



# Integrative developmental ecology: a review of density-dependent effects on life-history traits and host-microbe interactions in non-social holometabolous insects

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## Abstract

Population density modulates a wide range of eco-evolutionary processes including inter- and intra-specific competition, fitness and population dynamics. In holometabolous insects, the larval stage is particularly susceptible to density-dependent effects because the larva is the resource-acquiring stage. Larval density-dependent effects can modulate the expression of life-history traits not only in the larval and adult stages but also downstream for population dynamics and evolution. Better understanding the scope and generality of density-dependent effects on life-history traits of current and future generations can provide useful knowledge for both theory and experiments in developmental ecology. Here, we review the literature on larval density-dependent effects on fitness of non-social holometabolous insects. First, we provide a functional definition of density to navigate the terminology in the literature. We then classify the biological levels upon which larval density-dependent effects can be observed followed by a review of the literature produced over the past decades across major non-social holometabolous groups. Next, we argue that host-microbe interactions are yet an overlooked biological level susceptible to density-dependent effects and propose a conceptual model to explain how density-dependent effects on host-microbe interactions can modulate density-dependent fitness curves. In summary, this review provides an integrative framework of density-dependent effects across biological levels which can be used to guide future research in the field of ecology and evolution.

**Keywords** Niche theory · Ecological specialisation · Ecological theory · Population density · Microbiome · Host-microbiome interaction

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## Introduction

Population density is a key factor affecting life-history trait expression and trade-offs (Mueller et al. 1991). Individuals from low-density populations often display higher expression of fitness-related traits (e.g., higher fecundity, larger size) compared to individuals from high-density populations (Dey and Joshi 2018; Prasad and Joshi 2003). This is because high-density increases intraspecific competition which limits per capita resource acquisition (Klepsatel et al. 2018). On the other hand, social interactions may benefit individuals through cooperative feeding (Denno and Benrey 1997), predator defence (Breviglieri and Romero 2019), or potentially by sharing beneficial microbial communities that are horizontally transmitted between individuals in the group (idea developed in this paper).

Early life conditions influence fitness traits and life-history trade-offs (Nijhout 2015; Stearns 1982). As a result, early life conditions can induce long-lasting effects on fitness and population dynamics, shaping populations' evolutionary trajectories, species distribution range and extinction risks (Criscuolo et al. 2008; Lindström 1999; Monaghan 2008). In insects, population density at larval stage modulates resource availability during development that can have both negative and positive effects on development and fitness (Applebaum and Heifetz 1999). In non-social holometabolous insects in particular, competition for resources at the larval stage is known to underpin changes in larval growth as well as adult morphology and fitness (Yang 2001). Adults have limited scope to compensate for poor developmental conditions later in life, particularly in traits such as body size because adults do not moult (Belles 2011). Therefore, the larval stage is paramount for resource acquisition, with density-dependent effects being particularly notable. Interestingly, population density at the larval stage can lead to faster adaptation to novel resources through increased intraspecific competition (Bolnick 2001), a factor that can increase the ability of populations to adapt to changing environments as well as population range shifts (Lawrence et al. 2012). Thus, the implications of density-dependent effects during development are many. Yet, we still do not have a deep understanding of the far-reaching effects of early life conditions on individual life-history traits (Lindström 1999). For instance, we still do not know whether responses to high population densities are conserved across taxa or to what extent population density during development has carry-over effects to adulthood and offspring that mediate eco-evolutionary processes. As a result, we lack a generalised understanding of density-dependent effects of larval stage on life-history traits expression, trade-offs and population dynamics (Applebaum and Heifetz 1999). This is likely a product of (1) the lack of a functionally consistent definition of density and (2) the absence of a taxonomically diverse perspective about density-dependent effects on life history. With the current decline in insect biodiversity—where the most affected insect species are holometabolous—gaining a better understanding of how different taxa respond to density-dependent conditions during development can provide important knowledge of species' life-histories that might be useful for population forecasts and conservation (Kunin 2019; Rada et al. 2019; Wagner 2019; Welti et al. 2020).

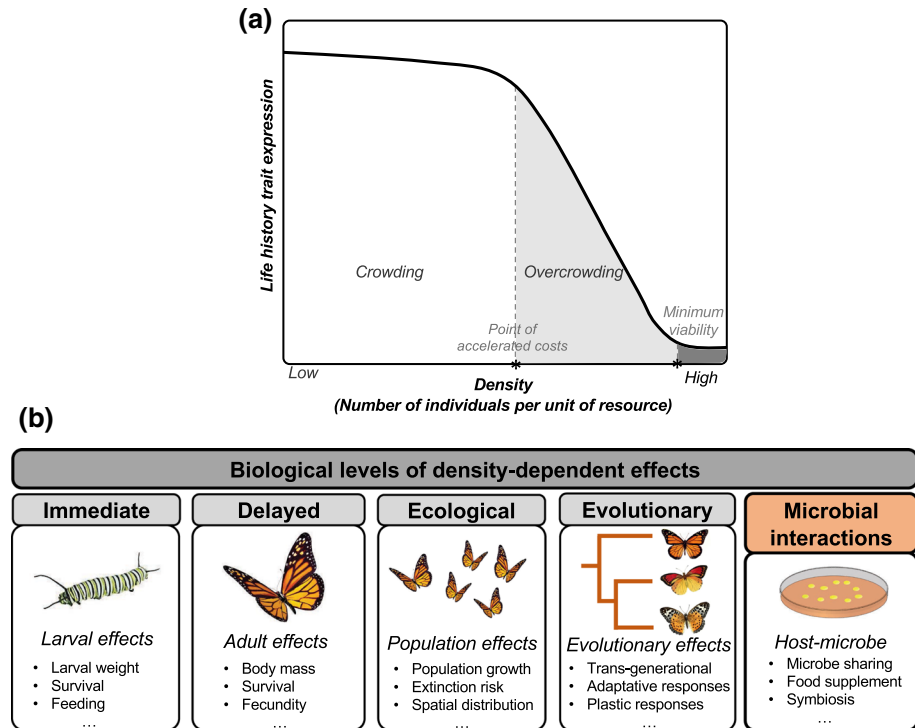
Here, we reviewed the literature on the plastic and evolutionary effects of population density at larval stage on life-history trait expression in non-social holometabolous insects. First, we provide a functional definition of density aimed to standardise the terminology used in density-dependent studies—for our own reference while writing the review and also for future studies, where a functional definition of density will allow for comparative analysis across taxa. Next, we identify the biological levels at which density-dependent

