Ecological Entomology

*Ecological Entomology* (2021), DOI: 10.1111/een.13073

INVITED REVIEW

# Host repertoires and changing insect–plant interactions

MARIANA P. BRAGA[1,2] and NIKLAS JANZ[1] [1]Department of Zoology, Stockholm University, Stockholm, Sweden and [2]Department of Biology, Washington University in St. Louis, St. Louis, Missouri, U.S.A.

**Abstract.** 1. One of the main challenges faced by ecologists today is to understand and predict how species interactions will respond to the current environmental change. It is likely that these changes will have a stronger effect on phylogenetic lineages that depend on intimate and specialised ecological interactions, such as most herbivorous insects.

2. In this review, we highlight the aspects that we consider are fundamental for understanding how species interactions change over time. We start by reviewing terminology and conclude that commonly used terms have undesired connotations with regard to what we know about how hosts are acquired and lost over time.

3. Based on that, we suggest *host repertoire* as a better term to describe the use of multiple hosts than the host range or diet breadth, both of which fail to capture that host use is often non-contiguous and tend to emphasise the total number of hosts, while ignoring host identity.

4. Another important issue that we highlight is the differentiation between fundamental and realised host repertoires, where the latter is the set of hosts that are actually used in nature, whereas the first includes all hosts that can potentially be used by the species. We show that the characterisation of the fundamental host repertoire is key to understanding how insect–plant interactions will respond to the ecological opportunities instigated by environmental change.

**Key words.** Diversification, host range, host shifts, specialisation.

## Introduction

Current rapid changes in environmental conditions constitute major challenges for all species on earth and may also disrupt or otherwise change existing species interactions. It is a double-edged sword. On the one hand, we see an increased risk of loss of species interactions, potentially leading to accelerated extinction rates (Strona & Lafferty, 2016; Strona & Bradshaw, 2018). On the other hand, changing environmental conditions are also likely to lead to new ecological interactions being formed, which can potentially lead to problems with invasive species, new crop pests, and zoonotic diseases (e.g. Nylin *et al.*, 2018; Brooks & Boeger, 2019). The challenge that faces us is how to predict which species will respond in which way. This is of no small consequence, since among other things, it can help us prevent future emerging infectious disease outbreaks and potential pandemics (Apari *et al.*, 2019; Brooks *et al.*, 2020). In order to predict such changes, we need to better understand what exactly is changing during the formation of new ecological interactions, and we need to understand the mechanisms involved.

Insect–plant systems can serve as a good model for understanding parasitic interactions, since compared to most other such systems, they are intensely studied and the interactions are comparatively well documented. As a consequence, the interaction between herbivorous insects and their host plants has become one of the most important model systems for evolving species interactions (Ehrlich & Raven, 1964; Boggs *et al.*, 2003; Tilmon, 2008; Janz, 2011), as well as for responses to climate change (Parmesan *et al.*, 1999; Parmesan, 2006). It has become increasingly clear that the evolutionary dynamics of all parasitic interactions – despite large superficial differences – share key similarities (Agosta *et al.*, 2010; Nylin *et al.*, 2018), which strengthens the case for using the insect–plant system as a general model for understanding parasitic interactions. Insights from insect–plant systems have, for example, been a major influence behind the ‘Stockholm Paradigm’ – a general framework that has been used to understand and predict infectious disease under climate change (Agosta *et al.*, 2010; Nylin *et al.*, 2018; Brooks *et al.*, 2019).

Correspondence: Niklas Janz, Department of Zoology, Stockholm University, 10691 Stockholm, Sweden. Email: niklas.janz@zoologi.su.se

The considerable effort to understand the remarkable diversification of insect–plant systems has yielded important insights both on taxonomical diversification (through host-driven speciation) and ecological diversification (through host colonisations, host shifts, and specialisation), and on how these processes are interrelated (e.g. Janz, 2011). Although the interaction with host plants certainly seems to influence speciation rates (Janz *et al.*, 2006; Fordyce, 2010; Hardy & Otto, 2014; Hamm & Fordyce, 2015; Hardy, 2017; Braga *et al.*, 2018), much of this diversification appears to have coincided with dramatic Cenozoic climatic perturbations (Peña & Wahlberg, 2008; Wahlberg *et al.*, 2009; Heikkilä *et al.*, 2012; Nyman *et al.*, 2012). This indicates the important roles of both biotic (e.g. host plant) and abiotic (e.g. climate) factors in the diversification process and that they can have complex synergistic effects (Condamine *et al.*, 2018; Kergoat *et al.*, 2018). It appears that even if the periods of the environmental change are perilous for species that live through them, they will also provide opportunities for colonisation of novel habitats and hosts, which can promote diversification (Janz & Nylin, 2008; Hoffmann & Sgrò, 2011). Still, species will respond differently to such challenges. Some may simply go extinct (locally or globally), others may shift their geographic ranges, still others may adapt through phenotypic or evolutionary modifications, such as forming novel species associations. The key question is to understand, and ultimately predict, the response of any given species.

The cause of these disparate responses is bound to be multifaceted, to a large extent because ecological interactions are determined by multiple factors, each potentially responding differently to change. Still, an important key to the answer lies in what cards a species holds at the onset of the climatic perturbance, which to a large extent will determine its ability to respond to change. Certain traits, evolved in response to other situations, may prove to be useful in the novel environment (Janzen, 1985; Agosta, 2006).

Some species, or groups of species, may just ‘win the lottery’, in the sense that they happen to specialise on habitats or hosts that themselves will expand and proliferate as a consequence of the changing climate. For example, the impressive diversification of the grass-feeding Satyrinae butterflies may have been facilitated by their ability to take advantage of the vast grasslands that opened up during the unusually dry and cool climate in the Oligocene (Peña & Wahlberg, 2008; Peña *et al.*, 2011). However, it is also possible that species have evolved traits – such as polyphagy, high mobility, or broad habitat use – which allow them to better track the changing climate (Warren *et al.*, 2001; Chen *et al.*, 2011; Betzholtz *et al.*, 2013; Fecchio *et al.*, 2019). As a consequence, it is important to understand not only which these traits are but also how and when they evolved. What selective pressures and ecological contexts favour traits that may be beneficial when coping with environmental perturbations?

The purpose of this review is to provide a better foundation to understand how insects (and other parasites) respond to environmental change. First, what traits are changing? Terminology in the field has been inconsistent, which leads to ambiguity, but we also suggest that misleading terminology has invited erroneous thinking about how host interactions change. Getting terminology right is not so much a matter of precise definitions as a matter of how the terms assist in truly understanding the phenomena they are meant to describe. We show how a modified terminology can help us think about how species interactions *change*. Moreover, we discuss the importance of recognising the complex nature of the ‘trait’ that is host plant use, and the need to understand how ecological opportunity interacts with evolutionary compatibility to affect the change. Finally, we suggest how a better understanding of the mechanisms involved in the change can help us bridge the gap between micro- and macroevolutionary scales.

## What is changing?

From the point of view of a phytophagous insect, a change in its host plant interaction is typically manifested as a change in the number or identity of plants that are used, or in the relative frequency of interaction with these plants. These seemingly simple changes can potentially have diverse mechanistic causes and lead to a variety of outcomes (Hardy *et al.*, 2020). To make matters worse, the terminology used to describe these changes is not very consistent. For example, the process of adding or dropping plants as hosts has been referred to as *specialisation/generalisation*, *colonisation*, *host switches*, and *host shifts*. Likewise, the result of this process is typically referred to as an insect’s *host range*, *diet breadth*, *diet width*, *specificity*, or *degree of specialisation*. While many of these terms have different connotations, there is a substantial overlap in their use. These terms are also applicable for any organism with a parasitic lifestyle, including herbivorous insects, internal parasites, microbes, and parasitoids, and there could thus also be potential cultural differences in how they are used.

A search on Clarivate Analytics Web of Science™ (Table 1) reveals that *host switch* and *host shift* are about equally common overall. However, while insect scientists seem to strongly lean towards *host shift*, *host switch* is about twice as common in conjunction with the term “parasit*”, indicating a terminology difference between the fields of parasitology and insect–plant associations. We believe this difference in usage points to a historical difference between the fields in how the species associations are expected to be shaped. A ‘shift’ is more ambiguous than a ‘switch’, in the sense that the latter more clearly alludes to an exchange of host A for host B, whereas the former could be said to more broadly refer to any change in host use, including situations like shifting from A to A + B. This reflects the strong tradition among parasitologists to assume extreme specialisation and tight coevolution of parasites with their hosts (Nylin *et al.*, 2018). In such associations, colonisations should be rare, and when they happen, they should indeed lead to complete switches from A to B. While similar notions have been present among insect–plant researchers, there has been a higher tendency to see host colonisations themselves as the important drivers of the patterns of association (Ehrlich & Raven, 1964; Jermy, 1984; Janz, 2011; Suchan & Alvarez, 2015). As it has become increasingly clear that the assumptions of extreme specialisation and cospeciation are highly dubious also for parasite–host interactions (Nylin *et al.*, 2018), we caution against using *host switch* unless one specifically wants to emphasise that there has indeed been a complete exchange of hosts.

