host, may influence a species ability to respond to shifting selective pressures.

In summary we may conclude that, in response to invasion events and host-shifting, adaptation in phytophagous insects exist. Although multiple ways of adaptation are thoroughly described for some species, the understanding of adaptation and evolution remains complex and needs further evaluation. Plasticity and adaptation may sometimes only lead to weak population divergence, in other cases coevolution or even complete speciation occurs. Currently the predictability of these events is low, the question what factors determine the extent to which speciation proceeds to completion needs to be evaluated for more insight (Matsubayashi, Ohshima, & Nosil 2010) . Few studies address effects of species that appear to blend into native communities without noticeable adaptations. Species with traits that appear unaffected by invaders may have evolved, phenotypically masking substantial genetic change that affects evolutionary potential (Carroll et al. 1997) . The importance of such hidden changes may be significant and may provide valuable information, which may help provide insight into the structure and functioning of ecological communities.