effects are manifested in non-social holometabolous insects and review the empirical evidences underpinning density-dependent effects on the larvae (density-dependent immediate effects), adults (density-dependent delayed effects), as well as populations (density-dependent ecological effects) and across generations (density-dependent evolutionary effects) (Agnew et al. 2000; Bhavanam and Trewick 2017; Couret et al. 2014; Creland et al. 1986; Gimmig et al. 2002; Hawley 1985; Morimoto et al. 2019a; Morimoto et al. 2017a). We then discuss recent evidences that density-dependent effects could affect the interactions between the host and its microbial community (density-dependent microbial interactions) and conclude by proposing a conceptual model to explain how density-dependent host-microbial interactions can modulate the strength of density-dependent effects across biological levels. We focused on non-social holometabolous insects as sociality adds an additional layer of complexity that is beyond the scope of this review. Overall, this review aims to guide and stimulate future research within an integrated framework of insect developmental ecology [see also (Mueller 1997) for a historical review in the topic and (Applebaum and Heifetz 1999; Stiling 1988) for reviews of density-dependence in other contexts].

## How did we define density?

The literature of density-dependent effects in holometabolous insects is a fruitful ground for terms referring to population density, including (but not limited to) ‘low and high density’ [e.g., (Henry et al. 2020; Ower and Juliano 2019)], ‘aggregation’ (Inouye and Johnson 2005; Morimoto et al. 2018), ‘crowding’ [e.g. (Lushchak et al. 2019; Morimoto et al. 2019a)] and ‘overcrowding’ (Ikeshoji and Mullai 1970; Roberts 1998) (the authors are themselves guilty of contributing to such panacea of terms). All of these terms capture the idea that in one treatment or condition, there are more individuals per unit of resource compared with another treatment or condition. However, the multiplicity of terms precludes appropriate comparisons of effect sizes within and between taxa. Questions such as ‘is high density equivalent to crowding or overcrowding, or both?’ and ‘what is the difference between the levels of crowding across species (e.g., maggots vs. caterpillars)?’ are highly-species and context-dependent.

Ideally, the terminology should reflect changes in density relative to the natural history of a species [see also (Travis 2020) for an appeal to natural history] but this is not always possible. The terminology is important because the effects of density can vary greatly even with small differences in experimental design for the same species [see e.g., (Mueller et al. 1993; Roper et al. 1996)] and thus a ‘ruler’ can help estimate and compare density-dependent effects and gain insights across taxa. In this Review, where we had to navigate through existing terminology, we opted to define density in a broad sense which allowed for general patterns of ‘low’ and ‘high’ density conditions across species to be derived (for consistency, we refer to different densities as low and high densities throughout the paper). In particular, we refer to low density treatments that include anything from one to few individuals whereas high density treatment includes large groups, aggregates and overcrowded conditions (Fig. 1a). This coercion should be taken with caution, but this broad definition allowed us to draw general conclusions. Note that our functional terminology does not attempt to provide the solution for the issue of defining low versus high density for each species and context. Nonetheless, this definition could potentially be adopted more widely in studies of density-dependent effects in insects; terminology is certainly an area for further improvements in the field.



**Fig. 1** Density-dependent effects across biological levels. **a** A simple functional definition for the terminology of density in insects. We considered low density studies that investigated single individuals (in butterflies) or small groups (in flies) and high density, studies that investigated large groups, crowding and overcrowding conditions. Note that low and high density are relative to each other and to the study species (i.e., low density in caterpillars is different from low density in maggots). This classification was necessary to conciliate the variety of terms used in density-dependent literature in ways that general insights could be obtained. We propose that, if this terminology is used more widely, crowding should reflect changes in density up to the point where the costs of density on life-history trait accelerates. For higher densities (overcrowding; light grey shaded region), the expression of life-history traits is expected to reach a minimum viable level, after which life-history trait expression does not decrease due to selection (dark grey shaded region). **b** The biological levels of density-dependent effects

## Multiple biological levels of density-dependent effects

Density-dependent effects are observed at multiple biological levels. Here, based on a previous framework (Mueller 1997), we classified these levels as (Fig. 1b):

1. *Immediate density-dependent effects*, which refers to density-dependent effects that occur at the same stage at which population density is sensed. For instance, density-dependent effects on larval traits in response to larval density.
2. *Delayed density-dependent effects*, which refers to effects at future life stages in the response to the developmental population density. For instance, density-dependent effects on adult traits in response to larval density.
3. *Ecological density-dependent effects*, which refer to the density-dependent effects at the population level as a result of immediate and delayed density-dependent effects. For

instance, changes in social interactions between individuals of a population in response to density.

4. *Evolutionary density-dependent effects*, which refer to density-dependent adaptations and trans-generational effects, emerging from the combination of effects in previous biological levels. For instance, density-dependent effects on offspring traits in response to parents' density.