**Table 1.** Popularity of terms used to describe variations in, or changes in, host use.

| Search terms | Hits | Search terms | Hits |
|---|---|---|---|
| TS = (“host switch*” OR “host plant switch*”) | 1176 | TS = (“host shift*” OR “host plant shift*”) | 1191 |
| AND TS = insect* | 209 | AND TS = insect* | 517 |
| AND TS = parasit* | 637 | AND TS = parasit* | 299 |
| TS = (“host range*” OR "host plant range*”) | 18 261 | TS = “Host specificity” | 8913 |
| AND TS = insect* | 2052 | AND TS = insect* | 1244 |
| AND TS = parasit* | 2067 | AND TS = parasit* | 2998 |
| TS = “Diet breadth” | 1005 | TS = “Diet width” | 20 |
| AND TS = insect* | 318 | AND TS = insect* | 3 |
| AND TS = parasit* | 57 | AND TS = parasit* | 1 |

Hits are the number of times the search terms matched entries in the ‘Core collection’ of Clarivate Analytics Web of Science™ on 2020-10-22.

As for describing the pattern of multiple host use, *host range* is the overwhelmingly most common term, followed by *host specificity* (Table 1). These two terms do have rather different connotations though, as host specificity refers more to the shape of the relative distribution of host use than its limits. Two species with similar host ranges can differ in specificity; one species may, for example, use some hosts more than others, whereas the other uses all hosts to a similar degree. Terms like diet breadth and diet width can be seen as more synonymous with host range, although distinctly less popular (especially diet width).

Curiously, *diet breadth* appears to be disproportionally popular among entomologists compared with parasitologists. Even though the terms are similar, diet breadth differs from host range in that it explicitly refers to food. Since the location of the host in herbivorous insects is often nontrivial, so that oviposition is typically an important aspect of host use (Singer, 1971; Wiklund, 1975; Thompson & Pellmyr, 1991; Janz & Nylin, 1997), this is somewhat surprising. We believe that the difference in meaning between diet breadth and host range could potentially be useful, but it appears that the difference is rarely reflected in practical usage. The relative widespread use of diet breadth among entomologists is therefore more likely to reflect a cultural preference, which makes the distinction between the alternatives meaningless in practice.

With regard to changes in host use, there has been a strong emphasis on trying to explain specialisation, that is, why host use become restricted to one or a few hosts (Futuyma & Moreno, 1988; Devictor *et al.*, 2010; Forister *et al.*, 2012; Cooper, 2014). This is not surprising, since such specialisation is a pervasive feature among herbivorous insects as well as other parasites (Forister *et al.*, 2015; Nylin *et al.*, 2018). There are many potential mechanisms that can contribute to specialisation (Sexton *et al.*, 2017; Hardy *et al.*, 2020), including neutral processes (Forister & Jenkins, 2017; Peterson *et al.*, 2020). However, specialisation only refers to one direction of change in host use, the loss of one or several hosts, and does not help us understand multiple host use.

Since adding new hosts should be difficult, it is something of a paradox that we see so many problems associated with the inclusion of new hosts, such as invasive species and emerging infectious disease (Agosta *et al.*, 2010). Multiple host use in general appears to be associated with changing environments (Warren *et al.*, 2001; Mangels *et al.*, 2017; Wilson & Fox, 2020), and one reason for the predominance of specialists could simply be that over long time periods, change is relatively rare. On the other hand, the Earth is currently experiencing intense environmental change (IPCC, 2013), and we believe there is a case to be made for an increased effort to understand the reversal of specialisation, that is diet expansions.

This is an aspect of host use where current terminology falls short, since it invites erroneous thinking about how host associations evolve. We want to point out a number of realisations that require a different way of thinking and communicating about multiple host use. In short, these are (i) that ‘host ranges’ (or ‘diet breadths’ etc.) are not necessarily contiguous, (ii) that host choice (preference) and larval performance are separate traits, shaped by different selection pressures and with distinct (but hopefully overlapping) evolutionary identities, and (iii) that host use is not binary – all hosts are not equally good. Moreover, the last two points combine into a fourth point with far-reaching consequences: (iv) the number of realised interactions at any given time can be smaller than the number of potential interactions. We will deal with these points in the following section.

## Host repertoires

The first problem is that all terms commonly used to describe multiple host use – such as *range*, *breadth*, and *width* – imply a contiguous distribution of hosts across one or several trait axes. This leads to an expectation of phylogenetically contiguous host ranges. We argue that this invites misleading views of the processes behind multiple host use. One reason is simply that plant characteristics do not always follow phylogeny. Plant secondary compounds have long been recognised as the important determinants of plant–herbivore interactions (Dethier, 1941; Fraenkel, 1959; Ehrlich & Raven, 1964), but even if there is a broad phylogenetic conservatism in plant secondary chemistry, their distribution can still vary within groups in complex ways (Uckele *et al.*, 2020). In terms of plant defences, there are examples not only of defence escalation, but also of de-escalation and convergence (Agrawal *et al.*, 2009; Agrawal, 2010; Edger *et al.*, 2015; Defossez *et al.*, 2018; Livshultz *et al.*, 2018; Volf, 2018). Moreover, in addition to functioning as feeding barriers, plant secondary metabolites can be used by insects to locate plants, creating a situation where plants may also benefit by diversifying their chemical signals to obfuscate insects searching for hosts (Zu *et al.*, 2020).

Broad phylogenetic conservatism may still lead to a pattern of groups of insects being associated with groups of plants (Ehrlich & Raven, 1964; Janz & Nylin, 1998; Weiblen *et al.*, 2006), but at the same time, these groups of plants are often not monophyletic (Becerra, 1997; Wahlberg, 2001; Nyman, 2010). In fact, a recent study on phylogenetic butterfly–plant networks revealed that while butterflies in the same module tended to have lower phylogenetic diversity than expected by chance, this was not true for plants in the same module (Braga *et al.*, 2018). In other words, there is a strong conservatism in host use among butterflies, but the plants they are tracking are phylogenetically diverse and often also chemically diverse.

It may be worth pointing out that the term 'range' is also used to describe the extent of geographic distribution of a species. This is a possible cause of confusion, but it also serves as an illustrative analogy. Geographic ranges are typically contiguous, so here the term is apt. There are examples of disjunct distributions, but this calls for an explanation and has to be pointed out, because it breaks with expectations from a 'range'. In contrast, the set of plants that insects feed on are *typically* phylogenetically disjunct. As a consequence, it is unhelpful to have an insect's (or any parasite's) hosts represented as a 'range', as it implies variation between upper and lower limits on a continuous scale that simply is not true.

Even if 'host range' is understood as an ordinal or nominal scale (i.e. the number of hosts), it is not an independently evolving trait as such, but an emergent property of the process of gaining and losing individual hosts over time (Braga *et al.*, 2018, 2020). The trait that actually evolves through history is the *host repertoire*: the set of hosts that are used (or can be used, see below) by an insect or parasite at a given time. The probability of colonising new hosts has been shown to be correlated to 'host range' (Janz *et al.*, 2006), but not primarily because of the number of hosts used, but because the abilities to use this collection of hosts overlap in significant ways with other plants. A larger number of host plants only increase this overlap if these hosts are different enough to require different sets of genes when feeding on them. The host repertoire thus represents not only the number of hosts used but also their identities (Fig. 1). It is a representation of the 'genetic toolbox' of the herbivore that determines the set of plant traits it can successfully locate, identify, and metabolise (Peterson *et al.*, 2015). Two insects with identical host ranges can thus have different host repertoires, and it is the latter that determines the functional overlap with potential novel hosts.

Importantly, the hosts in the repertoire have typically been added sequentially over evolutionary time, potentially leading to different sets of adaptations to each. Insects (or other parasites) may evolve more fine-tuned adaptations to hosts with a long history of association, whereas others are recent colonisations where adaptation is incomplete. In a study of the highly polyphagous butterfly *Vanessa cardui*, Celorio-Mancera *et al.* (2016) divided the hosts in the repertoire into *a priori* categories based on the history of association: older hosts were labelled the 'core' repertoire, and recently, colonised hosts were labelled the 'extended' repertoire. The study showed that the global gene expression of larvae clustered more strongly with this core/extended subdivision than with groupings based on the phylogenetic relationships of the host plants (Celorio-Mancera *et al.*, 2016).

Indeed, such 'core' hosts may play a large role in the evolutionary dynamics of insect–host interactions. There is evidence on several scales suggesting that all hosts in the repertoire are not equal. Phylogenetic analyses of diverse groups of herbivorous insects (Janz *et al.*, 2001; Nylin & Wahlberg, 2008; Scriber *et al.*, 2008; Peterson *et al.*, 2015; Larose *et al.*, 2018) as well as evolving digital parasites (Zaman *et al.*, 2014) have indicated an important role of recurrence, that is ancestral hosts that are temporarily lost and later recolonised. It is not uncommon to see such hosts 'pop up' deep within clades that have long since switched to another host group (Nylin *et al.*, 2014; Braga *et al.*, 2018). A similar pattern of the recurrent use of a limited set of host plants can be seen on smaller scales as well. This is perhaps most well documented in *Euphydryas editha* in the western USA. All populations of *E. editha* use different combinations of a number of hosts in the order Lamiales, although most populations are monophagous on one of these hosts, creating a geographic mosaic of host use across its range (Singer & Wee, 2005). Colonisations and recolonisations of hosts within this repertoire are common, and populations seem to mix and match between a set of hosts across its geographic distribution, depending on, for example, availability, suitability, and local history of selection (Singer & Wee, 2005; Singer *et al.*, 2008; Bennett *et al.*, 2014; Singer & Parmesan, 2021).

Interestingly, there is another striking similarity between this interpopulation dynamics and what is seen on phylogenetic levels: unless the mixing and matching between hosts is caught in the process, much of the actual dynamics will be invisible. Indeed, if the system returns to its ancestral state after a change in the patterns of interaction, it can appear in retrospect as if nothing much has happened (Singer *et al.*, 2008; Singer & Parmesan, 2018). As a consequence, the role of such recurrence for shaping host repertoires – on micro- as well as macroevolutionary scales – is probably underrated.

