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Are exotic host plants a life raft or a trap for butterflies?

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Many landscapes across the world are dominated by exotic (non-native) plant species. These plants can directly impact native species, including insect herbivores. There are many reported cases of native butterfly species using exotic host plants, and these new interactions have had diverse effects on butterfly populations. In this mini-review, I highlight recent developments in the study of the effects of exotic host plants on butterflies, focusing on two areas that have seen major advances: the genetic basis of host use and the influence of other trophic levels on butterfly–plant interactions. Understanding how these multiple factors interact is a key outstanding question for better predicting if an exotic plant might be a trap or a life raft for a herbivorous insect.

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Introduction

Human activities have directly impacted the frequency with which species are moved from their historical range to new geographic areas [1]. Some of these species thrive in the new locations, increasing their abundance and their influence on the native community. Among the most obvious examples of introduction are plant species of agricultural interest, such as crops for human or live-stock consumption. Non-native plants can quickly dominate large parts of the landscape and form new ecological interactions with native species [1]. For herbivorous insects, exotic plants might potentially become new host plants, but these resources are less predictable

than native hosts [2,3]. Insects and plants have a long shared evolutionary history, which has produced the overall positive correlation between female oviposition preference and larval performance on native host plants [4]. This correlation is weaker among insects using exotic host plants, perhaps due to the lack of shared evolutionary history [5].

If a female recognizes an exotic plant as acceptable for oviposition, the ability of larvae to feed and develop can be less than, equal to, or greater than that on the native host. In the extreme case where the larvae die, the previously reliable oviposition cue is now associated with a maladaptive choice and the new host may constitute an ecological trap [6]. On the other hand, if the larvae are able to ecologically fit to this new condition and survive [7,8], selection can act and may increase larval performance. In the extreme case where the native hosts become locally extinct, the exotic host may act as a life raft for the insect by facilitating population persistence [9]. With the new host plant comes changes in other ecological interactions (mutualists, competitors, parasitoids, and predators), which can tip the balance in favor or against population persistence [10]. The exotic host might provide enemy-free space for the caterpillars, increasing butterfly fitness [11], or it might attract butterfly enemies using indirect defense mechanisms [12].

Given the large number of factors at play, understanding the circumstances where an exotic host is an ecological trap or a life raft demands field data from a number of natural populations [13]. Butterflies are among the most studied insect groups and that is also true for investigations of new interactions with exotic host plants. Butterflies are often specialized on a few host plants [14], but that does not prevent them from probing new plants that might be potential hosts for their larvae [15]. Research on recent introductions has indeed found that butterflies can quickly colonize newly available plants [16–18] with outcomes ranging from populations relying solely on an exotic host plant after local extinction of native hosts [9] to the exotic host being completely lethal to the larvae [19,20]. This variation means that butterfly–plant systems are suitable for studying the drivers and consequences of colonization of exotic host plants.

The use of exotic hosts by butterflies has been reviewed before. Twenty years ago, Graves and Shapiro [21] thoroughly reviewed reported interactions between

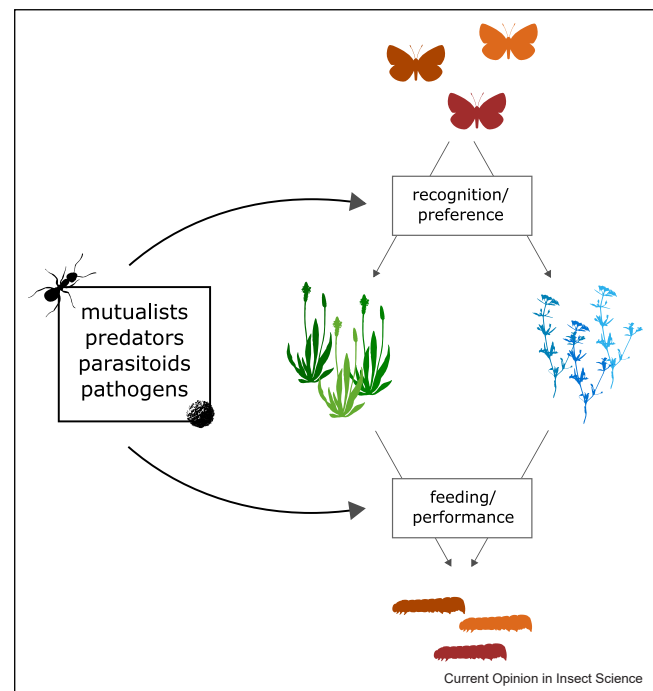
butterflies and exotic host plants in California, where more than 1000 naturalized exotic plants had been reported by then. More recently, Yoon and Read [22] did a meta-analysis on the impacts of exotic hosts on butterfly and moth communities, as well as on their preference and performance on native versus exotic hosts. Early studies on oviposition preference and larval performance already highlighted the importance of understanding the genetic architecture underlying these traits and the need to study natural populations so that the effects of other interacting species, such as natural enemies, could be accounted for [13]. However, only recently, the technologies necessary to investigate these questions in a multidisciplinary framework became available. In this mini-review, I highlight recent developments in our understanding of the factors determining the ecological and evolutionary outcomes of interactions between native butterflies and exotic host plants, with a focus on two areas that have seen major advances in the past two years: the genetic basis of traits related to host use and the effects of other trophic levels (including microorganisms) on interaction dynamics (Figure 1).

