The population ecology of novel plant–herbivore interactions

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Many native herbivores are known to attack exotic plants, and we can expect these interactions to occur with increasing frequency in coming years as invasive plants become naturalized and new invaders arrive in native communities. In some cases, evolutionary biologists and ecologists have learned a great deal from insects adapting to novel hosts. However, there is more to be learned and we suggest that the ecological study of exotic host colonization by native insects has been impeded by a lack of focus in the questions being asked, and also from overlap with other areas of plant–insect ecology, including the study of specialization. In the present paper, a conceptual model is described for the colonization of a novel host-plant, which focuses on the relationship between occupancy and availability. Occupancy is the fraction of patches of novel hosts that are utilized by an herbivore, and availability is the abundance or presence of a novel host on the landscape. Considering the slope of that relationship (between occupancy and availability), hypotheses are suggested that involve dispersal and, most important, population growth rate of an insect herbivore associated with an exotic host. A focus on the occupancy–availability relationship highlights the strengths and weaknesses of common experimental approaches, such as preference–performance experiments. Suggestions for future work are offered that include integration with evolutionary theory and exploration of more complex demographic and ecological scenarios.

Herbivorous insects are characterized not only by enormous species richness, but also by great variation in diet (Price et al. 2011). The number and type of plants attacked constitute the host-range of an herbivore, and many fields of research have been occupied with understanding variation in host range among herbivore species (Jaenike 1990, Olff et al. 1999). These areas of research include studies of host detection, larval physiology, natural enemies and oviposition behavior, among other topics (Crawley 1983, Bernays and Chapman 1994). A prominent and unifying theme in these areas of research has been ecological specialization (Singer et al. 2008, Poisot et al. 2011, Barrett and Heil 2012, Forister et al. 2012a), and workers in the field of specialization have typically focused on issues of relative host-range (Ali and Agrawal 2012). In other words, why do certain herbivore species attack a greater number of hosts than other herbivore species? This question can be addressed with reference to a particular feature of herbivorous insect biology. For example, the physiological efficiency hypothesis posits that growth rates will be higher for a specialized insect relative to a more generalized species when compared on a common host-plant, perhaps the primary host of the specialist and one of the hosts of the generalist (this is also known as the 'jack of all trades is a master of none' hypothesis; Fry 1996, Scriber 2005, García-Robledo and Horvitz 2012). Other hypotheses have focused on different facets of plant–insect ecology, such as the importance of natural enemies in determining the relative number of hosts attacked (Bernays 1989, Dyer 1995, Singer and Stireman 2005), and recent work has stressed the need for integration across hypotheses (Mooney et al. 2012) and life history stages (Altermatt and Pearse 2011). In contrast to the study of specialization, which focuses on comparative diet breadth or the relative number of host associations for a given herbivore, we are interested in changes in host-range: the incorporation of novel hosts, either with or without the loss of previously used hosts.

The issues of dietary specialization and the colonization of new hosts are interrelated, but not completely overlapping. We will argue that there are questions that can be asked and elements of plant–insect ecology that can be profitably pursued with respect to the colonization of new hosts that are complementary to issues of relative diet breadth or specialization. Our emphasis on the colonization of novel hosts can be illustrated with reference to the schematic presented in Fig. 1, which includes factors affecting diet breadth for a single, hypothetical herbivore species. The study of specialization has often asked how a particular factor determines or constrains diet breadth. For example, neural limitations might affect the number of potential hosts that are considered by an ovipositing female (in the case of Fig. 1, a total of four hosts are recognized), and that range of hosts need not be identical to the list of hosts that are suitable for juvenile development (Solarz and Newman 2001). However, knowing that neural limitations or physiological tradeoffs cause one herbivore species to attack a
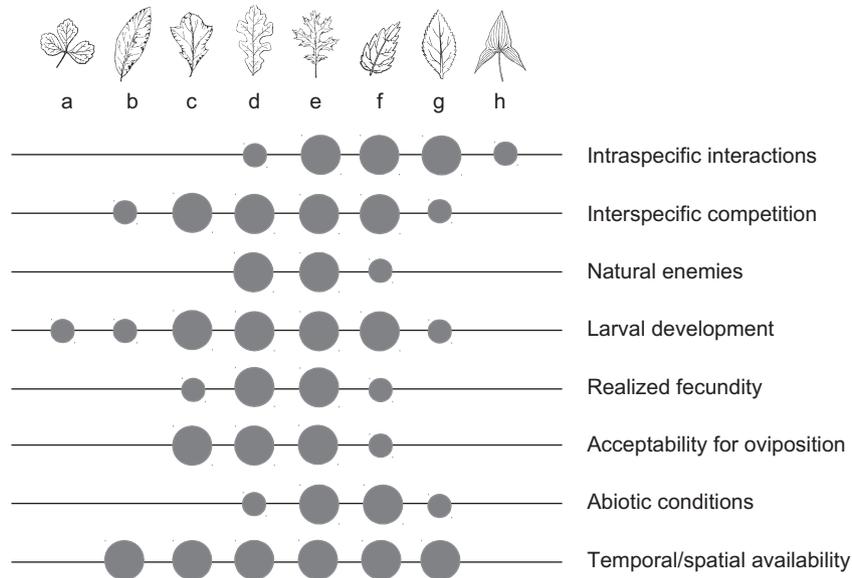
Figure 1. Factors affecting host range for a hypothetical species of insect herbivore. Each lowercase letter and leaf illustration represents a single host-plant species, and the gray circles indicate the suitability of hosts with respect to particular factors; the smaller circles indicate less suitability, and the absence of a circle indicates the least favorable host-specific conditions. For example, hosts b through g are either temporally or spatially available to the herbivore, while only plants d through g are associated with abiotic conditions that allow for persistence of an herbivore population. Circles associated with 'acceptability for oviposition' indicate plants that are recognized by females as oviposition substrates, while 'realized fecundity' suggests variation in host-specific factors that influence the number of eggs that a females lays during her life (for example, a larval host-plant that is also a nectar resource could be associated with high realized fecundity compared to a situation in which the larval host does not offer nectar, forcing females to move between nectar plants and hosts). Other factors are more self-explanatory, with the exception of 'intraspecific interactions', which is meant to encompass a number of phenomena, including intraspecific competition for feeding or competition for oviposition sites. Different host-species (or potential host-species, as for example in the case of host h) could grow in spatial distributions that either enhance or impede the ability of individuals to find mates, which would also be a host-specific effect associated with intraspecific interactions.

