Insects in their environments: *eco-devo* and *evo-devo* perspectives

Erica M Nadolski, **Phillip L Davidson**, **Joshua A Jones**, **Rebecca R Westwick**, **and Armin P Moczek**, Department of Biology, Indiana University, Bloomington, IN, United States

Abstract

How organismal development, behavior, and physiology are shaped by ecological circumstances, how organisms may be altering these interactions through their own actions, and how the resulting dynamics evolve - as well as shape subsequent evolutionary trajectories - are all subjects central to ecological and evolutionary developmental biology, or *ecoevodevo*. Yet this rapidly growing field is more than just another incarnation of integrative biology; instead it constitutes in many ways the first comprehensive attempt to examine what can be learned by viewing environment, development, phenotype, and evolution all as cause and effect of each other. In this chapter we begin by exploring the relationships between insects and their environment as traditionally conceived. We then examine how our understanding of this relationship changes once we incorporate into our assessment additional and interacting environments, environments that contain other organisms including their genes, environments that are created or shaped by organismal action themselves, and environments that may be inherited. More generally, this chapter is intended to relate insect *ecoevodevo* perspectives to allied conceptual frameworks, and to explore how doing so may broaden where and how we look for *causes* in development, ecology, and evolution.

https://doi.org/10.1016/B978-0-323-95424-2.00007-8

Key points

- *Ecoevodevo* focuses on how organismal development, behavior, and physiology are shaped by ecological circumstances, how organisms may be altering these interactions through their own actions, and how the resulting dynamics evolve as well as shape evolutionary trajectories
- We explore the relationships between insects and their environment as traditionally conceived, then broaden our assessment to include additional and interacting environments, environments that contain other organisms, environments that are created or shaped by organismal action themselves, and environments that may be inherited
- More generally, this chapter aims to relate insect *ecoevodevo* perspectives to allied conceptual frameworks, and to explore how doing so may broaden where and how we look for *causes* in development, ecology, and evolution.

Introduction

How organismal development, behavior, and physiology are shaped by ecological circumstances, how organisms may be altering these interactions through their own actions, and how the resulting dynamics evolve - as well as shape subsequent evolutionary trajectories - are all subjects central of ecological and evolutionary developmental biology, or *ecoevodevo* (Abouheif et al., 2014; Sultan, 2015; Gilbert and Epel, 2015). Yet this rapidly growing field is more than just another incarnation of integrative biology; instead it constitutes in many ways the first comprehensive attempt to examine what can be learned by viewing environment, development, phenotype, and evolution all as cause and effect of each other. The field itself is young, yet insects have already featured prominently in highlighting how *ecoevodevo* perspectives can advance our understanding of longstanding questions in development and evolution, as well as motivate novel research programs (e.g. Snell-Rood et al., 2010; Rohner et al., 2023). The sections to follow are intended to provide examples of some of these efforts, to relate insect *ecoevodevo* perspectives to allied conceptual frameworks, and to explore how doing so may broaden where and how we look for *causes* in development, ecology, and evolution.

Insects and their environment

Environmental conditions affect all organisms, including insects, in principally two ways. First, by shaping selective conditions, environmental circumstances allow fitness differences among genotypes to emerge, thereby delineating evolutionary trajectories and facilitating subsequent adaptation. Second, environmental conditions directly affect phenotype formation. At a minimum, this dependency arises due to the biochemical and biophysical dependencies of living systems to abiotic factors such as temperature or *pH*. More often, however, such plastic responses to environmental conditions are exquisitely complex and may affect morphological, physiological, and behavioral traits, often all at once. Consequently, environmental conditions facilitate both the production of phenotypic variation via plasticity and its sorting via selection (Ananthakrishnan and Whitman, 2009).

Temperature

Among abiotic environmental conditions, temperature is among the most widely appreciated, researched, and consequential factors influencing insect development and evolution, and one in which recent work has begun to illustrate particularly well the complex interplay between developmental plasticity on one side, and developmental evolution on the other. Most insects respond to colder temperatures by growing slower, and to larger body sizes, a pattern so common it has been named the temperature size rule (Atkinson, 1994). However, taxa differ in the developmental means by which they achieve this interaction: in the tobacco horn worm *Manduca sexta* temperature affects late mass gain, whereas in *Drosophila melanogaster* it alters the relative timing of metamorphosis (Davidowitz and Nijhout, 2004; Ghosh et al., 2013). Furthermore, temperature dependent growth dynamics are often complex, non-linear, necessitating measurements across a gradient of rearing temperatures, a difficult challenge for taxa not amenable to lab rearing.

Temperature and seasonality

Temperature-size interactions pose interesting challenges to insects themselves, in particular those colonizing new habitats and extending their ranges poleward into cooler climates. While prolonging insect growth by virtue of average cooler temperatures, cooler environments are also generally associated with shorter summer seasons within which to complete immature growth, metamorphosis, and reproduction. As such, taxa expanding poleward may find themselves under strong selection to *reduce* development time while simultaneously biased to *prolong* it by virtue of their physiology. Disentangling the relative contributions of both influences to local insect development is difficult. One possible approach is to rear individuals derived from different latitudes under controlled conditions in the laboratory. A recent successful example involves the bull-headed dung beetles *Onthophagus taurus*, a species native to the Mediterranean (Rohner and Moczek, 2020). In 1974, *O. taurus* was first recorded in Northern Florida, and manage to reach the Canadian border by 2011, a roughly 1700 km northward expansion within just 40 years, involving likely no more than 1–2 generations per year (Hoebeke and Beucke, 1997; Rounds and Floate, 2012). Rearing *O. taurus* derived from four different locations along a longitudinal gradient (Michigan, Indiana, North Carolina, Florida) as well as from the native range (Italy) at two temperatures (19C and 27C, reflecting average soil temperatures in the northern and southern-most distribution of the species) found little difference in development time among populations when reared at 27C, but dramatic differences at 19C. Specifically, northern populations managed to complete larval development at 19C considerably faster than individuals derived from further south, consistent with selection favoring fast-developing genotypes when season length is curtailed. More generally, findings such as these show that local adaptation to shorter seasons was achieved through evolutionary changes in the interactions between temperature and larval development, or the degree of thermal plasticity across populations.

Nutrition

Nutritional conditions likewise constitute a fundamental environmental variable shaping both phenotype production and selective conditions. Organismal growth necessitates nutrients, and dealing with changes in nutritional conditions therefore constitutes a fundamental challenge to all organisms, insects included. Not surprisingly, the precise nature of variation in nutritional conditions has played a critical role in shaping how insects respond to their nutritional environment.

Nutrition and body size

Insects obtain nutrition in an amazing variety of ways, as the consumers of plant materials, as predators, parasitoids, or by utilizing the dead bodies or excretory products of other organisms. One fundamental variable shared by all types of insect diets is the significance of food *quantity*: for example, to complete larval development, holometabolous insects require a minimum amount of food to reach *minimal viable weight*, a body mass resulting from a corresponding food quantity below which individuals simply cannot continue their development, metamorphose, and pupate (Mirth and Riddiford, 2007). Likewise, nutrition in excess of reaching *minimal viable weight* allows holometabolous insects to attain *critical weight*, i.e. a threshold mass that once reached triggers the onset of metamorphosis regardless of any subsequent weight gain (Davidowitz et al., 2003). However, exactly how insects are able to utilize their larval food supply to reach a given mass critically depends to a considerable degree on their feeding ecology: caterpillars short of having attained critical weight may have the option of finding additional host plants by virtue of their morphology and locomotory abilities. In contrast, larval dung beetles contained within a maternally provisioned underground brood ball have, in a sense, nowhere else to go on their own should they run out of food (e.g. Shafiei et al., 2001). It is in such taxa that we often find the greatest disparity between minimal viable weight and critical weight, and the greatest variation in adult body sizes within populations, reflecting on one side the immense variation in larval food quantity available under natural conditions, and on the other the extreme degree of nutritional plasticity that has evolved in some taxa in response.

Nutrition and relative trait size

Nutrition does not just affect body size as a whole, but also impacts the sizes of specific traits *relative* to body size. Remarkably, traits differ in how their growth is affected by nutrition, even if they reside within the same individual organism. Put another way, different growing structures interpret the same nutritional conditions, or the same *change* in nutritional conditions, on a trait-by-trait basis, resulting in scaling relationships specific to each trait (Casasa et al., 2017; Casasa and Moczek, 2018, 2019). For example, insect legs and wings tend to scale relatively isometrically with body size, that is larger individuals resemble enlarged versions of smaller individuals. Genitalia and components of the central nervous system, in contrast, tend to scale only modestly with body size (Macagno et al., 2011; Parzer et al., 2018). Put another way, large, high-nutrition individuals possess relatively similarly sized genitalia and brains (on an absolute scale) than much smaller, low nutrition individuals. Secondary sexual traits such as the horns of rhinoceros beetles, the mandibles of male stag beetles, or the eye stalks of stalk-eyed flies are different yet again, in that they are disproportionately enlarged in large, high-nutrition males, but greatly reduced in smaller males (Emlen, 2008). Lastly, nutrition mediated differences in phenotype expression are most extreme in *polyphenic* species, i.e. taxa in which individuals adopt one of two or more *discretely different alternative forms* depending on the specific environmental conditions encountered at earlier stages of development. Diverse environmental factors may cue the developmental of alternate morphs, from photoperiod to crowding, yet nutritional conditions appear to be especially relevant, for instance in the determination of seasonal polyphenisms in inchworm caterpillars, castes in social Hymenoptera, or the alternate horned and hornless male morphs of many horned beetle species (Moczek, 2009).

The evo devo of scaling

Trait-specific growth responses to the same nutritional conditions occur even though all cells within an individual organism possess the exact same genome and experience the exact same nutritional conditions. This seeming contradiction is resolved through a partial autonomy of trait primordia to pursue their own growth trajectory, enabled for instance through trait-specific implementation of the same signaling pathway or the trait-specific combination of multiple signaling pathways. For example, across diverse insects nutritional conditions are transduced into circulating levels of insulin-like peptides (ILPs), which in turn are sensed by membrane-bound insulin receptors (InR) to then promote cell proliferation and structural growth (Brogiolo et al., 2001). However, traits may diverge in their growth response to the *same* level of circulating ILPs via the differential expression of other pathway members (e.g. FOXO; Tang et al., 2011), or via differential interactions with other growth regulating pathways: for example, the experimental downregulation of insulin receptors affects horn, leg, and genitalia growth in horned dung beetles, but co-regulation of growth via the hedgehog signaling pathway is restricted to horns (Casasa and Moczek, 2018; Kijimoto and Moczek, 2016).

Adjusting body size to nutrient availability, and relative trait size to body size as a function of trait type, are typically viewed as adaptive, allowing organisms to maintain functionality and integration in the face of an uncertain food supply during development. However, because selection may favor different scaling relationships in different populations or species, evolutionary changes in relative trait size are essentially ubiquitous, and as such an important contributor to phenotypic diversity in the wild. This evolutionary lability of scaling is in turn made possible through the evolutionary lability of the underlying developmental mechanisms: for example, while the insulin signaling pathway plays key role in the regulation of the relative sizes of legs, horns, and genitalia in two species of onthophagine dung beetles as well as one species of rhinoceros beetle, the exact functions of pathway components not only diverge among traits but also across phylogenetic distances, including among the two relatively closely related onthophagine species (Rohner et al., 2023; reviewed in Casasa, 2024).

