CONCEPTS & SYNTHESIS
EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

Ecology, 101(12), 2020, e03152

A framework and standardized terminology to facilitate the study of predation-risk effects

Scott D. Peacor,[1,6] Brandon T. Barton,[2] David L. Kimbro,[3] Andrew Sih,[4] and Michael J Sheriff[5]

[1]*Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824 USA*
[2]*Department of Biological Sciences, Mississippi State University, Mississippi State, Mississippi 39762 USA*
[3]*Department of Marine and Environmental Science, Northeastern University, Nahant, Massachusetts 01908 USA*
[4]*Department of Environmental Science and Policy, University of California Davis, Davis, California 95616 USA*
[5]*Biology Department, University of Massachusetts Dartmouth, Dartmouth, Massachusetts 20747 USA*

Citation: Peacor, S. D., B. T. Barton, D. L. Kimbro, A. Sih, and M. J. Sheriff. 2020. A framework and standardized terminology to facilitate the study of predation-risk effects. Ecology 101(12):e03152. 10.1002/ecy.3152

Abstract. The very presence of predators can strongly influence flexible prey traits such as behavior, morphology, life history, and physiology. In a rapidly growing body of literature representing diverse ecological systems, these trait (or "fear") responses have been shown to influence prey fitness components and density, and to have indirect effects on other species. However, this broad and exciting literature is burdened with inconsistent terminology that is likely hindering the development of inclusive frameworks and general advances in ecology. We examine the diverse terminology used in the literature, and discuss pros and cons of the many terms used. Common problems include the same term being used for different processes, and many different terms being used for the same process. To mitigate terminological barriers, we developed a conceptual framework that explicitly distinguishes the multiple predation-risk effects studied. These multiple effects, along with suggested standardized terminology, are risk-induced trait responses (i.e., effects on prey traits), interaction modifications (i.e., effects on prey–other-species interactions), nonconsumptive effects (i.e., effects on the fitness and density of the prey), and trait-mediated indirect effects (i.e., the effects on the fitness and density of other species). We apply the framework to three well studied systems to highlight how it can illuminate commonalities and differences among study systems. By clarifying and elucidating conceptually similar processes, the framework and standardized terminology can facilitate communication of insights and methodologies across systems and foster cross-disciplinary perspectives.

Key words: behaviorally mediated trophic cascade; ecology of fear; higher-order interaction; interaction modification; nonconsumptive; nonlethal effects; non-trophic interaction; phenotypic plasticity; predation-risk effects; sublethal effects; trait-mediated effects.

Introduction

The study of predation-risk effects, under the envelope of such terms as nonconsumptive effects, ecology of fear, trait-mediated indirect interactions, and nonlethal effects, has exploded in recent decades. The underlying concept is that prey modify flexible traits, such as growing thicker shells, being more vigilant, or increasing refuge use, as a function of predation risk (Lima and Dill 1990). While these trait responses can have an overall positive effect on prey fitness by reducing predation risk, they are typically associated with a trade-off that has a negative effect on fitness of the prey, such as growth or reproduction (Abrams 1984, Brown 1988, Houston et al. 1993, Lima 1998*a*, *b*, Werner et al. 1983). Further, the flexible trait responses of prey may affect other species including resources, competitors, and predators of the prey (Werner and Peacor 2003, Sih et al. 1998). The large number of well-cited reviews on this topic (Sih 1987, Lima and Dill 1990, Peckarsky et al. 2008, Schmitz et al. 2004, Miner et al. 2005,

Manuscript received 12 September 2019; revised 14 March 2020; accepted 8 June 2020. Corresponding Editor: Joel C. Trexler.
[6] E-mail: peacor@msu.edu

Preisser et al. 2005, Creel and Christianson 2008, Heithaus et al. 2008, Abrams 2010, Ohgushi et al. 2012, Sheriff et al. 2020) illustrates the significant interest and effort being expended to advance the study of predation-risk effects.

Unfortunately, advancement is being impeded by ambiguous terminology. Here, we discuss the need and motivation for standardizing terminology within the study of predation-risk effects. We explicitly define the overall process of predation-risk effects and evaluate the merits of different terms used for it. In the spirit of recommendation by Velland (2010), we address terminology problems by developing a conceptual framework that partitions the overall process into four distinct effects. Using this framework, we demonstrate the magnitude of the terminology problem by examining the multiple terms used to describe each of four effects of predation risk. Based on this evaluation, we advocate for particular standardized terms. Finally, we show how the framework and associated terminology can be used to establish commonality and communication among researchers studying different systems (e.g., freshwater, marine, and terrestrial) and different taxa, and thus foster interdisciplinary perspectives that advance progress in the study of predation-risk effects.