smaller number of hosts relative to some more generalized herbivore, while clearly important, does not necessarily help us understand the conditions under which any particular new host might be added to the diet of either species (Larsson and Ekbom 1995), which is our focus here.

Of the hosts diagrammed in Fig. 1, host e is the most suitable with respect to the factors shown. We can imagine a situation in which host e is currently being used by a hypothetical herbivore in a hypothetical area, and plants d and f invade the area. Will they be colonized given the balance of survival and fitness effects associated with the factors shown? Is the effect of abiotic conditions (perhaps microclimate around a particular plant species) as a limiting factor more or less important than the effect of natural enemies? Are there certain demographic or landscape scenarios that might lead to the utilization of hosts c or g, despite the fact that the herbivore is poorly preadapted to those plants? Questions of this type can be asked of particular herbivores and plants, and we might also seek generalities among related herbivores or within feeding guilds or among species that utilize a common suite or lineage of hosts.

The factors illustrated in Fig. 1 are not meant to be exhaustive, even for a hypothetical herbivore; they are meant to illustrate the complexity of diet breadth (Bowers et al. 1992, Karban and English-Loeb 1997, Keeler et al. 2006, Smilanich et al. 2009). Numerous additional factors could be added for any real plant–insect interaction. For example, heterophylly (the production of various leaf types within the

lifespan of an individual plant) has been suggested as an important axis of variation influencing the colonization of *Eucalyptus* trees by native herbivores in areas where the trees are cultivated (Paine et al. 2011). Voltinism, or the number of generations produced per year, is yet another factor by which populations associated with different hosts can vary in ways that might affect the colonization of new host-plants (Sims 1983, Scholl et al. 2012). Interactions among factors could also be considered in any real-world scenario, as between oviposition preference and the abundance of mutualists (Pierce and Elgar 1985) or competitors (Hanks et al. 1993).

Investigations into the colonization of new hosts are of course not new, and research has involved both causes and consequences of changes in host range (Thompson and Pellmyr 1991). Substantial progress has been made in the realm of consequences: ecologically, changes in host range can produce novel inter- and intraspecific interactions and community dynamics (Lambrinos 2004, Tylianakis et al. 2008). Evolutionarily, changes in host range can lead to divergence in host-associated traits, such as the evolution of oviposition behavior that has been observed in *Euphydryas editha* butterflies in the presence of an exotic host (Thomas et al. 1987, Singer et al. 2008). On a longer timescale, evolutionary consequences of changes in host-range can lead to reproductive isolation and contribute to the diversification of insect lineages (Fordyce 2010, Janz 2011; but see Nyman et al. 2010). Janz and Nylin (2008) posit a particular

interaction between host-range shifts and diversification: in the oscillation hypothesis, lineages of herbivores oscillate between periods of host range expansion and periods of host-range contraction, with the latter (contraction) being associated with diversification and speciation.

