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Scaling up our Understanding of Non-Consumptive Effects in Insect Systems

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Abstract: 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.

Keywords: Non-consumptive effects, trait-mediated interactions, predator-prey interactions, insect behavior, biological control

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. (2012) 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.

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Non-Consumptive Effects of Predators

Insect Responses to Predation Risk

78 Shifts in insect prey traits in response to predators include behavioral changes [7–11], life
79 history adjustments [12–14], and physiological changes [15–19] (See **Table 1 & 2** for behavioral
80 and physiological changes, respectively). The majority of studies to date link NCEs to changes in
81 behavior, including changes in feeding [20–22], oviposition [23,24], colonization or dispersal
82 [25–27], host-plant preference or habitat use [28–30] and increased predator avoidance
83 [31,32]. As a whole, prey tend to respond to predators by modifying their behavior to become
84 less apparent and reduce predator encounters (i.e. less risky). Understanding the mechanisms
85 by which prey detect and respond to predation risk is key to the ability to manipulate NCEs for
86 pest suppression.

87

Mechanisms of Predator Detection

89 Mechanisms for detecting predators with sufficient time/space to avoid predation is essential
90 for prey. This could result in selective pressure favoring eavesdropping behaviors that allow
91 them to respond before a predation event, and conversely for predators to become stealthier.
92 In studies where the mechanism of NCEs is considered, the vast majority focus on chemical
93 cues whereas other mechanisms including visual or tactile cues are currently understudied.
94 Moreover, the potential for multiple mechanisms of predator detection has hardly been
95 considered in insect systems, with only a few studies directly investigating a combination of
96 cues [33–36].

97

98 **Visual Detection of Predators:** Insect visual ability is often underestimated, but has been shown
99 to contribute to predator detection [37]. For example, predator models made to look like crab
100 spiders (Thomisidae) decreased visitation by pollinators to floral resources [38]. In addition,
101 dead ants (*Camponotus* and *Cephalotes*) - dried and pinned to plants - to serve as a visual
102 predator proxy, decreased oviposition by butterflies (*Eunica bechina*) [23]. Other evidence of
103 visual cues driving prey perception of risk has been found by isolating a dragonfly predator
104 (*Anax*) behind a clear barrier, which led to slower growth, reduced escape speed and increased
105 oxidative damage to its damselfly prey (*Enallagma cyathigerum*) [33,34]. The visual ability of
106 insects is not considered to be exceptional and may underestimate its potential to play a role in
107 NCEs, especially for juvenile insects. However, visual cues could provide important information
108 in conjunction with other predator cues and should not be discounted.

109

110 **Chemical Detection of Predators:** It is well established that insect predators use chemical cues
111 to locate prey [39] and more recently it has been shown that prey have the ability to eavesdrop
112 on predator chemical cues [8,32,36,40]. Studies examining the role of chemical cues in NCEs
113 have investigated isolated semiochemicals [9,28], chemicals associated with consuming
114 conspecifics [33], footprints or previous foraging of predators [41], and crushed predators
115 applied to plants as a slurry [40]. Using an experimental arena where predators had previously
116 foraged and were subsequently removed, researchers can isolate specific contact chemical cues
117 as a source of information for prey. For example, one experiment revealed significantly fewer
118 bird cherry-oat aphids (*Rhopalosiphum padi*) colonize plants where the ladybeetle predators

(*Coccinella septempunctata*) had previously foraged relative to control plants [25]. Furthermore, the potential for volatile cues to affect prey behavior has been demonstrated by observing Colorado potato beetle (*Leptinotarsa decemlineata*) feeding behavior while under a constant airflow containing volatiles from their stink bug predator (*Podisus maculiventris*). Here, beetle feeding was significantly reduced compared to beetles feeding under a blank airflow which suggests that beetles are capable of detecting and responding to specific volatile chemical cues just as they would to the physical presence of the predator [36].

