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Phenotypic Plasticity of Cuticular Hydrocarbon Profiles in Insects

Tobias Otte[1] · Monika Hilker[1] · Sven Geiselhardt[1]

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Abstract

The insect integument is covered by cuticular hydrocarbons (CHCs) which provide protection against environmental stresses, but are also used for communication. Here we review current knowledge on environmental and insect-internal factors which shape phenotypic plasticity of solitary living insects, especially herbivorous ones. We address the dynamics of changes which may occur within minutes, but may also last weeks, depending on the species and conditions. Two different modes of changes are suggested, i.e. stepwise and gradual. A switch between two distinct environments (e.g. host plant switch by phytophagous insects) results in stepwise formation of two distinct adaptive phenotypes, while a gradual environmental change (e.g. temperature gradients) induces a gradual change of numerous adaptive CHC phenotypes. We further discuss the ecological and evolutionary consequences of phenotypic plasticity of insect CHC profiles by addressing the question at which conditions is CHC phenotypic plasticity beneficial. The high plasticity of CHC profiles might be a trade-off for insects using CHCs for communication. We discuss how insects cope with the challenge to produce and "understand" a highly plastic, environmentally dependent CHC pattern that conveys reliable and comprehensible information. Finally, we outline how phenotypic plasticity of CHC profiles may promote speciation in insects that rely on CHCs for mate recognition.

Keywords Assortative mating · Chemical communication · Mate recognition · Sensory drive · Ecological speciation · Self-referent phenotype matching

Introduction

Organisms need to cope with a huge variety of environmental conditions that may change in space, time, intensity, and quality. The response of an individual to novel environmental conditions can take many forms, ranging from changes in physiology, alterations of morphology to shifts in behavioral responses (Schlichting and Pigliucci 1998; Wund 2012). This variation in phenotypic expression is defined as "phenotypic plasticity" – the ability of a single genotype to produce different phenotypes in response to different abiotic and biotic environmental conditions (Moczek et al. 2011; Pfennig et al. 2010; Pigliucci et al. 2006; Via et al. 1995). Phenotypic plasticity of a certain genotype plays a role in many evolutionary processes like selection within and between species (Salamin et al. 2010), formation of host races (Drès and Mallet 2002), or the establishment of reproductive isolation barriers between and within populations (Coyne and Orr 2004). Thus, phenotypic plasticity may promote speciation processes (Pfennig et al. 2010), and facilitate or even speed up the process of (adaptive) evolution (Ghalambor et al. 2007; West-Eberhard 2003). In order to understand the mechanisms and adaptive value of phenotypic plasticity, we need to investigate the responses of an organism to changing environmental factors and the costs and/or benefits of phenotypic changes (Moczek 2010; Snell-Rood 2012).

In this review, we focus on the phenotypic plasticity of cuticular hydrocarbons (CHCs) in solitary insects, with special emphasis to herbivorous species (Chung and Carroll 2015; Thomas and Simmons 2011). We do not consider CHCs of eusocial insects like termites, ants and bees because the chemistry and ecological relevance of their CHC profiles in social life have been excellently addressed in several recent reviews (Leonhardt et al. 2016; Oi et al. 2015; Smith and Liebig 2017).

CHCs are of enormous functional significance in insects which have evolved a wide range of CHCs differing with respect to chain length (typically 20 to about 40 carbons), methyl branching pattern, and position and number of double bonds (Geiselhardt et al. 2011; Martin and Drijfhout 2009). CHCs

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✉ Sven Geiselhardt
sven.geiselhardt@fu–berlin.de

[1] Institute of Biology, Freie Universität Berlin, Haderslebener Str. 9, 12163 Berlin, Germany

are covering the insect's integument and protect them from abiotic and biotic environmental stress, as will be outlined below. Insects can adjust the chemical composition of their CHC profiles to the environmental needs. CHCs do not only serve as protective device, but are also used by many insect species for intra- and interspecific communication (Blomquist and Bagnères 2010). When communicating by these highly variable chemical cues, insects need to be able to cope with this environmentally dependent, flexible chemical information.

A major issue of this review is to outline current knowledge and resulting ideas on the ecological processes that shape phenotypic plasticity of insect CHC profiles which may contribute to speciation of insects. We first provide a brief overview on factors influencing insect CHCs and address the dynamics of phenotypic changes. We further analyze two modes of phenotypic change and differentiate between saltatory and gradual adaptive changes. Finally, we critically discuss consequences of phenotypic plasticity in insect chemical communication systems, speciation processes and evolutionary biology. We address costs and benefits of the plasticity of insect CHC profiles with respect to the dynamics of changes of CHC patterns, the modes of changes, and the individual and evolutionary consequences of changes.