Taken together, developmental plasticity is thus not only ubiquitous in insects, but so are evolutionary changes in plasticity as a means to adapt to local conditions (see also photoperiod-dependent diapause in pitcher plant mosquitoes (Bradshaw and Holzapfel, 2001) and lacewing (Tauber and Tauber, 1970, 1982); size-dependent expression of weaponry in earwigs (Tomkins, 1999), habitat-dependent induction of dispersal morphs in planthoppers (Denno et al., 1986; Zhang et al., 2022)). Collectively, these and many other studies underscore the complex roles of environment-responsive development in facilitating insects' ability to both persist and adjust. The same as well as other complexities emerge, when our conceptualization of the environment is expanded to include social conditions, as discussed next.

The social environment

Though not all insects include sociality in their life histories, those that do are often profoundly affected in their ecology, evolution, and development as a result of group living and social interactions. The social environment in particular stands out in that it is shaped in large part by the same individuals that are responding to it. This phenomenon echoes dimensions of the more general phenomenon of niche construction, which occurs when organisms modify their environment in ways that alter the selective conditions that they themselves are subject to (see Section "Niche construction" below). At the same time, insect species differ in how social they are, how plastic their level of sociality is, and how much their biology is impacted by social conditions. In the sections that follow we begin with a brief overview of the diversity of social systems found in insects; we then discuss how sociality affects developmental, physiological, and ecological dimensions of insect biology; next, we cover how *ecoevodevo* perspectives may help us illuminate the evolution of sociality; and finally, we close by examining the dynamics that can emerge when social insects form close interactions with other taxa.

The scope of sociality in insects

Insects display a wide range of social organizations from solitary to advanced eusocial. Historically, different categories of social organization have been particularly well described in relation to bees, ants, and wasps (Hymenopterans) and were grouped by a number of social criteria (Linksvayer, 2019; Michener, 1969). *Solitary* species spend their lives alone and typically only come together with conspecifics for the purposes of mating. Parents leave eggs shortly after they are laid, sometimes on or near a suitable food source for the offspring, but they depart before the offspring hatch. The vast majority of insects (including the majority of Hymenopterans) fall into this category. *Aggregations* and *communal groups* then describe cases in which many individuals live near one another but do not cooperate. For example, females may build nests in the same area or use a composite nest, such as ground-nesting *Andrenid* bees (Paxton et al., 1999). Each female makes and provisions her own compartments within the nest, and different females do not assist one another. Insects may also aggregate in other ways, such as bark beetles using "strength in numbers" to overcome the defenses of a host tree (Birch, 1984). *Subsocial* species are distinguished by showing parental care. At least one parent provides ongoing care to the offspring and/or defends them as they develop. For instance, earwig mothers construct a chamber to lay their eggs and will remain with the young after they hatch. Mothers defend offspring from predators and even clean them to keep them free of pathogens (Boos et al., 2014; Butnariu et al., 2013). *Quasisocial* groups in turn contain multiple females of the same generation that all lay their own eggs, then cooperatively work together to raise them. Every female participates in both reproduction and rearing. Some Afrotropical *Allodapine* bees are quasisocial (Schwarz, 1987). Lastly, *semisocial* groups are similar to quasisocial groups in that they contain multiple females of the same generation that are reproductively capable. In semisocial groups, however, some division of labor begins to emerge—some of the same-generation females lay most of the eggs while others spend more time on construction and provisioning, even though they are capable of reproduction. Some *Augochlorini* sweat bees are an example of a semisocial insect (Michener, 2007).

The most complex social group, however, are the *eusocial* insects. There are three requirements for a species to be considered eusocial: cooperative brood care, where many individuals work together to raise the brood; overlapping generations, where adult parents and adult offspring coexist within the same nest (which differentiates them from quasi-and semi-social groups); and reproductive division of labor, where some individuals primarily reproduce ("queens" and "kings") while others forego reproduction to focus on maintenance tasks such as nest construction, foraging, brood care, and defense ("workers," who are the offspring of the reproductives in eusocial colonies; Hölldobler and Wilson, 1990). Eusociality can be further divided into two groups, primitively/facultatively eusocial and advanced/obligately eusocial (Crespi and Yanega, 1995). In primitive/facultative eusociality, queens and sterile workers are morphologically indistinguishable (or nearly so), as is the case in many bumblebees (Wilson, 1971). For advanced/obligately eusocial species, queens and workers show strong morphological differences between reproductive queens and nonreproductive workers due to differences that arise relatively early in development. Honey bees, ants, and termites are all classic examples of advanced/obligately eusocial species (Wilson, 1971).

Recently, there have been calls to update our terminology with regards to social organization in insects. Firstly, the above schema was developed heavily based on hymenopterans. Many social interactions seen in other insect taxa do not fit neatly into these categories. Second, the categories described above have a hierarchical structure that does not necessarily fit with a modern understanding of how the evolution of sociality has occurred. Other classifying systems have been proposed, such as classifying insect societies by the relational composition of the group and the context in which the social interaction occurs, i.e.: maternal and biparental care; paternal care; resource defenders; and larval or nymphal "herds" (Costa, 2018).

Social conditions as cause and effect of insect ecoevodevo

Individuals contribute to the social environment they exist in by virtue of their behaviors, metabolic products, excretory products, and diverse other activities. This social environment in turn shapes how an insect experiences yet other environmental conditions. For example, group living inherently affects the dynamics of microbial transmission, which has implications for the spread of both beneficial symbionts and pathogens. The unique pressures caused by pathogens in high-density social settings have led to the evolution of a suite of adaptations, called "social immunity," that combat this heightened risk in social species (Cremer et al., 2007; see also Section "Endosymbiosis" below). Many social species also experience different nutritional conditions than their solitary counterparts, particularly during early life (Lihoreau et al., 2018). Specifically, parental provisioning buffers offspring against foraging risks and variance in larval food supply during this highly vulnerable stage. For highly social species, the benefits of a collective adult foraging workforce further decrease the pressure on any one individual to provide completely for its own needs. This large workforce can also allow the colony to efficiently exploit resources in a given area, often to an extent not accessible to solitary species (Clark and Mangel, 1986). Some highly social species are even able to cultivate their own stable nutritional resources rather than relying on traditional foraging (e.g. aphid-herding "rancher" ants (Ivens and Kronauer, 2022); herbivory by fungus "farmer" ants (Mehdiabadi and Schultz, 2010). Finally, many social species build physical environments in the form of complex nest structures. These nests are perhaps one of the most obvious forms of niche construction, able to shape diverse abiotic and biotic factors, from temperature and moisture experienced during larval development to the ability to store food reserves (AbdUllah et al., 2018; Hess, 1926; Jones and Oldroyd, 2006; Turner and Soar, 2008; see also Section "Niche construction"). These environmental modifications can be critical for both developmental processes and adult survival (Groh et al., 2004; Korb and Linsenmair, 2000; Powell and Stradling, 1986). As such, social conditions created by insects for themselves and the members of their social group profoundly alter the selective conditions experienced by individuals compared to solitary taxa, in turn promoting the extraordinary colony-level behaviors observed in highly social insects.

Social conditions may, however, also affect the ecology, evolution, and development of insects apart from their influence on conventional environmental conditions. One prominent example of this phenomenon can be seen in aggression. Aggression is expressed in many contexts in insects. Aggression is sometimes used as a way to defend resources or personal safety. While many solitary insects will defend themselves or their resources, defensive aggression has become a highly coordinated, collective behavior in many social insects. For example, some insects have evolved the use of complex communication systems to synchronize defense, such as honey bees; others have evolved specialized castes that are morphologically adapted specifically for combat, such as in some ants (Breed et al., 2004; Powell, 2009). Resource defense aggression by social groups can influence the ecology of a geographic region or habitat, as it often allows these groups to monopolize and exploit far more of an area's resources than solitary individuals can (Wilson and Kinne, 1990). Aggression can further affect species' evolutionary trajectories via systems such as intra-group dominance hierarchies. Some facultatively eusocial wasps determine which females get to reproduce and which are relegated to be mainly workerlike based on these strict dominance hierarchies. Because these interactions determine which individuals reproduce, they strongly affect heritable variation visible to selection (and therefore responses to selection) in species with these types of social systems. Social wasps in particular have been used to study topics such as reproductive skew theory and kin selection (also see Section "The evolution of sociality" below). Lastly, due to the physical nature of these dominance contests, dominance both affects and is affected by a range of physiological traits, from body size to brain structure to endocrine function (Jandt et al., 2014).

However, not all examples of social conditions involve antagonistic interactions. Affiliative interactions, such as allogrooming and parental care, can also affect insect ecology and development. For example, allogrooming (where one individual cleans the body surface of another) is widespread in social species, including insects. These interactions are associated with colony health since they can affect hygiene and disease transmission (Theis et al., 2015). Additionally, allogrooming can function as an important communication behavior to disperse social pheromones throughout the group (Naumann et al., 1991). Likewise, parental care also affects insect biology in a surprising number of ways. As mentioned already, parental protection of offspring often enhances survival, and parental provisioning during the early-life period can buffer developing insects against the risks of early life malnutrition. These buffering effects have been shown to enable the accumulation of cryptic genetic variation invisible to selection (Snell-Rood et al., 2016; see also Box 1 for entry on *cryptic genetic variation*). Such hidden variation may, however, be released and become visible to selection when the buffering capacity of parental care is compromised, e.g. during periods of stress, ecosystem-wide environmental changes, or the colonization of new habitats.

Box 1 Concepts central to *eco evo devo.*

Reciprocal causation

A concept central to *ecoevodevo* that extends the field beyond traditional ways of thinking is viewing phenotype/organism, environment, development, and evolution all act as cause and effect of each other. For example, conventional perspectives view development as the means by which genotype is translated into phenotype. Viewed this way, development is solely a product of evolution. *Evodevo* extends this perspective by adding that once evolved, developmental mechanisms shape subsequent evolutionary trajectories by biasing phenotypic variation available for evolutionary processes to act upon, either by constraining phenotype space or by facilitating some phenotypic transitions more so than others. Conventional perspectives also view the environment as external and separable from the organism (in the absence of the organism the environment still exists) and passive (the organism responds to the environment, less so the other way around). *Ecoevodevo* also emphasizes that organisms constantly modify environments in non-random ways (niche construction) that have the potential to feedback to influence both development and evolution. While niche construction, too, is an evolved property, it may feed back to influence the evolutionary process by contributing evolutionarily relevant heritable variation in those cases in which aspects of the environment are passed on to descendants, and providing alternate routes toward organism-environment fit (adaptation).

Phenotypic/developmental plasticity

Ability of a single genotype (or individual organism) to change phenotype expression in response to changes in the environment. Plastic responses may be neutral, detrimental, or adaptive with respect to fitness, gradual or non-linear, reversible or not, and may even transcend generations such that environments experienced in one generation affect phenotypes in the next. Further, plastic responses to environmental changes such as seasonality or nutrition may involve well-choreographed, integrated, and robust changes in behavior, morphology, physiology, and life history, allowing organisms to maintain high fitness in the face of environmental change.