At each biological level, the mechanisms underpinning the density-dependent effects likely vary. For example, immediate density-dependent effects are likely a result of resource acquisition and direct intraspecific competition, delayed density-dependent effects result of resource allocation trade-offs and plasticity, and evolutionary density-dependent effects is a combination of plasticity (within-generations) and evolutionary history (between generations). This classification allowed us to organise the evidence gathered here, providing a starting-point for interpreting density-dependent effects across taxa with appropriate speculation of the underlying mechanisms. Finally, we will define an additional biological level, host-microbe interactions, subject to density-dependent effects (Fig. 1b). Note that this classification does not preclude the density-dependent effects of one level to influence another (e.g., density-dependent effects on individual reproduction affects population growth and vice versa), but it allows for the formulation of clear expectation of processes leading to density-dependent effects.

## Density-dependent effects on life-history traits

### Immediate and delayed density-dependent effects

Immediate and delayed plastic responses to density determine individual fitness and are the roots of long-term density-dependent effects. In general, increasing larval density strengthen life-history trade-offs and lead to longer larval developmental time (but see section on eco-evolutionary adaptations below), lower adult body mass and reproductive success, as well as both larval and adult survival. For instance, in mosquitoes and flies, high larval density increases developmental time [flies: *D. melanogaster* and *Ceratitis capitata*; (Diamantidis et al. 2019; Henry et al. 2018); mosquitoes: *Ae. aegypti* and *A. gambiae*; (Agnew et al. 2002; Couret et al. 2014; Gimmig et al. 2002; Muriu et al. 2013)]. In addition, high larval density also decreases larval and adult body mass and reproductive success [flies: *D. melanogaster* and *B. tryoni* (Diamantidis et al. 2019; Morimoto et al. 2016, 2017a, 2019a); mosquitoes: *Ae. aegypti*, *Ae. Albopictus*, *A. gambiae* and *Culex quinquefasciatus*; (Agnew et al. 2000; Davis et al. 2016; Gimmig et al. 2002; Maciá 2017; Manorenjitha and Zairi 2012)] as well as larval and adult survival [flies: *Drosophila willistoni* and *C. capitata* (Baldal et al. 2005; Diamantidis et al. 2019; Dukas et al. 2001; Pearl et al. 1927); mosquitoes: *Ae. aegypti*, *A. gambiae* and *C. quinquefasciatus* (Agnew et al. 2000, 2002; Jannat and Roitberg 2013)]. However, adult survival was not affected by larval density in *Ae. albopictus* or *Ae. sierrensis* (Hawley 1985; Reiskind and Lounibos 2009) and high larval density increases larval survival in experimental evolution *D. melanogaster* lines [e.g., (Shenoi et al. 2016a)] at the expense of energy efficiency (Mueller 1990, 1997). High larval density also leads to an increase in adult lipid storage in *D. melanogaster* (Zwaan et al. 1991)] but a decrease in adult lipid storage in *B. tryoni* (Morimoto et al. 2019a) even in sugar-rich diets (Nguyen et al. 2019). Moreover, high larval density

increases local temperature (Appleby and Credland 2007) and promotes a generalised stress response which can mediate individual's thermotolerance (Henry et al. 2018). Given the ongoing environmental changes and the rapid decline in insect species worldwide (Wilson and Maclean 2011), it is appealing that population density could mediate the ability of populations to overcome extreme temperature shocks (Lushchak et al. 2019). Similar general effects of larval density are observed in Hymenoptera (Kuno 1962; Milonas 2005; Taylor 1988) although more studies in parasitoids, which poses a more complex relationship between developmental density and resource (e.g., host size), are needed.

Despite the general trends described above, some fly species benefit from high density via faster developmental pace. For instance, high larval density in some blowfly and fruit fly species can lead to benefits of group feeding that shortens developmental time [e.g., *Calliphora vicina* (Saunders and Bee 2013); *Phormia regina* (Green et al. 2002); *B. tryoni* (Morimoto et al. 2018)]. In blowflies in particular, shorter developmental time in high larval densities is likely an evolutionary response to the nutritional ecology of Calliphoridae species which feed on carcass, an ephemeral resource attractive to many species. High larval density could signal to the larva that the resource is likely to become fully depleted in a shorter period of time due to intra- and inter-specific competition, thereby accelerating larval development (Reis et al. 1999). Nonetheless, these species still respond to high larval densities by developing into smaller pupae and adults [*C. vicina* and *C. vomitoria* (Ireland and Turner 2006; Saunders et al. 1999)] and having lower adult reproductive success [*C. vicina* (Fantinou et al. 2008)].