Less progress has been made on the side of causes of host-range evolution, though this failing has not been due to a lack of effort or attention. Futuyma et al. (1995) used breeding experiments and quantitative genetics to suggest that the history of host-shifts in the leaf beetle genus *Ophraella* has been constrained or at least guided in part by the existence of genetic variation in traits related to the use of alternative host-plants. The desire to predict changes in host-range extends beyond ecology and evolutionary biology into applied fields of pest control, forest management and conservation biology (Waters and Stark 1980). Our ignorance regarding the ecology of host-range shifts is well illustrated by examples of insect biocontrol agents attacking unintended targets (Louda et al. 2003). Here we propose a conceptual framework to hopefully advance our study of causes and processes associated with the colonization of novel hosts. We define a problem utilizing a hypothetical herbivore species, we place previous work in a particular context, and we suggest avenues for future research.

Related theories

Before moving on to describe our conceptual framework and related hypotheses, we digress to describe and address related bodies of theory. The hypotheses and questions implicit in Fig. 1, and mentioned above, are compatible with the conceptual framework of 'ecological fitting' put forward first by Janzen (1985) and most recently articulated by Agosta (2006) and others (Brooks et al. 2006, Gillespie and Wratten 2011). The concept of ecological fitting suggests that observed ecological interactions among contemporary species are not necessarily the product of evolutionary processes (Janzen 1985). Instead, the 'fit' of parasites to contemporary hosts results from an ecological 'match' of traits and environments, with the traits themselves having been the result of evolution in association with hosts or environments that are either extinct or geographically removed from the currently-observed host–parasite interaction. This concept is closely related to the idea of exaptation (Gould and Vrba 1982), and was offered as an alternative to the adaptationist expectation that any observed ecological interaction is the product of coevolutionary processes (Janzen 1985). Agosta (2006) applied the idea of ecological fitting directly to host shifts by herbivores, and pointed to different lines of evidence suggesting that host shifts provide good evidence for the ubiquity of ecological fitting. In the context of Fig. 1, if host e were currently utilized by the herbivore species and hosts d or f invaded the range of the herbivore, one might speak of the colonization of those hosts as an example of ecological fitting. The fact that the fit is not perfect to either d or f (indicated by the smaller circles) could further be encompassed by Agosta and Klemens' (2008) concept of 'sloppy fitness space' associated with plasticity and the ability to use novel and possibly sub-optimal resources or environments.

In addition to the idea of ecological fitting, there are bodies of theory in ecology that are important for understanding changes in diet breadth, including a large amount of work on niche width (Holt 2009, Chase 2011). The framework of fundamental and realized niches could be used to discuss factors that constrain or facilitate the utilization of certain hosts (Fig. 1). Another body of theory, on range limits and adaptation to marginal habitats, is also relevant, but slightly beyond the aims of the present paper (Holt 2003). Our goal is neither to present completely novel theory, nor to translate theory from other subfields into the issues of novel host colonization. Instead, the goal is to present a simple conceptual model that might help to organize empirical and theoretical research on the ecology of insects interacting with novel hosts. We hope that this model will complement other recent reviews on related topics involving both invasive species and diet breadth in herbivorous insects (Strauss et al. 2006, Vellend et al. 2007), as well as continue the dialog related to ecological fitting (Agosta 2006). Processes of recent and rapid adaptation have been considered elsewhere (Thompson 1998, Hairston et al. 2005), thus we (mostly) keep a narrow focus on ecological interactions and ecological dynamics in the process of host range shifts, acknowledging the need for future work integrating ecological and evolutionary aspects of the host-range issue (Schoener 2011).

A conceptual framework

A number of different starting points could be (and have been) suggested for research investigating the colonization and utilization of novel hosts by herbivorous insects. For example, a reasonable starting point could be as straightforward as asking if a potential host is acceptable to ovipositing females, or if a novel host is a viable larval resource (Shapiro and Masuda 1980, Barre et al. 2002, DiTommaso and Losey 2003, Mattila and Otis 2003, Stefanescu et al. 2006)? Other questions involve phylogenetic distance between novel hosts and hosts already in the diet of an herbivore (Agrawal and Kotanen 2003, Bertheau et al. 2009, Pearse and Hipp 2009, Hill and Kotanen 2011), or phytochemical similarity between current and potential hosts (Cappuccino and Arnason 2006, Murphy and Feeny 2006). All of these approaches are commonsensical, and have been productive areas of research. After all, a novel host must presumably be recognized by an ovipositing female, and that recognition will often be predicted by phylogenetic or phytochemical distance to previously-used hosts. However, rather than giving priority to any one feature of plant–insect ecology (such as oviposition), we start with a more general model that hopefully highlights multiple features of the plant–insect relationship that are worthy of study.