A Need for Standardized Terminology

Standardized terminology specific to given disciplines, i.e., jargon, plays an important role in scientific communication by making explicit the assumptions that underlie concepts (Fauth et al. 1996) and, by compressing language, allows specialists to communicate about technical terms without long explanations (Jones et al. 1997, Vilhena et al. 2014). But in the absence of standardized terminology, there can be miscommunication as well as run-away creation and use of new jargon that enables long-established ideas to be presented as novel, and thereby hinders the maturation of ideas (Velland 2010). In ecology, the absence of frameworks and consensus on terminology in the literature has impeded progress on many issues, including the study of ecosystem engineers (Jones and Gutierrez 2007), keystone species (Mills et al. 1993), and animal personality (Carter et al. 2013).

Several factors underlie a particular need for standardized terminology of predation-risk effects. First, predation-risk effects are complex, with multiple factors interacting over different time scales, which challenges the connection between terms and processes. Second, the study of predation-risk effects is increasing at a high rate; the number of papers found using the search term “predation risk” in the Web of Science increased from 65 in 1989 to 926 in 2019. Third, ecologists are strongly grouped by different natural or organismal systems (e.g., marine or terrestrial) and by science and management application (Meadows et al. 2017). Without a conceptual framework and standardized terminology, this segregation could foster a lack of recognition of published work across different systems that address conceptually similar problems (Velland 2010).

Indeed, the terminology describing predation-risk effects has succumbed to these very problems. Explicit problems include the same process being described by different terms (Box 1) including differences among researchers of different systems (e.g., marine and terrestrial), different processes being described by the same term, and the meaning of particular terms changing over time. Consider a researcher searching the literature on how a predator affects prey fecundity by inducing the prey into costly anti-predator behavior. A search on “predation risk” yields almost 1,000 papers per year, and it is unclear which terms should be used to narrow the field to the topic of costs associated with anti-predator behavior. Further, some terms used to describe the costs such as “nonlethal effect” are also used to describe other predation-risk processes (e.g., the trait change itself, Box 1) or other ecological processes (Box 2). These problems impede researchers from finding relevant papers and likely prevent them from even knowing there is missing literature of importance. In fact, motivation of this paper has arisen in part from our own difficulties encountered while trying to review and synthesize studies of predation-risk effects.

Defining the Overall Process of Predation-Risk Effects

We must first explicitly define the overall process that is the topic of this synthesis because it can be ambiguous in the literature. “Predation-risk effects” (term justified in *A Framework for the Study of Predation-Risk Effects*) arise from two fundamental factors: predation risk *varies* and prey traits are *flexible* (i.e., are phenotypically plastic) in response to a change in predation risk. The overall process of predation-risk effects encompasses the actual flexible trait response of the prey to predation risk, the ensuing effects on interactions between prey and other species, the fitness consequences of the flexible trait response for the prey, and the ensuing effects on species abundances and community composition (Fig. 1).

Before proceeding, it is prudent to consider the differences between predation-risk effects and three other processes that also involve variation in prey traits and predator–prey interactions. First, individuals within a population may exhibit variation in a trait that is in large part constitutive (i.e., inflexible; Sih 1987) that reduce predation risk. An example includes shells, in which there could be among-individual variation in shell thickness in the absence of any environmentally induced change in shell thickness. Other examples include porcupine quills, poisonous skin, and refuge use. Whereas such traits may also be flexible, the nature of constitutive and flexible components of traits is not the subject of this paper. Second, predators may affect an individual’s traits in the absence of flexible traits, such as when a predator only consumes the arms of a sea star. Third, predators may select for constitutive defensive traits over

Box 1.

A non-exhaustive list of terms used to describe the different predation-risk effects defined in Fig. 1, including those that encompass all of the risk effects. Terms marked with a dagger appear in more than one group. Within each group, we recommend use of the term in boldface type.