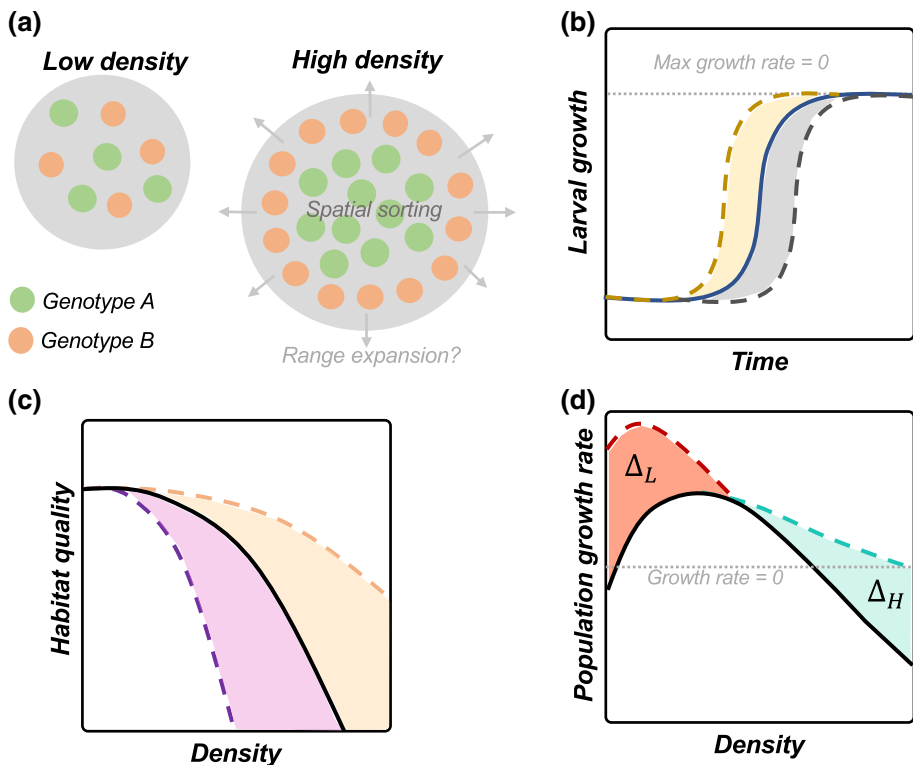
In Coleoptera and Lepidoptera, the responses to larval density are less consistent across taxa with some species displaying positive and others negative responses to larval density. For example, some species respond to increased larval density by increasing the number of larval moults and delaying development [i.e., Lepidoptera: *Pararge aegeria* and *Sesamia nonagrioides* (Fantinou et al. 2008; Gibbs et al. 2004)]; Coleoptera: *Zophobas atratus* (Quenedey et al. 1995)], other species maintain the same [*Tenebrio molitor*; (Connat et al. 1991; Weaver and McFarlane 1990)] or even display faster development with increasing larval densities [Lepidoptera: *Bicyclus anynana* (Bauerfeind and Fischer 2005) and *Chiasma clathrata* (Välimäki et al. 2013)]. High larval densities can have negative [butterfly: *Pieris napi* (Kivelä and Välimäki 2008)] or positive effect on larval survival by increasing larval feeding efficiency ['feeding facilitation' (Nahrung et al. 2001)] and group anti-predatory defence [e.g., (Aukema and Raffa 2004)]. For instance, in burying beetles *Nicrophorus vespilloides*, a species where adults display parental care for the larvae, larval density facilitates feeding depending on the level of parental care. In the presence of parental care, there is a negative relationship between larval density and larval mass, likely due to increased larval competition. In the absence of parental care, there is a quadratic relationship, with larval mass being maximised at intermediate larval densities because groups of larvae could better penetrate the carcass upon which they were feeding (Schrader et al. 2015). Feeding facilitation also increased larval survival in the butterfly *Chlosyne lacinia* (Clark and Faeth 1997). In the moth *Hylesia nigricans*, high larval density allow for groups to display longer anti-predatory responses when exposed to acoustic stimuli from predators (Breviglieri and Romero 2019), a behaviour that likely increase individual and group survival probabilities. In first instar larvae of the mountain pine beetle *Dendroctonus ponderosae* (Cole 1973) and the eucalypt-feeding beetle *Chrysophtharta Agricola*, high larval density also result in higher larval survival likely due to the combination of both feeding facilitation and anti-predatory responses (Nahrung et al. 2001).

Another way in which larval density can exert positive effects on Lepidoptera and Coleoptera larvae (and potentially in other insect orders) is by increasing immune function

(known as ‘density-dependent prophylaxis’) which increases resistance against parasites as well as bacterial and viral infections (Barnes and Siva-Jothy 2000; Cotter et al. 2004; Wilson and Cotter 2008; Wilson and Graham 2015) [but see (Piesk et al. 2013) for contrary evidence in *P. napi*]. Nonetheless, increasing larval density still lead to lower adult body mass survival in both Coleoptera and Lepidoptera [Lepidoptera: *Elachista* sp, *Cnaphalocrocis medinalis*, *Plodia interpunctella*, *S. nonagrioides*, *Lymantria dispar*, *P. aegeria* and *Chiasma clathrata* (Dai et al. 2019; Fantinou et al. 2008; Gage 1995; Gibbs et al. 2004; Lazarevic et al. 2004; Reilly and Hajek 2007; Välimäki et al. 2013); Coleoptera: *Callosobruchus maculatus*, *O. sulcatus* and *Gnathocerus cornutus* (Clark et al. 2011; Creland et al. 1986; Savvidou and Bell 1994; Smallegange and Tregenza 2008; Tsuda and Yoshida 1985)]. These discrepancies likely emerge through the combination of species-specific responses to density as well as experimental design.