## A complex trait

A large body of work on insect–plant interactions has been devoted to understanding the correlation – or the lack of correlation – between female oviposition preference and larval performance (Thompson, 1988; Mayhew, 1997; Gripenberg *et al.*, 2010). We have no intention of reviewing this topic here, suffice to say that all reviews above pointed at a good deal of variation in the strength of the correlation. This is hardly surprising considering that both preference (Wiklund, 1974; Singer, 1986; Scriber, 1993) and performance (Nylin *et al.*, 1996) can be measured in many ways and that it has been known for a long time that they are indeed two different traits with different genetic backgrounds (Wiklund, 1974, 1975). Since selection pressures should not be identical on the two traits, we should expect some degree of independent evolution (Friberg *et al.*, 2015). On the other hand, the two traits should also exert a strong selection pressure on each other, so that correlations should strengthen if the interaction persists over long time periods. And indeed, the correlation does appear stronger

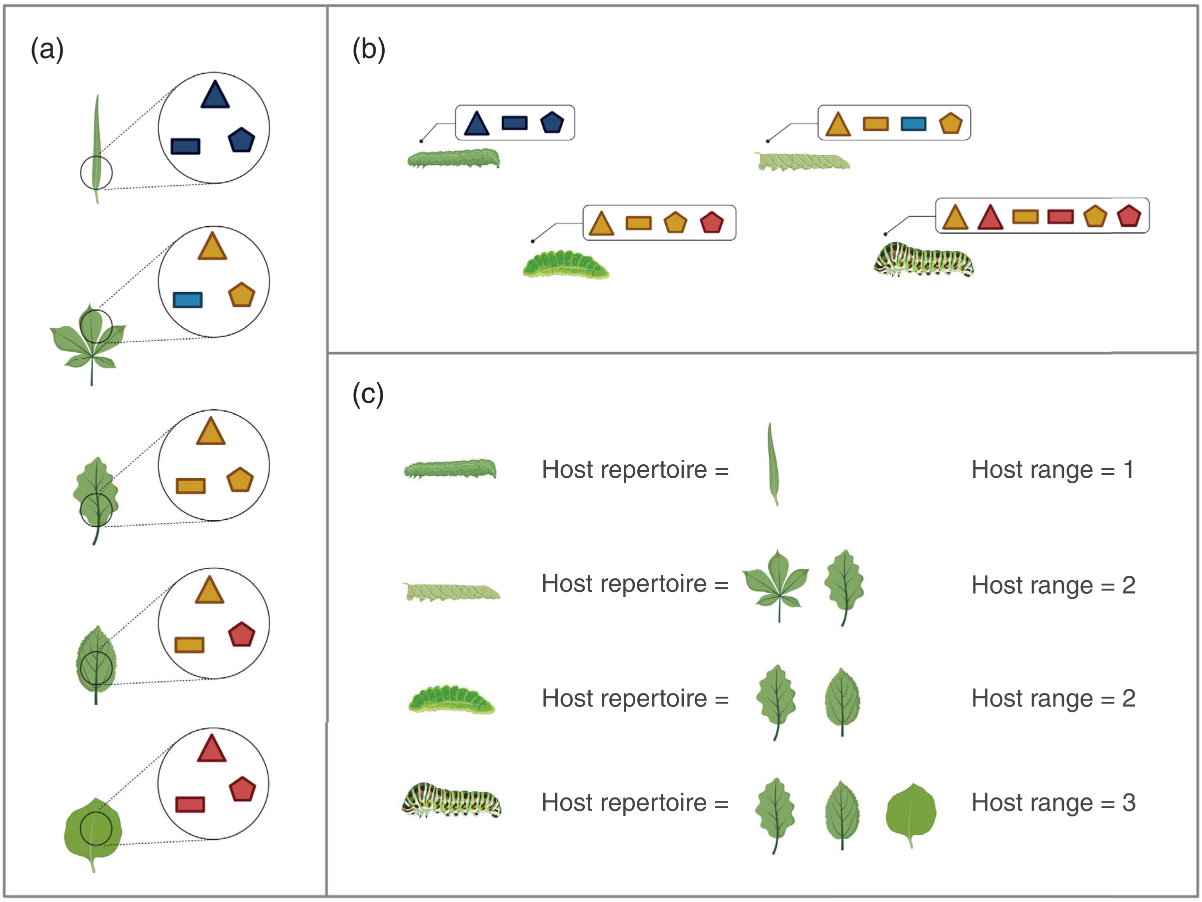

**Fig. 1.** Abilities that underlie host use. (a) Plant species are characterised by different trait combinations. (b) Insect species possess different tools to deal with plant traits. (c) The interaction between plant traits and insect genetic tools defines the host repertoire, and consequently, the host range of an insect. Created with BioRender.com.

in insects feeding on native plants, with a longer history of correlated selection, than that on exotic plants (Jones *et al.*, 2019).

Nevertheless, the genetic independence of the traits has some interesting evolutionary consequences. It grants females some degrees of freedom when searching out plants for oviposition. If the 'best' plant is not currently available, it will not continue to search for that plant indefinitely, thus assuring that eggs will be laid even under suboptimal conditions (Wiklund, 1975, 1981; Singer, 1983). The plant that is best from a purely nutritional perspective might also be dangerous for the offspring because they will be particularly exposed to natural enemies (Murphy, 2004). Moreover, the strength of the correlation may also be influenced by maternal care, where species with precocious larvae and less time to devote to search may invest more in total fecundity rather than assuring optimal conditions for each offspring (Wiklund & Persson, 1983; Abbott & Dukas, 2016; Schäpers *et al.*, 2016; Masselière *et al.*, 2017; Javoiš *et al.*, 2019). Hence, we should expect variation in the strength of correlation between preference and performance, and we should not be surprised to see a certain degree of mismatch – especially in the face of change – as the traits involved will respond differently to spatiotemporal variation. Rather than seeing this as a problem, we should acknowledge this as an important source of variation that can allow species to respond faster to environmental change.

In fact, we believe that the several decades long search for preference–performance correlations has led to a somewhat one-sided view of the interaction and precluded certain insights. The strength in correlation is, in our opinion, less interesting than how the traits evolve and in response to what. Such a shift in focus will allow us to differentiate between the *fundamental repertoire* – the set of hosts that can potentially be used; and the *realised repertoire* – the set of hosts that are actually used at any given time and place (Onstad & McManus, 1996; Braga *et al.*, 2018, 2020; Larose *et al.*, 2018; Nylin *et al.*, 2018). We use these terms in a similar way as they are commonly used in relation to niches, without claiming full parity. 'Niche' is a difficult term, where the multiple niche concepts and their many interpretations have created inconsistency and confusion (Sales *et al.*, 2021). We have chosen to steer away from the niche concept, so as not to add to this confusion. In essence, the niche is also a holistic concept and we believe derivations such as 'feeding niche' are misconceived. By using 'host repertoire', we are clear about this restriction. Moreover, since a rationale for promoting the concept of host repertoires was to avoid associating it with continuous variation, this makes for another reason to avoid the niche concepts, which have similar connotations (*niche space*, *hypervolume*, etc).

There is also one subtle but important difference in how we think about fundamental and realised repertoires in comparison with how these terms are commonly used in relation to niches. While one could argue that the Hutchinsonian realised niche (Hutchinson, 1957) is the part of the fundamental niche that an organism is squeezed into by the presence of competitors (and to some extent, the rest of the community), the fundamental host repertoire instead represents excess abilities that are currently not used, but that could be realised if conditions change. Even the insects with the most extensive host repertoires tend to commonly use only a fraction of their potential hosts (Rafter & Walter, 2020). A good example is the Painted Lady butterfly (*Vanessa cardui*), which is able to use plants from 25 families as hosts (Scott, 1986). Among these, only a small set of ‘core’ host plants receive the majority of eggs (Celorio-Mancera *et al.*, 2016), even if the local realised host repertoires may vary considerably, due to, for example, local availability (Stefanescu *et al.*, 2017), phenology matching (Audusseau *et al.*, 2016), natural enemies (Stefanescu *et al.*, 2012), or proximity to nectar sources (Janz, 2005). Hence, we also want to emphasise that we make no *a priori* assumptions about what mechanisms explain the difference between fundamental and realised host repertoires; they may be biotic or abiotic, or a combination of both.

The realised repertoire is the interface between the fundamental repertoire and the environment. It is where selection acts and thus what determines how interactions will change within the limits of the fundamental repertoire. Sometimes, the environment may challenge these limits, forcing the fundamental repertoire to change (Agosta & Klemens, 2008; Agosta *et al.*, 2010). At the same time, the ability to retain hosts in the fundamental repertoire even after they have been lost from the realised repertoire allows rapid colonisations and host shifts in response to changes in plant availability, thus providing an explanation for the pattern of the widespread recurrence of host interactions discussed above. Such recurrent colonisations also set the stage for the ‘oscillations’ in the host repertoire that have been suggested to drive diversification of plant-feeding insects under the oscillation hypothesis (Janz & Nylin, 2008; Nylin & Janz, 2009; Janz *et al.*, 2016). Incidentally, a more extensive fundamental repertoire should also provide the source of the ‘lability’ in host use that drives diversification under the musical chairs hypothesis (Hardy & Otto, 2014). In a longer perspective then, the decoupling of preference and performance may facilitate rapid responses to changing environments, and even act as a buffer against extinction, by increasing evolvability instead of adaptation to the current state (Derry *et al.*, 2019).