All risk effects
- **Predation-risk effect**
- Risk effect
- Fear effect
- Nonconsumptive effect†
- Nonlethal effect†
- Sublethal effect†
- Trait-mediated effect†
- Trait-mediated interaction†

E1
- **Risk-induced trait response**
- Anti-predator phenotypic response
- Anti-predator behavior
- Anti-predator strategy
- Anti-predator response
- Adaptive prey response
- Induced trait change
- Fear response
- Predator-induced trait changes
- Trait-mediated effect†
- Trait-mediated interaction†

E2
- **Interaction modification**
- Higher-order interaction
- Non-additive effect
- Trophic modification
- Non-trophic interaction

E3
- **Nonconsumptive effect† (NCE)**
- Indirect interaction
- Nonlethal effect†
- Sublethal effect†
- Trait-mediated interaction†

E4
- **Trait-mediated indirect effect (TMIE)**
- Trait-mediated indirect interaction
- Behaviorally mediated indirect interaction
- Behaviorally mediated trophic cascade
- Behaviorally transmitted indirect effects
- Trait-transmitted indirect effects
- Trait-mediated interaction†

short-term ecological time scales (i.e., rapid evolution). Although researchers have applied terms such as trait-mediated and sub-lethal to these three processes, they fundamentally differ from predation-risk effects by not involving flexible traits of individuals.

A change in habitat preference (including immigration and emigration) of prey warrants special attention due to the potential confusion of this trait response directly influencing prey population density. When risk alters habitat selection by prey, it changes prey density within habitats (local density), but will only affect the overall prey population density if there are significant fitness costs associated with the habitat shift (Abrams 2007, Sheriff et al. 2020). In the present paper, we examine the influence of the predator on the spatial scale of the prey population. Changes in local density due to modifications in habitat preferences should thus be considered trait responses (a predation-risk effect), not effects on density.

A Framework for the Study of Predation-Risk Effects

Fig. 1 illustrates a framework that explicitly distinguishes multiple predation-risk effects and their connections. Next, we describe the key interactions and

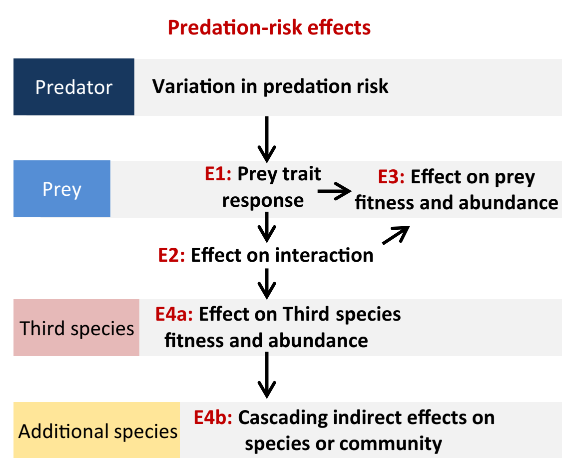


Fig. 1. Conceptual framework of predation-risk effects. An increase in predation risk will induce a trait response(s) in prey (E1; risk-induced trait response), which benefits the prey by reducing predation risk. The prey's trait response(s) will modify the nature and strength of the prey's interactions with other species (E2; an interaction modification). A prey's trait response (E1) that reduces predation risk can come with a cost to prey's fitness measures via effects on demographic rates and, in turn, abundance (E3; NCE), both directly (horizontal arrow) and through the effect on interactions with other species (upward pointing arrow). The effect on the interaction (E2) can also affect other (third) species in the system (E4a; TMIE), which can, in turn, affect yet other species and community properties (E4b; TMIE). [Color figure can be viewed at wileyonlinelibrary.com]

Box 2.

Alternative uses of terms that are also used to describe the different predation-risk effects (Box 1). The list provides examples and is not intended to be exhaustive.

Sublethal
- Negative effects of toxins, such as pesticides, without mortality
- Negative effects of hydrologic disturbances without mortality
- Predator consumption of part of prey (used often in sea star research)

Nonconsumptive
- Background death due to causes other than predation (primarily found in zooplankton literature)
- Abandonment of a killed prey before consuming it
- Mortality by predator through unintended means (e.g., caught in mucus trail) in absence of consumption

Nonlethal
- Human reduction in large-carnivore damage to livestock by means other than killing the carnivore
- Sampling method of stomach contents of an animal without killing it

Trait-mediated effects
- Effect of prey traits on predation rate

processes involved for each distinct effect, discuss extant terminology used for them, and advocate for an optimal term moving forward.