Consider a species of insect herbivore that has localized population dynamics and locally specialized, host–associated behaviors: most individuals spend their lives associated with a particular patch of plant, and many elements of the life cycle (larval development, eclosion, mating) are in direct association with that plant. This hypothetical herbivore is locally specialized in the sense that one plant species is used in a given location, and locations are separated by matrix

that exceeds in areal extent the average distance moved by most individuals (i.e. dispersal between locations is uncommon). Different locations might utilize different host-plants (the herbivore can be regionally polyphagous while being locally specialized), and we are interested in the possibility that a plant species that is novel to the region becomes colonized and utilized by the herbivore species. The ecology of this hypothetical metapopulation corresponds to many real species, including some butterflies, beetles and other insects.

In Fig. 2a, linear relationships are drawn between 'occupancy' and 'availability'. Occupancy refers to the fraction of the plant that is utilized by an herbivore in a landscape or regional context: in other words, as new patches of host-plants are colonized, 'occupancy' increases. An increase in occupancy could also be interpreted as an increase in the probability that any one plant or patch of plants is utilized. Availability is meant to capture the landscape-presence of the resource: the origin of Fig. 2a can be seen as the start of an invasion of a novel plant into an area (we acknowledge that 'availability' is not a simple factor,
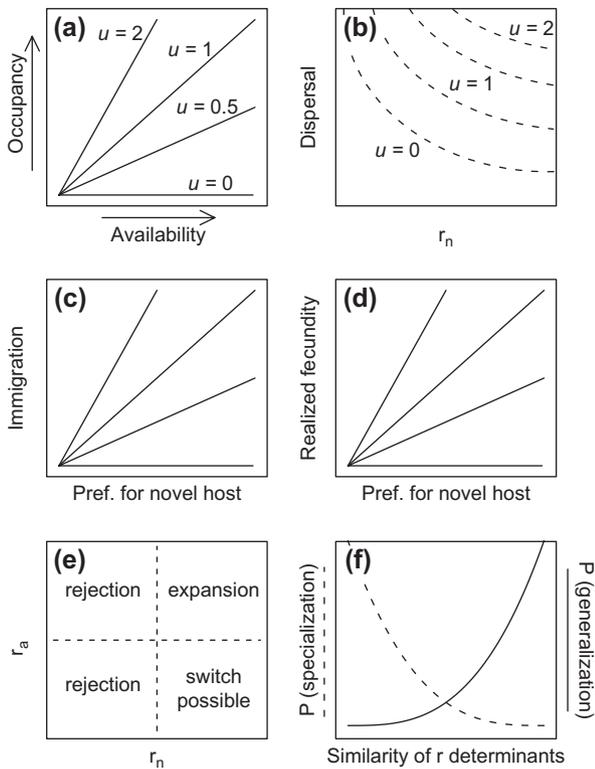

Figure 2. Hypotheses relating to the colonization of novel host plants. (a) The relationship between the availability of a host on the landscape and the extent to which the plant is utilized by an herbivore; occupancy here could be interpreted in different ways, including the fraction of the resource that is utilized as well the probability that any one patch of host is utilized. Arrows on the axes are meant to indicate the dynamic nature of these quantities, and the slopes of the lines are labelled with u, the utilization coefficient. (b) An illustration of two properties, dispersal and population growth rate (r_n, on the novel resource), and how they might predict u. (c and d) Two sets of relationships illustrating variables that could be investigated with respect to plant preference. (e and f) Hypothetical relationships related to the probabilities of specialization or host range expansion, see text for more details.

and certainly involves detectability by the herbivore, but that complexity is not needed at this stage). The line in Fig. 2a with a slope equal to one corresponds to an herbivore that utilizes a novel plant in proportion to its availability on the landscape: as the plant becomes more common, it is incorporated to a greater extent into the diet of the herbivore. When the slope is greater than one, the plant is utilized at a relatively greater rate, and the converse applies to the slope less than one. When the slope is zero, a plant is never utilized.

The relationships in Fig. 2a concern a particular herbivore species and a particular plant species. At a broader, community level, a positive relationship has long been recognized between herbivore community richness and both the geographic area of host-plants and the amount of time that hosts have been in a particular area (Southwood 1961, Opler 1974, Brändle et al. 2008). At the more narrow scale that is our focus here (involving the interaction between an herbivore species and a particular plant species), we suggest that the slope of the occupancy–availability relationship (Fig. 2a), which we refer to as u (for utilization coefficient) captures something essential that we would like to know when thinking about the interaction between an herbivore and a (potentially) novel host-plant. In other words, if we consider the potential interaction between a native herbivore and an exotic plant, we want to know more than 'is a potential host acceptable to ovipositing females?' or 'can larvae survive on the host tissue?' Rather, we would like to know the rate at which a host is utilized in proportion to its availability to the herbivore. This rate (u) is important not only for predicting the future of the interaction, but also for the future of the herbivore in a conservation context (Westman 2005).