Interestingly, even predator byproducts have been shown as a source of predator chemical information for prey. A series of small-scale field experiments examined whether spider silk could affect the feeding behaviors of two agricultural pests, the Japanese beetle (*Popillia japonica*) and the Mexican bean beetle (*Epilachna varivestisi*). Herbivory was measured in response to strands of silk from the spider (*Tetragnatha elongate*) as a proxy for predation pressure, compared to no silk and silkworm (*Bombyx mori*) silk controls (controlling for potential tactile or visual cues) in bush style snap-bean (*Phaseolus vulgaris*) fields. A significant reduction in plant damage was found when spider silk was present, suggesting that manipulating NCEs can have implications for crop protection [20]. NCEs have diverse consequences on focal prey but the cascading effects that may occur as a result of NCEs influence target prey, their hosts and other key players within the community. While early evidence is promising, larger field-scale studies that span a growing season are necessary to understand long-term effects and potential benefits to crop yield.

Ecological Consequences of Non-Consumptive Effects

Trophic Interactions

Although NCEs are typically evaluated in a manner that emphasizes prey responses, the ecological consequences of NCEs can cascade through trophic systems. Predators can influence food web dynamics by direct consumption of prey [42] (**Figure 1**). As a result, there can be indirect changes mediated by prey removal, which are beneficial to the prey's host plant (depicted by the double lined arrows, **Figure 1a**). Trophic dynamics resulting from NCEs increase the complexity of interactions, as there can be either positive or negative effects of the predator on prey, the prey's host plant and possibly even from the prey on the predator itself (depicted by the double lined arrows, **Figure 1b**). These indirect interactions may have particularly important effects that can add to our understanding of how biological control agents impacts pests. For example, the presence of the convergent ladybeetle (*Hippodamia convergens*) risk predators, which are commonly used biological control agents, reduced the population growth of potato aphids (*Macrosiphum euphorbiae*) without direct consumption. Further, the presence of the predators also lead to an increase in the formation of winged prey, indicating preparation for dispersal away from the host plant. Increased dispersal in response to predator risk can have an indirect benefit on the host plant by reducing the probability of negative pest impacts. The indirect impact on the host plant was not measured in the aforementioned study, however, there are an increasing number of studies that attribute trophic cascades to NCEs. For example, Antiqueira & Romero (2016) examined the possibility for indirect effects driven by behavioral changes in pollinator response to models of predatory crab spiders (after Thomisidae). Visual models alone resulted in decreased visitation by

pollinators which led to a 33% reduction in fruit biomass and a 28% reduction in seed production [38]. Clearly, predators can play a large role in regulating prey host seeking behaviors and thus have a large effect on lower trophic levels [42].

In addition to affecting pollinator visitation, predation risk can also alter prey host plant choice in ways that affect plant communities [43]. The ability to sense predator cues on plants where potential threat level is the highest allows prey to modify their choice of host plant, which may lead to a selection tradeoff between safe and nutritious host plants. For example, grasshopper prey (*Melanoplus femurrubrum*) were shown to switch from preferred grasses to less nutritive forbs in the presence of risk spider predators (*Pisaurina mira*) in field mesocosms [43]. The observed habitat shifts have strong impacts on both the preferred host (increased biomass from lack of grasshopper damage) as well as the less-suitable host (decreased biomass). These community level changes may increase competition for insects that seek refuge in new habitats or even change nutrient dynamics through altered plant abundance and composition [6].

Landscape Level Considerations

Landscape structure has a well-known influence on communities of beneficial, natural enemies and their impact on prey populations. Habitats with a high level of plant diversity harbor an increased abundance and diversity of predatory and parasitic natural enemies [44]. Increased habitat diversity at the local landscape scale also leads to a decrease in prey abundance [45]. What remains unclear is the role of NCEs in these relationships. Since we know predator communities change with landscape structure, it is important to understand how associated

NCEs may also change and how prey may respond. If key mechanisms of NCEs are understood, it may be possible to manipulate cues to create a landscape of fear for pest species.