Phenotypic Plasticity of CHCs – Drivers and Temporal Dynamics

Several studies suggest that CHC profiles largely depend on the insect's genetic background (e.g. Dembeck et al. 2015). In turn, numerous abiotic and biotic environmental factors (Ingleby 2015; Leonhardt et al. 2016) shape the internal status of an insect and expression of genes (Ferveur 2005; Martin and Drijfhout 2009; Menzel et al. 2017) (Fig. 1). The enormous impact of the environment on an insect's CHC profile has been shown long ago by a study of Toolson and Kuper-Simbron (1989) who transferred *Drosophila pseudoobscura* from the field to the laboratory; the flies showed altered CHC profiles already in the first laboratory generation. However, the cause of this shift remained unclear. Below, we will outline the impact of several environmental and insect-internal factors on insect CHC patterns. Examples are listed in Table 1. Furthermore, the dynamics by which insect CHC phenotypes adapt to changing environmental conditions will be addressed and discussed.

Abiotic Environmental Factors as Drivers of Insect CHC Phenotypes

When insects are exposed to high temperature and/or low relative humidity, they face a high risk of desiccation because of their large surface-to-volume ratio. CHCs act as waterproofing agents and support prevention of dehydration in interaction with other cuticular compounds and respiratory regulation. The lipophilic, long-chained CHCs form a protective film on the insect's integument which impairs permeation of water molecules to the outside. In addition, the hydrophobic CHCs prevent wetting and passage of water into the insect (Gibbs et al. 1998; Wang et al. 2016, and references therein). Insects can prevent critical water loss in response to high temperature and low humidity by a fast change of their CHC phenotype (Chown et al. 2011). They start to change their CHC phenotype in response to changing temperature or humidity within a day (Howard et al. 1995; Kwan and Rundle 2010; Savarit and Ferveur 2002; Stinziano et al. 2015). In general, desiccation stress leads to an adaptive shift towards increased levels of longer chain CHCs, a higher proportion of saturated CHCs, and/or greater proportions of straight- *versus* branched-chain CHCs.

Furthermore, CHCs can protect from harmful, cytotoxic sun radiation in combination with other cuticular compounds. Cockroaches are known to even increase their hydrocarbon content in the cuticle upon exposure to UV radiation (Gingrich 1975).

Also the photoperiod or time of day can significantly impact on the CHC phenotype of an insect. In male *D. melanogaster*, CHCs are dynamic traits that vary in response to time of day, and this diurnal pattern is sensitive to light (Gershman et al. 2014; Kent et al. 2007; Krupp et al. 2008). However, while trait values of CHC-based attractiveness in males are highest during day and low throughout the dark phase, females show exactly the opposite temporal pattern (Gershman et al. 2014). Jurenka et al. (1998) used short-day-conditions to induce reproductive diapause in face flies, *Musca autumnalis*. Diapausing flies had lower proportions of alkenes and higher proportions of methyl-branched alkanes compared to reproductive face flies reared under long-day conditions.

Biotic Environmental Factors as Drivers of Insect CHC Phenotypes

CHCs serve a crucial role in protection against pathogen infection. They contribute to formation of a physical barrier which prevents pathogens to penetrate into the insect. Especially fungal pathogens which require some water for germination are impaired by the hydrophobic interaction with CHCs (Hajek and St. Leger 1994). However, some entomopathogenic fungi can rapidly degrade insect CHCs (Napolitano and Juárez 1997) and thus, significantly alter the CHC phenotype of its host within a few hours after infection, depending on the insect species (Lecuona et al. 1991) and the age of the host (Zurek et al. 2002) (Table 2). In addition, other ecto- and endoparasites, (e.g. viruses, mites, tapeworms) or even an artificial immune stimulation may also elicit rapid modifications of CHC profiles (Beros et al. 2017 and references therein; Nielsen and Holman 2012).