Density-dependence can be a signal to the level of competition individuals are likely to encounter in the future. Thus, immediate and delayed plastic responses to population density are thought to represent ways through which individuals attempt to maximise fitness given the level of expected competition in the population. For instance, *D. melanogaster* males raised in high density evolve higher courtship rates (Shenoi et al. 2016b) and invest relatively more in ejaculates relative to their body mass compared with males from low density larval environments (Wigby et al. 2016) although they do not increase the expression levels of seminal proteins (McGraw et al. 2007). These plastic responses can be tailored to maximise fitness in habitats where population density is high and sperm competition is likely, although males from high larval density have lower fertilization success in general (Morimoto et al. 2016, 2017a). Males of the armyworm *Mythimna separata* (aka *Pseudaletia separata*) from high larval have significantly more apyrene (non-fertilising) sperm than males from solitary larval environments, but with no differences in eupyrene (fertilising) sperm (He and Miyata 1997). While apyrene sperm is not capable of fertilising eggs it may nonetheless affect egg fertilisation in sperm competitive contexts (Silberglie et al. 1984; Watanabe 2016). Similarly, in the gum-leaf skeletonizer moth *Uraga lugens*, males from high larval densities invest more in testis size but have relatively shorter wing and antenna length, revealing a trade-off between investing in finding mates versus winning paternity (Johnson et al. 2017). Female antenna and wing sizes are density-independent or social-dependent, respectively, which uncovers sex-specific responses to population density at the larval stage (Johnson et al. 2017). In the moth *P. interpunctella*, males from high larval density emerge with relatively larger abdomens, testis, and with greater number of sperm when reared in high density conditions (Gage 1995), which can be interpreted as an adaptation to higher sperm competition in high-density population (Gage 1995). Experimental evolution in *P. interpunctella* also revealed that males evolving in low (not high) larval density transfer overall more sperm and both sexes invest less in immunity (McNamara and Simmons 2017), contradicting the predictions of standard density-dependent theory and density-dependent prophylaxis (see above). Interestingly, high larval density compounded with food shortage leads to plastic phenotypic adaptations in the adult of the flour moth *Ephestia kuehniella* whereby males have lower body weight but disproportionately longer wings which could facilitate migration (Bhavanam and Trewick 2017). Whether or not migratory individuals have higher fitness remains to be tested (Stamps 2006). From a spatial perspective, high larval density in the caddisfly *Cheumatopsyche* sp. (Trichoptera) leads to homogenous distribution of individuals in space, where some individuals are displaced to the edge of the group in poor habitats (Glass and Bovbjerg 1969). Displaced individuals might experience poorer environments and emerge

as adults that are prone to dispersal, thereby influencing population range distribution (Dethier 1959) as well as generating spatial sorting of genotypes that can lead to spatial evolution (Shine et al. 2011) (Fig. 2a). This remains untested but is an important topic for future studies. Lastly, it is important to mention that low larval density is positively associated with direct development rather than diapause in the butterfly *C. clathrata* (Välimäki et al. 2013), suggesting that larval density can also modulate modes of development. More studies are needed in this area.



**Fig. 2** Population density, spatial sorting and density-dependent effects on host-microbe interactions. **a** High larval densities may displace individuals (and consequently, their genotypes) towards the periphery of the population. These individuals at the periphery might be more prone to migrate (either as a response to density *per se* or as a result of other factors [e.g., interactions between density and nutrition; see main text]). This can in theory contribute to population range expansion and spatial evolution. **b** Density-dependent host-microbe interactions can generate the potential for accelerated or decelerated growth rates during larval development. As a result, maximum growth rate might be achieved faster or slower depending on the population density and the microbial community present in the environment. Changes in maximum growth rate are not displayed here but are nevertheless possible. **c** As microbes can serve as food, host-microbe interaction can modulate the rate of habitat degradation by population density. Scenarios where microbes increase (orange) or decrease (pink) environmental quality are shown. **d** At the population level, density-dependent host-microbe interactions can mediate population growth rates. For example, population growth rates may increase in low (red) or high (turquoise) densities due to the sum of the density-dependent effects on host-microbe interactions at the individual level



## Ecological and evolutionary density-dependent effects

Larval density-dependent effects can modulate how a species interact with itself (e.g., intraspecific competition) and with other species (e.g., predators, preys), or both [e.g., (Arditi et al. 2001; May et al. 1981)]. This will determine both the ecological significance of the species within the ecosystem (ecological density-dependent effects) as well as the evolutionary trajectory of the species over generations (evolutionary density-dependent effects) [e.g., (Cappuccino 1992; Hassell and May 1986; Liu et al. 2007)].

Many insights into within-species ecological and evolutionary density-dependent effects emerged from studies in *Drosophila* (Mueller 1997). For instance, *D. melanogaster* populations evolved at high larval densities displayed increased population growth rates, which is the opposite pattern observed for populations evolving at low densities that evolved reduced population growth rates. (Mueller and Ayala 1981; Mueller et al. 1991); this is evidence for the evolution of increased population carrying-capacity at high population densities. In addition, *D. melanogaster* larval feeding rates (a measure of larval competitive ability), cannibalism, and ability to withstand toxic waste (i.e., ammonia and urea) also increase (although not for all species) in populations experiencing or evolving high larval densities [(Belloni et al. 2018; Borash et al. 1998; Borash and Shimada 2001; Vijendravarma et al. 2013); see also review in (Joshi et al. 2001)], albeit creating a trade-off with larval energy efficiency (Joshi and Mueller 1996; Joshi et al. 2001; Mueller 1990). However, this trade-off is not necessarily observed in other *Drosophila* species (Nagarajan et al. 2016) suggesting that the natural history of species may lead to different responses to population density. Interestingly, even within a single cohort of individuals in a high-density population, density-dependent effects generate and maintain genetic polymorphism. This is because individuals that develop faster (early developers) have higher feeding rates but lower viability and tolerance to toxic waste compared with individuals that develop later (late developers) (Borash et al. 1998). Furthermore, density-dependent selection also leads to differential allelic composition for a single locus foraging (*for*) gene, corroborating that high population density can maintain genetic polymorphism in populations (Sokolowski et al. 1997). Population density at the larval stage also mediates plastic reproductive strategy responses at the population level which ultimately affects population survival and growth. For example, *D. melanogaster* populations with individuals raised in high larval density have significantly faster reproductive rates but lower survival than populations with individuals from low larval density or populations with mixed compositions (low and high larval density individuals) (Morimoto et al. 2016, 2017a). Such changes in reproductive rate also lead to changes in sexual selection and sexual conflict (Morimoto et al. 2016, 2017a) [see also (Prasad et al. 2001)]. In addition, parental larval density can affect offspring body mass, opening up the potential for long-term trans-generational effects of larval density (Morimoto et al. 2017a).