The genetic basis of native butterfly–exotic plant interactions

One of the best-characterized interactions between a native butterfly and an exotic plant is the one between the Melissa blue (*Lycaeides melissa*, Lycaenidae) and alfalfa (*Medicago sativa*, Fabaceae) introduced in western North America about 200 years ago [23]. The Melissa blue uses native Fabaceae hosts and has colonized alfalfa at least twice [24], mainly in areas where the plant has escaped from cultivated fields and established into wild environments. Overall, alfalfa is a poor food plant for Melissa blue caterpillars, with clear negative effects on larval performance. However, there is variation in the ability to use this exotic host [24,25]. The spatial heterogeneity of this butterfly–plant interaction and the variability in preference and performance across *L. melissa* populations offers the opportunity to investigate the genetic basis for this variation.

Gompert et al. [25] sequenced, assembled, and annotated a draft genome of the Melissa blue, which opened the doors for statistical and functional genetic analyses of host use traits. The original study investigated larval performance and genomic variation in *Lycaeides melissa* and found that genetic variants that affected performance on one host (native or exotic) had little-to-no effect on performance on the other host [25]. The main conclusion of the study was that the genetic architecture of variation in larval performance in *L. melissa* is characterized by many loci of small and independent effects across native and exotic host plants [25]. Thus, there should be enough genetic variation in *L. melissa* for selection to act upon and increase larval performance on

Figure 1



Interactions between butterflies and plants are determined by many factors, including i) the ability of the butterfly to recognize a plant as an adequate host, ii) the ability of the larvae to feed and develop on the plant, iii) whether the plant is native (blue) or exotic (green), iv) butterfly and plant intraspecific genetic variation (represented by color variation), and v) other interacting species such as mutualists and natural enemies.

the exotic host without necessarily affecting performance on the native host.

However, this is only one side of the interaction. The genetic variation within host species can also affect the outcome of the interaction. Gompert et al. [26••] addressed this question by quantifying the relative contributions of genetic variation in *L. melissa* and the exotic host (*Medicago sativa*), and how these interact. They accomplished this by conducting common garden rearing experiments, multilocus genetic mappings, and genotype–phenotype modeling to predict larval performance [26••]. Larval growth and survival (i.e. performance) depended on genetic variation from both butterfly and host plant, with butterfly genetic variation being more determinant of performance early in larval development and host plant genetics coming into play later. The effect of host plant genetics was associated with heritable variation in phytochemicals, to a large extent. Taking one step further, the authors found that the identified effects of plant genetics were consistent across four *L. melissa* populations and two other butterfly species, *Colias eurytheme* (Pieridae) and *Vanessa cardui* (Nymphalidae) [26••]. Taken together, these results support a

scenario of diffuse coevolution where the formation of new butterfly–plant interactions is not necessarily constrained by genetic trade-offs in larval performance [25,26••].

Recent years have also seen advances in our understanding of the genetic basis of oviposition preference. In this area, an emerging model system for studying maladaptation is the butterfly *Pieris macdunnoughii* using native and exotic Brassicaceae hosts in North America. *Pieris macdunnoughii* females have laid eggs on the Eurasian mustard (*Thlaspi arvense*) for decades, despite the plant being lethal to the larvae. Steward et al. [27••] found that genetic variation in host preference is maintained in a population of *P. macdunnoughii* despite strong selection to avoid the exotic, toxic host. Analysis of heritability of preference for the toxic host versus a common native host uncovered sex-linked genetic variation, which is unexpected for a trait under strong negative selection given that females are heterogametic and so the effects of recessive alleles in sex-linked genes are not masked [27••]. The authors suggest that this maladaptation is likely maintained in the population by other processes such as gene flow from naive populations, temporal and spatial variation in selection, or pleiotropic constraints. Future studies can take advantage of the recently assembled *P. macdunnoughii* genome [28•] to investigate the genomic basis of preference for both native and exotic hosts and uncover the mechanisms maintaining this butterfly in an ecological trap.

Another model system in the study of insect–plant interaction dynamics is *Euphydryas* butterflies using the exotic plant *Plantago lanceolata* [29–31]. Among these, populations of Edith’s checkerspot (*Euphydryas editha*) in western North America are the best known in terms of temporal changes in host use and their demographic consequences [3,16]. Opposite to the interaction between *Pieris macdunnoughii* and *Thlaspi arvense*, *Euphydryas editha* achieved higher fitness on *Plantago lanceolata* than on the native host. This happened because the perennial exotic is available for a much longer time than the ephemeral native host, freeing the butterflies from a trade-off imposed by time constraints [32]. Even though the butterfly was originally able to use both hosts, selection for using the new host was strong and the population quickly evolved preference for *Plantago lanceolata*, ultimately abandoning the native host. This meant that the butterfly population was completely dependent on a host that is controlled by human activity. When land management changed, *P. lanceolata* was overgrown by grass and *Euphydryas editha* lost its sole host plant. Three years later, the population was extinct [3]. Even though much is known about the life-history and host use dynamics in *Euphydryas* butterflies, the genetic basis of these traits is still understudied. An important recent development was the assembly of a

genome for *Euphydryas editha* [33•], which will allow future studies to investigate the genetic basis of host preference and performance on native and exotic hosts, as well as the genetic consequences of rapid changes in host use.