The overall process: Predation-risk effects

Of the many terms used to describe the overall process reviewed here (Box 1), we advocate for the term predation-risk effects (sensu Creel and Christianson 2008, Zanette et al. 2014). Unlike some other terms used, this term is general to all species because it relates directly to the underlying factor that drives the effects, namely variation in predation risk. This term also has historical precedence with prominent usage in foundational studies such as Werner et al. (1983), Brown (1988), Martin and Roper (1988), Lima and Dill (1990), Sih et al. (1990), Kotler et al. (1991), Houston et al. (1993), and Peckarsky et al. (1993).

The choice of one term requires us to explain the exclusion of other terms. The terms indirect effect, sublethal effect, nonlethal effect, trait-mediated interaction, and trait-mediated effect, are also used to describe distinct effects within the overall process of predation-risk effects (Box 1). The rationale for excluding these terms is given in subsequent sections. The term nonconsumptive effect is not problematic, however, we believe there are stronger reasons to reserve its use for one of the specific distinct effects (E3, Fig. 1).

We acknowledge that use of the terms fear, ecology of fear (Brown et al. 1999), and landscape of fear (Laundre et al. 2001) are popular in the current literature especially in wildlife studies, where an understanding of the stress physiology and neurobiology associated with avoiding predators may be studied (Clinchy et al. 2013, Boonstra 2013, Gaynor et al. 2019). But they do not apply generally across taxa and systems because studies of fear are associated with psychological stress, thoughts, and feelings (Clinchy et al. 2011, 2013). To reduce this ambiguity and the potential misapplication of fear terminology, we support the argument of Gaynor et al. (2019) that "fear" terms should be reserved for studies focusing on the neurological, cognitive, and emotional aspects of prey perception of and response to the risk of predation. We recognize that "ecology of fear" has the advantage of sounding more compelling than "predation-risk effects" and we do not suggest that researchers necessarily stop using the term "fear." If fear terminology is used, however, studies should also include general terms of predation-risk effects to ensure reference to the general theory and ecological context to which it applies.

Effect 1: Risk-induced trait response

The first effect of predation risk involves prey reducing risk from a focal predator by modifying phenotypically-plastic traits including behavior, morphology, physiology, and life history (E1 in Fig. 1). The terminology for this effect is particularly diverse and unstandardized (Box 1). We advocate for the term risk-induced trait response, because it best captures key features of Effect 1. Namely, the inclusion of "induced" captures the *flexible* nature and phenotypic plasticity of the prey's trait and therefore distinguishes E1 from terms that could describe constitutive traits in contrast to many of the other terms used for E1, such as anti-predator behavior. The recommended term also includes a key element that the prey is responding to risk. Whereas the term does not specify that risk is due to predation, this feature would be clear in any paper on the subject. We also advocate against the commonly used "trait-mediated effect" and "trait-mediated interaction" terms based on arguments made in Abrams (2007). Finally, we argue against the use of terms that include "fear" for E1 based on the same reasoning regarding terminology for the overall process.

Effect 2: Interaction modifications

The risk-induced trait response often affects the nature of the *interaction* between the prey and other species (E2 in Fig. 1). For instance, a predator-induced reduction in prey foraging activity can reduce the interaction strength between the prey and its resource, or it could modify (positively or negatively) the interaction strength between prey and a second predator. In this circumstance, the interaction between two species is not only a function of the density of those two species, but is also a function of the density of a third species; e.g., the prey–resource interaction is a function of predator density. In the theoretical literature, such three-species interactions are termed higher-order interactions (HOI; Vandermeer 1969, Abrams 1983, Billick and Case 1994). HOIs are important because they are predicted to profoundly influence species coexistence and the dynamics, stability, and persistence of ecological communities (Abrams 2010, Peacor and Cressler 2012).

There have been a number of statistical and empirical terms used to describe E2 (Box 1). Interestingly, we are not aware of a specific term for the effects of predation risk on species interactions. Rather, the terms used encompass all ecological processes in which one species affects the interaction between two other species (Peacor and Cressler 2012). For E2, we propose using the term interaction modification, which was first introduced by Wootton (1993) to describe the biological effect, as opposed to the mathematical HOI term. In the case of predation-risk effects, the "modifier" of the interaction is the predator affecting prey traits. We also suggest reserving the term "non-additive effect" for the statistical testing of interaction modifications, rather than for the process itself. We note that interaction modification is a broad term that encompasses other mechanisms that can influence species interactions.