Given the relationships depicted in Fig. 2a, a key question becomes: what determines the slope (u) of the occupancy–availability line? One possible perspective on that answer is presented in Fig. 2b, with u determined by a combination of dispersal and population growth rate associated with the novel host. The population growth rate (r_n) refers to populations associated with the novel host (remember that the hypothetical herbivore has localized population dynamics, with rare or infrequent dispersal between host-plant patches). Dispersal is a complex facet of populations and organisms (Nathan et al. 2008), and a precise definition will not be offered here, rather it is used as a measure of the extent to which individuals of our hypothetical species 'get up and move' from their natal host patches and potentially encounter patches of the novel resource. When either dispersal or r_n are very low, then u is predicted to be also very low (the novel plant will not be successfully utilized, or will be utilized at only a very small rate relative to its availability on the landscape). If dispersal is quite high, then a range of potential r_n values could still be associated with utilization of the novel host. This outcome encompasses more than one potential mechanism: for example, high dispersal could facilitate colonization by increasing the probability that a novel patch is encountered, or by supplementing populations on a novel resource with occasional demographic input from a source associated with an ancestral host, which would obviously be important if r_n is low ('ancestral' is used here and throughout to refer simply

to native hosts as opposed to more recently contacted, exotic plants). If one accepts the argument that u could be determined by some combination of dispersal and r_n, then the question is raised of what should be studied regarding dispersal and r_n? In the next section, aspects of herbivore behavior and performance are considered with respect to the relationships in Fig. 2a and 2b.

Preference and performance

Female insects make complex decisions regarding egg oviposition that include sensory inputs at multiple spatial scales and involving multiple organs of touch and smell (Courtney et al. 1989, Scheirs and De Bruyn 2002, Cunningham 2012). Oviposition behavior is typically assayed in preference arenas that can either be choice or no-choice, involving plants presented to females either singly or in groups, with the numbers of eggs counted as a measure of preference (Thompson and Pellmyr 1991). Because many herbivorous insects mate on their host-plants, oviposition behavior has been studied in the context of ecological speciation (Drès and Mallet 2002), often as a proxy for host preference in general (host preferences of males are not as easily assayed in many systems). If populations on different host-plants evolve divergent oviposition preferences, this could translate into reproductive isolation if individuals from different populations look for mates in association with different host-plant species (Funk et al. 2002, Nosil et al. 2003, Matsubayashi et al. 2010). Thus, in the context of herbivores interacting with novel hosts, it is clearly of interest to ask if oviposition behavior evolves, but we should be clear as to whether variation in oviposition behavior is of interest as a cause or as a consequence of the utilization of a novel host. With respect to causes of novel host colonization, Fig. 2c and 2d illustrate two things that we might want to know about variation in oviposition preference.

First, does greater oviposition preference for a novel host equate to increased immigration rates (Fig. 2c)? In other words, as an individual is moving across the landscape, does 'preference' as typically measured in small experimental arenas translate to probabilities of detecting and alighting on patches of host plants? At this point in time, we can only conclude that we do not know in any general sense, though the question is not new (Prokopy and Owens 1983, Thompson and Pellmyr 1991, Jonsen and Fahrig 1997, Conradt et al. 2001). Exceptions to the lack of work on this topic are the well-studied metapopulation systems of the butterflies *Melitaea cinxia* and *Euphydryas editha*. In the former, *M. cinxia*, it seems to be the case that individual-level oviposition preferences are associated with regional patterns of host use (Kuussaari et al. 2000). Hanski and Singer (2001) released *M. cinxia* individuals with known differences in preference for two different host-plant species, and recorded biased presence at two artificial host patches such that individuals with a certain preference were more likely to be found in the corresponding plant patch. A complementary finding with *E. editha* is that immigration is not higher into areas with the preferred host, but emigration out of those areas is lower (Boughton 2000), suggesting that butterflies do not discriminate before

arriving in an area, but that host-preference does ultimately matter (by affecting emigration) for the utilization of a new patch of plants. Workers in the field of biocontrol have developed 'open field' tests that have great potential to address these issues (Briese 2005). The design and implementation of these large-scale tests is controversial, and they are at present too rarely used to allow for general conclusions (Heard 2000).