The landscape of fear is defined as varying levels of predation risk that prey perceive across space, often depicted as peaks and valleys of threat versus safety [46]. As prey seek enemy free space, i.e. safe places to feed, oviposit, and rest [47], their distribution in the landscape is altered to facilitate predator avoidance. For vertebrates, it has been demonstrated that spatial and temporal land use by prey is driven by fear of predation [48]. This can result in parts of the landscape where resources may be over or under exploited. To date, there has been no study that has attempted to understand or manipulate similar landscape of fear in an insect system.

In order to understand the impact of habitat and landscape factors on insect NCEs, studies done in open field settings are necessary. Behavioral observations of pests, coupled with yield measurements may help to illustrate the impact of landscape on pest management. Since NCEs do not necessarily lead to reduced pest populations but can reduce pest pressure, surveys of pest abundance across landscape may not capture the net effect of predators on prey and the impact of those interactions on crops. In addition, some landscape factors may also influence the strength of the response a given prey has to its predator. For example, if more refuges or alternative habitats are available in a complex landscape, the strength of NCEs on prey may be reduced since the refuge provides added safety. Understanding the impact of landscape factors on trophic interactions will allow for better predictions of the strength and outcome of insect predator-prey interactions in managed and natural systems.

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Arguments for Scaling-Up

209 Current studies of insect NCEs largely focus on short time scales in laboratory settings. Of the
210 studies we reviewed, 41% were completed solely in a laboratory setting, 35% were performed
211 in the field, less than 1% in a greenhouse and 20% used a combination of settings (see **S1** for a
212 table indicating both the experimental setting and the length of experiments within each
213 reviewed study). In order to investigate potential cascading effects as a result of NCEs, there is a
214 need to increase studies that combine meaningful laboratory/greenhouse results and
215 investigate them in open field settings. By investigating the spatial and temporal scale of
216 predator risk effects on prey populations, as well as the resulting effects on plants, we can
217 gather essential insights into important community dynamics as well as possible non-target
218 effects. Additionally, the consumptive effect of predators has a relatively short range effect on
219 prey populations since it is limited to the area within a habitat that predators physically reach.
220 NCEs of predators, however, have the potential to be farther reaching if predator cues can be
221 detected by prey at a distance. Yet, the effective spatial scale of predator cues and NCEs in
222 terrestrial insect systems has not yet been investigated.

223 In addition to spatial scale, the temporal scale of predator cues is understudied. Only 32% of
224 papers reviewed were on a time scale that lasted longer than one week (see **S1**). Furthermore,
225 over 50% of the reviewed studies performed experiments that lasted 24 hours or less. By
226 limiting experiments in both space and time, our current understanding of cue persistence, and
227 potential prey habituation are nearly absent. Understanding the temporal dynamics of these
228 interactions in a field setting is essential if NCEs are to be useful as an alternative pest

management strategy. Further, by scaling up our understanding of NCEs to larger spatial and temporal scales, we can then ask how habitat and landscape diversity may influence these interactions.

Conclusions

Evidence for influences of NCEs in insect systems is growing. However, spatial and temporal scales of previous work is limited. More work in terrestrial insect systems where insects are both predators and prey is needed to elucidate effects of scale. Studies in agroecological systems would be particularly crucial, as farmers are increasingly manipulating habitats to increase predator abundance and improve pest suppression through consumptive effects of natural enemies [49]. However, there has been no attempt to manipulate pest communities and alter species interactions through the landscape of fear by taking advantage of NCEs.

We know insects use visual and chemical cues to assess habitat suitability, and pest taxa likely have similar mechanisms to detect habitats/landscapes with increased predation risk. Identifying specific cues that elicit prey fear will allow us to better understand systems and begin manipulating them. There is also the potential to utilize chemical cues, predator mimics, or crop planting patterns that signal increased predator risk and reduce pest damage. In push-pull pest management, plant defensive chemistry or pest alarm pheromones can be manipulated to repel, or push, pests away from a crop while plant-derived attractants or alternative attractive hosts act to pull pests away from the crop plants. Predator cues have yet to be used in these systems to alter behavior or physiology of pests but could be applied as an alternative tool for pest management in push-pull systems [50].