Effect 3: Nonconsumptive effects

Predation risk can also alter prey fitness measures and abundance via the costs associated with risk-induced trait responses (E3 in Fig. 1). By fitness measure we refer to the multiple components of fitness such as reproduction, recruitment, mortality due to risk, and, in some cases, condition or growth rate (Sheriff et al. 2020). The distinction between the effect of a risk-induced trait response (E1) and an effect on fitness measures (E3) can be complex, because some prey responses including fecundity, growth, and condition can be either, or both. For example, an effect on fecundity could be a risk-induced trait response (E1), such as when zooplankton modify life history strategies when exposed to fish cues (Tollrian 1995). Or the effect on fecundity could represent the fitness cost of a risk-induced trait response (E3), such as when zooplankton seek refuge in a lower quality habitat (Pangle et al. 2007).

Effects on prey fitness measures or abundance (E3) occur in two general ways. First, predation risk can influence prey fitness via interaction modifications (arrows to and from E2, Fig 1). For instance, a risk-induced reduction in foraging activity can affect the interaction between the prey and its resource, thereby reducing resource acquisition and, ultimately, prey growth rate, condition, and reproduction. It could also alter the interaction between the prey and other predators, thereby modifying mortality risk from those predators. Second, predation risk can influence prey fitness measures and abundance through the risk-induced trait responses without additional interacting species (horizontal arrow, Fig. 1). As an example, vertebrate prey respond to predation risk by modifying hormones (Maher et al. 2013) and incurring an associated physiological cost that reduces reproduction and survival (Zanette et al. 2011, Macleod et al. 2018). Other examples include morphological defenses (e.g., thicker shells, larger spines) that incur a cost to fitness (Harvell 1992), and habitat shifts associated with changes in abiotic factors such as temperature that affect fitness (Pangle et al. 2007).

Ecologists have used a diversity of terms to describe E3 (Box 1). We advocate using nonconsumptive effect (NCE) for E3. It does not have the disadvantages of the other terms used to describe E3, it is mechanistically accurate in that the effect of a predator on prey fitness is not due to consumption, and it parallels the contrasting term of "consumptive effect" that describes how predators affect prey abundance through consumption. NCE is also a widely used term. Whereas NCE has also been used to describe the overall process of predation-risk effects (Box 1), we argue that it would promote communication and synthesis if its use is restricted to describe E3 (sensu Sih et al. 2010).

The other terms used for E3 have disadvantages relative to NCE. Terms such as nonlethal (Pangle et al. 2007) and sublethal effects (Peckarsky et al. 1993) are not technically accurate because the risk-induced trait response may result in nonconsumptive mortality, which has been shown for anuran larvae (Werner and Anholt 1996), dragonflies (McCauley et al. 2011), zooplankton (Bourdeau et al. 2016), and hares (Macleod et al. 2018). Terms such as "trait-mediated effects" or "trait-mediated interaction" have been used to describe E3 (Preisser et al. 2005). However, we concur with Abrams (2007), who argued that "trait-mediated" be reserved as a descriptor of how predation risk can act indirectly among trophic interactions via plastic trait changes in prey (i.e., E4). Last, we especially advocate for discontinuing the use of the term "indirect effect" for E3 (LaManna and Martin 2017), because "indirect effect" should be reserved for effects between more than two species as is consistent with the ecological literature (Billick and Case 1994).

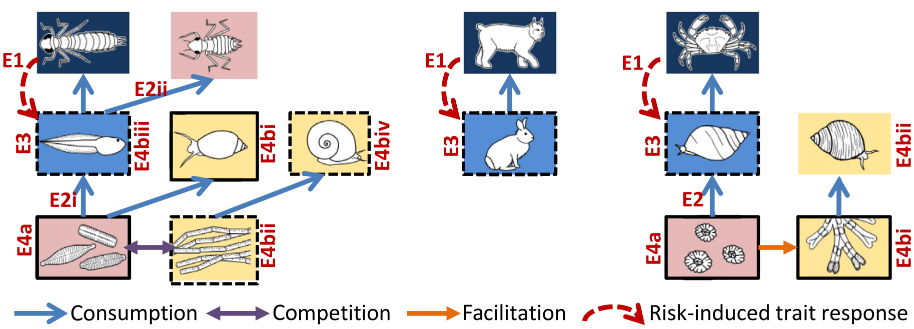
Effect 4a: Trait-mediated indirect effects