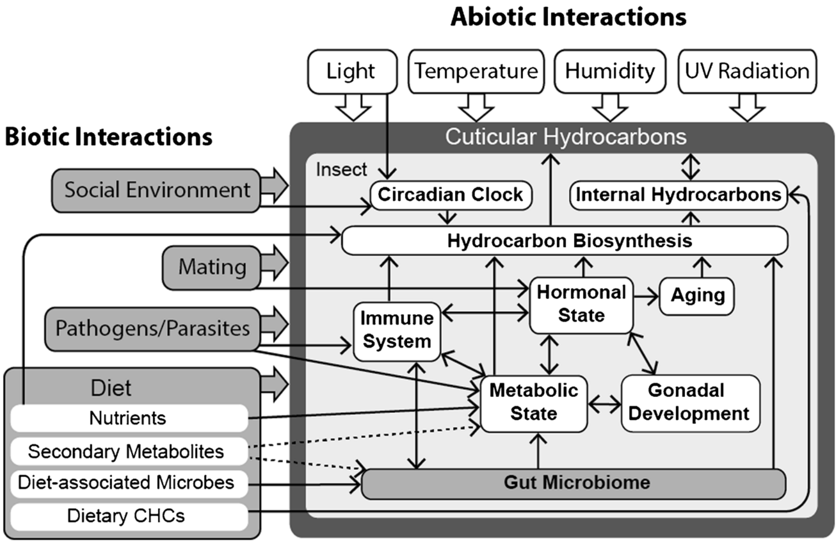

Fig. 1 Scheme of biotic and abiotic environmental triggers and internal effectors of phenotypic plasticity of cuticular hydrocarbons in insects and their interactions

Numerous studies have demonstrated a significant role of diet in phenotypic plasticity of CHCs in various insect orders (Table 2). For example, caterpillars of several lepidopteran species (Espelie and Bernays 1989) and grasshoppers (Blomquist and Jackson 1973) have been shown to incorporate dietary CHCs into their CHC profiles. Caterpillars of some polyphagous species use ingested dietary CHCs to mimic the cuticular chemistry of their actual host plant (chemical phytomimesis) to avoid predation by ants (Akino et al. 2004; Piskorski et al. 2010; Portugal and Trigo 2005;). Dietary effects on the CHC phenotype might also be triggered by varying compositions of CHC precursors in different diet, e.g. fatty acids (Otte et al. 2015; Pennanec'h et al. 1997; Steiger et al. 2007). When the mustard leaf beetle *Phaedon cochleariae* switches to a novel host species, it takes about two weeks until its novel CHC profile significantly differs from the former one (Geiselhardt et al. 2012). Not only herbivorous insects, but also parasitic and predatory insects have been shown to produce different CHC patterns when developing in different host species (e.g. Khidr et al. 2013; Kühbandner et al. 2012).

The type of diet affects the gut microbiome which may also impact on the insect's CHC pattern. Sharon et al. (2010) have demonstrated that *D. melanogaster* flies (Oregon-R) reared on different diets show altered gut microbiomes and divergent CHC phenotypes, which in turn leads to diet-assortative mating because mating in these flies is mediated by their CHC patterns. However, follow-up studies led to inconsistent results about the role of the gut microbiome on mate preference and CHC phenotype (Leftwich et al. 2017; Ward 2017). Ward (2017) found a significant effect of diet on the CHC phenotype of Canton-S flies, but no effect of the gut microbiome on the CHC profile. Moreover, Leftwich et al. (2017) failed to show a significant role of diet or gut microbiome on mate preferences in two wild-type strains (Dahomey and Oregon-R). Thus, the significance of the gut microbiome as a trigger for CHC-mediated behavioral isolation remains ambiguous and needs further investigations.

Not just the type of diet and the depending microbiome, but also the quantity of diet significantly affects the insect's CHC profile. Starvation leads to a significant change in insect CHC patterns (Peschke 1987a, b). In earwigs, which show parental care, the offspring CHC profile signals the nutritional need and thus, affects foraging and reproductive activities of the mother (Mas et al. 2009; Mas and Kölliker 2011). The mother's CHC profile signals the nutritional provision, and thus, affects sibling cannibalism (Wong et al. 2014a).

The encounter of conspecifics can trigger rapid changes of CHC phenotypes. For example, males of *D. serrata* change their CHC profiles within a few minutes after exposure to female flies (Petfield et al. 2005). Moreover, in *D. serrata*, the attractiveness of male CHC profiles depends on the presence and absence of conspecific males and females, and their sex ratio (Gershman et al. 2014; Gershman and Rundle 2016, 2017). Similarly, the CHC profiles of male *D. melanogaster* are also affected upon encounter with conspecifics, and this in turn infers with the diurnal cycle of CHC expression (Kent et al. 2008; Krupp et al. 2008). Furthermore, in orthopteran species, the dominance of rivalling males (Thomas and Simmons 2011), experience of conspecific song (Thomas et al. 2011), and population density (Genin et al. 1986; Heifetz et al. 1998) affect the insect's CHC profile. Biparental burying beetles are able to discriminate between breeding and non-breeding conspecifics based on the CHC profile of their counterpart (Scott et al. 2008; Steiger et al. 2007).