## Mechanisms of change

In order to actually realise an interaction, it is not enough to have overlapping preference and performance on a given host. Such evolutionary compatibility with the host is necessary, but so is ecological opportunity (Araujo *et al.*, 2015). Even if a plant is perfectly capable of supporting larval growth and females accept it for oviposition, it will not be used if it is not encountered in the habitats occupied by the insects. As with most parasite–host interactions, this is an important source of variation in the association between insects and their host plants (Wehling & Thompson, 1997; Bergstrom *et al.*, 2004; Thompson, 2005; Friberg *et al.*, 2008; Wiklund *et al.*, 2017). Figure 2 depicts a sequence of changes in the host repertoire of a hypothetical butterfly. Interactions can change as a result of new ecological opportunities that arise from changing distributions of species in time and space (Fig. 2b–d), as well as a result of evolutionary changes (Fig. 2e). Because the fundamental host repertoire (all compatible hosts) is usually more extensive than the realised host repertoire (compatible and available hosts), new interactions can easily be formed when a butterfly encounters a new compatible host (Fig. 2b). Likewise, the recolonisation of an ancestral host is also easy if the ability to use that host is retained (Fig. 2c,d).

It is important to recognise the roles of evolutionary compatibility and ecological opportunity when studying the evolution of parasite–host interactions (such as those between insects and host plants), as well as community assembly, climate-driven movement of species, etc. If we want to predict the outcomes of such complex processes, it is necessary to take the species’ initial abilities (compatibility) into account and explicitly investigate how these interact with new ecological opportunities that may emerge as a result of changes in community composition and host availability. In other words, it is important to understand if an absence of interaction is caused by mismatching compatibility or lack of opportunity (Brooks *et al.*, 2019; D’Bastiani *et al.*, 2020). It is also worth noting that ‘opportunity’ here is not merely availability in the direct sense (as in co-occurrence), but also includes the role of other ecological interactions, such as with competitors or natural enemies, which may affect the suitability of a plant as a viable host.

As with most evolutionary modifications, changes in host use are challenging to observe in real time. There are, however, some examples where it was possible to study the process on shorter timescales. One scenario that is useful for this purpose is when species are introduced to new habitats and form new interactions within the local community. These are by definition cases of rapid changes in the host repertoire. One such example is the colonisation of the exotic *Plantago lanceolata* by a population of the butterfly *E. editha* in western North America (Singer & Parmesan, 2018). Following the introduction of *P. lanceolata*, *E. editha* instantly achieved higher fitness on the exotic host than that on its native host, without the need for evolutionary change. This led to a quick response to natural selection for preference of the exotic host. In this case, adaptation to the novel host meant loss of the ancestral host, which then led to the extinction of the population after a change in human land management that rendered the novel host inaccessible for the butterflies (Singer & Parmesan, 2018). But that is not always the case. A different population of the same butterfly species has colonised a novel host while keeping the ability to use the ancestral host, even though some adaptations to the ancestral host were maladaptations to the novel host (Singer & Parmesan, 2019). Singer and Parmesan (2021) suggested that even when the plant that is colonised represents an ancestral host (and thus part of the fundamental repertoire), conspecific plant populations may be different enough from each other to promote additional modifications in the insect, which in turn can draw additional plants into the repertoire. However, over time, local selection will favour specialisation, thus creating a microevolutionary equivalent of the 'oscillation hypothesis' (Janz & Nylin, 2008), which may potentially provide a mechanistic explanation for its larger-scale dynamics (Singer & Parmesan, 2021).

Another example of the interplay between evolutionary compatibility and ecological opportunity is the colonisation of introduced alfalfa by the Melissa blue butterfly (*Lycaeides melissa*). Even if populations show local adaptation to their local host, performance on other potential hosts is not constrained by such adaptation (Gompert *et al.*, 2015). In other words, the fundamental repertoire is relatively unaffected by variable local selection and the potential for colonising an alternative or novel host is maintained. Moreover, in populations that have colonised introduced alfalfa, there is a mismatch between variants that elicit the highest oviposition and the highest larval performance (Harrison *et al.*, 2016), emphasising the complexity of host adaptations, and that correlations between different aspects of such adaptations may take time to evolve (Jones *et al.*, 2019).

Similar patterns have also been found in other plant-feeding insects. For example, *Ophraella communa* beetles introduced from North America to Japan have colonised and rapidly adapted to the novel host *Ambrosia trifida* (Fukano *et al.*, 2016; Fukano & Nakayama, 2018). This plant is also introduced from North America but is not used as a host in its native range. However, American beetles are able to feed on the Japanese *A. trifida*, suggesting that the plant lost some of its resistance after the introduction to Japan. Interestingly, the Japanese beetles, which have adapted to the novel host, can now also use the American ancestral variant. This elegantly demonstrates how the fundamental repertoire makes colonisation of a novel host possible, but also how subsequent local adaptation to the novel host makes it possible to attack previously resistant variants by expanding the fundamental repertoire (Fukano *et al.*, 2016). Moreover, as in the butterfly examples, the performance of Japanese beetles on the native North American host *Ambrosia artemisiifolia* was not affected by local adaptation to the new host (Fukano & Nakayama, 2018).

Detailed studies like these show that plant-feeding insects can evolve host preference and performance rapidly (though often not synchronously), but it all has to start with some level of overlap between the fundamental repertoire and the novel host, enough to result in nonzero fitness (Janz & Thompson, 2002; Singer *et al.*, 2008; Agosta *et al.*, 2010; Yoon & Read, 2016).

The findings outlined above provide a promising path to gain insight into how ecological and microevolutionary processes can give rise to the macroevolutionary patterns of large-scale conservatism, recurrence, and diversification of plant-feeding insects. They also highlight that compatibility is a match between insect and plant traits, and that both may be affected by ecological and geographical variations. Just as individual insects may react differentially to plant defences, there can be a significant intraspecific genetic variation within and between plant populations in traits that affect the interaction (Utsumi *et al.*, 2009;

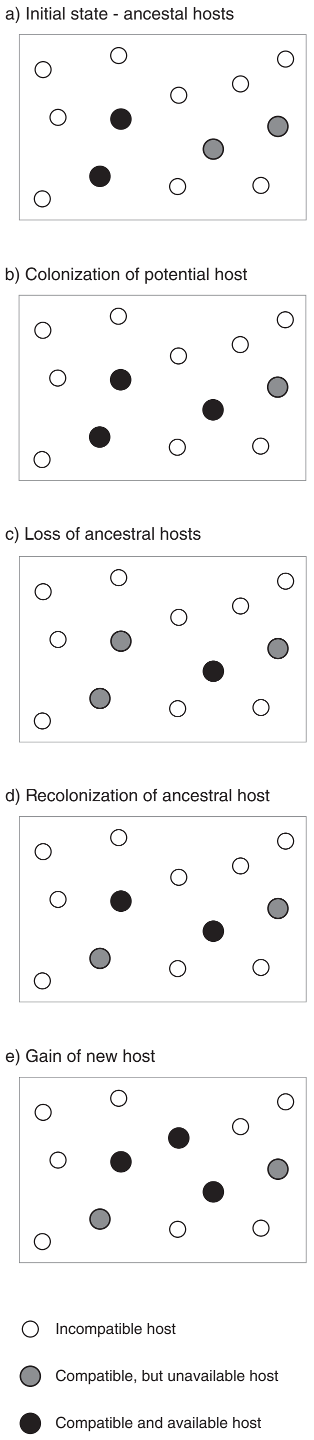

**Fig. 2.** Temporal changes in host repertoire. The host repertoire of a hypothetical butterfly is determined by the compatibility and by the overlap in time and space with the host plants. Each circle in a panel represents one host species. White circles are incompatible hosts, grey circles are compatible but unavailable hosts (potential hosts), and black circles are compatible and available hosts (actual hosts). Host availability is here determined by the distribution of the butterfly, represented by the grey area. As this distribution changes, so does the realised host repertoire.

Gompert *et al.*, 2019; De-la-Cruz *et al.*, 2020). Moreover, plant defence traits are also affected by environmental variation (Audusseau *et al.*, 2016), which can render some populations more susceptible to attack (Mason, 2016), promote divergent evolution in the herbivores (Utsumi *et al.*, 2013), or constrain their realised host repertoires (Robinson & Strauss, 2020). Thus, as the environment changes, genetic and plastic variations in both plants and insects can open and close spatiotemporal windows of opportunity and determine how the interacting species will cope in the face of climate change. Such modulation of realised host repertoires within more extensive fundamental repertoires can also scale up to affect community assembly (Utsumi, 2015) and provide the necessary fuel for large-scale macroevolutionary patterns of variability and diversification (Janz & Nylin, 2008; Janz *et al.*, 2016).

## Conclusions

The widespread occurrence of invasive species and emerging infectious diseases indicate that realised repertoires are often significantly smaller than fundamental repertoires in all parasitic taxa, including herbivorous insects. This suggests that there is a substantial amount of ecological redundancy at the community level in the form of latent interactions that are not realised, but that could be, should conditions change. In a community context, this can affect both the rates that species go extinct and form new interactions. It is a possible cause of emerging infectious disease, as previously inaccessible hosts become accessible due to changes in climate, animal husbandry, and habitat (Agosta *et al.*, 2010; Nylin *et al.*, 2018; Brooks & Boeger, 2019; Brooks *et al.*, 2019). On a more positive note, it may be the reason why the rates of co-extinction are not as severe as some models predict (Strona & Bradshaw, 2018), but can also explain the striking observation that whole ecosystems can be assembled by means of introduced species, as with the reforestation of Green Mountain on Ascension Island (Wilkinson, 2003).