251

252 In addition, multiple predator cues (visual, chemical, vibrational) could have additive effects on
253 prey and should be investigated further. While visual cues that provide information about
254 habitat suitability could be recognized at larger scales, visual information about predator
255 presence is likely more localized. The distance over which chemical cues play a role is also
256 unclear but has the potential provide information from a distance. More research on the
257 mechanism that drives NCEs across terrestrial insect systems as well as their temporal and
258 spatial effectiveness is needed to determine if the use of predator cues that influence the
259 behavior and physiology of pests, coupled with habitats that maintain or enhance consumptive
260 effects could provide the infrastructure for sustainably pest-suppressive landscapes [51].

261

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References and Recommended Reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Sih A: **Antipredator responses and the perception of danger by mosquito larvae.** *Ecology* 1986, 67:434–441.
 2. Turner AM, Bernot RJ, Boes CM: **Chemical cues modify species interactions: the ecological consequences of predator avoidance by freshwater snails.** *Oikos* 2000, 88:148–158.
 3. Hajek AE: *Natural Enemies: an introduction to biological control.* Cambridge University Press; 2004.
 4. Werner E, Peacor S: **A Review of Trait-Mediated Indirect Interactions in Ecological Communities.** *Ecology* 2003, 84:1083–1100.
 5. Preisser E, Bolnick D, Benard M: **Scared to death? The effects of intimidation and consumption in predator-prey interactions.** *Ecology* 2005, 86:501–509.
 6. Hawlena D, Strickland MS, Bradford M a., Schmitz OJ: **Fear of predation slows plant-
•• litter decomposition.** *Science* 2012, 336:1434–1438.
- This study found a physiological stress response in grasshoppers reared with risk spiders that increases grasshopper body C:N ratio compared. Further, while this alteration in physiology did not change the decomposition time of grasshopper bodies themselves, the stressed body carcasses altered soil community function by slowing plant mineralization/decomposition of leaf litter in the experimental arena.
7. Ballantyne G, Willmer P: **Floral visitors and ant scent marks: Noticed but not used?** *Ecological Entomology* 2012, 37:402–409.
 8. González FG, Rodríguez-Gironés MA: **Seeing is believing: information content and behavioural response to visual and chemical cues.** *Proc R Soc B* 2013, 280:20130886
 9. Li J, Wang Z, Tan K, Qu Y, Nieh JC: Giant Asian honeybees use olfactory eavesdropping to detect and avoid ant predators. *Anim. Behav.* 2014, 97:69–76.
 10. Tan K, Hu Z, Chen W, Wang Z, Wang Y, Nieh JC: **Fearful foragers: honey bees tune colony and individual foraging to multi-predator presence and food quality.** *PLoS One* 2013, 8(9):e75841.
 11. Siepielski AM, Wang J, Prince G: **Nonconsumptive predator-driven mortality causes natural selection on prey.** *Evolution* 2014, 68:696–704.
 12. Elliott KH, Betini GS, Dworkin I, Norris DR: **Experimental evidence for within- and cross-seasonal effects of fear on survival and reproduction.** *J. Anim. Ecol.* 2015, 85:507–515.
 13. Xiong X, Michaud JP, Li Z, Wu P, Chu Y, Zhang Q, Liu X: **Chronic, predator-induced stress
• alters development and reproductive performance of the cotton bollworm, *Helicoverpa armigera*.** *BioControl* 2015, 60:827–837.
- This study showed significant life history and physiological implications (increased weight, wing deformity, development, and fecundity as well as reduced survival) associated with NCEs over multiple generations of exposure in an agriculturally relevant system.
14. Sitvarin MI, Breen K, Rypstra AL: **Predator cues have contrasting effects on lifespan of *Pardosa milvina* (Araneae: Lycosidae).** *J. Arachnol.* 2015, 43:107–110.
 15. Rendon D, Whitehouse MEA, Taylor PW: **Consumptive and non-consumptive effects of**