Although relatively less common, studies in other species have allowed us to gain insights into both within- and between-species density-dependent effects of larval density. For instance, previous studies have shown that when density of larvae (prey) from the shield beetle *Cassida rubiginosa* increased, they were more likely a preferred target for the generalist paper wasp parasitoid *Polistes dominulus*, which showed a type III functional response to prey density (Schenk and Bacher 2002). Moreover, higher densities of strawberry ground beetle *Pterostichus melanarius* larvae (predator) are more efficient at reducing biomass of two slug species (between-species density-dependent

effects), although higher larval density also resulted in higher cannibalism rates due to stronger intraspecific competition (within-species density-dependent effects) (Thomas et al. 2009). Together though, these findings demonstrate that larval density-dependent effects have long-lasting ecological and evolutionary consequences to populations, species, and ecosystems.

## Host-microbe interactions as a missing factor

Based on the evidences provided above, one could ask: why do responses to high larval density vary greatly between insect populations, species and Orders? A definite answer to this question is difficult to answer due to the lack of empirical work across taxa. While part of this emerge from differences in experimental design, it is likely that some portion of this variation in responses to larval density are rooted in differences of developmental biology processes. For instance, while Diptera, Coleoptera and Lepidoptera larvae need to reach a threshold size (critical mass) for pupation, Diptera has a fixed number of larval instars while Coleoptera and Lepidoptera larvae possess flexibility on the number of larval instars that can precede metamorphosis (Belles 2020; Mirth et al. 2005; Truman 2019). The last stages of Coleoptera and Lepidoptera larval development are particularly sensitive to nutrients, and commitment to metamorphosis can be adjusted based on environmental and nutritional conditions (Belles 2020; Truman 2019). The ecological factors that interact with population density [e.g., temperature (Pétavy et al. 1997)] can also contribute to developmental plasticity. Despite this, many ecological factors have not yet been fully integrated within the framework of density-dependent effects in developmental ecology. In the next section, we discuss recent evidence that shows that the relationship between individuals and microbes can promote developmental plasticity and enable individual development in challenging conditions. We then argue that host-microbe interactions can be an additional unit of density-dependent effects, which can mitigate or accentuate density-dependent effects across all biological levels.

## Interactions between host and microbes

Microbial communities can modulate the expression of life-history traits in insects via an intricate communication network involving the immune system (Newton et al. 2013) and which, as a result, affect the expression of traits not only related to the immune system (Genta et al. 2006; Gonzalez-Ceron et al. 2003) but also to metabolism and development (Ben-Yosef et al. 2014, 2015; Morimoto et al. 2019b; Warnecke et al. 2007; Zhou et al. 2007). Microbial communities also help insect hosts overcome chemical defenses (Ben-Yosef et al. 2015), acquire nutrients (Ben-Yosef et al. 2014; Bing et al. 2018; Sannino et al. 2018), and serve as direct source of nutrients (Nguyen et al. 2019). Furthermore, microbes also interact with insect host to modulate adult oviposition behaviour (Jose et al. 2019), foraging (Wong et al. 2017), reproductive success (Morimoto et al. 2017b) and potentially mate choice (Sharon et al. 2011) [but see (Leftwich et al. 2017)]. Microbes are therefore the ‘gatekeepers of organism fitness’ (Colombani and Andersen 2020).

Population density can influence host-microbe interactions directly, via horizontal transmission of strains through social interactions, or indirectly, by modulating the diversity of strains present in a given population as well as the physico-chemical conditions of the substrate for microbial growth. For instance, increased larval density is associated

with accumulation of toxic compounds (i.e., urea, ammonia) excreted in the substrate which are known to modulate the microbial composition of the substrate [see e.g., (Henry et al. 2020)]. The underlying mechanisms remain unknown, but at higher larval densities, chemical changes (e.g., pH) likely favour the growth of some microbial strains over others (Gibson et al. 1988; Rousk et al. 2009; Russell and Dombrowski 1980). Moreover, microbial strains might interact with each other via metabolites in order to promote growth of a cohort of strains which together, influence larva's development and life history trait (Consuegra et al. 2020; Lesperance and Broderick 2020; Sommer and Newell 2019). Given that a large proportion of microbes are acquired from interactions between the host and the surrounding environment, larval density might be important, yet an overlooked factor, in modulating host-microbe interactions (Broderick et al. 2004; Colman et al. 2012; Tang et al. 2012; Vacchini et al. 2017; Yun et al. 2014; Zhang et al. 2018; Zhao et al. 2017). Below, we summarise the main consequences of host-microbe interactions (especially microbes in the gut) to insect life-history trait expression while discussing potential ways through which larval population density could influence these effects. Note that our goal was not to review the (gut) microbe literature as extensive reviews have been published elsewhere [e.g., (Bährndorff et al. 2016; Bordenstein and Theis 2015; Douglas 2009, 2015, 2019; Lesperance and Broderick 2020; Lewis and Lizé 2015)]. Instead, our aim is to demonstrate potential links between population density and (gut) microbe effects on fitness.