Phenotypic/developmental robustness

Robustness in development refers to the ability of an organism (or component part thereof) to output the same phenotype in the face of perturbations. However, robustness in development or physiology is *not* the same as insensitivity, instead it is commonly made possible by plastic, compensatory changes at other levels of biological organization. Developmental robustness in the face of *genetic* perturbations such as new mutations has the added effect that it shields such mutations from becoming phenotypically manifest and thus visible to selection. Developmental robustness is therefore thought to be a major facilitator of the accumulation of *cryptic genetic variation* in natural populations.

Niche construction

Niche construction occurs when an organism modifies environmental conditions in ways that alter selection pressures on a recipient organism, which may be the niche constructor itself, its offspring, or members of the same or other species (Matthews et al., 2014). Niche construction emphasizes organisms' capacity to alter environmental conditions in ecologically, developmentally, and evolutionarily impactful ways, and may be an important source of extended inheritance (e.g. when parents pass on to their offspring antibodies, symbionts, knowledge, or territories) as well as serve as a buffer to genetic and environmental perturbations, thereby contributing to both robustness and (in case of buffering against genetic perturbations) cryptic genetic variation.

G x E, E x E, and G x E x E

Quantitative and evolutionary genetic models partition the phenotypic variation V_P observable in natural populations into contributing fractions. While V_G and V_E denote the variation contributed by genetic and environmental factors, respectively, $V_{G\,x\,E}$ captures the variation contributed by *gene x environment* (*G x E)* interactions, or the phenotypic variation attributable to different genotypes responding differently to the same environmental change. $V_{E\,x\,E}$ in turn refers to the phenotypic variance generated by *environment x environment (E x E)* interactions, that is influences of the environment on the phenotype that are themselves dependent on yet another environmental variable. Lastly, when genotypes differ in the degree to which their responses to the environment are affected by yet other environmental influences, this reveals the existence of *genotype x environment x environment (G x E x E)* interactions*,* a likely common but hard to detect source of phenotypic variation in nature.

Cryptic genetic variation

Cryptic genetic variation (CGV) refers to genetic differences between individuals that do not manifest in phenotypic differences, and therefore remain invisible to selection. CGV is the expected outcome of *developmental robustness* channeling genotypic differences during development toward uniform phenotypic outcomes (*genotypic equivalence*). CGV is also predicted to accumulate as a consequence of developmental buffering occurring at other levels of biological organization, such as parental care, which similarly buffers developing organisms against genetic (and environmental) perturbations. Lastly, CGV may also accumulate as a consequence of relaxed selection resulting from certain types of context-specific gene expression, e.g. when genes exhibit strict maternal, sex-, or environment-specific expression; in each case gene copies residing in non-expressing individuals are shielded from selection, and population-wide mutational variation is able to accumulate to a greater degree than in comparable genes expressed in every individual. CGV may stop being cryptic and instead contribute to phenotypic variation for instance when organisms encounter novel or especially stressful environmental conditions (causing buffering mechanisms to reach their limits) or when populations transition from heterogenous to uniform environments (thereby exposing variation that accumulated in non-inducing environments).

Genetic accommodation/assimilation

Genetic accommodation occurs when a novel phenotype, generated through a newly arriving mutation, environmental change, previously cryptic genetic variation, or their interactions is refined into an adaptive phenotype through quantitative genetic changes over generations. While genetic accommodation may yield increased or decreased environmental sensitivity of a plastic phenotype, genetic assimilation refers to the extreme outcome when environmental sensitivity is lost entirely, and a trait acquires constitutive, canalized expression. Genetic accommodation provides a critical conceptual bridge from the interactions between development and environment and their ability to bring about novel phenotypes on one side to heritable genetic changes in phenotype induction in subsequent generations on the other.

Non-genetic/extended/inclusive inheritance

Eco evo devo extends the concept of inheritance beyond genetic and Mendelian boundaries. Instead, the field recognizes that variation in what can be inherited across generation and thus may shape evolutionary trajectories may reside not just in the nuclear genomes of parent populations, but also include ecological factors (e.g. through the differential inheritance of constructed environments), culture (through the differential transmission of learned knowledge) and symbioses (through the vertical transmission of microorganisms and their products).

Holobiont, and hologenome theory of evolution

The holobiont refers to the community formed by a host organism and the often very diverse other species living in, on, or around it (aka metaorganisms). The holobiont concept views the holobiont as a discrete ecological unit and emphasizes that host development, responses to the environment, defense, and disease may emerge through the complex interactions among holobiont members, rather than be causally attributable to host genes, behaviors, or physiology alone. The hologenome theory of evolution in turn views the composite of genomes contained within a holobiont as the discrete unit of selection (Zilber-Rosenberg and Rosenberg, 2008), yet level of discreteness and thus evolutionary significance (to hosts, symbionts, or both) likely depend heavily on mode of symbiont acquisition and degree of specialization.

Box 1 (Continued)

Evolutionary addiction

Hosts organisms commonly depend on microbial taxa to execute functions their own genomes are unable to support. However, frequently hosts also depend on microbial symbionts to provide functions hosts were ancestrally able to execute on their own. In these cases host secondarily outsourced these functions to symbionts, which is then often followed by a loss of their own corresponding genetic underpinnings (e.g. the ability to synthesize select amino acids). When this happens, the evolutionary persistence of the host lineage thus becomes dependent upon, or 'evolutionarily addicted' to, select microbial symbionts (Moran, 2002; Hammer, 2023).

Environmental conditions can also affect the immediate fitness effects of parental care. For example, the European earwig (*Forficula auricularia*) provides facultative maternal care which increases offspring survival under many conditions, except under conditions of food restriction, when increased maternal care *reduces* offspring fitness (Meunier and Kölliker, 2012). In this way, the evolutionary consequences of sociality can depend on environmental conditions in ways that are often complex and nonintuitive.

Finally, parental care can also be exploited by other individuals. As one example, some species will perform "egg dumping," during which eggs are abandoned with the clutch of another conspecific who then provides the parental care for them. The fitness effects of this behavior on the dumper and the recipient can be similarly complex; the recipient may have to expend more energy caring for a larger clutch, but the recipients are often related to the dumpers and therefore may benefit from kin selection (Loeb, 2003). Thus, sociality both affects and is affected by the ecology, evolution, and development of insects in wide-ranging contexts.

Social life affects insect physiology

The physiology of insects has changed in a number of important ways in response to life in social groups. First, because the social environment is the product of the individuals that comprise it, group members experience changes in their physiology that help promote the maintenance of the social group. For example, the transition from solitary to any kind of social group living is thought to be associated with the elaboration of communication systems to coordinate these groups. This elaboration of communication systems in turn relies on evolutionary changes in the neural and sensory structures that are necessary for sending and receiving signals (Kocher and Cocroft, 2019; Nehring and Steiger, 2018). Some social groups have even evolved *individual* recognition, in particular in taxa that rely on strict dominance hierarchies that require individuals to remember who is who (Tibbetts, 2002). Other changes to insect physiology are associated with sociality more broadly. For example, many advanced eusocial colonies persist under one queen for a long time, despite the queen only mating once. Long-lived queens therefore need to store sperm to be able to keep producing fertilized eggs throughout their tenure as the colony's sole reproductive. Evolutionary responses to this selective pressure include greatly enlarged spermathecae (sperm storage organs) and the physiological ability to maintain sperm viability over years or even decades (Pascini and Martins, 2017). Other physiological changes have evolved hand in hand with the evolution of eusociality. Workers in advanced eusocial colonies develop into sterile adults that often have diminished reproductive structures, changes to body size and allometry, altered endocrinology, and even changes to brain structure relative to reproductives (Bloch et al., 2002; Bourke., 1999; Jaumann et al., 2019; O'Donnell et al., 2011; Roat and da Cruz Landim, 2008; Wheeler, 1986). Finally, while social immunity behaviors have evolved in response to the increased disease pressure in social settings, social immunity may be associated with an intriguing trade-off, as at least some social insects have evolved *decreased* investment in personal immunity (Meunier, 2015). We can see therefore that the transition to group living is associated with highly diverse, body-wide consequences for insect health and physiology.

The evolution of sociality

The evolution of insect sociality is an area of active investigation and continued debate. Early theories included the "social ladder" hypothesis, which suggests that more complex forms of sociality evolve from less complex ones. For example, using the social categorization scheme described earlier, this theory suggests that subsociality evolved first, which then progressed to quasi- and/or semisociality, which eventually transitioned into eusociality. Often, though, this hypothesis is not supported by empirical data (Wcislo and Tierney, 2009). It additionally contains the subtle implication that species that are lower on the "ladder" are all evolving toward some end goal of eusociality, rather than strategies like parental care and aggregations being highly derived, evolutionary endpoints in and of themselves (Costa, 2018).

More recent theories therefore focus on exploring the genetic and/or ecological circumstances that may selectively favor group living (kin selection: Hamilton, 1964; reciprocal altruism: Fletcher and Zwick, 2006; Trivers, 1971; ecological constraints: Emlen, 1982; reproductive skew theory: Nonacs and Hager, 2011; Reeve and Keller, 2001; molecular evolution: Toth and Rehan, 2017). One common critique leveled at many of these frameworks is that all struggle to clearly distinguish between cause and effect: did eusociality evolve because it allowed cooperating individuals to exploit resources previously inaccessible, or did the latter become possible once the former was achieved? Are highly social groups often comprised of closely related individuals because kin selection shaped the evolution of social insects, or are high levels of relatedness a secondary byproduct of social group living? Here, *ecoevodevo* perspectives are beginning to provide complementary opportunities to assess causes and mechanisms in the evolution of insect sociality (West-Eberhard, 2003; Toth and Rehan, 2017). For instance, the many examples of extant, facultatively (eu)social taxa raise the possibility that certain forms of sociality may have initially evolved as alternative phenotypes, expressed in some conditions (e.g. prolonged season and ample food supply) but not others (e.g. Halictid and *Ceratina* bees, Shell and Rehan, 2018). Phylogenetic analyses further suggest that persistence of environmental states (e.g. consistently short or long seasons in higher and lower latitudes, respectively) may result in the secondary loss of alternate states, rendering populations obligately solitary *or* eusocial, depending on their geographic location (West-Eberhard, 2003). Such plasticity-first perspectives on the evolution of insect sociality do not diminish the potential explanatory value of more traditional frameworks, but instead illustrate how *ecoevodevo* perspective are able to supplement additional perspectives potentially amenable to experimental assessment (see also Moczek et al., 2011).

Cross-species interactions

Even though sociality is classically used to describe cooperation among groups of conspecifics, there are also ample cases of beneficial *cross*-species interactions in the insect world. These situations may be mutualistic if both parties benefit, as is the case in the relationship between so-called "rancher ants" and aphids. Colonies of these ants tend herds of aphids, providing protection and hygiene to the aphids and in return receiving nutritious honeydew that the aphids secrete. Many facets of the physiology and coevolutionary trajectories of mutualistic species are altered by these interactions, including diet, morphology, and communication (Ivens and Kronauer, 2022).