Acknowledging the need for more studies of individual behavior and dispersal, we can move on and ask if variation in oviposition preference has an effect on fitness or population growth rate for populations inhabiting patches of a novel host: does increased preference for the novel host result in higher r_n? Clearly, if preference and performance are correlated (Mayhew 1997, Gripenberg et al. 2010), then increased preference could be associated with higher r_n (Cogni 2010), and a dramatic mismatch between preference and performance can be associated with novel hosts as ecological 'traps' (Keeler and Chew 2008). However, it is interesting to consider more direct (and less-often studied) mechanisms involving preference, and one mechanism by which variation in preference might be important for local population dynamics could be if higher preference was associated with higher realized fecundity, as diagrammed in Fig. 2d. There is some reason to think that this could be true, as specialists with more narrow behavioral preferences (stronger preference for a particular host) can make more efficient decisions with respect to host choice (Janz and Nylin 1997, Egan and Funk 2006). The few studies on this topic have found supportive evidence and suggest a link between preference and fitness or realized fecundity, but clearly more studies are needed before a connection between oviposition preference and u (the slope of the occupancy–availability line) can be established.

The relevance of juvenile performance to the colonization of novel hosts is perhaps less subtle. After all, individual growth and survival must clearly inform population growth rates (r_n) and hence persistence on a novel host. However, one does not have to look far to find examples where rearing experiments suggest that a novel host might be inferior and perhaps unlikely to support populations in the wild, which nevertheless do persist on the novel host; for example, *Papilio zelicaon* on citrus trees (Shapiro and Masuda 1980), or *Lycaeides melissa* on alfalfa, where individuals reared on the novel host in the lab can be up to 70% smaller than individuals reared on a native host (Forister et al. 2009). In the latter example involving poor lab performance on the novel host, an interaction with mutualistic ants in the field is key to understanding population persistence (Forister et al. 2011).

With respect to performance, there are also a priori demographic considerations that might profitably be kept in mind, but which are often not mentioned in studies of dynamic host-ranges. Most insects have fairly high potential fecundity, with individual females laying hundreds or thousands of eggs. Given that potential fecundity, how much does variation in larval performance matter? If juveniles are 10 or 20% more likely to survive when reared on a novel host, does this translate into an effect on population growth rate, or might such differences in larval performance be swamped by, for example, variation in female realized

fecundity or variation in the probability of finding a mate? If factors such as habitat configuration, weather, predators or mate availability have any impact on the number of eggs that a female can lay during her lifetime, then those factors could be more important for r_n than larval performance, particularly if one considers that larval performance is typically measured in a laboratory setting, removed from many abiotic and biotic factors (e.g. other factors in Fig. 1; for an example of host-specific effects of natural enemies in the wild, see Yamaga and Ohgushi 1999).

Specialization, host switching and generalization

We have referred throughout to the colonization of novel hosts without explicitly discussing outcomes with respect to ancestral or previously-used hosts; that is because we believe there is much to be learned by focusing on, for example, demographic processes associated specifically with the novel host. However, it is of inherent interest to ask: under what conditions is the colonization of a novel host likely to involve a process of specialization or generalization (i.e. a narrowing or a broadening of diet breadth)? Considering the invasion of a potential host-plant into the geographic range of an insect herbivore, specialization would be involved if contact with the novel host resulted in either (a) a true host switch, such that populations become behaviorally or physiologically restricted to that novel resource (i.e. they loose the ability to utilize the ancestral host), or (b) populations associated with the ancestral host that eventually discriminate against the novel resource (i.e. discrimination against the novel plant is acquired). In contrast, a process of generalization would result if the species utilizes both ancestral and novel hosts at a regional or metapopulation scale following the invasion of the novel plant. In Fig. 2e and 2f, demographic processes are related to the outcomes of specialization, host-switching and generalization. If population growth rates are high on both ancestral and novel hosts (the upper right of Fig. 2e), then we could predict generalization as an outcome. In contrast, if the novel host is a particularly good resource and r_n is higher than r_a (lower right of Fig. 2e), this could be at least one condition facilitating a host-switch (loss of use of an ancestral host). As a purely ecological mechanism, populations on the novel host might be more stable, and thus the region or metapopulation might come to be characterized only by the use of that host over time. As another possibility, elevated demographic output from the novel host could, for example, have a negative impact on ancestral-host populations, if the former flood the latter with particular alleles or combinations of alleles that are beneficial on the novel but not the ancestral host (see Fry 1996 for a related perspective on specialization involving alleles with host-specific effects). Finally, if r_n is generally low relative to population growth rates on the ancestral host, then a situation exists in which discrimination against the novel host could evolve.