An important outcome of the interaction modification (E2) between the prey and a third species is the potential effect on the fitness measures and abundance of the third species such as the resource or another predator of the prey (Fig. 1, E4a and Fig. 2). A risk-induced trait response of reduced foraging activity (E1) will cause an interaction modification (E2) between the prey and its resource, which could then affect the resource's growth rate, biomass, and abundance (Werner and Peacor 2003). The risk-induced trait response of prey could also modify the interaction between the prey and a second predator, hence affecting the second predator's fitness.

This latter process has been shown to occur when snails strengthen shell morphology to deter crab predation in a manner that makes the snails more vulnerable to sea star predators (Bourdeau 2009), which would increase sea star fitness.

We advocate for the term trait-mediated indirect effect (TMIE) to describe E4a because it captures the underlying mechanisms explicitly (Abrams 2007). That is, the effect is transmitted indirectly and "mediated" by the trait of the intermediate species. In addition, TMIE appears to be the most common term used in the literature. The term TMIE was introduced by Abrams et al. (1996) as a contrast to classic density-mediated indirect effects (DMIEs) caused by indirect effects of a predator on other species through reduction in prey density via consumption. We advocate discontinuing the use of the nearly identical term "trait-mediated indirect interaction" (TMII; Peacor and Werner 1997). The term TMII offers no improvement on TMIE, and it refers to the *interaction* between the prey and the third species, rather than the *effect* on the third species, which is more often the intent. Importantly, the term TMIE is not restricted to interactions in which the initiator of the effect is a predator (reviewed in Werner and Peacor 2003). Thus, when using the term TMIE to describe E4a, it is necessary to make clear that the initiator species is a predator.

TMIEs have been described with more specific terms that are subsets or types of TMIEs (Box 1). These



	Freshwater system	Terrestrial system	Marine system
Predator	*Anax* dragonfly larva	Lynx	European green crab
Prey	Frog tadpoles	Hare	*Nucella* snail
Third species	Large diatom periphyton (resource) *Tramea* larvae (second predator)		Barnacles (resource)
Additional species	Green algae (competition for space) *Physa* snail (competition for diatoms) Planorbid snail (consumes green algae)		Fucoid algae (facilitated by barnacles) *Littorina* snail (consumes fucoid algae)
E1	Habitat shift to substrate ↓ % Percentage of time active Change in tail morphology	↑ Time in refuge ↑ Stress hormones	↑ Time in refuge ↓ Foraging rate
E2	i. Tadpole – Periphyton ii. Tadpole – *Tramea* larvae		*Nucella* snail – Barnacle
E3	↓ Tadpole growth rate ↑ Increased tadpole mortality	↓ Body condition ↓ Fecundity ↑ Mortality Abundance cycles affected	↓ *Nucella* snail growth rate
E4a	↑ Large diatom periphyton density		↑ Barnacle density
E4b	i. ↑ *Physa* snail growth rate ii. ↓ Biomass green algae iii. ↑ Tadpole prey growth rate vi. ↓ Planorbid snail growth rate		i. ↑ Fucoid algal biomass ii. No observed effect on *Littorina* snail growth rate

FIG. 2. Application of the framework (Fig. 1) to multiple systems. Diagrams depicting predation-risk effects found in three predator–prey systems: freshwater dragonfly and tadpole, terrestrial lynx and hare, and marine crab and snail (see The Application of the Framework to Multiple Study Systems for citations). We use these systems to illustrate how the framework can help identify similar theoretical and methodological findings across systems. In each system, the particular predation-risk effects are labelled and colored to correspond to the color code of the effect in Fig. 1. Solid, dashed, and dotted box outlines indicate risk effects that were positive, negative, or examined but not found, respectively. In the corresponding table, the top four rows list species of focal predator, focal prey, third species that interact directly with the focal prey including resources and competitors, and additional species with other roles. Other roles include competitor of focal resource, a second predator (freshwater system), a second resource in the refuge habitat (terrestrial system), and a resource species that is facilitated by the focal resource (marine system). Lower rows list predation-risk effects as depicted in Fig. 1. Down arrows and up arrows represent reduced and increased, respectively. [Color figure can be viewed at wileyonlinelibrary.com]