Social living, however, also opens up avenues of exploitation by heterospecifics, as in the case of *social parasitism*. Social parasitism occurs when an individual incorporates itself into the social group of another species and exploits it for resources, to the benefit of the parasite and the detriment of the host group. Social parasitism is best studied, and perhaps most elaborate, within the ants. Prominent examples include diverse insects and non-insect arthropods who conceal themselves by mimicking ant chemical ecology and behavior, enabling them to utilize ant nests as a source of food and protection for some or all of their life cycle (Kronauer and Pierce, 2011). However, some of the most extreme forms of social parasitism are executed by ants *on other ants*. Forms of social parasitism by ants include xenobiosis (where a smaller colony of ants uses the nest and nutritional resources of a larger ant colony of a different species, but still cares for its own brood), temporary parasitism (where a foundress queen kills the queen of an existing colony of another species, forcing the host colony's workers to raise her first generation of young), dulosis (the capture of pupae from a heterospecific host colony to create a work force supporting the invading species), and inquilinism (where a single queen spends her entire life clinging to members of a still-queened, still-functional host colony, begging for food from the host-colony workers as she spends all of her time on reproduction, having secondarily lost all castes but the queen; Buschinger, 2009).

Social parasitism is predicted to create selective pressure on hosts to detect and evade parasites, and on parasites to overcome host evasion efforts, setting up an evolutionary arms race of sensory characteristics and defensive capabilities (Davies et al., 1989). Further, several hypotheses aim to explain under which conditions social parasitism may be especially likely to evolve. For example, Emery's rule states that social parasites should be the closest phylogenetic relatives of their host species as a consequence of sympatric speciation and/or because it may be easier for a parasite to evade detection when it is closely related to its host. Experimentally, however, Emery's rule has been found to be more prevalent for some forms of social parasitism than others (Huang and Dornhaus, 2008). More generally, while the potential fitness benefits of social life are without doubt, sociality also incurs risks and costs. As such, the social environment insects experience and create does not just affect their own ecology, evolution, development, and physiology, but frequently extends to diverse other insects engaged in mutualistic and parasitic interactions.

Endosymbiosis

The preceding section emphasized the roles played by social conditions generated in part by conspecifics (e.g. colony members) or symbiotic insects (e.g. farmed Hemiptera, social parasites) in shaping environmental conditions to which insects respond to both in development and evolution. These interactions are, however, not limited to those occurring between insect taxa, but can also occur in the context of insect-*microbe* interactions. The field of microbiome science - interested in the communities of microbial organisms which macroscopic host organisms interact with and the nature and consequences of these interactions - has undergone extraordinary growth in recent decades, with research focused on insects having played pivotal roles in many advances. As detailed below, modern molecular methods and manipulative experiments have uncovered intimate interactions between insects and their microbiomes, whereas phylogenetic reconstructions show that many of these interactions may have evolved over many millions of years of co-evolutionary history (Cornwallis et al., 2023). As we will also see, these interactions may occur over varied physical distances, on host exterior or interior epithelia, and even within host cells. We will begin with an overview of the most important facets of insect ecology shaped by the association with symbionts, then explore how some insects have evolved specific physiological, morphological, and behavioral phenotypes to ensure symbiont maintenance, and end by touching on recent work suggesting that symbionts may actively drive evolution, radiation, and speciation of their hosts.

The role of endosymbionts in host-environment interactions

Resource utilization

Insects have long been known for their diverse range of dietary specializations (e.g. nectar, blood, dung, carrion, wood, etc.), yet only recently has it become clear exactly how much of this ability is made possible through the association with beneficial microbial symbionts. For example, many insects consume diets rich in hard to break down complex polysaccharides such as plant matter. Plant cell walls are particularly difficult for animals to digest as they are composed of crystalline arrays of cellulose interwoven with various hemicelluloses. Herbivorous insects are therefore often reliant on microbial enzymes (cellulases) to break down plant matter into simpler sugars which they may then be able to metabolize using enzymes encoded within their own genomes (Martin, 1983). Termites and cockroaches, for instance, are known for their ability to feed entirely on wood fiber yet only achieve this feat because of a diverse community of symbionts in their hindguts able to break down cellulose (Slaytor, 1992). Similarly, leaf cutter ants (*Atta, Acromyrmex*) meticulously collect leaves and grasses not to consume directly but to feed fungal cultivars growing throughout the colony, which in turn serve as the ant's primary diet (Chapela et al., 1994).

Other common insect diets, such as nectar and phloem sap, are rich in easily digested sugars yet are often deficient in other nutrients such as essential amino acids (Lee et al., 2015; Douglas, 2006; Parish et al., 2022). Insects may be able to subsist on such deficient diets by synthesizing all missing components on their own. Yet genomic analysis and phylogenetic reconstruction (Payne and Loomis, 2006) suggest that arthropods have lost as many as 10 of the pathways needed to synthesize essential amino acids alone. Again, it is through association with microbial symbionts that insects overcome these challenges. Hemiptera, many of which are sap feeders, are an especially illustrative example. For instance, the pea aphid, *Acyrthosiphon pisum*, evolved a symbiotic relationship with *Buchnera* bacteria between 160 and 280 million years ago, and now stores *Buchnera* within specialized host cells called bacteriocytes located adjacent to the ovarioles within the aphid body cavity (Braendle et al., 2003). Pea aphids benefit from this association because the *Buchnera* genome encodes the enzymatic machinery needed to synthesize all the essential amino acids the aphids are either unable to synthesize on their own or which are not provided by the aphid's diet (Shigenobu and Wilson, 2011).

While many insects use breakdown and synthesis of resources as direct ways to utilize their microbes to access resources, some insects utilize microbial dietary mediation much more indirectly. For example, burying beetles (*Nicrophorus*), which rely on nutrient rich carrion as a diet and reproductive resource, must compete with putrefying microbes (Shukla et al., 2018). The time limit on carrion viability, based on the gradual proliferating microbial competitors, loss of nutrient content, and accumulation of toxic metabolites, would normally quickly limit larval ability to consume carrion throughout their development. However, research has shown that parental beetles inoculate carrion with a community of microbes which lower the concentrations of putrescine and cadaverine, polyamines which are toxic and can reveal carrion location to competitors and predators, in the carrion (Shukla et al., 2018), as well as decrease the prevalence of pathogenic bacteria in both carrion and offspring (Wang and Rozen, 2017). These and many other examples illustrate how insects have gained or improved their access to otherwise challenging and recalcitrant food resources through their association and interactions with beneficial symbionts.

Defense

Symbiotic microbes also play pivotal roles in how insects interact with potential pathogens in their environments. Many insects maintain microbial communities that limit the ability of pathogens to colonize host tissues, while others have tailored microbiome-mediated defenses to select taxa to confront niche-specific challenges. Lagriinae beetles, for example, harbor communities of *Burkholderia.* If removed from the surface of host eggs, these become significantly more susceptible to fungal infection (Flórez et al., 2018). The European beewolf, *Philanthus triangulum*, provides another example of symbiont-associated defensive benefits. Beewolves spread *Streptomyces* bacteria from a specialized gland in their antenna onto the brood cell, which contains an offspring along with food provisions. The *Streptomyces* is then taken up by the larvae and woven into the walls of the cocoon prior to pupation. Research suggests that *Streptomyces* increases the survival of offspring by decreasing the prevalence of fungal infestation via the production of antibiotics (Kaltenpoth et al., 2005).

Symbionts may also provide defensive services by boosting host immunity. For example, *Wolbachia* is a bacteria found in 40%–60% of all insect species, and of growing interest to human health because of its *pathogen blocking* effects in insect vectors. Work in *Aedes aegypti* demonstrates that certain strains of *Wolbachia* are capable of inhibiting viral replication thus decreasing vectoral potential of populations of mosquitoes (Lindsey et al., 2018). Similarly, aphids in parasitoid-rich environments often associate with a bacteria, *Hamiltonella defensa*, which confers resistance to parasitoid infections (Oliver et al., 2005; Cayetano and Vorburger, 2014). This example is particularly unique as *H. defensa* confers a cost on host fitness, thus individuals infected with *H. defensa* will be rare if parasitoids are uncommon, but prevalence quickly increases as parasitoids become more abundant (Oliver et al., 2005). More generally, microbe-mediated defenses thus provide a critical, spreadable, and extraordinarily varied interface between insects and their selective environment.

Development

A growing body of literature shows that in at least some instances symbionts can evolve to manipulate host gene expression and development. Similarly, hosts may lose ancestral metabolic pathways thus evolving reliance on symbionts for the synthesis of compounds essential to development, a phenomenon referred to as *evolutionary addiction* (see Box 1). For instance, insect molting is a deeply ancestral aspect of insect growth and metamorphosis, the control of which has been lost in certain taxa which instead now require microbial interactions toward its initiation. For example, molting in the mosquito *Aedes aegypti* is induced by an axenic gut environment, which occurs when microbial growth in the gut reaches a threshold, depletes gut oxygen levels in the process, which in turn activates hypoxia-induced transcription factors which then initiate molting (Coon et al., 2017; Valzania et al., 2018a,b). In the absence of the proper gut microbiome this cascade fails to be initiated. Similar constraints have evolved in a stingless bee, *Scaptotrigona depilis*, which must feed on a cultivar of *Zygosaccharomyces* to acquire ecdysteroids, a class of hormones critical for the initiation of the molting cycle (Menezes et al., 2015; Paludo et al., 2018).

As hosts evolved dependencies on symbionts to complete their own development, symbionts also acquired increased ability to control host development. This is perhaps best observed in *Wolbachia*. To understand the specific manipulations carried out by *Wolbachia*, it is important to note that male hosts are often evolutionary dead ends for symbionts as they rarely pass their symbionts on to their offspring. Thus, *Wolbachia* improves its own fitness by manipulating the sex of its host, changing populations to predominantly, or entirely, female via a suit of mechanisms including parthenogenesis induction in arrhenotokous taxa such as *Trichogramma* and *Franklinothrips* (Stouthamer et al., 1990; Arakaki et al., 2001), feminization in *Eurema* and *Zyginidia pullulan* (Hiroki et al., 2002; Negri et al., 2006), and male killing in *Tribolium*, *Drosophila*, and *Acraea* (Fialho and Stevens, 2000; Dyer and Jaenike, 2004; Jiggins et al., 2001).

Mechanisms underlying microbiome maintenance

When symbionts evolve to become important for normative niche function of their hosts, the mechanisms that ensure the reliable association between hosts and microbial partners have the potential to become major drivers of host ecology and evolution. Here, the mode of symbiont acquisition plays a critical role in shaping the fidelity and heritability of insect microbe associations, as discussed next.

Mode of acquisition

Symbionts can be passed on vertically from one generation to the next, thereby contributing to extra-genetic inheritance. This vertical transmission may be enabled by packaging of symbionts inside gametes, combining them into food provisions, or adding them to other components of the offspring's developmental environment. This strategy can be advantageous to the insect host as it can ensure the reliable maintenance of a specific community of beneficial symbionts (Hammer and Moran, 2019). To that end, insects have evolved diverse behavioral, morphological, and physiological mechanisms to ensure the faithful passage of select symbionts across generations.