Under what circumstances might population growth rates (r_a and r_n) on the two hosts be positively or negatively correlated? In our final set of hypothetical relationships (Fig. 2f), we offer a perspective that is perhaps narrowly focused on ecological dynamics, as opposed to, for example, a quantitative genetic perspective (Holzman et al. 2011) or a perspective derived from a balance of gene flow and selection (Holt et al. 2003). The abscissa of Fig. 2f, 'similarity of r determinants', is meant to capture an idea of turnover or consistency in ecological factors (as in Fig. 1) affecting population dynamics across two habitats or hosts (Strauss and Irwin 2004, Singer and McBride 2010). Consider populations on an ancestral and a novel host where an ability to detoxify a specific phytochemical is highly beneficial in both cases; thus one 'determinant' of r is similar or identical across hosts. Then consider that populations on both hosts benefit from a similar cryptic coloration, and also benefit from having particular behaviors associated with recognizing and avoiding competitors on the two hosts. If all of those 'determinants' are in common between populations on the ancestral and novel hosts, then generalization can be predicted (the upper right portion of Fig. 2e). The relationship for increased probability of generalization in Fig. 2f (the solid line) is depicted as steeply curved to illustrate the possibility that there might be some threshold past which having enough ecological traits favored in common on the two hosts would essentially make the host-range expansion very easy or even unnoticed from the perspective of the herbivore (thus colonization of the novel host could be thought of as ecological fitting in the sense of Agosta 2006; and see Nyman 2010 for a consideration of similar issues but at a different temporal scale, relating in particular to diversification and host-associated speciation). Of course, the probability of specialization (on either host) as an outcome then drops as the similarity of determinants increases (the dotted line in Fig. 2f). If a given colonization scenario is close to the origin of Fig. 2f, such that the herbivore is in the region of specialization, then the two outcomes of 'switch' versus 'rejection' would perhaps again depend on demographic factors and survival associated with the two hosts (Fig. 2e). At an intermediate range of 'similarity of r determinants' (Fig. 2f), the metapopulation might be unlikely to fully reject one or the other host (specialization) but it also might not fully use both hosts to a comparable extent (generalization); instead the use of more than one host might involve, as one possibility, a more complicated source–sink system across populations associated with the alternative hosts.

Discussion

Empirically, the topic of novel host colonization is ripe for exploration simply because one does not have to look very far to find native insects using novel hosts. As an example, approximately one-third of the butterflies of California have been reported attacking exotic plants (Graves and Shapiro 2003). There are applied reasons to be interested in the colonization of exotic hosts, including non-target effects associated with biocontrol agents, and also conservation challenges associated with the management of rare insects that have adopted exotic hosts (Shapiro 2002, Severns and Warren 2008). In addition, the opportunities for basic science are many as we have the chance to watch food webs and entire ecosystems being assembled (Agrawal et al. 2005, Brändle et al. 2008, Harvey et al. 2010, Almeida-Neto

et al. 2011). Lau and Strauss (2005) took advantage of recently-formed plant–insect interactions to disentangle direct and indirect effects of herbivory and competition involving a native plant and exotic alfalfa, *Medicago sativa*. The presence of novel host associations allowed Jahner et al. (2011) to consider the importance of the geographic range of herbivores as a factor influencing the process of host-range expansion in a macroecological sense, involving a large number of butterfly and plant species (butterfly species with wider geographic and host-ranges were more likely to be observed attacking exotic hosts). These studies illustrate the utility of novel plant–insect interactions for ecological questions, and we suggest that other studies along similar and complementary lines would be profitably informed by a more detailed understanding of the processes and causes of host-range shifts. We have attempted to articulate hypothetical relationships that could be used as a framework in which to study that process. The relationships depicted in Fig. 2 are not meant to be exhaustive, but they are meant to spur conversation and theoretical work.

Ultimately, demographic considerations must be key to the process of novel host colonization (Fig. 2b), as we need to know how populations are regulated to predict persistence in a novel environment (Carey 2001). And there is much that we have yet to learn about the demography of insects in general (Nylin 2001). Does preference for a host-plant affect colonization and persistence (Fig. 2c and 2d)? Given the enormous number of elements that might affect realized fecundity of adults in the wild (Fig. 1), how important is variation in larval performance as typically measured in studies of 'preference and performance'? The work of Howard Cornell and colleagues has set a high bar for the comparative study of insect herbivore demography: they have reviewed hundreds of life table studies to synthesize information on sources of mortality (Cornell and Hawkins 1995, Cornell et al. 1998). Among their findings was the importance of natural enemies, which were associated with approximately half of the deaths across 124 studies (Cornell et a. 1998; and see Gentry and Dyer 2002 for a broad experimental perspective on the diversity of caterpillar defenses against enemies). Ultimately, we could hope to have similar work comparing sources of mortality between native and novel hosts.