### Density-dependent effects on host-microbe interactions and the modulation of fitness curves

Insects depend on their microbiome for successful development which opens up the possibility for density-dependent effects to modulate host-microbe interactions in ways that benefit (or harm) individuals. We therefore propose that host-microbe interaction is an additional biological level on its own right which is subjected to density-dependent effects. For instance, the mosquitoes *Ae. aegypti*, *A. gambiae* and *Georgescraigius atropalpus* fail to complete larval development in the absence of commensal microbes (Coon et al. 2014; Correa et al. 2018). The developmental arrest is rescued upon re-inoculation with the enterobacteria *Escherichia coli* into germ-free larvae (Coon et al. 2014), suggesting that host-microbe interactions drive development. Similar effects were described in the mosquito *C. quinquefasciatus* where the presence of the phosphorus-rich bacterium *Pseudomonas aeruginosa* increases growth rate in phosphorus-poor diet (Peck and Walton 2006) although high concentration of the phosphorus-rich bacteria inhibited the development of another mosquito, *Culex tarsalis*, which highlights the species-specific interactions amongst host and microbes (Peck and Walton 2006). Studies in *D. melanogaster* also showed that some microbial strains can decrease larval survival and adult sizes due to toxic compounds and competition for nutrients ('animal-microbe competition') [see both (Trienens et al. 2010; Wertheim et al. 2002) for similar results]. Conversely, two microbes—*Lactobacillus plantarum* and *Acetobacter pomorum*—can rescue developmental time and larval growth in nutrient-deficient diets by acting on major hormonal signalling pathways (i.e., Insulin and TOR) (Shin et al. 2011; Storelli et al. 2011, 2018; Westfall et al. 2019). Interestingly, these microbes rely on metabolites from each other to grow and to provide developmental benefits to the host (Consuegra et al. 2020; Henriques et al. 2019; Sommer and Newell 2019). In particular, a recent study has revealed that the cross-feeding between *L. plantarum* and *A. pomorum* is mediated by lactate, amino acids, and vitamins (e.g., biotin) which together

promote microbial growth that stimulate the endocrine and metabolic systems of *D. melanogaster* larvae (Consuegra et al. 2020). These interactions are important because high larval density is known to decrease the availability of protein in the diet (Klepsatel et al. 2018) and the cross-talk between microbes can buffer against nutritional stress. Also, microbial strains modulate adult reproductive success and offspring body mass in *D. melanogaster* (Morimoto et al. 2017b), corroborating the long-lasting effects of host-microbe interaction. Together, these findings reveal a complex host-microbe relationship that modulates host development and fitness.

Population density can modulate the microbial diversity in the substrate as well as in the population and facilitate the horizontal transmission of microbial strains between individuals due to increased levels of social interactions. In *D. melanogaster* larvae from high density conditions show a trend for elevated microbial richness (Henry et al. 2020). Likewise, the diet of high density larval conditions showed significantly higher microbial richness and diversity compared to the diets of low density larval conditions (Henry et al. 2020). Microbial growth is also known to buffer against nutritional stress caused by high larval density, aiding the expression of life-history traits such as pupal weight, adult weight and to a smaller extent, lipid storage (Nguyen et al. 2019). Microbes can also be food supplements for the developing larvae and thus, an important way to modulate the strength of density-dependent effects (Augustinos et al. 2015; Drew et al. 1983; Kaznowski et al. 2005; Salem et al. 2014). Thus, microbial diversity, transmission, and host-microbe interactions are likely density-dependent.

In this study, we propose that the effects of density-dependence on host-microbe interactions can modulate the distribution of life history trait values, the shape of individual's fitness curves and ultimately, the opportunity for—and strength of—selection in populations. Using the framework proposed by (Edelaar and Bolnick 2019), we hereby describe a conceptual model of how density-dependent effects on microbe interactions can affect individual and population fitness. According to the framework in (Edelaar and Bolnick 2019), a non-stochastic Gaussian fitness curve  $W_{ij}$  links trait and fitness whereby changes in individual fitness through time is given by

$$\frac{dW_{ij}}{dt} = \frac{\partial W_{ij}}{\partial x_{ij}} \frac{\partial x_{ij}}{\partial t} + \frac{\partial W_{ij}}{\partial X_j} \frac{\partial X_j}{\partial t} + \frac{\partial W_{ij}}{\partial \omega_j} \frac{\partial \omega_j}{\partial t} + \frac{\partial W_{ij}}{\partial c_j} \frac{\partial c_j}{\partial t} \quad (1)$$

[reproduced integrally here from (Edelaar and Bolnick 2019) for clarity].  $W_{ij}$  refers to the fitness of an individual  $i$  in environment  $j$ .  $x_{ij}$  refers to the value of trait  $x$  of individual  $i$  in environment  $j$ ,  $X_j$  is the optimum trait value for environment  $j$ ,  $\omega_j$  is inversely related to the strength of stabilizing selection in trait  $x$  in environment  $j$  and  $c_j$  is the maximum achievable fitness for environment  $j$  (Edelaar and Bolnick 2019). Below, we firstly explain the meaning of each of the terms according to (Edelaar and Bolnick 2019) followed by recent evidence which suggest that density-dependent effects can act upon each of the terms:

- $\frac{\partial W_{ij}}{\partial x_{ij}} \frac{\partial x_{ij}}{\partial t}$  represents the change in individual fitness through time via temporal changes in individual's trait value; it is subdivided into two components: constitutive growth (i.e., growth rate) and the interaction between the trait value and the environment (Edelaar and Bolnick 2019).

Density-dependent effects on host-microbe interactions can affect individual's growth rates by accelerating (or decelerating) individual's nutrients uptake as well as influencing hosts' metabolism (Fig. 2b) (Henriques et al. 2019; Jing et al. 2020;

Morimoto et al. 2019b; Sommer and Newell 2019). Note that density-dependent effects on host-microbe interactions are likely time-dependent given that the individual, the environment and the microbes change over the developmental period of an individual, thereby influencing the nature of host-microbe interactions [e.g., (Chen et al. 2016; Johnston and Rolff 2015)].

- $\frac{\partial W_{ij}}{\partial X_j} \frac{\partial X_j}{\partial t}$  represents the change in individual's fitness through time via temporal changes in local environment optimum (e.g., social group, (micro)habitat quality) (Edelaar and Bolnick 2019).