For example, adult burying beetles inoculate their carrion diet with a community of symbionts. By feeding this microbially inoculated carrion alongside additional microbe-rich oral secretions to their offspring, parents ensure the inheritance of their particular community of beneficial microbes (Shukla et al., 2017). Adult dung beetle mothers, conversely, oviposit eggs inside subterranean brood balls but in most taxa do not provide further care and do not interact with their larval offspring. In these cases, vertical transmission of microbiota is instead accomplished indirectly via the *pedestal*, a fecal pellet left under the egg which larvae will eat immediately upon hatching, thereby inoculating their own gut with maternally derived symbionts (Estes et al., 2013; Schwab et al., 2016). Alternatively, or in addition, hosts may use diverse means of *internal* symbiont transmission: weevils store symbionts within their ovarioles and transmit them directly into or onto developing eggs (Vigneron et al., 2014), and pea aphids are born with symbiotic *Buchnera* in their bacteriocytes (Braendle et al., 2003). Likewise, at least some symbionts have themselves evolved intriguing means to ensure their own passage from one host generation to the next, as perhaps best understood in *Wolbachia*, which is capable of coopting host cellular machinery to facilitate its own transmission into developing host eggs (Herren et al., 2013; Newton et al., 2015, see also Rafiqi et al., 2020).

Diverse insects also rely on symbionts yet do not acquire them directly or indirectly from parents. In many of these cases, host-symbiont associations are made possible through specific mechanisms that allow hosts to filter through the diversity of microbes available in the external environment to establish an endosymbiotic population of select microbes anew each host generation and possibly life stage. Such horizontal acquisition may be favored over vertical acquisition when symbionts are needed during only a subset of host life stages or when maintaining symbionts across life stages is simply difficult. Coconut rhinoceros beetles (*Oryctes rhinoceros*) and squash bugs (*Anasa tristis*) both obtain essential symbionts from their environments. The beetles acquire them from their the plants they consume as adults (Han et al., 2024) while the squash bugs acquire them from their plant or soil environment after their first molt (Acevedo et al., 2021).

Lastly, many insects implement a mixed-mode transmission strategy to assemble their microbiome, relying on vertical transmission for one portion and horizontal transmission for the other (Ebert, 2013). This can be observed in dung beetles which have larval stages whose microbial community is sculpted by both inherited maternal microbes and horizontally acquired environmental microbes (Suárez-Moo et al., 2020; Jones et al., 2025).

Symbiont maintenance across complex life cycles

Holometabolous insects in particular display major shifts in morphology, physiology, experienced environments, and behavioral interactions across their life cycle, which in turn may bring about corresponding changes in their microbiota (Hammer and Moran, 2019; Manthey et al., 2023). If so, this poses two major questions: how might insects maintain associations with their beneficial symbionts in the face of major life stage transitions? And conversely: do holometabolous insects possibly modulate their microbial communities to suit life stage-specific needs, and if so by what means?

To address the first question, recent work has examined the significance of the pupal stage, a developmental stage that undergoes dramatic organ system metamorphosis and generally does not feed. Yet despite these apparent constraints, the pupal stages of some Lepidoptera, Hymenoptera, and Coleoptera have all been found to retain microbial communities within (Johnston and Rolff, 2015; Jones et al., 2025; Suárez-Moo et al., 2020; Wang and Rozen, 2017; Zhukova et al., 2017; see also Fig. 1 for an example on dung beetles). Others, such as burying beetles do not retain symbionts internally, but instead evolved mechanisms to pass their

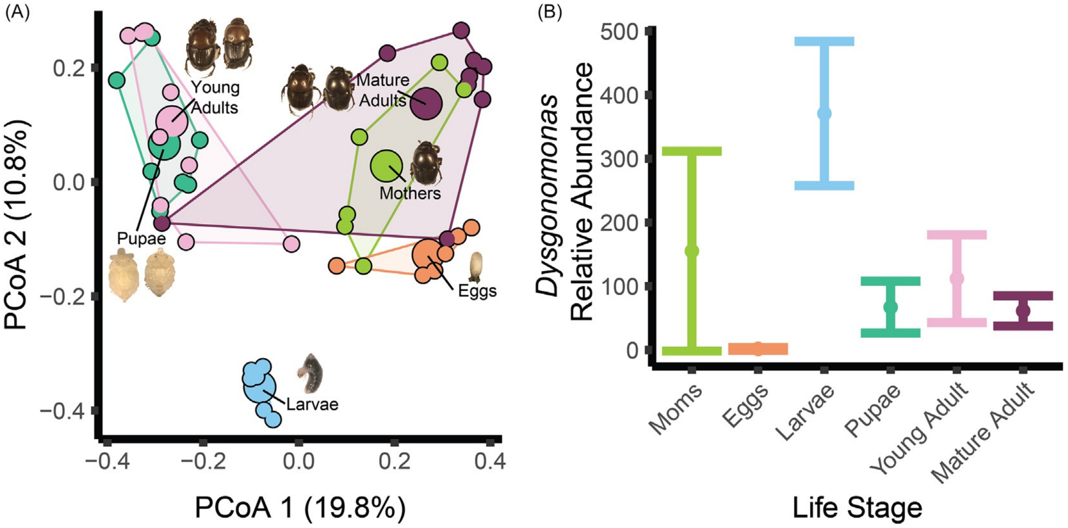

Fig. 1 Composition and turnover of insect microbiota. (A) The composition of the microbiome associated with the bull-headed dung beetle *Onthophagus taurus* diverges as a function of host life stage. Shown are Bray-Curtis dissimilarities based on the bacterial abundances of the beetle microbiome. Host life stages are differentiated by colors, large circles represent the average microbiome composition within a given life stage, whereas small circles represent the microbiomes of individual samples. Results suggest that microbiome composition changes in a cyclical manner, from adults mothers to those of the eggs produced by them, followed by the very distinct microbiome of larvae and then pupae, followed further by young adults who have yet to eclose from their natal brood ball. The microbiome of mature adults then returns in overall composition to that of adult mothers. (B) Example of microbiota whose abundance change dynamically as a function of host life stage. *Dysgonomonas* has been shown to play critical roles in the digestion of complex carbohydrates in diverse insects. In *O. taurus*, *Dysgonomonas* is among the most abundant bacteria, reaching its by far highest relative abundance during larval development when hosts consume cellulose-rich dung in support of rapid larval mass gain. Points represent the mean relative within each life stage and error bars represent a 95% confidence interval. Figures modified after *Jones J, Newton IG, and Moczek M (2025) Microbiome composition and turnover in the face of complex lifecycles and bottlenecks: Insights through the study of dung beetles. Applied and Environmental Microbiology 91 (1): e01278-24*.

symbionts “around” pupation. During pupation, burying beetles surround themselves with pupal chambers which contain the same microbial taxa found later in emerging adults (Wang and Rozen, 2017). This suggests that when late larvae purge their gut in anticipation of pupation, microbes contained within are retained in the immediate, surrounding environment for later reacquisition.

Life stage transitions, such as between larva and adult via the pupal stage, may not just reflect a constraint on microbiome maintenance, but also an opportunity to adjust symbiont composition to meet life stage specific needs (Hammer and Moran, 2019). In the bull-headed dung beetle (*Onthophagus taurus*) for instance, larvae consume the fibrous dung rich in cellulose provisioned by its adult mother, while the corresponding adults filter feed on the liquid portions of above-ground dung produced directly by cattle. As a consequence, whereas the larval microbiome is dominated by taxa presumed to assist it with cellulose digestion, such as *Dysgonomonas*, those same taxa are comparatively much less abundant in the filter-feeding adult stage (Jones et al., 2025; Fig. 1).

Microbial contributions to insect evolution, diversification and speciation

Given the key roles played by symbiotic microbes in both insect development and ecology it may not be surprising that insect-microbe symbioses may also shape insect evolution. For example, phylogenetic analyses reveal that dietary specializations (xylem, phloem, blood, and wood) have relatively few and deep evolutionary origins, and those cases that do exist are either commonly (wood) or always (xylem, phloem, and blood) associated with obligate symbionts, compared to other sources such as omnivory, herbivory, or predation (Cornwallis et al., 2023). The same work documents that such obligate insect symbiont relationships - once formed - may drastically affect diversification rates: herbivorous insect families with obligate symbionts contain 12 times as many species as insect families on average, and 15 times as many species as herbivorous insect families without obligate symbionts.

Yet symbionts may not just help enhance ecological opportunities for insect specialization and diversification, but may also directly contribute to the evolution of reproductive isolation, and thus species formation. For example, reproductive isolation may affect mate selection as a result of microbial community differences, and may appear surprisingly quickly with lasting effects. This was demonstrated in *D. melanogaster*, where rearing flies on one of two diet types caused flies to prefer to mate with individuals reared on the same diet for at least 37 generations (Sharon et al., 2010). This preference, the result of microbially influenced cuticular hydrocarbons, could be eliminated with an antibiotic treatment or induced by transferring microbes across individuals reared under different treatment conditions. Even more extreme impacts on reproductive isolation may be observed with intracellular symbionts such as *Wolbachia* (also *Rickettsia* and *Cardinium*), via their ability to induce parthenogenesis in insects with haplodiploid sex-determination to maximize their own transmission via the female germline (Adachi-Hagimori et al., 2008; Zchori-Fein et al., 2004). If occurring over many generations, this may result in the accumulation of mutations in traits involved in sexual reproduction, creating reproductive barriers between asexual and sexual populations (Gottlieb and Zchori-Fein, 2001; Brucker and Bordenstein, 2012). Likewise, *Wolbachia* and *Cardinium* are also capable of inducing *cytoplasmic incompatibility* in host populations i.e. the inability of infected males to mate with uninfected females or females infected with a different strain (Perlman et al., 2008), causing differentially infected populations to become bidirectionally incompatible (Bourtzis and Miller, 2003; Bordenstein and Werren, 2007; Werren et al., 2008).

Lastly, insect symbionts may also affect the evolution of their hosts simply by shaping nature and amount of heritable variation in host traits available for selection to act upon. For example, recent work in the gazelle dung beetle *Digitonthophagus gazella* revealed that disrupting microbiome inheritance increases additive genetic variation, heritability, and evolvability for development time (Rohner et al., 2024; Rohner and Moczek, 2024). This raises the possibility that natural (e.g. during range expansion) or artificial (e.g. via the use of antibiotics in agriculture) disruptions of dung beetle microbiome associations may influence host populations' responses to their selective environment.

Conclusions

As shown above, the symbiotic environments of insects play critical roles in insects' ability to utilize recalcitrant diets, instruct their own development, confront immune challenges, select mates, among others. As such, insect-microbe interactions emerge as major drivers of insect evolution and diversification. Moreover, in many insects microbial symbionts are passed on to the next generation alongside parents' genes, thereby contributing to extra-genetic inheritance, heritable variation, and thus the ability to respond to selection (Rohner and Moczek, 2024). In such cases, natural selection may act on the combined phenotypes and underlying genomes of both host insects and microbial symbionts, a notion at the heart of the *holobiont* (or *hologenome*) *theory of evolution* (see Box 1). While the merits of this concept remain to be fully assessed, it is without doubt that the symbiotic environment of insects plays a formidable role in insect *ecoevodevo*.