- wolf spiders on cotton bollworms. *Entomol. Exp. Appl.* 2016, 158:170–183.
16. Wineland SM, Kistner EJ, Joern A: **Non-consumptive interactions between grasshoppers (Orthoptera: Acrididae) and wolf spiders (Lycosidae) produce trophic cascades in an old-field ecosystem.** *J. Orthoptera Res.* 2015, 24:41–46.
 17. Kaplan I, Thaler JS: **Phytohormone-mediated plant resistance and predation risk act independently on the population growth and wing formation of potato aphids, *Macrosiphum euphorbiae*.** *Arthropod. Plant. Interact.* 2012, 6:181–186.
 18. Janssens L, Stoks R: **Chronic predation risk reduces escape speed by increasing oxidative damage: A deadly cost of an adaptive antipredator response.** *PLoS One* 2014, 9:1–6.
 19. Thaler JS, McArt SH, Kaplan I: **Compensatory mechanisms for ameliorating the fundamental trade-off between predator avoidance and foraging.** *Proc. Natl. Acad. Sci.* 2012, 109:12075–12080.
 20. Rypstra AL, Buddle CM: **Spider silk reduces insect herbivory.** *Biol. Lett.* 2013, 9.
 21. Kaplan I, McArt SH, Thaler JS: Plant defenses and predation risk differentially shape patterns of consumption, growth, and digestive efficiency in a guild of leaf-chewing insects. *PLoS One* 2014, 9:20120948.
 22. Thaler JS, Contreras H, Davidowitz G: **Effects of predation risk and plant resistance on *Manduca sexta* caterpillar feeding behaviour and physiology.** *Ecol. Entomol.* 2014, 39:210–216.
 23. Sendoya F, Freitas VL, Oliveira PS: **Egg-laying butterflies distinguish predaceous ants by sight.** 2015, 174:134–140.
 24. Wasserberg G, White L, Bullard A, King J, Maxwell R: **Oviposition site selection in *Aedes albopictus* (Diptera: Culicidae): are the effects of predation risk and food level independent?** *J. Med. Entomol.* 2013, 50:1159–1164.
 25. Ninkovic V, Feng Y, Olsson U, Pettersson J: **Ladybird footprints induce aphid avoidance behavior.** *Biol. Control* 2013, 65:63–71.
 26. Bucher R, Menzel F, Entling MH: **Risk of spider predation alters food web structure and ●● reduces local herbivory in the field.** *Oecologia* 2015, 178:571–577.
- The authors demonstrated that predator cues (bagged spiders, removed prior to 3-day long surveys) can affect the overall colonizing community of prey in an open field setting which resulted in reduced leaf damage of the host plant.
27. Kersch-Becker MF, Thaler JS: **Plant resistance reduces the strength of consumptive and non-consumptive effects of predators on aphids.** *J. Anim. Ecol.* 2015, 84:1222–1232.
 28. Sidhu SC, Wilson Rankin EE: **Honey bees avoiding ant harassment at flowers using scent cues.** *Environ. Entomol.* 2016, 45:420–426.
 29. Lagrue C, Besson AA, Lecerf A: **Interspecific differences in antipredator strategies determine the strength of non-consumptive predator effects on stream detritivores.** *Oikos* 2015, 124:1589–1596.
 30. Wilson MR, Leather SR: **The effect of past natural enemy activity on host-plant preference of two aphid species.** *Entomol. Exp. Appl.* 2012, 144:216–222.
 31. Lee DH, Nyrop JP, Sanderson JP: **Non-consumptive effects of the predatory beetle *Delphastus catalinae* (Coleoptera: Coccinellidae) on habitat use patterns of adult whitefly *Bemisia argentifolii* (Hemiptera: Aleyrodidae).** *Appl. Entomol. Zool.* 2014, 49:599–606.