Still, fundamental repertoires are not infinite and compatibility will also vary substantially between species in a community, so that such redundancy is likely to be highly variable and cannot be taken for granted. Insects can and do evolve rapidly, but humans can alter habitats even faster than insects can evolve (Singer & Parmesan, 2018). Moreover, ecological opportunity is determined not only by the co-occurrence of the parasite and host but also by co-occurrence with enemies, mutualists, and competitors (Price *et al.*, 1986; Strauss, 1991; Shikano *et al.*, 2016; Vidal & Murphy, 2018; Opedal *et al.*, 2020; Audusseau *et al.*, 2021). This is illustrated by the fact that environmental models can predict species co-occurrence rather well but not necessarily interactions; even when species distributions do overlap, the predictability of the actual formation of interactions can be low (Gravel *et al.*, 2018). Hence, while climate envelope models may be able to predict where a species could move, they may not be particularly good in predicting which species it will interact with. Clearly, this is an area where much remains to be understood (Sax *et al.*, 2007; Simberloff, 2010; Sagoff, 2019). Still, if we want to predict how a species should respond to climate change, we should not only be asking what the species is currently doing but we should also ask what it is able to do (Onstad & McManus, 1996; Agosta *et al.*, 2010; Feronato *et al.*, 2021).

## Future directions

Over 50 years after Ehrlich and Raven (1964) drew attention to the coevolutionary interaction between butterflies and plants, the intensive study of this system continues to yield vital insights into the evolution of species interactions. As always, new insights also lead to new questions and reveal areas that need more focus. There are a number of topics that we feel need attention in the near future.

First, there are potentially many selection pressures that influence the realised repertoires. While many of these are known and described, we still lack a proper understanding of their relative importance and how they interact with each other across time and space to actually shape the realised repertoire. We believe that framing host interactions in terms of their fundamental and realised repertoires should highlight the need for additional studies along these lines, rather than continuing to ask if females make the ‘right’ egg-laying decisions with regard to larval performance.

We also need to properly understand and characterise fundamental host repertoires. Such knowledge is valuable for the general understanding of host repertoire evolution and to better predict future changes in host interactions as a response to, for example, climate change. As recent events have shown, the significance of such predictions is not only a matter of academic interest, but also immensely important for the well-being of our own species, as it may help us to avoid future zoonotic diseases (Brooks & Boeger, 2019; Brooks *et al.*, 2020). However, mapping fundamental repertoires may not be an easy task, simply because its full extent is not necessarily expressed under current conditions. Hence, we need methods to map such unexpressed variation in a systematic way. Janz *et al.* (2001) pioneered the use of larval establishment tests to survey unexpressed host use capabilities. While such surveys are valuable, it is tedious work and is likely to be riddled by false negatives. Recent developments in the phylogenetic reconstruction of host repertoires (Braga *et al.*, 2020) may make it possible to make more informed predictions for what plants to test, thus making such surveys more tractable.

Another path that is opening up is to use genomic tools to identify and characterise hidden aspects of the fundamental repertoires. The reported differences in tempo of host repertoire evolution are quite striking. We previously described rapid changes in host preference and/or performance in response to changing conditions, with examples from butterflies and beetles. This stands in contrast to other examples where host preference was remarkably inert and virtually unaffected by the local variation in host availability (e.g. Wehling & Thompson, 1997; Bergstrom *et al.*, 2004; Chandra & Hodge, 2021), sometimes even at a considerable cost, as in the case of the persistent acceptance for the oviposition of the introduced plant *Thlaspi arvense*, which is lethal to the larvae, by the butterfly *Pieris macdunnoughii* (Chew, 1977; Steward & Boggs, 2020).

Most likely such differences in tempo of host repertoire evolution are caused by differences in the genetic architecture of the traits involved, something that we are only beginning to unravel. Investigations into the evolutionary modifications involved in host repertoire expansions (Suzuki *et al.*, 2018), as well as identification of common patterns of gene expression on different hosts (Celorio-Mancera *et al.*, 2013, 2016; Christodoulides *et al.*, 2017; Huang *et al.*, 2020b; Petre *et al.*, 2020) or on the same hosts across insect species (Huang *et al.*, 2020a; Malka *et al.*, 2021) help us to not only map the fundamental repertoires but also yield insights into their genetic architecture and, in extension, potential pathways of change (Birnbaum & Abbot, 2020).

The shift in perspective implied by thinking of multiple host use as a collection of abilities (host repertoires), rather than a continuous range, will allow us to ask better questions. For example, many 'generalists' are probably better thought of as *polyspecialists* (West-Eberhard, 2003; Nylin & Janz, 2009; Agosta *et al.*, 2010); they have host-specific adaptations, but to more than one plant. With this perspective, questions such as if specialisation is caused by performance trade-offs also need to be more refined, since there can exist positive and negative correlations between individual hosts within a repertoire. Again, the existence of such correlations will depend on the genetic architecture behind the adaptations, which in turn will depend on the history of acquisition and subsequent evolution. Adaptation to a novel host may lead to epistatic or pleiotropic interactions with existing hosts in the repertoire, but these can be positive as well as negative (Remold, 2012). It has been claimed that trade-offs should not be expected immediately after colonisation, but should evolve as a consequence of adaptation to the novel host (Joshi & Thompson, 1995). However, it is also possible that as time continues to pass, hosts that are involved in antagonistic epistatic or pleiotropic interactions with other hosts may be pruned from the repertoire, leading to the assembly of more stable fundamental repertoires, where interactions among the remaining hosts are mainly positive. Consequently, understanding the genetic architecture of traits involved in multiple host use is of prime importance.

Species ranges may shift rapidly as a consequence of human activities, and range expansions appear to have a significant effect on host repertoires (Slove & Janz, 2011; Lancaster, 2020; Singer & Parmesan, 2021). The nature of this effect will largely depend on the shape of the fundamental host repertoire in relation to the effective change in ecological opportunity. In the introduction, we stated that a key question is to understand what determines which species will proliferate, flee to more benign habitats, or go extinct in the face of climate change. This remains a question that needs much and urgent attention, and we need more knowledge to assess generalities and understand the mechanisms involved. We believe that this necessitates an approach that explicitly investigates fundamental and realised host repertoires and that embraces the distinct roles of compatibility and opportunity in shaping interactions.

Doing so will not only help us to understand how species will cope with climate change, but also provide important tools to investigate species invasiveness and emerging infectious diseases, both of which are examples of species taking advantage of new ecological opportunities, by exploring their fundamental host repertoires.

## Acknowledgments

We wish to thank three anonymous reviewers for constructive comments on the manuscript. The authors have no conflicts of interest to declare.

## Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

## References

Abbott, K.R. & Dukas, R. (2016) Substrate choice by ovipositing mothers and consequent hatchling behaviour: the exploration sharing hypothesis. *Animal Behaviour*, **121**, 53–59.

Agosta, S.J. (2006) On ecological fitting, plant-insect associations, herbivore host shifts, and host plant selection. *Oikos*, **114**, 556–565.

Agosta, S.J., Janz, N. & Brooks, D.R. (2010) How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. *Zoologia*, **27**, 151–162.

Agosta, S.J. & Klemens, J.A. (2008) Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. *Ecology Letters*, **11**, 1123–1134.

Agrawal, A.A. (2010) Current trends in the evolutionary ecology of plant defence. *Functional Ecology*, **25**, 420–432.

Agrawal, A.A., Fishbein, M., Halitschke, R., Hastings, A.P., Rabosky, D.L. & Rasmann, S. (2009) Evidence for adaptive radiation from a phylogenetic study of plant defenses. *Proceedings of the National Academy of Sciences*, **106**, 18067–18072.

Apari, P., Bajer, K., Brooks, D.R. & Molnár, O. (2019) Hiding in plain sight: an evolutionary approach to the south American Zika outbreak and its future consequences. *Zoologia*, **36**, 1–7.

Araujo, S.B.L., Braga, M.P., Brooks, D.R., Agosta, S.J., Hoberg, E.P., von Hartenthal, F.W. et al. (2015) Understanding host-switching by ecological fitting. *PLoS One*, **10**, e0139225.

Audusseau, H., de la Paz Celorio-Mancera, M., Janz, N. & Nylin, S. (2016) Why stay in a bad relationship? The effect of local host phenology on a generalist butterfly feeding on a low-ranked host. *BMC Evolutionary Biology*, **16**, 144.

Audusseau, H., Ryrholm, N., Stefanescu, C., Tharel, S., Jansson, C., Champeaux, L. et al. (2021) Rewiring of interactions in a changing environment: nettle-feeding butterflies and their parasitoids. *Oikos*, **130**, 624–636.

Becerra, J.X. (1997) Insects on plants: macroevolutionary chemical trends in host use. *Science*, **276**, 253–256.

Bennett, N.L., Severns, P.M., Parmesan, C. & Singer, M.C. (2014) Geographic mosaics of phenology, host preference, adult size and microhabitat choice predict butterfly resilience to climate warming. *Oikos*, **124**, 41–53.

Bergstrom, A., Nylin, S. & Nygren, G.H. (2004) Conservative resource utilization in the common blue butterfly - evidence for low costs of accepting absent host plants? *Oikos*, **107**, 345–351.

Betzholtz, P.-E., Pettersson, L.B., Ryrholm, N. & Franzén, M. (2013) With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20122305.

Birnbaum, S.S.L. & Abbot, P. (2020) Gene expression and diet breadth in plant-feeding insects: summarizing trends. *Trends in Ecology & Evolution*, **35**, 259–277.

