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Scaling up our understanding of non-consumptive effects in insect systems

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Non-consumptive effects (NCEs) of predators on prey is an important topic in insect ecology with potential applications for pest management. NCEs are changes in prey behavior and physiology that aid in predation avoidance. While NCEs can have positive outcomes for prey survival there may also be negative consequences including increased stress and reduced growth. These effects can cascade through trophic systems influencing ecosystem function. Most NCEs have been studied at small spatial and temporal scales. However, recent studies show promise for the potential to manipulate NCEs for pest management. We suggest the next frontier for NCE studies includes manipulating the landscape of fear to improve pest control, which requires scaling-up to field and landscape levels, over ecologically relevant time frames.

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Introduction

Predator–prey interactions are among the most important topics in insect ecology and have significant implications for pest management. Understanding how arthropod predators alter prey abundance through direct consumption is critical to understanding population structure and community dynamics. However, prey are not defenseless and constantly make adjustments in behavior and physiology to avoid predation [1]. Increasingly, it is apparent that prey also detect and utilize a variety of cues to avoid encounters with predators [2]. Predator-mediated changes in prey biology that do not involve direct consumption are termed non-consumptive effects (hereafter, NCEs). Further understanding of how NCEs alter predator–prey dynamics is particularly needed in managed ecosystems where biological control seeks to manipulate insect natural enemies for pest management [3].

Non-consumptive effects—also referred to as non-lethal effects, risk effects or trait-mediated interactions—are changes in prey biology driven by predation threat. Predator induced NCEs are well studied in aquatic and terrestrial vertebrate systems and can manifest as changes in prey behavior, life history, reproduction, physiology, as well as other phenotypic traits [4]. These diverse predator effects can alter species interactions, and are critical for understanding community and ecosystem dynamics. In fact, NCEs have been shown to be equally or more important in altering prey population dynamics than consumptive effects [4,5]. Far less is known about NCEs in terrestrial insects, although the field is rapidly expanding.

Most of our current knowledge of how insect predators affect insect prey comes from small-scale laboratory or mesocosm experiments over relatively short time scales. In small-scale experiments, NCEs have been shown to have impacts that cascade to non-prey organisms and even further into the ecosystem processes and functions themselves [4]. For example, Hawlena *et al.* described an increase in the body C:N ratio of grasshoppers (*Melanoplus femurrubrum*) in response to hunting spider (*Pisuarina mira*) presence compared to predator-free controls [6••]. The resulting physiologically stressed body carcasses altered soil community function by slowing decomposition of leaf litter in small mesocosms. The indirect effects of insect NCEs could have wide-reaching impacts at the community and ecosystem level, further investigation of this understudied aspect of insect science is critically needed at more realistic scales.

Here we review studies of terrestrial insect NCEs to identify recent advances in the field and knowledge gaps. Given the relative youth of this field, we reviewed studies published within the last five years (n = 34) that examined the NCEs of terrestrial arthropod predators on prey in the absence of lethal encounters. Authors established predator risk to prey in the absence of a lethal encounter by; (1) manipulation of mouthparts (physical removal or gluing them shut), (2) physically isolating predators from prey with a barrier, or (3) by using isolated predator cues (visual models or predator odors). Such studies allow isolation of the impact of fear of predation on prey behavior and biology. Below we discuss ways that insect prey may respond to predation risk, the mechanisms that allow for risk detection, the ecological consequences of these interactions, and implications for using this knowledge to increase pest suppression.