32. Hoefler CD, Durso LC, McIntyre KD: **Chemical-mediated predator avoidance in the european house cricket (*Acheta domesticus*) is modulated by predator diet.** *Ethology* 2012, 118:431–437.
 33. Janssens L, Stoks R: **Synergistic effects between pesticide stress and predator cues: Conflicting results from life history and physiology in the damselfly *Enallagma cyathigerum*.** *Aquat. Toxicol.* 2013, 132–133:92–99.
 34. Janssens L, Stoks R: **Predation risk causes oxidative damage in prey.** *Biol. Lett.* 2013, 9:20130350.
 35. Bray A, Nieh J: **Non-consumptive predator effects shape honey bee foraging and recruitment dancing.** *PLoS One* 2014, 9(1):e87459.
 36. Hermann S, Thaler J: **Prey perception of predation risk: volatile chemical cues mediate**
 - **non-consumptive effects of a predator on a herbivorous insect.** *Oecologia* 2014, 176:669–676.
- This study identified the mechanism for prey detection and behavioral response to predators in an agriculturally relevant system. Experiments show that isolated volatile chemical cues from predators alter the feeding behavior of prey that leads to reduced herbivory similar to that caused by the presence of a non-lethal or risk predator.
37. Sendoya SF, Freitas AVL, Oliveira PS: **Ants as selective agents on herbivore biology: effects on the behaviour of a non-myrmecophilous butterfly.** *J. Anim. Ecol.* 1996, 65:205–210.
 38. Antiqueira PAP, Romero GQ: **Floral asymmetry and predation risk modify pollinator**
 - **behavior, but only predation risk decreases plant fitness.** *Oecologia* 2016, 181:475–485.
- This study illustrated a significant cascading effect of NCEs by placing spider models on observing subsequent pollinator behavior in response to the predator visual cue. Pollinator visitation was reduced and increased avoidance of plants with visual predator models were observed, which led to a decrease in fruit biomass as well as reduced seed production.
39. Hatano E, Kunert G, Michaud JP, Weisser WW: **Chemical cues mediating aphid location by natural enemies.** *Eur. J. Entomol.* 2008, 105:797–806.
 40. Gonthier DJ: **Do herbivores eavesdrop on ant chemical communication to avoid predation?** *PLoS One* 2012, 7:e28703.
 41. Cembrowski AR, Tan MG, Thomson JD, Frederickson ME: **Ants and ant scent reduce bumblebee pollination of artificial ants and ant scent reduce bumblebee pollination of artificial flowers.** *Am. Nat.* 2014, 183:133–139.
 42. Hairston NG, Smith FE, Lawrence: **Community structure, population control, and competition.** *Am. Nat.* 1960, 94:421–425.
 43. Schmitz OJ: **Direct and indirect effects of predation and predation risk in old-field interaction webs.** *Am. Nat.* 1998, 151:327–42.
 44. Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C: **Landscape perspectives on agricultural intensification and biodiversity on ecosystem service management.** *Ecol. Lett.* 2005, 8:857–874.
 45. Gardiner MM, Landis DA, Gratton C, Schmidt N, O’Neal M, Mueller E, Chacon J, Heimpel GE, Difonzo CD: **Landscape composition influences patterns of native and exotic lady beetle abundance.** *Divers. Distrib.* 2009, 15:554–564.
 46. Laundre JW, Hernandez L, Ripple WJ: **The landscape of fear: ecological implications of being afraid.** *Open Ecol. J.* 2010, 3:1–7.

- 401 47. Jeffries MJ, Lawton JH: **Enemy free space and the structure of ecological communities.**
402 *Biol. J. Linn. Soc.* 1984, 23:269–286.
- 403 48. Laundré JW, Hernández L, Altendorf KB: **Wolves, elk, and bison: reestablishing the**
404 **“landscape of fear” in Yellowstone National Park, U.S.A.** *Can. J. Zool.* 2001, 79:1401–
405 1409.
- 406 49. Gurr G, Wratten SD, Landis DA: **Habitat management to suppress pest populations:**
407 **progress and prospects.** *Annu. Rev. Entomol.* 2017, 62, *in press*.
- 408 50. Landis DA: **Designing agricultural landscapes for biodiversity-based ecosystem services.**
409 *Basic Appl. Ecol.* 2016, doi:10.1016/j.baee.2016.07.005, *in press*.
- 410

Figure 1. Food web dynamics considering consumptive effects of predators (a.) and non-consumptive effects of predators (b.). Solid lines indicate consumptive effects while dashed lines indicate behavioral/trait changes and double lines indicate indirect effects. Modified from Schmitz et al. 1998.