Boggs, C.L., Watt, W.B. & Ehrlich, P.R. (2003) *Butterflies: Ecology and Evolution Taking Flight*. Chicago: University of Chicago Press.

Braga, M.P., Guimarães, P.R., Wheat, C.W., Nylin, S. & Janz, N. (2018) Unifying host-associated diversification processes using butterfly–plant networks. *Nature Communications*, **9**, 5155.

Braga, M.P., Landis, M.J., Nylin, S., Janz, N. & Ronquist, F. (2020) Bayesian inference of ancestral host-parasite interactions under a phylogenetic model of host repertoire evolution. *Systematic Biology*, **69**, 1149–1162.

Brooks, D.R. & Boeger, W.A. (2019) Climate change and emerging infectious diseases: evolutionary complexity in action. *Current Opinion in Systems Biology*, **13**, 75–81.

Brooks, D.R., Hoberg, E.P. & Boeger, W.A. (2019) *The Stockholm Paradigm: Climate Change and Infectious Disease*. Chicago, Illinois: University of Chicago Press.

Brooks, D.R., Hoberg, E.P., Boeger, W.A., Gardner, S.L., Araujo, S.B.L., Bajer, K. et al. (2020) Before the pandemic ends: making sure this never happens again. *World Complexity Science Academy Journal*, **1**, 7–16.

Celorio-Mancera, M.d.l.P., Wheat, C.W., Huss, M., Vezzi, F., Neethiraj, R., Reimegård, J. et al. (2016) Evolutionary history of host use, rather than plant phylogeny, determines gene expression in a generalist butterfly. *BMC Evolutionary Biology*, **16**, 59.

Celorio-Mancera, M.d.l.P., Wheat, C.W., Vogel, H., Söderlind, L., Janz, N. & Nylin, S. (2013) Mechanisms of macroevolution: polyphagous plasticity in butterfly larvae revealed by RNA-Seq. *Molecular Ecology*, **22**, 4884–4895.

Chandra, V. & Hodge, S. (2021) Fijian swallowtail butterfly *Papilio schmeltzi* (Papilionidae: Lepidoptera) shows clear preference–performance relationships on both native and exotic host plants. *Austral Entomology*, **60**, 225–233.

Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Chew, F.S. (1977) Coevolution of pierid butterflies and their cruciferous foodplants. II. The distribution of eggs on potential foodplants. *Evolution*, **31**, 568–579.

Christodoulides, N., Dam, A.R.V., Peterson, D.A., Frandsen, R.J.N., Mortensen, U.H., Petersen, B. et al. (2017) Gene expression plasticity across hosts of an invasive scale insect species. *PLoS One*, **12**, e0176956.

Condamine, F.L., Rolland, J., Höhna, S., Sperling, F.A.H. & Sanmartín, I. (2018) Testing the role of the red queen and court jester as drivers of the macroevolution of Apollo butterflies. *Systematic Biology*, **67**, 940–964.

Cooper, V.S. (2014) The origins of specialization: insights from bacteria held 25 years in captivity. *PLoS Biology*, **12**, e1001790.

D'Bastiani, E., Campião, K.M., Boeger, W.A. & Araújo, S.B.L. (2020) The role of ecological opportunity in shaping host–parasite networks. *Parasitology*, **147**, 1452–1460.

de la Masselière, M.C., Facon, B., Hafsi, A. & Duyck, P.-F. (2017) Diet breadth modulates preference - performance relationships in a phytophagous insect community. *Scientific Reports*, **7**, 16934.

Defossez, E., Pellissier, L. & Rasmann, S. (2018) The unfolding of plant growth form-defence syndromes along elevation gradients. *Ecology Letters*, **21**, 609–618.

De-la-Cruz, I.M., Merilä, J., Valverde, P.L., Flores-Ortiz, C.M. & Núñez-Farfán, J. (2020) Genomic and chemical evidence for local adaptation in resistance to different herbivores in *Datura stramonium*. *Evolution*, **74**, 2629–2643.

Derry, A.M., Fraser, D.J., Brady, S.P., Astorg, L., Lawrence, E.R., Martin, G.K. et al. (2019) Conservation through the lens of (mal)adaptation: concepts and meta-analysis. *Evolutionary Applications*, **12**, 1287–1304.

Dethier, V.G. (1941) Chemical factors determining the choice of food plants by *Papilio* larvae. *American Naturalist*, **75**, 61–73.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W. et al. (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology*, **47**, 15–25.

Edger, P.P., Heidel-Fischer, H.M., Bekaert, M., Rota, J., Glöckner, G., Platts, A.E. et al. (2015) The butterfly plant arms-race escalated by gene and genome duplications. *Proceedings of the National Academy of Sciences*, **112**, 8362–8366.

Ehrlich, P.R. & Raven, P.H. (1964) Butterflies and plants: a study in coevolution. *Evolution*, **18**, 586–608.

Fecchio, A., Wells, K., Bell, J.A., Tkach, V.V., Lutz, H.L., Weckstein, J.D. et al. (2019) Climate variation influences host specificity in avian malaria parasites. *Ecology Letters*, **22**, 547–557.

Feronato, S.G., Araujo, S. & Boeger, W.A. (2021) 'Accidents waiting to happen' – insights from a simple model on the emergence of infectious agents in new hosts. *Transboundary and Emerging Diseases*. https://doi.org/10.1111/tbed.14146

Fordyce, J.A. (2010) Host shifts and evolutionary radiations of butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3735–3743.

Forister, M.L., Dyer, L.A., Singer, M.S., Stireman, J.O. & Lill, J.T. (2012) Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions. *Ecology*, **93**, 981–991.

Forister, M.L. & Jenkins, S.H. (2017) A neutral model for the evolution of diet breadth. *The American Naturalist*, **190**, E40–E54.

Forister, M.L., Novotny, V., Panorska, A.K., Baje, L., Basset, Y., Butterill, P.T. et al. (2015) The global distribution of diet breadth in insect herbivores. *Proceedings of the National Academy of Sciences*, **112**, 442–447.

Fraenkel, G.S. (1959) The raison d'être of secondary plant substances. *Science*, **129**, 1466–1470.

Friberg, M., Olofsson, M., Berger, D., Karlsson, B. & Wiklund, C. (2008) Habitat choice precedes host plant choice - niche separation in a species pair of a generalist and a specialist butterfly. *Oikos*, **117**, 1337–1344.

Friberg, M., Posledovich, D. & Wiklund, C. (2015) Decoupling of female host plant preference and offspring performance in relative specialist and generalist butterflies. *Oecologia*, **178**, 1181–1192.

Fukano, Y., Doi, H., Thomas, C.E., Takata, M., Koyama, S. & Satoh, T. (2016) Contemporary evolution of host plant range expansion in an introduced herbivorous beetle *Ophraella communa*. *Journal of Evolutionary Biology*, **29**, 757–765.

Fukano, Y. & Nakayama, S. (2018) An experimental test of trade-offs associated with the adaptation to alternate host plants in the introduced herbivorous beetle, *Ophraella communa*. *Journal of Insect Behavior*, **31**, 490–502.

Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, **19**, 207–233.

Gompert, Z., Brady, M., Chalyavi, F., Saley, T.C., Philbin, C.S., Tucker, M.J. et al. (2019) Genomic evidence of genetic variation with pleiotropic effects on caterpillar fitness and plant traits in a model legume. *Molecular Ecology*, **28**, 2967–2985.

Gompert, Z., Jahner, J.P., Scholl, C.F., Wilson, J.S., Lucas, L.K., Soria-Carrasco, V. et al. (2015) The evolution of novel host use is unlikely to be constrained by trade-offs or a lack of genetic variation. *Molecular Ecology*, **24**, 2777–2793.

Gravel, D., Baiser, B., Dunne, J.A., Kopelke, J., Martinez, N.D., Nyman, T. et al. (2018) Bringing Elton and Grinnell together: a quantitative framework to represent the biogeography of ecological interaction networks. *Ecography*, **42**, 401–415.

Gripenberg, S., Mayhew, P.J., Parnell, M. & Roslin, T. (2010) A meta-analysis of preference–performance relationships in phytophagous insects. *Ecology Letters*, **13**, 383–393.

Hamm, C.A. & Fordyce, J.A. (2015) Patterns of host plant utilization and diversification in the brush-footed butterflies. *Evolution*, **69**, 589–601.

Hardy, N.B. (2017) Do plant-eating insect lineages pass through phases of host-use generalism during speciation and host switching? Phylogenetic evidence. *Evolution*, **71**, 2100–2109.

Hardy, N.B., Kaczvinsky, C., Bird, G. & Normark, B.B. (2020) What we don't know about diet-breadth evolution in herbivorous insects. *Annual Review of Ecology, Evolution, and Systematics*, **51**, 1–20.

Hardy, N.B. & Otto, S.P. (2014) Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132960.

Harrison, J.G., Gompert, Z., Fordyce, J.A., Buerkle, C.A., Grinstead, R., Jahner, J.P. et al. (2016) The many dimensions of diet breadth: phytochemical, genetic, behavioral, and physiological perspectives on the interaction between a native herbivore and an exotic host. *PLoS One*, **11**, e0147971.

Heikkilä, M., Kaila, L., Mutanen, M., Peña, C. & Wahlberg, N. (2012) Cretaceous origin and repeated tertiary diversification of the redefined butterflies. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 1093–1099.

Hoffmann, A.A. & Sgrò, C.M. (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Huang, H.-J., Cui, J.-R. & Hong, X.-Y. (2020a) Comparative analysis of diet-associated responses in two rice planthopper species. *BMC Genomics*, **21**, 565.