Niche construction

The term niche construction can be applied to all cases in which an organism modifies environmental conditions in ways that alter selection pressures on a recipient organism, be that the niche constructor itself, its offspring, or members of the same or other species (Matthews et al., 2014, Box 1). The construction of nests and cocoons and the induction of galls are all prominent examples of niche construction in insects. Niche construction thus emphasizes organisms' capacity to alter environmental conditions in ecologically, developmentally, and evolutionarily impactful ways, yet it is neither the first nor only conceptual framework to do so (see Box 2). For example, alteration of selective conditions due to the activities of organisms is central to theories of density-dependent selection, sexual selection, and social and co-evolutionary theory, all of which seek to understand of how interactions between individuals, mates, groups, or species influence the outcomes of selection (Scott-Phillips et al., 2014; Schwab et al., 2017). Likewise, eco-evolutionary feedback theory explores how organismal (e.g. predator–prey) interactions produce feedback loops between

Box 2 Niche construction theory and allied conceptual frameworks.

Niche construction theory is one of multiple conceptual frameworks that emphasizes the capacity of organisms to alter their environmental conditions in ecologically, developmentally, and evolutionarily important ways, and has been advanced mainly by evolutionary biologists in the last 30 years. Additional evolutionary frameworks have highlighted dynamics of organismal activity that create or modify selection pressures within populations. Sexual selection, first introduced by Darwin, explains how dynamic processed occurring within populations such as female mate choice and male-male competition over mating opportunities can impose selection pressures, the outcomes of which can rival natural selection in their propensity to generate evolutionary change (Lyon and Montgomerie, 2012). Density-dependent selection can also dramatically alter phenotypic patterns within a population as it promotes different trait optima at different population densities, selecting for phenotypes that counter the effect of whatever environmental condition or ecological agent is limiting population growth (Clarke, 1972; Travis et al., 2023).

A related framework that has stemmed from ecological research and thinking is the concept of ecosystem engineering, when the activity of one species creates, alters, or destroys habitats that modulate the availability of resources for other species (Jones et al., 1994; Erwin, 2008). In partial contrast, descriptions of niche construction focus on interactions between a species and its environment that modify the species' own niche, resulting in altered selective pressures on the species itself (Odling-Smee et al., 1996). In the simplest case, niche construction can involve moving to a more appropriate environment, but the most interesting cases tend to involve the physical modification of specific environmental conditions, which may then persist during future generations and constitute an ecological inheritance. As such, ecosystem engineering is a natural consequence of niche construction, although in specific cases it may not be clear if the engineering activities of organisms have a selective impact on the species that induce them (Erwin, 2008).

Thus, a key component that differentiates a niche construction framework from other frameworks is that in niche construction theory, organism mediated activity is understood as a source of localized, individual (self)-level phenotypic variation *within* populations, with the added potential to mediate in population-level shifts in ecological parameters. Furthermore, niche construction theory emphasizes the importance that non-genetic inheritance can have on micro-evolutionary processes when genotypes are inherited alongside environments pre-modified by and for related individuals.

ecological and evolutionary dynamics, generating a conceptual framework that is independent of, though broadly overlapping with, niche construction theory (Kylafis and Loreau, 2008; Post and Palkovacs, 2009; Odling-Smee et al., 2013; Matthews et al., 2014). Where the conceptual framework of niche construction diverges from others, however, is in its explicit emphasis on environment-modifying abilities as sources of *individual* phenotypic variation, and as an avenue for non-genetic inheritance in those cases in which environments are passed on to offspring. Furthermore, the concept of niche construction makes room for viewing the process of adaptation from a new perspective, whereby the fit between organism and environment is enhanced not only via organisms evolving to suit environmental circumstances, but also via organisms evolving ways of actively changing environments in a manner that suits their needs and objectives.

Insect biology abounds with extraordinary examples of niche construction. From the complex nests built by social insects to the parental care behaviors of burying and dung beetles, insects generate and modify their physical and social environments in ways that are strongly suggestive of the adaptive value of environment-modifying behaviors. Yet experimental assessments of the mechanisms and consequences of niche construction are challenging, in part because of a relative paucity of model organisms in which phylogenetic assessments and field studies can be complemented by controlled manipulations in laboratory conditions. Using taxa where some or all of these aspects align, the field is beginning to expand our understanding of the broader patterns of mechanisms and consequences of niche construction in insects. Below, we will survey larval and parental niche construction in necrophagous *Nicrophorus* beetles and coprophagous beetles in the subfamily *Scarabaeinae*, and a diversity of niche construction activities across eusocial Hymenoptera and Blattodea (Isoptera).

Evolution of and through niche construction: Burying beetles

Burying beetles, *Nicrophorus* species, compete as adults for access to ephemeral carrion which they bury and craft into a nursery and food source for their young. Working alone or as a breeding pair, adults will strip the carrion of fur, cover the animal in antibacterial secretions, manipulate it into a ball, and bury it. The mother will lay her eggs nearby in the soil; as the larvae hatch, the mother and her mate, if present, will then feed their offspring pre-digested carrion material (Fig. 2, left). Larvae of *Nicrophorus* species vary from facultatively to obligately dependent on maintenance of parental food provisioning throughout juvenile development (Smiseth and Moore, 2004; Capodeanu-Nägler et al., 2016). Together, parents thus construct and then maintain a physical and nutritional niche for their offspring. In studies that have assessed the consequences of parental care on larvae, it has been shown that larval survival and mass increased significantly in the presence of active bi-parental care, and the size of this effect increased with the duration of care, indicating that this nutritional niche constructed by attentive parents affects fitness-relevant traits in offspring. (Eggert et al., 1998). Quantitative genetic studies of the larval responses to facultative maternal care have been performed utilizing a half-sib split-family breeding experiment – raising half of a brood in the presence of their mother and raising the other half in the presence of

Fig. 2 Examples of niche construction activities in insects. *Left*: Parents of *Nicrophorus* burying beetles construct and maintain nurseries made of carrion for their larval offspring, and in some cases provide pre-digested food for the larvae throughout their development. Photo courtesy of Allen J. Moore. *Right*: Larvae of *Onthophagus* dung beetles spend their entire juvenile development alone inside their natal brood ball. Adult mothers provision these brood balls with carefully selected dung and a fecal pellet which will serve as a microbial inoculate for each offspring, who upon hatching further manipulate the brood ball environment through rounds of dung digestion and excretion, effectively creating an ‘external rumen.’ Parental care and environment-modifying behaviors such as these exemplify how organismal activities can impact the selective environment experienced by individuals and their offspring.

prepared carrion alone (Rauter and Moore, 2002). Resulting estimates revealed substantial additive genetic effects for development time but minimal effects for body mass, and characterizations of genotype-by-environment interactions indicated substantial variation among maternal families in response to active maternal care. These results indicate that parental care in this group can conceal heritable variation, highlighting one mechanism by which niche-constructing activities can affect responses to selection by buffering the extent to which standing genetic variation gets revealed to selective processes. Furthermore, this evidence for *G x E* interactions affecting life-history traits in the presence or absence of parental care may additionally help account for the maintenance of additive genetic variation even under strong selection on body size and development time (Rauter and Moore, 2002), a phenomenon difficult to explain under more traditional models of population responses to environmental selection pressures. The variation in larval response to lack of parental care may help to explain why variation in parental care strategies is maintained in facultatively-caring species and indicates a potential avenue by which maternal effects may evolve, hinting at potential for such niche-constructing activities to feed back on evolutionary trajectories. Other work has shown how parental care buffers against inbreeding depression by counteracting its attenuating effects on fitness related traits, in species with both facultative and obligate parental care (Pilakouta et al., 2015; Hughes et al., 2023). Together, this body of work indicates that niche construction in the form of parental care can shield genetic variation from selection in multiple potentially interacting ways and highlights one mechanism by which niche constructing behaviors have the potential to influence both individual fitness and population-level evolutionary outcomes. Recent work is beginning to characterize an additional component of parental effects on larval ecology in burying beetles: vertical transmission of gut microbes from parents to offspring during feeding (Wang and Rozen, 2018; Shukla et al., 2018, Miller et al., 2021). This emerging field is a theme we will return to in the following section.

Studies of niche construction in insects have also begun to probe how these dynamics originate in a lineage. Recent studies have suggested that simple environment modifying behaviors may also facilitate the evolution of more sophisticated means of niche construction. For instance, recent work assessed the ability of three *Nicrophorus* species to conceal carrion odors to prevent resource discovery and poaching of a buried nursery in comparison to two other necrophagous silphid beetle relatives. The three *Nicrophorus* species - all of which also exhibit extended parental care - were able to successfully conceal carcass odors and avoid competitor interaction three times as often as the two more distantly related species (Trumbo and Sikes, 2021). These findings support the notion that the evolution of carcass burying and modification behaviors was a key early step in the evolution of the more complex nesting and parental care niche construction behaviors in *Nicrophorus* burying beetles. These findings highlight that even more simplistic environment-modifying behaviors may impact the selection dynamics acting on subsequent insect-environment interactions.

When the constructed environment contains genes: Dung feeding scarab beetles

Mothers from dung-feeding beetle species like those in the genus *Onthophagus* also provision each of their eggs with a nursery, termed a brood ball, which in this case is constructed entirely from dung. Further, mothers provide their offspring with a fecal pellet of their own excrement, termed the pedestal, which serves as her offspring's first food source and a means of inoculation with their mother's microbiome. In the case of *Onthophagus* and other coprophagous beetles, vertical transmission of a maternally acquired microbiome emerges as an integral component of maternal niche construction. Larvae grow to larger adult sizes over shorter timescales when provisioned with pedestal microbiota and are able to offset negative effects of temperature and desiccation stressors compared to siblings deprived of their pedestal (Schwab et al., 2016), thus shaping important fitness components in these animals. Furthermore, the adaptive benefit of maternal microbiome transfer exhibits a certain degree of species-specificity. Larvae reared with a pedestal excreted by an ecologically similar but distantly related *Onthophagus* species suffered significant growth and fitness consequences (Parker et al., 2019), yet cross-fostering of larvae on pedestals derived from a sister species attenuated the severity of these negative effects (Parker and Moczek, 2020). These findings are also consistent with a signal of phylosymbiosis across the clade, i.e. the co-evolution and co-divergence of *Onthophagus* hosts with their host associated microbiota. Intriguingly, a corresponding signal also appears detectable on the level of populations. For example, the microbial community compositions associated with individuals of the bull-headed dung beetle *O. taurus* belonging to populations introduced to Eastern Australia and the Eastern United States were found to be more similar to those of native Mediterranean *O. taurus* than to those of other dung beetle species now sympatric and syntopic in both exotic ranges (Parker et al., 2020). Taken together, these results indicate that mechanisms of microbial inheritance across generations can be important contributors to both fitness and evolutionary diversification in taxa that have evolved complex niche construction behaviors.