Mating is also known to trigger changes of the CHC phenotype in various insect groups (Table 2). Male rove beetles, *Aleochara curtula*, rapidly (within 30 min) change their CHC profile after onset of copulation (Peschke 1987a). In *D. serrata*, courtship results in a very rapid change in the CHC profile even without physical contact of the partners

Table 1 Environmental (abiotic and biotic) and internal factors affecting cuticular hydrocarbon profiles insects

Factor	Insect taxon	Mode of CHC change	Communicative function	References
Abiotic environmental factors				
Temperature	Orthoptera	Quantitative	–	Gibbs and Mousseau 1994
	Coleoptera	Qualitative/ Quantitative	–	Hadley 1977; Peschke 1987b; Geiselhardt et al. 2006
	Diptera	Quantitative	Sex pheromone	Toolson 1982; Gibbs et al. 1998; Noorman and Den Otter 2002; Savarit and Ferveur 2002; Rouault et al. 2004; Bontonou et al. 2013; Ingleby et al. 2013; Ingleby et al. 2014; Rajpurohit et al. 2017
Humidity	Diptera	Quantitative	–	Noorman and Den Otter 2002; Stinziano et al. 2015
UV radiation	Blattodea	Quantitative		Gingrich 1975
Circadian rhythm/ Light	Diptera	Quantitative	Sex pheromone	Jurenka et al. 1998; Kent et al. 2007; Kent et al. 2008; Krupp et al. 2008; Gershman et al. 2014
Biotic environmental factors				
Pathogens	Coleoptera	Qualitative/ Quantitative	–	Lecuona et al. 1991
	Lepidoptera	Qualitative/ Quantitative	–	Lecuona et al. 1991
	Diptera	Quantitative	Sex pheromone	Zurek et al. 2002
Type of diet	Orthoptera	Qualitative/ Quantitative	–	Blomquist and Jackson 1973; Espelie et al. 1994; Weddle et al. 2012
	Hemiptera	Quantitative	–	Gemeno et al. 2012; Chen et al. 2017
	Hymenoptera	Qualitative/ Quantitative	Sex pheromone	Howard 1998; Howard 2001; Howard and Pérez-Lachaud 2002; Howard and Baker 2003; Kühbandner et al. 2012; Khidr et al. 2013;
	Coleoptera	Qualitative/ Quantitative	Sex pheromone	Steiger et al. 2007; Geiselhardt et al. 2012; Fujiwara-Tsujii et al. 2013; Otte et al. 2015; Otte et al. 2016; Xue et al. 2016
	Lepidoptera	Qualitative/ Quantitative	Phytomimesis	Espelie and Bernays 1989; Akino et al. 2004; Portugal and Trigo 2005; Piskorski et al. 2010
	Diptera	Quantitative	Sex pheromone	Pennanec'h et al. 1997; Stennett and Etges 1997; Etges et al. 2006; Delcourt and Rundle 2011; Fedina et al. 2012; Ingleby et al. 2013; Ingleby et al. 2014; Bousquet et al. 2016; Ward 2017
Diet quantity	Dermaptera	Quantitative	Solicitation pheromone	Mas et al. 2009; Mas and Kölliker 2011; Wong et al. 2014a
	Orthoptera	Quantitative	Sex pheromone	Weddle et al. 2012
	Hymenoptera	Quantitative	Sex pheromone	Howard 1998; Howard and Baker 2003
	Coleoptera	Qualitative/ Quantitative	Sex pheromone	Peschke 1985; Peschke 1987a, b
	Diptera	Quantitative	Sex pheromone	Wicker and Jallon 1995a; Kuo et al. 2012; Lebreton et al. 2016
Commensal bacteria	Diptera	Quantitative	Sex pheromone	Sharon et al. 2010
Social environment	Orthoptera	Quantitative	Phase transition/ Dominance status	Genin et al. 1986; Heifetz et al. 1998; Thomas and Simmons 2009; Thomas et al. 2011; Thomas and Simmons 2011
	Coleoptera	Qualitative	Partner recognition	Steiger et al. 2007; Scott et al. 2008; Steiger et al. 2008
	Lepidoptera	Qualitative	Chemical mimicry	Akino et al. 1999; Elmes et al. 2002; Schönrogge et al. 2004, Thomas et al. 2013
	Diptera	Quantitative	Sex pheromone	

Table 1 (continued)