Huang, X., Ullah, H. & Wang, Y. (2020b) Growth performance and transcriptomic response of *Calliptamus abbreviatus* Ikonn (Orthoptera: Acrididae) to suitable and unsuitable host plant species. *Arthropod-Plant Interactions*, **14**, 605–612.

Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

IPCC. (2013) *Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, New York: Cambridge University Press.

Janz, N. (2005) The relationship between habitat selection and preference for adult and larval food resources in the polyphagous butterfly *Vanessa cardui* (Lepidoptera: Nymphalidae). *Journal of Insect Behavior*, **18**, 767–780.

Janz, N. (2011) Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 71–89.

Janz, N., Braga, M.P., Wahlberg, N. & Nylin, S. (2016) On oscillations and flutterings–a reply to Hamm and Fordyce. *Evolution*, **70**, 1150–1155.

Janz, N., Nyblom, K. & Nylin, S. (2001) Evolutionary dynamics of host-plant specialization: a case study of the tribe Nymphalini. *Evolution*, **55**, 783–796.

Janz, N. & Nylin, S. (1997) The role of female search behaviour in determining host plant range in plant feeding insects: a test of the information processing hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, **264**, 701–707.

Janz, N. & Nylin, S. (1998) Butterflies and plants: a phylogenetic study. *Evolution*, **52**, 486–502.

Janz, N. & Nylin, S. (2008) The oscillation hypothesis of host plant-range and speciation. In: Tilmon, K.J. (Ed.) *Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects*. Chicago: University of California Press, pp. 203–215.

Janz, N., Nylin, S. & Wahlberg, N. (2006) Diversity begets diversity: host expansions and the diversification of plant-feeding insects. *BMC Evolutionary Biology*, **6**, 4.

Janz, N. & Thompson, J.N. (2002) Plant polyploidy and host expansion in an insect herbivore. *Oecologia*, **130**, 570–575.

Janzen, D.H. (1985) On ecological fitting. *Oikos*, **45**, 308.

Javoiš, J., Davis, R.B. & Tammaru, T. (2019) A comparative morphometric study of sensory capacity in geometrid moths. *Journal of Evolutionary Biology*, **32**, 380–389.

Jermy, T. (1984) Evolution of insect/host plant relationships. *The American Naturalist*, **124**, 609–630.

Jones, L.C., Rafter, M.A. & Walter, G.H. (2019) Insects allocate eggs adaptively across their native host plants. *Arthropod-Plant Interactions*, **39**, 1–11.

Joshi, A. & Thompson, J.N. (1995) Trade-offs and the evolution of host specialization. *Evolutionary Ecology*, **9**, 82–92.

Kergoat, G.J., Condamine, F.L., Toussaint, E.F.A., Capdevielle-Dulac, C., Clamens, A.-L., Barbut, J. et al. (2018) Opposite macroevolutionary responses to environmental changes in grasses and insects during the Neogene grassland expansion. *Nature Communications*, **9**, 5089.

Lancaster, L.T. (2020) Host use diversification during range shifts shapes global variation in lepidopteran dietary breadth. *Nature Ecology & Evolution*, **4**, 963–969.

Larose, C., Parker, D.J. & Schwander, T. (2018) Fundamental and realized feeding niche breadths of sexual and asexual stick insects. *Proceedings of the Royal Society B*, **285**, 20181805.

Livshultz, T., Kaltenegger, E., Straub, S.C.K., Weitemier, K., Hirsch, E., Koval, K. et al. (2018) Evolution of pyrrolizidine alkaloid biosynthesis in Apocynaceae: revisiting the defence de-escalation hypothesis. *New Phytologist*, **218**, 762–773.

Malka, O., Feldmesser, E., Brunschot, S., Santos-Garcia, D., Han, W., Seal, S. et al. (2021) The molecular mechanisms that determine different degrees of polyphagy in the *Bemisia tabaci* species complex. *Evolutionary Applications*, **14**, 807–820.

Mangels, J., Fiedler, K., Schneider, F.D. & Blüthgen, N. (2017) Diversity and trait composition of moths respond to land-use intensification in grasslands: generalists replace specialists. *Biodiversity and Conservation*, **26**, 3385–3405.

Mason, P.A. (2016) On the role of host phenotypic plasticity in host shifting by parasites. *Ecology Letters*, **19**, 121–132.

Mayhew, P.J. (1997) Adaptive patterns of host-plant selection by phytophagous insects. *Oikos*, **79**, 417–428.

Murphy, S.M. (2004) Enemy-free space maintains swallowtail butterfly host shift. *Proceedings of the National Academy of Sciences*, **101**, 18048–18052.

Nylin, S., Agosta, S., Bensch, S., Boeger, W.A., Braga, M.P., Brooks, D.R. et al. (2018) Embracing colonizations: a new paradigm for species association dynamics. *Trends in Ecology & Evolution*, **33**, 4–14.

Nylin, S. & Janz, N. (2009) Butterfly host plant range: an example of plasticity as a promoter of speciation? *Evolutionary Ecology*, **23**, 137–146.

Nylin, S., Janz, N. & Wedell, N. (1996) Oviposition plant preference and offspring performance in the comma butterfly: correlations and conflicts. *Entomologia Experimentalis et Applicata*, **80**, 141–144.

Nylin, S., Slove, J. & Janz, N. (2014) Host plant utilization, host range oscillations and diversification in nymphalid butterflies: a phylogenetic investigation. *Evolution*, **68**, 105–124.

Nylin, S. & Wahlberg, N. (2008) Does plasticity drive speciation? Host-plant shifts and diversification in nymphaline butterflies (Lepidoptera: Nymphalidae) during the tertiary. *Biological Journal of the Linnean Society*, **94**, 115–130.

Nyman, T. (2010) To speciate, or not to speciate? Resource heterogeneity, the subjectivity of similarity, and the macroevolutionary consequences of niche-width shifts in plant-feeding insects. *Biological Reviews*, **85**, 393–411.

Nyman, T., Linder, H.P., Peña, C., Malm, T. & Wahlberg, N. (2012) Climate-driven diversity dynamics in plants and plant-feeding insects. *Ecology Letters*, **15**, 889–898.

Onstad, D.W. & McManus, M.L. (1996) Risks of host range expansion by parasites of insects. *Bioscience*, **46**, 430–435.

Opedal, Ø.H., Ovaskainen, O., Saastamoinen, M., Laine, A. & Nouhuys, S. (2020) Host-plant availability drives the spatiotemporal dynamics of interacting metapopulations across a fragmented landscape. *Ecology*, **101**, e03186.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H. et al. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Peña, C., Nylin, S. & Wahlberg, N. (2011) The radiation of Satyrini butterflies (Nymphalidae: Satyrinae): a challenge for phylogenetic methods. *Zoological Journal of the Linnean Society*, **161**, 64–87.

Peña, C. & Wahlberg, N. (2008) Prehistorical climate change increased diversification of a group of butterflies. *Biology Letters*, **4**, 274–278.

Peterson, D.A., Hardy, N.B., Morse, G.E., Itioka, T., Wei, J. & Normark, B.B. (2020) Nonadaptive host-use specificity in tropical armored scale insects. *Ecology and Evolution*, **10**, 12910–12919.

Peterson, D.A., Hardy, N.B., Morse, G.E., Stocks, I.C., Okusu, A. & Normark, B.B. (2015) Phylogenetic analysis reveals positive correlations between adaptations to diverse hosts in a group of pathogen-like herbivores. *Evolution*, **69**, 2785–2792.

Petre, B., Lorrain, C., Stukenbrock, E.H. & Duplessis, S. (2020) Host-specialized transcriptome of plant-associated organisms. *Current Opinion in Plant Biology*, **56**, 81–88.

Price, P.W., Westoby, M., Rice, B., Atsatt, P.R., Fritz, R.S., Thompson, J.N. et al. (1986) Parasite mediation in ecological interactions. *Annual Review of Ecology and Systematics*, **17**, 487–505.

Rafter, M.A. & Walter, G.H. (2020) Generalising about generalists? A perspective on the role of pattern and process in investigating herbivorous insects that use multiple host species. *Arthropod-Plant Interactions*, **14**, 1–20.

Remold, S. (2012) Understanding specialism when the jack of all trades can be the master of all. *Proceedings of the Royal Society B: Biological Sciences*, **279**, 4861–4869.

Robinson, M.L. & Strauss, S.Y. (2020) Generalists are more specialized in low-resource habitats, increasing stability of ecological network structure. *Proceedings of the National Academy of Sciences*, **117**, 2043–2048.

Sagoff, M. (2019) When is it co-evolution? A reply to Steen and co-authors. *Biology and Philosophy*, **34**, 10.

Sales, L.P., Hayward, M.W. & Loyola, R. (2021) What do you mean by "niche"? Modern ecological theories are not coherent on rhetoric about the niche concept. *Acta Oecologica*, **110**, 103701.

Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D. et al. (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, **22**, 465–471.

Schäpers, A., Nylin, S., Carlsson, M.A. & Janz, N. (2016) Specialist and generalist oviposition strategies in butterflies: maternal care or precocious young? *Oecologia*, **180**, 335–343.

Scott, J.A. (1986) *The Butterflies of North America*. Stanford: Stanford University Press.

Scriber, J.M. (1993) Absence of behavioral induction in oviposition preference of *Papilio glaucus* (Lepidoptera, Papilionidae). *Great Lakes Entomologist*, **26**, 81–95.

Scriber, J.M., Larsen, M.L., Allen, G.R., Walker, P.W. & Zalucki, M.P. (2008) Interactions between Papilionidae and ancient Australian angiosperms: evolutionary specialization or ecological monophagy? *Entomologia Experimentalis et Applicata*, **128**, 230–239.