We hypothesise that density-dependent effects on host-microbe interactions can influence how individuals interact with conspecifics. One way this could occur is if density-dependent effects on host growth (see previous paragraph) affects phenotypic variation in the host (e.g., body size) (Crespi 1989). Another way in which density-dependent effects on host-microbe interactions can modulate social networks is via uneven spatial distribution of phenotypes (+ microbes) as a result of foraging decisions and mate selection. Previous studies have shown that fruit fly larvae (and adults) prefer to feed on diets that contain similar microbes as in their guts (Wong et al. 2017) while microbes also modulate locomotor activity in adults (Schretter et al. 2018). Previous studies have shown that population density can modulate eco-evolutionary processes that influence social networks (Vander Wal and Webber 2019). Moreover, as discussed above, host-microbe interactions can affect how individuals forage (Wong et al. 2017), move (Schou et al. 2013; Schretter et al. 2018) and mate (Sharon et al. 2011). Thus, population density can modulate the strength of mate choice and foraging choices, which in turn can generate higher or lower levels of assortativity (i.e., individuals interacting with similar or dissimilar individuals) in the social network, respectively (Crespi 1989; Jiang et al. 2013). For example, low density populations can have low assortativity as individuals are required to interact (e.g., mate choice, foraging site) with conspecifics with similar and different microbial profiles. Conversely, high density populations can have high assortativity whereby individuals preferentially interact with conspecifics with similar microbial profile in 'sub-networks' within populations. The opposite prediction is also possible, namely high assortativity in low density due to the potential for more structured populations, although if this persists throughout the reproductive stage, this could incur an opportunity cost for individuals in low density populations (e.g., low mating encounter rate). Recent studies have shown that groups of adult *Drosophila* tend to display some level of aggregation and social interactions that are density-dependent, with social distancing determined by specific neuronal circuits activated by contact amongst individuals in the groups and cluster formation dependent upon olfactory cues (Jiang et al. 2020; Rooke et al. 2020). These evidences suggest that density-dependent effects can modulate how individuals respond to social cues, ultimately affecting the propensity of individuals to form (dis)similar clusters within the social network structure.

- $\frac{\partial W_{ij}}{\partial \omega_j} \frac{\partial \omega_j}{\partial t}$  represents the change in individuals' fitness through time via the strength of stabilising selection (Edelaar and Bolnick 2019).

Theoretical and empirical work shows that strong stabilising selection eliminate genetic variability in the population [e.g., (Barton and Keightley 2002; Brooks et al. 2005; Hunt et al. 2007; Johnson and Barton 2005)]. Density-dependent host-microbe interactions can decrease frequency of extreme phenotypes by buffering against genetic variance of the host and negative ecological or nutritional conditions [see discussion above; (Ma et al. 2019)]. This can modulate the opportunity for and potentially the

strength of -stabilising selection in a population; a possible consequence of this process is that genetic variability in a population might be partly maintained in the population, as the frequencies of extreme phenotypes decrease due to the ‘buffering’ effects of host-microbe interactions.

- $\frac{\partial W_{ij}}{\partial c_j} \frac{\partial c_j}{\partial t}$  represents the change in individual fitness through time via increasing overall environmental quality (Edelaar and Bolnick 2019).

Density-dependent effect on host-microbe interactions can increase (or decrease) overall habitat quality via modulating availability of microbes as additional food source or competitors as well as the microbial diversity and horizontal transmission probabilities [see e.g., (Nguyen et al. 2019; Trienens et al. 2010; Wertheim et al. 2002)]. In fact, larval density modulates microbial composition of the substrate. The environment itself can feedback and modulate the amount of microbes and the types of host-microbe interactions during development (Zaada et al. 2019). Therefore, density-dependent effects on host-microbe interactions mediate changes in habitat quality and consequently, its carrying capacity (Fig. 2c).

The sum of density-dependent effects on microbe-host interactions at the individual level can affect population fitness and the strength of natural selection. For instance, low density populations (e.g., populations near the distribution edge), where habitat may have lower quality, can benefit from density-dependent host-microbe interactions in ways that population growth curve increases even in low densities (i.e.,  $\Delta_L$ , in Fig. 2d). Likewise, high-density populations (e.g., source population in a source-sink model) can mitigate the density-dependent negative effects of a reduction in nutrient per capita by sharing microbes that can support development in challenging conditions as well as using microbes as food. This may increase carrying capacity of the habitat and decelerate the decline in population growth rates at higher densities ( $\Delta_H$  in Fig. 2d). These population-level conceptual models assume that mothers lay eggs in the best resource for larval development (i.e., low mother-offspring conflict) and/or for beneficial microbial growth or transmit microbes vertically; these are somewhat realistic assumption and known to occur in insects [e.g., (García-Robledo and Horvitz 2012; Herren et al. 2013)]. Verbal models can overlook assumption that are only identified in more rigorous mathematical formulations (Mueller 1997). Thus, further theoretical and empirical work are needed to mathematically formalise this conceptual model and understand its assumptions. This conceptual model shows that density-dependent effects on host-microbe interactions can underpin changes in traditional density-dependent effects on life history traits.

## Conclusion

Density-dependent effects mediate life-history trait expression and trade-offs, affecting individual fitness and population dynamics (Mueller 1997). Here, we reviewed the evidence of density-dependent effects of population density during development in holometabolous insects. We provided a functional definition of density aimed at standardizing future studies and allowing for comparative research. We then discussed recent advances in our knowledge about the host-microbe interaction and suggest that the host-microbe interaction is an additional level upon which density-dependent effects can modulate individual fitness and eco-evolutionary processes acting on populations. We are still a long way from gaining comprehensive understanding of holometabolous insects’ developmental ecology.

A more taxonomically diverse exploration of the effects of larval density on life-history traits will allow us to better understand the plasticity in response to developmental conditions and how this varies across habitats (e.g., aquatic vs. terrestrial larva).

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## Compliance with ethical standards

**Conflict of interest** The authors declare no conflict of interests.

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