Factor	Insect taxon	Mode of CHC change	Communicative function	References
				Petfield et al. 2005; Kent et al. 2008; Krupp et al. 2008; Gershman et al. 2014; Gershman and Rundle 2016; Gershman and Rundle 2017
Mating status	Hymenoptera	Quantitative	Reproductive status/ Sex pheromone	Simmons et al. 2003; Mant et al. 2005; Polidori et al. 2017
	Coleoptera	Quantitative	Sex pheromone	Peschke 1987a; Booksmythe et al. 2017
	Diptera	Quantitative	Sex pheromone	Polerstock et al. 2002; Bontonou et al. 2015; Gershman and Rundle 2016; Gershman and Rundle 2017
Insect-internal factors				
Age/ Ontogeny	Plecoptera	Qualitative/ Quantitative	–	Armold et al. 1969
	Dermaptera	Qualitative/ Quantitative	Kin recognition/ Sex pheromone	Wong et al. 2014b
	Orthoptera	Quantitative	–	Tregenza et al. 2000
	Hemiptera	Qualitative/ Quantitative	–	Jackson 1983; Juárez and Brenner 1985; Yoon et al. 2012
	Hymenoptera	Quantitative	Sex pheromone	Howard 1998; Paulmier et al. 1999; Howard and Baker 2003; Steiner et al. 2005; Steiner et al. 2007; Ruther et al. 2011
	Coleoptera	Quantitative	Sex pheromone	Mody et al. 1975; Baker et al. 1979a, b; Peschke 1985, 1987a, b; Hebanowska et al. 1990; Nelson et al. 2003; Yocum et al. 2011; Booksmythe et al. 2017
	Lepidoptera	Quantitative	Sex pheromone	de Renobales and Blomquist 1983; Sappington and Taylor 1990
	Diptera	Quantitative	Sex pheromone	Armold and Regnier 1975; Jackson and Bartelt 1986; Trabalon et al. 1988; Pomonis 1989; Howard et al. 1990; Toolson et al. 1990; Gibbs et al. 1995; Wicker and Jallon 1995a; Gibbs et al. 1998; Mpuru et al. 2001; Polerstock et al. 2002; Nelson and Lee 2004; Zhu et al. 2006; Roux et al. 2008; Fedina et al. 2012; Kuo et al. 2012; Etges and de Oliveira 2014; Braga et al. 2016; Moore et al. 2016
Sexual maturation/ Gonad development	Blattodea	Quantitative	Sex pheromone precursor	Schal et al. 1994
	Hymenoptera	Quantitative	Sex pheromone	Steiner et al. 2005; Steiner et al. 2007; Ruther et al. 2011
	Coleoptera	Quantitative	Sex pheromone	Peschke 1985; Peschke 1987a, b
	Diptera	Qualitative/ Quantitative	Sex pheromone	Dillwith et al. 1983; Wicker and Jallon 1995b; Jurenka et al. 1998; Bilen et al. 2013; Fedina et al. 2017

(Petfield et al. 2005). In addition, successful copulation with sperm transfer has been shown to induce the development of male CHC phenotypes associated with high mating success in this species (Gershman and Rundle 2016). Also both sexes of *D. melanogaster* show altered CHC profiles immediately after mating which is most likely caused by reciprocal physical transfer of CHCs between the sexes (Everaerts et al. 2010). In contrast, Farine et al. (2012) found only a marginal effect of sexual interactions on volatile CHCs ($\leq n$-C23) of *D. melanogaster* flies kept in heterosexual groups for 2 h. However, the sex peptide ACP70A, a component in the seminal fluid of *D. melanogaster*, is involved in down-regulation of the biosynthesis of female sex pheromones (Bontonou et al. 2015). So far, in many cases the effects on CHC phenotypes could not unambiguously be assigned to mating or insemination because differences in ovary development could not be ruled out as an alternative explanation for altered CHC profiles (Booksmythe et al. 2017; Mant et al. 2005; Polidori et al. 2017; Polerstock et al. 2002; Simmons et al. 2003).

Insect-Internal Factors

The composition of the CHC profile of an insect is subjected to dynamic changes during development and ageing of the insect (Moore et al. 2017, and references therein) (Table 1).

Interestingly, phenotypic changes in CHC profiles are not only obvious when comparing different developmental stages, but also occur within the first days after adult eclosion. In several flies (Jackson and Bartelt 1986; Mpuru et al. 2001), parasitic wasps (Ruther et al. 2011; Steiner et al. 2005; Steiner et al. 2007), and in rove beetles (Peschke 1985), newly emerged adults of both sexes have similar CHC phenotypes that diverge and become sex-specific within a week (Table 2). Hence, a change in CHC phenotype in adults is often correlated with sexual maturation and development of the gonads (Dillwith et al. 1983; Fedina et al. 2012, 2017; Schal et al. 1994; Wicker and Jallon 1995b).

Changes in the CHC profile during insect development may be ascribed to changing CHC biosynthesis by the insect (Howard and Blomquist 2005). However, also CHCs of empty dipteran puparia change over time, a process which is due to weathering (Moore et al. 2017). Changes of an insect's CHC profile may be of quantitative nature when biosynthetic activities and thus quantities of CHC compounds vary (e.g. Krupp et al. 2008). But also qualitative changes over time are observed when novel CHC compounds are added to a CHC pattern by the insect's CHC transport activity or CHC biosynthetic activity (e.g. Schal et al. 1994; Steiner et al. 2007). A qualitative change of a CHC pattern may also be due to environmentally dependent changes (weathering) of already produced compounds on the insect's surface.