Aside from microbial transfer, dung beetle mothers also exhibit adaptive plasticity in niche-constructing behaviors. For example, mothers adjust brood ball size in response to changes in dung quality and construct larger brood balls out of lower quality dung, thereby compensating for reduced nutrient quality with increased quantity (Moczek, 1998). Further, mothers adjust brood ball burying depth to shield offspring from hotter ground surface temperatures (Macagno et al., 2018), an aspect of niche construction found to yield critical transgenerational effects. Offspring reared under hotter surface temperature conditions and thus buried more deeply by their mothers developed faster and to a smaller adult size. When this offspring generation was then raised to reproductive age the size of these second-generation mothers was found to be significantly positively correlated with two major components of maternal niche construction - brood ball mass and burial depth (Macagno et al., 2018). Together, these findings suggest that the size of a mother, affected by her own early life experiences, shapes her own maternal niche construction behaviors, which in turn affect fitness-relevant traits among her offspring including their own body size. Indeed, even when second-generation broods experienced favorable developmental environments, offspring of smaller mothers still grew to smaller adult sizes, indicating that the negative effects of stressful temperatures on body size can persist trans-generationally (Macagno et al., 2018).

Niche construction in this genus does not end with plasticity in maternal care behaviors during brood laying; Onthophagine larvae complete their entire juvenile development inside the brood ball, consuming, excreting, and re-consuming the inner layer of dung surrounding them, thereby constructing and re-constructing their physical niche as they develop (Fig. 2, right). Experimental manipulations that prevented larvae from accruing the benefits of modifying their natal brood ball resulted in lower survival to adulthood, longer development time, and emergence to smaller adult sizes (Rohner and Moczek, 2024). Furthermore, these manipulations significantly increased additive genetic variance and residual variance in development time, resulting in an increase in narrow-sense heritability and evolvability. These effects were mirrored and compounded in treatments where larvae were prevented from both modifying their brood balls and/or from receiving their maternal microbial pedestal (Rohner and Moczek, 2024). These data suggest that the range of niche constructing activities in these animals, encompassing both maternal provisioning with microbiota and the accumulation of larval modifications to the brood ball, all possess the potential to modify heritable variation, and thus shape responses to selection in natural populations. More generally, these results show that niche construction behaviors may buffer genetic variation from becoming expressed phenotypically, thus contributing to the accumulation of cryptic genetic variation. This in turn may have important implications for the evolutionary process, for example when a lineage encounters environmental conditions recalcitrant to modifications, thereby making previously cryptic variation phenotypically visible and thus available to selection, generating opportunities for niche construction to feed back onto organisms' ecology and evolution.

Niche construction in eusocial taxa

Eusocial taxa in the orders Hymenoptera and Blattodea (Isoptera) may offer some of the most profound examples of all insects of niche constructors. Through the combined efforts of dozens of individuals (e.g. in paper wasps, Ishikawa et al., 2010) to several hundreds of thousands (e.g. in army ants, Chandra et al., 2021) both mechanisms and consequences of niche construction activities can scale up in magnitude far past those observed in dung or burying beetles. For example, European honeybees *(Apis mellifera)* construct honeycomb-walled hives inside of which they coordinate the egg-laying of a fecund queen with the activities of foragers gathering pollen and nectar stores to feed the colony and brood-care nurses rearing thousands of offspring at once (Schmickl and Crailsheim, 2004). Leafcutter ants in the genera *Acromyrmex* and *Atta* and mound-building termites in the family *Termitidae* have independently evolved the capacity to collect and farm fungus inside their subterranean nests as a constant food source for workers and larvae (Quinlan and Cherrett, 1979; Mueller et al., 2018). Wood-feeding termites exhibit large-scale foraging networks, raising and protecting their brood either inside the same wood habitat chosen as their food source or harvesting material and returning to a separate nest location (Traniello and Leuthold, 2000). Beyond the construction of physical environments for shelter and food storage or cultivation, army ant colonies in the genus *Eciton* are nomadic, affording colony protection by the nightly formation of self-assembled temporary nests, clustering worker bodies together and carrying their brood (Baudier et al., 2019).

Despite the large-scale complexity of these colony-constructed environments, colonies maintain and regulate many internal environmental conditions to a striking degree. In honeybees, hive internal temperature is actively maintained to a range between 32-36C by worker migration within the hive and heat production by worker wing muscle exertion (Simpson, 1961; Stabentheiner et al., 2010). This tight thermoregulation is necessary for proper brood development, as temperatures ranging outside the optimum result in morphological and behavioral defects in developing broods (Tautz et al., 2003). Furthermore, in eusocial groups, tasks are performed by individual workers, yet selection for worker task phenotypes occurs in the aggregate at the colony level, potentially de-constraining the expression of phenotypic variation of individuals in colonies. However, when pushed to stressful extremes, some of this variation in individual-level behavioral phenotypes may have functional consequences for the colony, generating a major potential feedback loop between niche constructing tasks and evolution in these taxa (Jandt and Gordon, 2016).

The ecological reach of niche construction

The above discussion demonstrates that insects' niche construction activities possess strong potential to modify the selective regimes experienced by individuals, families, colonies, and even populations. However, in many instances, effects may range even further, allowing niche construction to blend into ecosystem engineering. For example, dung beetle manipulation of feces during the feeding and breeding process promotes a range of ecosystem functions, from carbon cycling and parasite suppression to seed dispersal (Nichols et al., 2008; Menéndez et al., 2016; Evans et al., 2019). In tropical savanna ecosystems, termites reach biomass densities comparable to those of large ungulates, and consequently have the potential to generate major ecosystem-wide effects as a result of their niche construction behaviors. For example, the density of termite mounds of *Macrotermes herus* explained the vast majority (89%) of variation in plant species composition and density (Moe et al., 2009). Similarly, the distribution of *Atta cephalotes* leaf-cutter ant colonies has been shown to significantly impact understory vegetation and canopy openness, as well as attenuating maximum soil temperatures in their tropical rainforest habitats, which in turn impact seed germination, plant growth, and plant survival across plant taxa (Meyer et al., 2011).

Collectively, investigations of the mechanisms, causes, and consequences of niche construction activities across taxa thus highlight the diverse ways in which the capacity of organisms to alter local environmental conditions impacts ecology, development, and evolution within and across generations and taxa. From self-imposed selection pressures to ecosystem-wide effects, the consequences of niche constructing activities of insects are therefore major determinants of the dynamics of insect-environment interactions.

Environment-by-environment interactions

Previous sections have illustrated that environmental conditions can have profound effects on development and resulting phenotype expression, and hence the phenotypic variation visible to selection. Further, we showed that the types of environmental changes that can exert such effects are themselves rather diverse, ranging from photoperiod and temperature to nutrition, social conditions, and symbionts, among many others. Consequently, over several decades research has focused on systematically assessing the significance of single environmental factors on organismal development, as well as on modelling how response to singular environmental variables may vary across genetic backgrounds (*G x E*: genotype-environment interactions, see also Box 1) (Moffitt et al., 2005). What was largely overlooked in this context was the notion that developmental or physiological responses to a given environmental variable may themselves be influenced by yet *other* environmental conditions, thereby resulting in *environment-by-environment* interactions (*E x E*) or multidimensional phenotypic plasticity (MDPP; Westneat et al., 2019). Put another way, magnitude and form of plasticity *may themselves be plastic.*

Background

There are theoretical reasons to expect *E x E* interactions to be a ubiquitous property of insect populations, yet experimental investigation of its impact on development, phenotypic variation, and evolution is challenging, especially in natural populations. As a result, the significance of *E x E* interactions remains poorly understood. Yet, understanding how insect populations respond to multi-dimensional ecological circumstances is likely essential to develop a more complete characterization of species' ability to respond to changes in their complex natural environments, including those occurring during global climate change, and to devise meaningful conservation measures (Rodrigues and Beldade, 2020). In this section, we briefly explain analytical principles of *E x E* interaction and why their application to insect populations is especially pertinent. We then highlight examples of published work assessing the impact of *E x E* interactions on insect biology, with an emphasis on insect development and evolution.

Significance of E x E for insects

Environment-by-environment interactions describe an organismal response to multiple environmental factors, a ubiquitous feature of single- and multicellular life (Westneat et al., 2019). *E x E* interactions can be broadly categorized as *additive*, where two or more environmental factors induce a linear phenotypic response, or *non-additive*, wherein multiple environmental factors generate more complex, interactive effects, including across biological levels of organization, yielding reinforcing, inhibitory, or even novel phenotypic responses in the process (Westneat et al., 2019). While additive relationships among environmental factors have been documented in natural populations, non-additive effects more commonly (and typically more accurately) model phenotypic responses to multiple environmental stressors due to the complex nature of organismal integration of environmental cues (Westneat et al., 2019).

Considering their extraordinary diversity, typically ectothermic nature, and small body sizes, insects represent especially powerful models for examining the evolutionary implications of *E x E* interactions. Two dimensions of *E x E* interactions are of particular relevance to insect evo devo, the first of which concerns the general, and increasingly broadly accepted role of plasticity in diversification. For example, plasticity may promote diversification by enabling populations to diverge in their location-specific optimal responses to environmental challenges, by providing new targets on which selection can act, and by generating novel trade-offs during trait development (Moczek et al., 2011). Further, over generations, plastic trait expression may become ameliorated in populations via genetic accommodation and assimilation (see Box 1, see also West-Eberhard, 2003, 2005; Waddington, 1942, 1959; Baldwin, 1896; Nijhout et al., 2021). In all of these contexts, considering *E x E* interactions rather than the effects of singular environmental variable affords a more comprehensive and nuanced appreciation of the role of plasticity in evolution, including that of insects.

Secondly, predicting the nature and consequences of insects' responses to global climate change likewise benefits from explicit incorporation of *E x E* interactions. Global climate change is by definition a multidimensional phenomenon, including range expansions, the introduction of alien species, changes in species synchrony, and simultaneous alterations of multiple and possibly interacting abiotic factors (e.g. temperature and humidity: Colinet et al., 2015; Rodrigues and Beldade, 2020). Thus, measuring how *one* environmental factor may impact insect fitness may fail to accurately capture the extent to which populations will or will not respond to real world changes. As a result, characterizing the interaction of multiple environmental factors on insect development is critical to predicting population responses and devise meaningful conservation measures. However, formal analyses of how multiple environmental cues are integrated during insect development are relatively scarce. Below, we first highlight and summarize the findings of select studies available to date and conclude by outlining promising conceptual and technical future directions that will shed additional light on the consequences of *E x E* interactions on insect developmental evolution.

Case studies

Some of the work to date assessing the impact of *E x E* interactions on insect biology concerns adult traits, such as pest survivability (*Alphitobius diaperinus*; Renault et al., 2015), offspring production (*Tribolium castaneum*; Koch and Guillaume, 2020), heat shock protein expression (*Drosophila simulans*; Bubliy et al., 2013) and adult behavior (*Drosophila melanogaster*; Yoshii et al., 2009;

Musca domestica; Schou et al., 2013). However, the majority of work has focused on immature development with a particular emphasis on thermal variation as one of the environmental variables of concern, in part due to the singular significance of thermal variation in insect development as well as the practical ease with which temperature can be manipulated experimentally (Colinet et al., 2015; Rodrigues and Beldade, 2020; Rohner and Moczek, 2023).