Table 1. Behavioral responses to predation risk in studies of non-consumptive effects of arthropod predators on prey in studies from 2012-16. Only significant results were included for simplicity.

Response Category	Predator spp.	Prey spp.	Measured Prey Response to Predation Risk	Reference
Δ Habitat/Resource Use	<i>Lasius niger</i>	<i>Bombus terrestris</i>	Reduced visitation (post-training in the lab)	Ballantyne & Wilmer 2012, [7]
	<i>Harmonia axyridis</i>	<i>Sitobion avenae</i> & <i>Rhopalosiphum padi</i>	Shifted to nutritionally inferior resource/avoided preferred host	Wilson & Leather 2012, [20]
	<i>centipede</i>	<i>Acheta domesticus</i>	Increased avoidance (less time spent near predator cue)	Hoefler et al. 2012, [32]
	<i>Oecophylla smaragdina</i>	<i>Nomia strigata</i>	Spent more time examining flowers	González & Rodríguez-Gironés 2013, [8]
	<i>Delphastus catalinae</i>	<i>Bemisia argentifolii</i>	Increased avoidance (more time spent in enemy-free space)	Lee et al. 2014, [31]
	<i>Oecophylla smaragdina</i>	<i>Apis dorsata</i>	Reduced landings, altered host choice location	Li et al. 2014, [9]
	<i>Myrmica rubra</i>	<i>Bombus impatiens</i>	Decreased pollen removal	Cembrowski et al. 2014, [41]
	<i>Tenodera sinensis</i>	<i>Apis mellifera</i>	Increased avoidance, reduced recruitment dancing	Bray & Nieh 2014, [35]
	<i>Linepithema humile</i>	<i>Apis mellifera</i>	Reduced acceptance of inflorescences	Sidhu & Rankin 2016, [28]
	modeled after Thomisidae spp.	Various Lepidopterans, Dipterans & Hymenopterans	Decreased visitation, Increased avoidance	Antiqueira & Romero 2016, [38]

Δ	Oviposition	<i>Tasmanicosa leuckartii</i>	<i>Helicoverpa armigera</i>	Increased avoidance (more time spent in enemy-free space)	Rendon et al. 2016, [15]
		<i>Erythemis simplicicollis</i> , <i>Plathemis Lydia</i> , or <i>Pachydiplax longipennis</i>	<i>Aedes albopictus</i>	Reduced oviposition	Wasserberg et al. 2013, [24]
		<i>Camponotus</i> & <i>Cephalotes spp.</i>	<i>Eunica bechina</i>	Reduced oviposition	Sendoya et al. 2015, [23]
Δ	Feeding and Activity	<i>Podisus maculiventris</i>	<i>Manduca sexta</i>	Reduced feeding	Thaler et al. 2012, [19]
		<i>Tetragnatha elongata</i>	<i>Popillia japonica</i> & <i>Epilachna varivestis</i>	Reduced feeding	Rypstra & Buddle 2012, [20]
		<i>Azteca instabilis</i>	<i>Margaridisa spp</i>	Reduced feeding & visitation	Gonthier 2012, [40]
		<i>Vespa velutina</i> <i>Vespa tropica</i>	<i>Apis crana</i>	Reduced individual foraging, feeding duration & colony foraging allocation	Tan et al. 2013, [10]
		<i>Anax spp.</i>	<i>Ischnura cervula</i>	Increased activity level	Siepielski et al. 2013, [11]
		<i>Podisus maculiventris</i>	<i>Leptinotarsa decemlineata</i>	Reduced feeding	Hermann & Thaler 2014, [36]
		<i>Podisus maculiventris</i>	<i>Manduca sexta</i> , <i>Leptinotarsa decemlineata</i> & <i>Trichoplusia ni</i>	Reduced feeding	Kaplan et al. 2014, [21]
		<i>Podisus maculiventris</i>	<i>Manduca sexta</i>	Reduced feeding, increased assimilation efficiency & resting metabolic rate	Thaler et al. 2014, [22]
		<i>Pisaura mirabilis</i>	Various Ants/Parasitoids/Aphids	Reduced herbivory (leaf damage)	Bucher et al. 2015, [26]
		<i>Hogna frondicola</i>	<i>Melanoplus borealis</i>	Reduced feeding	Wineland et al. 2015, [16]