In summary, the switch from one CHC profile to a novel, adaptive one may take minutes to weeks (Table 2). The dynamics and type of changes might depend on the need of a new CHC phenotype for survival or successful reproduction, as well as on the mechanisms which mount the insect's CHC pattern (Howard and Blomquist 2005). So far, it is difficult to predict which type of environmental stimulus induces a slow change of the CHC profile and which one triggers a highly rapid change.

Mechanisms of Phenotypic Plasticity of CHC Profiles

Rapid changes in insect CHC profiles are expected when an insect obtains CHCs from the environmental substrate and/or from other organisms by physical contact, e.g. during mating (e.g. Weddle et al. 2012). Nevertheless, fast changes in the CHC pattern may not only be possible by acquiring novel CHCs via contact, but may also depend on the dynamics of the transport of ingested CHCs to the cuticle via lipophorins (e.g. Schal et al. 1998).

If the change in an insect's CHC pattern requires a change in CHC biosynthesis, the dynamics of this change will depend on the insect's physiological state (e.g. the dynamics of changes in hormone levels) (Bagnères and Blomquist 2010), the availability of CHC precursors (Steiger et al. 2007; Otte et al. 2015), the uptake of compounds affecting biosynthesis and enzyme activities, and the expression activity of genes encoding the respective enzymes. Krupp et al. (2008) have demonstrated that oenocytes have functional molecular clocks that control the circadian rhythmicity of monoenes by controlling the expression of *desat1*, a gene that encodes a desaturase involved in pheromone biosynthesis of *D. melanogaster.* As mentioned above, several other studies show that abundance of CHCs on the insect's cuticle is dependent on the daytime (or nighttime) when measurements are taken (Gershman et al. 2014; Kent et al. 2007). So far, it is unclear how much the 24-h-temporal pattern of CHC profiles depends on CHC biosynthesis (expression levels of genes, enzyme bioactivities), transport activity of CHCs to the cuticle and/or loss of once produced CHCs due to offprint on the substrate.

Modes of Phenotypic Changes of Insect CHC Profiles

Exposure to different environmental conditions is suggested to result in different modes of phenotypic changes. We distinguish between (A) a stepwise (saltatory) shift and (B) a continuous (gradual) one. The stepwise shift from one CHC pattern to another occurs upon a saltatory environmental change (e.g. switch from one host species to another) and is lacking an adaptive intermediate CHC profile. In contrast, the continuous change of a CHC profile occurs in response to gradual changes of environmental conditions (e.g. increasing temperature) and shows many intermediate, adaptive CHC profiles (West-Eberhard 2003) (Fig. 2).

The stepwise (saltatory) type of plasticity (A) is characterized by a change in the mean CHC phenotype which is produced in (at least) two distinct environments. For example, when herbivorous beetles were exposed to a novel host plant species; they formed a different CHC pattern than conspecifics remaining on the original host plant species. The novel CHC phenotype enabled the beetles to distinguish between mates that had fed on the same plant species from mates feeding on the alternative plant species (Otte et al. 2016). This type-(A)-phenotypic plasticity may be quantified by the mean

Table 2 Dynamics of phenotypic changes in insect cuticular hydrocarbon profiles

Insect species	Trigger	Dynamics of change	References
Drosophila serrata	Courtship	< 15 min[a]	Petfield et al. 2005
Drosophila melanogaster	Courtship/mating	< 15 min[a]	Everaerts et al. 2010
Aleochara curtula	Mating	≤ 30 min	Peschke 1987a
Drosophila melanogaster	Humidity	< 5.5 h	Stinziano et al. 2015; Kwan and Rundle 2010
Ostrinia nubilalis	Fungal infection	< 6 h	Lecuona et al. 1991
Nicrophorus vespilloides	Breeding	< 16 h	Steiger et al. 2008
Drosophila melanogaster	Temperature	≤ 1 day	Savarit and Ferveur 2002
Drosophila melanogaster	Light regime	≤ 1 day	Kent et al. 2008
Melolontha melolontha	Fungal infection	< 1 day	Lecuona et al. 1991
Schistocerca gregaria	Social environment	≤ 1 day	Heifetz et al. 1998
Teleogryllus oceanicus	Social environment	≤ 1 day	Thomas and Simmons 2011
Tenebrio molitor	Immune challenge	1 day	Nielsen and Holman 2012
Oryzaephilus surinamensis	Humidity	1 day	Howard et al. 1995
Dibrachys cavus	Sexual maturation	1–2 days	Ruther et al. 2011
Drosophila melanogaster	Social environment	≤ 2 days	Krupp et al. 2008
Lariophagus distinguendus	Sexual maturation	≤ 3 days	Steiner et al. 2007
Phaedon cochleariae	Diet shift	14 days	Geiselhardt et al. 2012
Eleodes armata	Temperature	≥ 5 weeks	Hadley 1977