Multitrophic interactions

A number of recent studies have contributed to our understanding of mutualists and antagonists as one of the forces driving insect–plant interactions (see [10], for an overview). Direct tests of vulnerability to pathogen infection in butterflies reared in native versus exotic hosts have shown that feeding on the exotic host *Plantago lanceolata* changes immune response, even though the direction of change varies between species [34••,35••]. When larvae of the neotropical butterfly *Anartia jatrophae* (Nymphalidae) were infected with Junonia coenia densovirus (*Parvoviridae*), a naturally occurring pathogen of Lepidoptera, they exhibited higher survival on the exotic than on a native host [35••]. Thus, in situations where viral pressure is high, the exotic host could represent a life raft for *Anartia jatrophae*. In the other study however, larvae of a wild population of *Euphydryas phaeton* (Nymphalidae) using the same exotic plant exhibited reduced immunocompetence and higher viral burden [34••]. Despite having weaker immunity on the exotic host, butterflies achieved similar survival on exotic and native hosts by sequestering toxic compounds from the exotic plant and employing them in defense against the virus [34••].

These studies exemplify how insect immunity against pathogens is influenced by the nutritional quality and the phytochemistry of the host plant [36]. Other recent studies have focused on the role of microbiomes in shaping multitrophic interactions. For example, Yoon et al. [37] show that foliar microbial diversity has a negative effect on immune response in *Lycaeides melissa* fed with the exotic *Medicago sativa*, and Yoon et al. [38••] show that maternally transmitted microbes also reduce immunity in the same butterflies, particularly when they are reared on the native host. Some of the outstanding questions for future research are when are microbes beneficial and when are they harmful to herbivorous insects and how that affects the outcome of new interactions with exotic hosts.

Mutualists are also important players in insect–plant interaction dynamics. Among Lycaenidae butterflies, including the Melissa blue (*L. melissa*), ants are common mutualists [39]. Ant abundance was in fact the main determinant of the presence of Melissa blue in alfalfa patches, in a recent study [40]. The authors surveyed 56 patches of the exotic alfalfa where they sampled individuals of the Melissa blue (when present) and almost 300 species of other arthropods. They estimated

dispersal between patches from genomic data, characterized the physical structure and phytochemistry of individual plants, as well as quantified geographic and climatic variables in order to model the occurrence of the *Melissa* blue in alfalfa patches. The variables with the strongest negative effects on butterfly presence were plant phytochemical variation and arthropod enemies (such as other ant-tended herbivores that compete with butterflies, predators, and parasitoids), while the variables with the strongest positive effects were ant abundance, patch area, and butterfly dispersal [40]. This study presents a very thorough description of a system where the exotic plant is a suboptimal host for larval development and populations can only persist on this host when all important factors align, including mutualists, competitors, and predators.

Conclusion

The literature reviewed here highlights the complexity associated with predicting the outcome of interactions between native butterflies and exotic host plants. Among the many contributing factors, intraspecific variation within insect and plant species is an important determinant of whether an exotic plant might be an ecological trap [17,19,20,26••]. Understanding how this genetic variation translates into phenotypic variation that allows insects to ecologically fit to new plant resources remains a challenge left for future studies. Such research would support predictions of new interaction outcomes based on a more refined mechanistic knowledge of the dynamics that complements the more general knowledge about macroevolutionary patterns. At the same time, insect–plant interactions are embedded in larger ecological networks, and the other players in the network can directly increase or decrease insect fitness on exotic hosts. Mutualists and natural enemies are among the many biotic and abiotic factors that determine the ecological conditions in which a native insect survives on an exotic host [10,40]. This means that understanding interaction dynamics requires broad community sampling, and that demands a multidisciplinary approach that is more likely to be achieved by collaborative work.

One important limitation of the literature on the use of exotic hosts by butterflies is the geographical bias toward North America. In particular, long-term studies are concentrated in western North America. I have found few studies of tropical systems published in the past two years [9•,35,41,42], and even in regions where butterfly and plant diversity are well described, not much is known about interaction dynamics. For example, in Australia, at least six native butterflies seem to rely solely on exotic grass hosts and there are records of many other species using exotic hosts [43], but few studies demonstrate drawbacks [44] or benefits [45,46] of these interactions.

Overall, it seems that most exotic hosts are not instantaneous traps for butterflies (e.g. plants that are toxic to larvae), but they might become traps in the long term depending on the ecological context of the interaction and disturbances caused by human activities. Still, butterflies might evolve their way out of a trap if they have enough time [17,47].

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

Nothing declared.

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