Δ Dispersal & Colonization	<i>Hogna frondicola</i>	<i>Melanoplus dawsoni</i>	Reduced feeding, increased avoidance (more time spent in enemy-free space)	Wineland et al. 2015, [16]
	<i>Cordulegaster boltonii</i>	<i>Potamophylax sp.</i>	Increased feeding, more time spent in refuge	Lagrue et al. 2015, [29]
	<i>Coccinella septempunctata</i>	<i>Rhopalosiphum padi</i>	Reduced colonization and visitation	Ninkovic et al. 2013, [25]
	<i>Hippodamia convergens</i>	<i>Macrosiphum euphorbiae</i>	Increased dispersal, increased number of nymphs	Kersch-Becker & Thaler 2015, [27]

Table 2. Physiological responses to predation risk in studies of non-consumptive effects of arthropod predators on prey in studies from 2012-16. Only significant results were included for simplicity, two studies reported no effect on physiology in their experiment [21,22].

Response category	Predator spp.	Prey spp.	Measured Prey Response to Predation Risk	Reference
Δ Growth and Development	<i>Hippodamia convergens</i>	<i>Macrosiphum euphorbiae</i>	Increased alate production	Kaplan & Thaler 2012, [17]
	<i>Anax spp.</i>	<i>Enallagma cyathigerum</i>	Reduced growth rate, increased oxidative damage	Janssens & Stoks 2013a, [33]
	<i>Anax spp.</i>	<i>Enallagma cyathigerum</i>	Reduced growth rate, reduced oxygen intake	Janssens & Stoks 2013b, [34]
	<i>Harmonia axyridis</i>	<i>Helicoverpa armigera</i>	Increased development, weight (pupae), wing deformity (1st gen), & fecundity (3rd gen); reduced survival (3rd gen)	Xiong et al. 2015, [13]
	<i>Tasmanicosa leuckartii</i>	<i>Helicoverpa armigera</i>	Increased time spent in pupal stage	Rendon et al. 2016, [15]
	<i>Tenodera sinensis</i>	<i>Drosophila melanogaster</i>	Breeding: offspring developed faster and weighed less. Non-breeding: Increased mortality, decreased body mass, surviving flies had lower fecundity and fewer, lighter offspring.	Elliot et al. 2016, [12]
Δ Body Composition and Assimilation	<i>Pisuarina mira</i>	<i>Melanoplus femurrubrum</i>	Increased body C:N ratio	Hawlena et al. 2012, [6]
	<i>Podisus maculiventris</i>	<i>Manduca sexta</i>	Increased assimilation efficiency (short term), decreased assimilation efficiency (long term), decreased glycogen levels	Thaler et al. 2012, [19]
	<i>Podisus maculiventris</i>	<i>Manduca sexta</i>	Increased assimilation efficiency	Kaplan et al. 2014, [21]
	<i>Anax spp.</i>	<i>Enallagma cyathigerum</i>	Increased oxidative damage, decreased escape performance (reduced escape	Janssens & Stoks 2014, [18]

			speed)	
Δ Survival and Mortality	<i>Anax spp.</i>	<i>Ischnura cervula</i>	Increased mortality and size	Siepielski et al. 2013, [11]
	<i>Tigrosa helluo</i>	<i>Pardosa milvina</i>	Reduced lifespan of females (compared to ground beetle predator cues but not to control)	Sitarvin et al. 2015, [14]
	<i>Hogna frondicola</i>	<i>Melanoplus dawsoni</i> & <i>Melanoplus borealis</i>	Reduced survival	Wineland et al. 2015, [16]