[a] time to first contact/mating attempt; estimated based on published courtship behaviors

and variance of phenotypes within a population. A shift in a mean phenotype can occur when all individuals show a similar reaction norm, i.e. respond similarly to a change of an environmental cue. The variance can increase if different genotypes within a population respond differently to the same cue. Hence, type-(A)-phenotypes within a certain environment can show slight differences (but are mostly similar), but type-(A)-phenotypes occurring in two different environments are clearly different and separable (Ingleby et al. 2010).

The continuous (gradual) mode of phenotypic plasticity (B) focuses on a functional relationship between environmental conditions and phenotypes. Here organisms that are exposed to a continuously changing environmental gradient (e.g. increasing temperatures) express continuously different phenotypes (many intermediate phenotypes between different environments). For example, the chain length of CHCs may increase when temperature increases; the elongation of CHC chain length protects the organism from water loss (Geiselhardt et al. 2006). Such adaptation of the CHC pattern to temperature requires high plasticity because changes need to be reversible when temperature decreases again. Indeed, *D. melanogaster* shows reversible temperature-dependent cuticle permeability for an aqueous solution (Wang et al. 2016). However, whether this reversibility is due to a quick change in the chemical composition of the CHC profile has not been addressed in this study.

CHC Phenotypic Plasticity – A Challenge for Intraspecific Communication Via CHCs

Insects which use their CHCs for mediation of intra- and interspecific interactions are indeed challenged by high phenotypic plasticity of the CHC profile because intraspecific chemical communication requires high reliability and comprehensibility of the signals. If signals are not reliable, the receivers will be unable to gain fitness benefits. Moreover, if an expressed CHC phenotype does not match the receiver's preferences or demands, the signal - perceiver system will collapse.

Thus, how can insects successfully use CHCs for intraspecific communication, although these compounds are phenotypically so plastic?

- First, different CHCs or CHC classes might have differential importance for chemical communication (Dani et al. 2005). Thus, when insects change their behaviorally relevant CHC profiles due to different environmental conditions, these changes might be changes in compounds not relevant in intraspecific communication.
- Second, when the alteration of a CHC phenotype is a change in quantities of all behaviorally relevant CHCs, their ratios may stay the same. Here quantities might change, but ratios of informative compounds might be kept the same. Ratios of compounds are well known to play a role in numerous chemically mediated

intraspecific interactions (Geiselhardt et al. 2012; Weiss et al. 2013).

- Finally, if qualitative and quantitative changes in the chemical composition of a CHC profile occur, a mechanism is required to recognize the new CHC phenotype. The insect may recognize a conspecific individual by comparing its own chemical phenotype with the profile of the counterpart ("self-referent phenotype matching", Mateo 2010; Otte et al. 2016; Weddle et al. 2013). Assuming that insects use phenotype matching for recognition of conspecifics, the organisms exposed to the same environmental conditions match the chemical template more exactly than individuals from a different environment expressing an alternative CHC phenotype. This process corresponds with the signal matching process of the sensory drive hypothesis (Boughman 2002; Smadja and Butlin 2009). Thus, "self-referent phenotype matching" might help to cope with variable CHC phenotypes if these are important of intraspecific communication, but will also promote divergence in behavioral interactions (Geiselhardt et al. 2012; Otte et al. 2016).

Evolution of Phenotypic Plasticity of Insect CHC Profiles: Selective Advantages and Consequences

What are the benefits and costs of phenotypic plasticity of insect CHC patterns? An insect benefits from its phenotypic CHC plasticity when a certain phenotype induced by a specific environment has higher fitness in that environment than alternative phenotypes (DeWitt et al. 1998; Henneken et al. 2017; Snell-Rood et al. 2010). A CHC phenotype is expected to show higher fitness

(i) when it has improved abilities to cope with the conditions in this specific environment. As outlined above, many insects can change their CHC phenotype in response to certain abiotic and biotic conditions and thus, improve their abilities to cope with this environment.

(ii) when the costs for production and maintenance of the phenotype do not outweigh the benefit (Reylea 2002). These costs may especially occur when phenotypic plasticity requires continuous availability of the biosynthetic machinery and the maintenance of sensory and regulatory machinery to respond adequately to changing environmental conditions (DeWitt et al. 1998).