Non-consumptive effects of predators

Insect responses to predation risk

Shifts in insect prey traits in response to predators include behavioral changes [7–11], life history adjustments [12,13•,14], and physiological changes [15–19] (See

Table 1

Behavioral responses to predation risk in studies of non-consumptive effects of arthropod predators on prey in studies from 2012 to 2016. Only significant results were included for simplicity

Response category	Predator spp.	Prey spp.	Measured prey response to predation risk	Reference
Δ Habitat/ resource use	*Lasius niger*	*Bombus terrestris*	Reduced visitation (post-training in the lab)	Ballantyne and Wilmer [7]
	Harmonia axyridis	*Sitobion avenae* & *Rhopalosiphum padi*	Shifted to nutritionally inferior resource/avoided preferred host	Wilson and Leather [30]
	Centipede	*Acheta domesticus*	Increased avoidance (less time spent near predator cue)	Hoefler *et al*. [32]
	Oecophylla smaragdina	*Nomia strigata*	Spent more time examining flowers	Gonzálvez and Rodriguez-Gironés [8]
	Delphastus catalinae	*Bemisia argentifolii*	Increased avoidance (more time spent in enemy-free space)	Lee *et al*. [31]
	Oecophylla smaragdina	*Apis dorsata*	Reduced landings, altered host choice location	Li *et al*. [9]
	Myrmica rubra	*Bombus impatiens*	Decreased pollen removal	Cembrowski *et al*. [41]
	Tenodera sinensis	*Apis mellifera*	Increased avoidance, reduced recruitment dancing	Bray and Nieh [35]
	Linepithema humile	*Apis mellifera*	Reduced acceptance of inflorescences	Sidhu and Rankin [28]
	Modeled after Thomisidae spp.	Various Lepidopterans, Dipterans & Hymeonpterans	Decreased visitation, Increased avoidance	Antiqueira and Romero [38•]
	Tasmanicosa leuckartii	*Helicoverpa armigera*	Increased avoidance (more time spent in enemy-free space)	Rendon *et al*. [15]
Δ Oviposition	*Erythemis simplicicollis, Plathemis Lydia, or Pachydiplax longipennis*	*Aedes albopictus*	Reduced oviposition	Wasserberg *et al*. [24]
	Camponotus & *Cephalotes* spp.	*Eunica bechina*	Reduced oviposition	Sendoya *et al*. [23]
Δ Feeding and activity	*Podisus maculiventris*	*Manduca sexta*	Reduced feeding	Thaler *et al*. [19]
	Tetragnatha elongata	*Popillia japonica* & *Epilachna varivestis*	Reduced feeding	Rypstra and Buddle [20]
	Azteca instabilis	*Margaridisa* spp.	Reduced feeding & visitation	Gonthier [40]
	Vespa velutina Vespa tropica	*Apis crana*	Reduced individual foraging, feeding duration & colony foraging allocation	Tan *et al*. [10]
	Anax spp.	*Ischnura cervula*	Increased activity level	Siepielski *et al*. [11]
	Podisus maculiventris	*Leptinotarsa decemlineata*	Reduced feeding	Hermann and Thaler [36•]
	Podisus maculiventris	*Manduca sexta, Leptinotarsa decemlineata* & *Trichoplusia ni*	Reduced feeding	Kaplan *et al*. [21]
	Podisus maculiventris	*Manduca sexta*	Reduced feeding, increased assimilation efficiency & resting metabolic rate	Thaler *et al*. [22]
	Pisaura mirabilis	Various ants/ parasitoids/aphids	Reduced herbivory (leaf damage)	Bucher *et al*. [26••]
	Hogna frondicola	*Melanoplus borealis*	Reduced feeding	Wineland *et al*. [16]
	Hogna frondicola	*Melanoplus dawsoni*	Reduced feeding, increased avoidance (more time spent in enemy-free space)	Wineland *et al*. [16]
	Cordulegaster boltonii	*Potamophylax* sp.	Increased feeding, more time spent in refuge	Lagrue *et al*. [29]
Δ Dispersal & colonization	*Coccinella septempunctata*	*Rhopalosiphum padi*	Reduced colonization and visitation	Ninkovic *et al*. [25]
	Hippodamia convergens	*Macrosiphum euphorbiae*	Increased dispersal, increased number of nymphs	Kersch-Becker and Thaler [27]