While the number of published studies remains comparatively small, assessments of *E x E* interactions on insect growth rate and other traits have reported widespread and complex plasticity in response to multiple ecological interactions. Some of the most dynamic of these interactions have been documented between temperature and photoperiod. For example, De Block and Stoks (2003) found temperature, but not photoperiod, significantly impacted damsel fly (*Lestes viridis*) larval growth rate and foraging activity. However, they did detect an interaction between temperature and photoperiod stress on other development traits including age and body size at adult emergence. By comparison, Rodrigues et al. (2021) reported significant interactions between day- and night-time temperatures on development time of the butterfly *Bicyclus anynana*. The same study also found day and night temperatures confer additive-like effects on pupal mass and a separate dominant effect on eyespot size. Given the significance of photoperiod for insect seasonal cues and reproduction (Danks, 1994), additional studies are needed to characterize the extent to which insects integrate temperature and circadian responses into plastic developmental outcomes.

An especially compelling example of *E x E* interaction on insect development involves the roles of temperature and nutritional variation in the butterfly *Bicyclus anynana*. Early work reported evidence for several significant interactions between temperature and food limitation for development traits ranging from pupal mass and development time to resting metabolic rate and fat reserves, pointing to a dynamic tradeoff in energy storage and developmental regulation among body regions (Saastamoinen et al., 2013). Studies in another butterfly model (*Melitaea cinxia*), likewise, found developmental and life history traits to covary extensively with temperature and host-plant choice, a relationship that also revealed large family (genotypic) effects (Verspagen et al., 2020). Furthermore, recent experimental work in *Drosophila melanogaster* reported nutritional composition (protein-to-carbohydrate ratio) interacts significantly with developmental temperature for a range of developmental traits such as viability, development rate, and wing size (Kutz et al., 2019).

Lastly, recent work on *Onthophagus* dung beetles aimed to examine *E x E* interactions in the context of biological invasions and host range expansions. Recall that many *Onthophagus* species exhibit nutritional plasticity in the expression of male weaponry, and in many cases this phenomenon is so extreme that it results in the bimodal expression of two discrete horned and hornless male morphs within natural populations. At the same time, dung beetle development is also influenced considerably by temperature. Taking advantage of the northward range expansion of *Onthophagus taurus* from Florida to Michigan occurring over the past 50 years, Rohner and Moczek (2020) investigated how nutritional plasticity in weapon development responds to temperature, and whether *E x E* interactions had diverged among natural populations. This study found that rearing temperature had a profound effect on the nutrition-responsive allometric scaling relationship between body size and horn length within populations, most notably the size threshold separating alternate morphs. Intriguingly, the temperature-mediated shift in the body size threshold separating hornless from horned males was similar in magnitude to evolved differences among populations (Moczek and Nijhout, 2003; Rohner and Moczek, 2020). Further, the extent to which nutrition-dependent scaling of horns responded to temperature itself differed across populations reared in common conditions, suggesting that *E x E* interactions may themselves diversify during range expansions, or more generally when species encounter novel environments. As such, this work is among the few documenting that *E x E* interactions may contribute to population differentiation as much as microevolutionary divergences or genotype-by-environment interactions. More generally, these and other studies thus suggest that more explicit integration of *E x E* interactions into study designs may be much needed to better elucidate their potentially profound significance for predicting evolutionary responses of populations during introduction events, range expansions, or whenever confronted with rapid climate upheaval.

Future directions

Work examining the impact of *E x E* interactions cumulatively highlight how much more can be learned by considering multiple, potentially interacting environmental factors when assessing environmental impacts on insect developmental systems, and when aiming to predict evolutionary trajectories of populations and species. We posit that further advancing our understanding of the significance of *E x E* interactions in insect biology will require not only more studies across a wider range of taxa, but also incorporation of environmental factors often left unconsidered, as well as inclusion of a wider range of levels of biological organization and corresponding experimental approaches.

For example, temperature, nutrition, and photoperiod have so far been the main focal environmental variables subject of most *E x E* studies on insect development. However, two critically important biotic factors of development - social environment and microbiome composition - have yet to be integrated into *E x E* assessments of insect developmental evolution. As mentioned above, both social cues (Section "The social environment") and host-microbiome interactions (Section "Endosymbiosis") can individually impact crucial life history traits such growth rate, body size, metabolic capacity, neural development, morph determination, among many others. Yet developing organisms commonly integrate social and symbiotic conditions *alongside* diverse abiotic factors during ontogeny. Thus, considering differences in social and microbial conditions in a larger ecological context has the potential to create a more nuanced, but also likely biologically more realistic understanding of *ecoevodevo* dynamics of insect species and populations.

Likewise, past *E x E* work has largely focused on physical and life history traits, which has provided valuable insight into growth and fitness consequences associated with integrating multiple environmental cues during trait development. Yet, the underlying molecular, cellular, and tissue-level mechanisms regulating these developmental responses remain entirely unexplored.

Transcriptomic approaches in particular are now routine and affordable even in non-traditional model systems but have yet to be applied to *E x E* studies of insect development. Future work aimed at characterizing heterochronic, spatial, and/or magnitudinal shifts in plastic gene expression within and across body parts thus has exciting potential to begin generating a more mechanistic understanding of *E x E*-mediated developmental regulation through identification of causal genes underpinning environmental cue integration. In systems where contiguous genome assemblies are available, this work could be further expanded to assess the role of epigenetics and the non-coding genome in mediating multidimensional phenotypic plasticity. If non-additive *E x E* interactions detected at the organismal level are underlain by changes in gene expression, this approach may be especially insightful for untangling how pleiotropic interactions function and evolve to facilitate or inhibit plastic phenotypic responses.

Reconceptualizing the environment in insect development, ecology, and evolution

We began this chapter by highlighting work that has enabled us to build an increasingly deeper and nuanced understanding of the interplay between insects and their environment. We started out by providing an introduction into insects' developmental and physiological plasticity in response to key environmental variables (Section "Insects and their environment"), and then broadened our conception of what constitutes *environment* to also include: social partners and other ecological interactors (Section "The social environment"), internal and external microbial symbionts (Section "Endosymbiosis"), environments that are influenced by organismal activities (Section "Niche construction"), and finally, multiple and interacting environmental variables (Section "Environment-by-environment interactions"). Separately and in combination these sections highlighted diverse examples of how *ecoevodevo* perspectives add complexity and therefore depth of insight to our understanding of the mechanisms and consequences of insect-environment interactions, with three recurring themes emerging as particularly noteworthy: diffuse or reciprocal causation (see Box 1); the growing recognition of organisms not just as objects responding to external influences, but as agents able to influence what matters in their selective environment, thereby shaping their own trajectories in both development and evolution; and lastly and more generally, a blurring of the line between where the organism ends and its environment begins. We will therefore close this chapter by briefly examining each of these three themes in turn, highlighting emerging theoretical perspectives and conceptual frameworks amenable to understanding the growing complexity being uncovered by work in *ecoevodevo*.

On causes in ecoevodevo

Evodevo and *ecodevo* perspectives significantly enrich where we look for causal explanation of biological phenomena of interest to us, both within and across causal planes. For example, conventionally, we are accustomed to viewing phenotypes as being shaped at least in part by environmental influences. However, the increasing recognition of niche construction as a widespread if not universal property of organisms highlights that the arrow of causation can also go the other direction: environments - including those organisms respond to, are often shaped by organisms' own actions. Likewise, the growing realization of *E x E* interactions as likely similarly ubiquitous suggest that organisms' responses to environmental factors are likely dependent on yet other environmental circumstances, of course including those shaped by organisms themselves.

Across planes of causality, *ecoevodevo* perspectives sensitize us to view organismal responses to the environment not just as an evolved property conferring the ability to maintain high fitness across variable external conditions, but also as a phenomenon able to feedback to influence subsequent evolutionary trajectories, for instance by shaping the amount and type of phenotypic and genetic variation available for evolutionary processes to act upon (see *cryptic genetic variation* in Box 1). Further, in those cases in which plastic responses to environmental conditions transcend generations, *ecoevodevo* perspectives emphasize the evolutionarily significant contributions of heritable non-genetic environmental variation (e.g. via the inheritance of environmental states) and extra-genetic variation (e.g. via the genomes contained in vertically inherited microbial symbionts). More generally, *ecoevodevo* perspectives therefore provide a more complex and nuanced framework for understanding why development and evolution may unfold the way they do by highlighting sources of causation overlooked by the respective parent disciplines of the field.

Organismal agency and eco evo devo

An additional emerging theoretical perspective that is congruent with many of themes of *evodevo* and *ecoevo* research is that of biological agency: *"an organizationally closed system's capacity to build and maintain itself through the exchange of matter and energy, to differentiate itself from its environment through this capacity, and to exploit its environment in ways that promote its own continued persistence"* (Walsh, 2018). Conventional perspectives cast organisms as *objects*, subject to outside forces of environmental pressures and forms of selection. Yet, as we have seen, *ecoevodevo* perspectives champion the activities of organisms as central to their maintenance, both in terms of their own survival and the persistence of their lineage through evolutionary time. Thus, perspectives viewing organisms as *agents* place this capacity for flexible self-maintenance at center stage in our conceptualization of organism-environment interactions.

Furthermore, agency theories shift our conception of the environment itself away from a static, unchanging set of conditions toward a landscape of *affordances*, emergent properties of each unique organism-environment system, wherein an organism's state of being fundamentally shifts what a particular environment will offer them (Walsh, 2015; Nadolski and Moczek, 2023).

An organism's repertoire of behaviors and capacities is reciprocally constituted by its present set of affordances; its physiological, sensory, and behavioral capabilities not only determine what situations it can register and respond to, but these capabilities are themselves defined in relation to some present situation of relevance. *Ecoevodevo* perspectives highlight the myriad ways by which the activities of organisms shape their external surroundings, including abiotic conditions and biotic communities. Agency perspectives thus offer a framework in which organisms can be formally understood not simply to respond in static ways to a set of common environments, but to be fundamentally involved in creating the very conditions under which they develop and evolve, thereby expanding the foci of *ecoevodevo* research.

What is environment?

This chapter is part of a larger volume dedicated to insects in their environments. This very focus already implies their separability - insects as responding organisms on one side and environments as passive surroundings on the other. Another key implication of this perspective is that in the absence of the organism the environment with all its qualities still exists, not unlike a vacant niche (Moczek, 2015). Here *ecoevodevo* perspectives add important qualifications: first, because organisms frequently modify in non-random ways the environmental conditions that surround them, the environments we measure as experimenters or replicate in laboratory conditions may not always correspond to those *shaped* by organismal action in the field and *experienced* by our study organisms in nature. Assessing the relationship between environments as measured, as modified, and as experienced may therefore add important contexts to better understand nature and consequences of organism-environment interactions in the wild. Second, because aspects of the organism-constructed environment (e.g. symbionts, nesting sites, learned behaviors) may be passed on to subsequent generations, such non- or extra-genetic inheritance may contribute evolutionarily significant heritable variation, but this contribution is hardly ever assessed in quantitative genetic studies. Yet a more holistic view of the environment as both product and part of the organism may prove especially critical when we investigate insects' abilities to confront a planet that is changing rapidly in a number of environmental variables simultaneously, and when conservation efforts vary in their ability to support the environment modifying behaviors of their target organisms.

Acknowledgments

The authors thank Brent Sinclair for the opportunity to contribute this chapter and Ehab Abouheif for constructive feedback on earlier versions of the manuscript.

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