Sexton, J.P., Montiel, J., Shay, J.E., Stephens, M.R. & Slatyer, R.A. (2017) Evolution of ecological niche breadth. *Annual Review of Ecology, Evolution, and Systematics*, **48**, 1–24.

Shikano, I., Rosa, C., Tan, C.-W. & Felton, G.W. (2016) Tritrophic interactions: microbe-mediated plant effects on insect herbivores. *Annual Review of Phytopathology*, **55**, 1–19.

Simberloff, D. (2010) Invasions of plant communities - more of the same, something very different, or both? *The American Midland Naturalist*, **163**, 220–233.

Singer, M.C. (1971) Evolution of food-plant preference in the butterfly *Euphydryas editha*. *Evolution*, **25**, 383–389.

Singer, M.C. (1983) Determinants of multiple host use by a phytophagous insect population. *Evolution*, **37**, 389–403.

Singer, M.C. (1986) The definition and measurement of oviposition preference in plant-feeding insects. In: Miller, J.R. & Miller, T.A. (Eds.) *Insect-Plant Interactions*. New York: Springer Series in Experimental Entomology, Springer-Verlag, pp. 65–94.

Singer, M.C. & Parmesan, C. (2018) Lethal trap created by adaptive evolutionary response to an exotic resource. *Nature*, **557**, 238–241.

Singer, M.C. & Parmesan, C. (2019) Butterflies embrace maladaptation and raise fitness in colonizing novel host. *Evolutionary Applications*, **12**, 1417–1433.

Singer, M.C. & Parmesan, C. (2021) Colonizations cause diversification of host preferences: a mechanism explaining increased generalization at range boundaries expanding under climate change. *Global Change Biology*, **27**, 3505–3518. https://doi.org/10.1111/gcb.15656

Singer, M.C. & Wee, B. (2005) Spatial pattern in checkerspot butterfly-host plant association at local, metapopulation and regional scales. *Annales Zoologici Fennici*, **42**, 347–361.

Singer, M.C., Wee, B., Hawkins, S. & Butcher, M. (2008) Rapid natural and anthropogenic diet evolution: three examples from checkerspot butterflies. In: Tilmon, K.J. (Ed.) *Specialization, Speciation, and Radiation: The Evolutionary Biology of Herbivorous Insects*. Chicago: University of California Press, pp. 311–324.

Slove, J. & Janz, N. (2011) The relationship between diet breadth and geographic range size in the butterfly subfamily Nymphalinae – a study of global scale. *PLoS One*, **6**, e16057.

Stefanescu, C., Askew, R.R., Corbera, J. & Shaw, M.R. (2012) Parasitism and migration in southern Palaearctic populations of the painted lady butterfly, *Vanessa cardui* (Lepidoptera: Nymphalidae). *European Journal of Entomology*, **109**, 85–94.

Stefanescu, C., Puig-Montserrat, X., Samraoui, B., Izquierdo, R., Ubach, A. & Arrizabalaga, A. (2017) Back to Africa: autumn migration of the painted lady butterfly *Vanessa cardui* is timed to coincide with an increase in resource availability. *Ecological Entomology*, **331**, 296–211.

Steward, R.A. & Boggs, C.L. (2020) Experience may outweigh cue similarity in maintaining a persistent host-plant-based evolutionary trap. *Ecological Monographs*, **90**, e01412.

Strauss, S.Y. (1991) Direct, indirect, and cumulative effects of three native herbivores on a shared host plant. *Ecology*, **72**, 543–558.

Strona, G. & Bradshaw, C.J.A. (2018) Co-extinctions annihilate planetary life during extreme environmental change. *Scientific Reports*, **8**, 51–12.

Strona, G. & Lafferty, K.D. (2016) Environmental change makes robust ecological networks fragile. *Nature Communications*, **7**, 12462.

Suchan, T. & Alvarez, N. (2015) Fifty years after Ehrlich and Raven, is there support for plant–insect coevolution as a major driver of species diversification? *Entomologia Experimentalis et Applicata*, **157**, 98–112.

Suzuki, H.C., Ozaki, K., Makino, T., Uchiyama, H., Yajima, S. & Kawata, M. (2018) Evolution of gustatory receptor gene family provides insights into adaptation to diverse host plants in nymphalid butterflies. *Genome Biology and Evolution*, **10**, evy093.

Thompson, J.N. (1988) Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. *Entomologia Experimentalis et Applicata*, **47**, 3–14.

Thompson, J.N. (2005) *The Geographic Mosaic of Coevolution*. Chicago: University of Chicago Press.

Thompson, J.N. & Pellmyr, O. (1991) Evolution of oviposition behavior and host preference in Lepidoptera. *Annual Review of Entomology*, **36**, 65–89.

Tilmon, K. (2008) *Specialization, Speciation, and Radiation: the Evolutionary Biology of Herbivorous Insects*. Chicago: University of California Press.

Uckele, K.A., Jahner, J.P., Tepe, E.J., Richards, L.A., Dyer, L.A., Ochsenrider, K.M. et al. (2020) Evidence for both phylogenetic conservatism and lability in the evolution of secondary chemistry in a tropical angiosperm radiation. *bioRxiv*. https://doi.org/10.1101/2020.11.30.404855

Utsumi, S. (2015) Feeding evolution of a herbivore influences an arthropod community through plants: implications for plant-mediated eco-evolutionary feedback loop. *Journal of Ecology*, **103**, 829–839.

Utsumi, S., Ando, Y. & Ohgushi, T. (2009) Evolution of feeding preference in a leaf beetle: the importance of phenotypic plasticity of a host plant. *Ecology Letters*, **12**, 920–929.

Utsumi, S., Ando, Y., Roininen, H., Takahashi, J. & Ohgushi, T. (2013) Herbivore community promotes trait evolution in a leaf beetle via induced plant response. *Ecology Letters*, **16**, 362–370.

Vidal, M.C. & Murphy, S.M. (2018) Quantitative measure of fitness in tri-trophic interactions and its influence on diet breadth of insect herbivores. *Ecology*, **99**, 2681–2691.

Volf, M. (2018) Differential response of herbivores to plant defence. In: Merillon, J. & Ramawat, K. (Eds.) *Co-evolution of Secondary Metabolites, Reference Series in Phytochemistry*, Cham: Springer, pp. 1–24.

Wahlberg, N. (2001) The phylogenetics and biochemistry of host plant specialization in melitaeine butterflies (Lepidoptera: Nymphalidae). *Evolution*, **55**, 522–537.

Wahlberg, N., Leneveu, J., Kodandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V.L. et al. (2009) Nymphalid butterflies diversify following near demise at the cretaceous/tertiary boundary. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4295–4302.

Warren, M.S., Hill, J.K., Thomas, J.A., Asher, J., Fox, R., Huntley, B. et al. (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, **414**, 65–69.

Wehling, W.F. & Thompson, J.N. (1997) Evolutionary conservatism of oviposition preference in a widespread polyphagous insect herbivore, *Papilio zelicaon*. *Oecologia*, **111**, 209–215.

Weiblen, G.D., Webb, C.O., Novotny, V., Basset, Y. & Miller, S.E. (2006) Phylogenetic dispersion of host use in a tropical insect herbivore community. *Ecology*, **87**, S62–S75.

West-Eberhard, M.J. (2003) *Developmental Plasticity and Evolution*. New York: Oxford University Press.

Wiklund, C. (1974) Oviposition preferences in *Papilio machaon* in relation to the host plants of the larvae. *Entomologia Experimentalis et Applicata*, **17**, 189–198.

Wiklund, C. (1975) The evolutionary relationship between adult oviposition preferences and larval host plant range in *Papilio machaon* L. *Oecologia*, **18**, 185–197.

Wiklund, C. (1981) Generalist vs. specialist oviposition behaviour in *Papilio machaon* (Lepidoptera) and functional aspects on the hierarchy of oviposition preferences. *Oikos*, **36**, 163.

Wiklund, C., Norén, K., Ryman, N. & Friberg, M. (2017) Local monophagy and between-site diversity in host use in the European swallowtail butterfly, *Papilio machaon*. *Biological Journal of the Linnean Society*, **123**, 179–190.

Wiklund, C. & Persson, A. (1983) Fecundity, and the relation of egg weight to offspring fitness in the speckled wood butterfly *Pararge aegeria*, or why don't butterfly females lay more eggs? *Oikos*, **40**, 53–63.

Wilkinson, D.M. (2003) The parable of Green Mountain: Ascension Island, ecosystem construction and ecological fitting. *Journal of Biogeography*, **31**, 1–4.

Wilson, R.J. & Fox, R. (2020) Insect responses to global change offer signposts for biodiversity and conservation. *Ecological Entomology*, **46**, 699–717. https://doi.org/10.1111/een.12970

Yoon, S. & Read, Q. (2016) Consequences of exotic host use: impacts on Lepidoptera and a test of the ecological trap hypothesis. *Oecologia*, **181**, 985–996.

Zaman, L., Meyer, J.R., Devangam, S., Bryson, D.M., Lenski, R.E. & Ofria, C. (2014) Coevolution drives the emergence of complex traits and promotes evolvability. *PLoS Biology*, **12**, e1002023.

Zu, P., Boege, K., Del-Val, E., Schuman, M.C., Stevenson, P.C., Zaldivar-Riverón, A. et al. (2020) Information arms race explains plant-herbivore chemical communication in ecological communities. *Science*, **368**, 1377–1381.

Accepted 8 July 2021

Associate Editor: Takayuki Ohgushi