(iii) when the dynamics of a change in a CHC profile is fast enough to follow the dynamics of environmental changes inducing a CHC profile. Otherwise costs arise from poor phenotype–environment matching resulting from the time lag between sensing and responding to environmental cues (lag-time limits) (DeWitt et al. 1998).

(iv) when the phenotypic change of the CHC pattern is not outweighed by ecological costs. Which type of ecological costs might an insect need to "pay" when displaying phenotypic plasticity? For example, if an insect changes its CHC profile in response to changing temperatures, the novel profile might disrupt CHC-mediated communication systems (Geiselhardt et al. 2006; Peschke 1987b). If a novel CHC profile would no longer convey reliable and comprehensible information to those insects which communicate via CHCs, these costs would by far exceed the benefits of the adjustment of a CHC profile to a novel environment.

How can phenotypic divergence of CHC profiles affect speciation? If divergence of CHC profiles that affect sexual behavior leads to assortative mating, this might promote sexual isolation. For example, studies of the mustard leaf beetle *P. cochleariae* revealed that these beetles use their CHC profiles for mate recognition. They prefer partners with similar CHC profiles. The beetles show similar profiles when feeding on the same host plant species (Geiselhardt et al. 2009, 2012; Otte et al. 2016). Beetles of a given population of *P. cochleariae* may use different host plant species occurring in the population's habitat; if the beetles show fidelity to a certain host species, their mating preferences for similar CHC phenotypes feeding on the same plant species is expected to lead to genetic divergence and thus, to promote ecological speciation. Such diet-induced changes in CHC profiles that affect mate references have also been observed in other beetle species (Fujiwara-Tsujii et al. 2013; Xue et al. 2016), in *Drosophila* flies (Etges et al. 2006; Havens and Etges 2013; Rundle et al. 2005), and in parasitoid wasps (Howard 2001; Kühbandner et al. 2012). Hence, in these cases

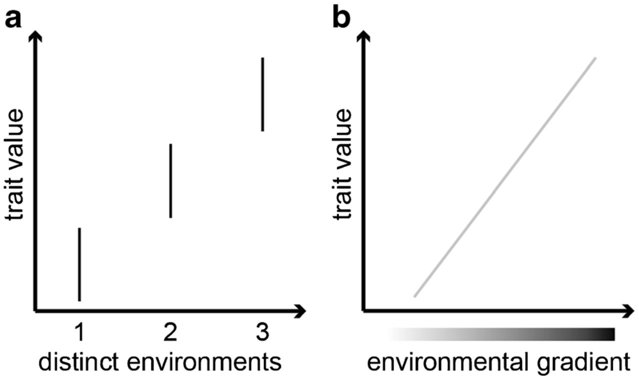

Fig. 2 Scheme of two modes of phenotypic plasticity: **a** stepwise (saltatory) shift from one CHC phenotype to another in individuals experiencing two distinct environments (e.g. different host species); no adaptive intermediate phenotype is formed (black lines) and **b** a continuous (gradual) change of a CHC phenotype in individuals experiencing a gradually changing environment (e.g. increasing temperature); many adaptive intermediate phenotypes are formed (grey line)

phenotypic divergence might promote genetic divergence, and thus finally impact on insect speciation.

Conclusions

A plethora of studies demonstrated the immense plasticity of insect CHC profiles. Nevertheless, further studies are needed on the question why insects use so highly variable chemical signals for intraspecific communication although signal reliability is needed (Henneken et al. 2017; Ingleby 2015; Kather and Martin 2015). These studies will provide a deeper understanding on the evolution of CHC-based mating signals, the respective recognition systems as well as on ecological speciation processes and the impact of phenotype divergence on genetic divergence. Furthermore, even though much knowledge is available on how insects biosynthesize their CHCs, still many questions remain to be answered as to how environmental, especially nutritional factors, influence the biosynthesis of CHCs and its dynamics.

Phenotypic plasticity of insect CHC profiles is favored in changing environments because it allows an individual to adapt its phenotype to novel environmental conditions. Furthermore, plastic CHC phenotypes allow organisms to invade multiple, disparate ecological niches, thus extending the geographic range and decreasing the probability of extinction caused by habitat loss or environmental stochasticity (Snell-Rood et al. 2010). Moreover, if insects use their CHCs for intraspecific communication, phenotypic changes may promote divergence of individuals within a population. If the diverging phenotypes are maintained, ecological speciation will be promoted.

Hence, phenotypic plasticity of insect CHC profiles may greatly impact on the fitness of an insect species, its ecological niche and geographical distribution, and thus on the diversity of insect species that evolve.

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