We have focused largely on ecological processes and mechanisms, partly because evolutionary processes associated with novel host-plant use have been more well studied, particularly processes resulting from the colonization of a novel host, such as adaptation in feeding morphology and competitive ability (Messina 2004, Carroll et al. 2005, Vellend et al. 2007), as well as shifts in behavioral preferences for different host-plant species (Singer et al. 1993, Forister et al. 2012b). Attention has also been given to the presence of genetic variation for host-related traits and the potential for adaptation to novel hosts (Futuyma et al. 1995, Forister et al. 2007, Fox 2006, Fricke and Arnqvist 2007). Because our model of host shifts merges well with the concept of ecological fitting, as discussed above, we would like to raise one evolutionary issue in the context of ecological fitting that points towards an area for future research. The concept of ecological fitting has been discussed in terms that juxtapose ecological processes

with 'evolutionary host shifts', with the latter being associated with novel mutations facilitating the use of novel host-plants (Agosta 2006). The well-studied example of *Euphydryas editha* butterflies colonizing the exotic host *Plantago lanceolota* is interpreted as being an ecological but not an evolutionary host-shift because some females in the population were pre-adapted to oviposit on the new host (Agosta and Klemens 2008). There was a change over many years in the population, such that the population-level preference shifted towards individuals that preferred *P. lanceolota* (Singer et al. 1993). Although no new mutation was involved, the *E. editha* example does involve evolution because there was a genetic shift in the composition of the population (Bell 2008). Thus we might suggest that the colonization of *P. lanceolota* by *E. editha* was indeed an 'evolutionary' host-shift, even though no new mutation was (as far as we know) needed.

More important than a difference in terminology, the case of *E. editha* and its novel host can be used to raise some relevant questions. How often does the colonization of a new host involve a new mutation, versus selection on standing genetic variation (as in *E. editha*), versus a plastic response sufficiently accommodating that it is not associated with a change in the genetic composition of the herbivore population? Agosta (2006) summarizes the very useful example of insects colonizing sugarcane, *Saccharum officinarum*, as it was planted around the world (Strong et al. 1977). The rate of colonization to sugarcane asymptotes within 100 years, and this is interpreted as evidence for the unimportance of evolution in the colonization process (Agosta 2006). We agree that the timeframe is too rapid to suggest novel mutations, but how often does the process involve selection on pre-existing genetic variation versus a purely plastic response, or (perhaps most likely) some combination of the two? Nylin and Janz (2009) posited plasticity as a bridge to new hosts prior to natural selection on host-specific traits. In any event, when considering evolutionary processes associated with novel host-use, we should continue to raise questions about the continuum from plasticity and ecological fitting to selection on standing and novel genetic variation.

Conclusion

Our goal has been to further the discussion of insects attacking novel host-plants, an area of research that has always been fruitful for ecologists and evolutionary biologists. The complexity of the relevant organismal interactions is daunting, which perhaps explains why so much of the 'host-range' literature (whether about specialization per se or about host shifts as we have discussed them) has revolved tirelessly around so few key issues. For example, issues with the most hefty attraction for researchers have included the 'jack of all trades' hypothesis (Scriber 2005) and the 'preference–performance correlation' (Gripenberg et al. 2010). While there is no denying the importance of repeated tests of core theory, the richness of plant–insect interactions should lend itself to a greater richness of theoretical expectations (Mooney et al. 2012). We hope that a focus on novel host use as complementary to the study of relative diet breadth (the traditional focus of studies of specialization),

along with a simple model (e.g. Fig. 1) and simple graphical relationships (Fig. 2) will be productive and compatible with other areas of research, and we have no doubt that others can pose more sophisticated theoretical hypotheses.

Some of the questions and issues that we have raised could readily be generalized to more realistic and complex evolutionary and demographic scenarios, for example involving the effect of maternal environment on the ability to utilize a novel host (Newman et al. 1997, Fox 2006). One could ask how the hypothetical relationships in Fig. 2 would be different for a species in which individuals are more dispersive and less localized (Holt et al. 2003). Questions similar to those that we have posed could also be addressed with pollinators, as issues of host-range in the two functional groups (pollinators and herbivores) have too often been pursued without reference to a common suite of questions. As acknowledged above, we have mostly neglected how evolutionary processes change ecological interactions (Pelletier et al. 2009). In other words, we have presented a mostly traditional picture of the ecological stage, feeling that it was necessary to specify certain questions about the architecture of that environment, and we leave it for others to ask how the stage might evolve (Facon et al. 2006). Finally, issues related to novel plant–insect interactions could encompass habitat (rather than host) use, which would make a clear connection to global change biology and the utilization of anthropogenic habitats by native animals. In all of these things, it is reasonable that studies of insects should lead the way: they are diverse and easily manipulated, but also fragile and inherently worth understanding in a world full of increasing upheaval and imperiled interactions.

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