include behavioral indirect interactions (Abrams 1984, Werner and Anholt 1996, Miller and Kerfoot 1987), behaviorally mediated indirect effects (Heithaus et al. 2008, Dill et al. 2003), and behaviorally mediated trophic cascades (Kauffman et al. 2010, Schmitz et al. 1997, Creel et al. 2005). Trait-specific terms like these may make the mechanism explicit (e.g., the behavior, morphology, or life history), but in doing so may create countless new terms that are difficult to navigate. If specific terms such as these must be used, then we advocate to also reference the term TMIE for generality and to ensure that the study is found in literature searches of the broader topic. Authors have also described TMIE (E4a) with the terms interaction modification and higher-order interaction, which have an established literature or mathematical connections to E2. Therefore, we suggest reserving those terms for the interaction E2.

Effect 4b: Further propagation of trait-mediated indirect effects

The ramifications of a risk-induced trait response can cascade further than the affected prey (E3) and species interacting with the prey (E4a) to other species in the system (E4b in Fig. 1). For example, if a predator has a TMIE on a resource through a risk-induced trait response in an herbivore, the change in the resource's growth rate or abundance could affect other herbivores, other resources (Fig. 2), community-level descriptors such as biodiversity, and ecosystem processes. In such cases, we advocate that the term TMIE still be used as it is in the three-species case (E4a), with of course an explanation of the multi-species interaction.

Different, unnamed, types of indirect effects caused by predation risk

Another effect of predation risk that could be confused for the TMIEs discussed here is that changes in the density of the prey due to a nonconsumptive effect (E3) on prey would likely affect other species (e.g., resources and predators). In this chain of events, the indirect effect is qualitatively different than the TMIE, as it occurs through the NCE on prey density rather than occurring through prey traits as with TMIEs. Similarly, a risk-induced trait response will influence predation rate of the focal predator, which can affect predator density, which could then affect the prey and other species in the system. We are unaware of terminology to describe these predation-risk effects.

The Application of the Framework to Multiple Study Systems

Fig. 2 illustrates the application of the framework to three predator–prey systems in which predation-risk effects have been studied: freshwater dragonfly and tadpole (Werner and Peacor 2006, Relyea 2001, Peacor 2002, Peacor and Werner 1997), terrestrial lynx and hare (Macleod et al. 2018, Sheriff et al. 2011, 2015), and marine crab and snail (Trussell et al. 2006, 2017). We have attempted to capture all of the food-web positions examined in these systems. If multiple species have been studied in a particular food-web position, we only included one species for simplicity. In the freshwater and terrestrial systems, for example, only one of several predators known to lead to risk-induced trait responses in the prey is shown.

This cross-system comparison of predation-risk effects highlights the congruence of concepts examined in different systems and helps to clarify the different effects (E1–E4) examined. Multiple risk-induced trait responses (E1) were shown in each system, but the traits that were modified varied among systems. Similarly, an NCE (E3) on prey fitness was shown in all three systems, but the fitness measures that were examined differed among systems (listed in Fig. 2). While some predation-risk effects were demonstrated in all three systems, others were not. Notably, evidence for NCEs of lynx on hares are extensive and strong, with NCEs affecting the nature of the classic hare population cycle through differential effects on fecundity at different periods of the cycle. Strong NCEs on growth have been found in the freshwater and marine food web, but only in highly controlled settings and not on population dynamics. Consequently, of the three study systems, the lynx–hare system is the only one that illustrates an NCE in a wild population (based on the papers identified for this overview) and as influencing longer term dynamics. This comparison also highlights an absence of research on TMIEs within the very same lynx–hare system, even though the risk-induced trait responses underlying such indirect effects have been demonstrated. Note that the above analysis is derived from the papers cited for each system, but we think those papers sufficiently capture the state of knowledge for the comparisons made.

Benefits of the Conceptual Framework

The framework and associated standardized terminology can assist in uniting studies of predation risk across systems by clarifying which of the multiple potential effects are examined. Rather than a vague notion that risk effects have been shown in different systems, using the framework to categorize the findings allows clearer comparisons of the explicitly studied risk effects across studies and systems. Consequently, we can more easily develop a synthesis of cross-system differences and similarities in the multiple risk effects, sharpening our understanding of the overall process of predation-risk effects. In contrast, when explicit effects are not referenced with a standardized terminology, not only can the terminology be difficult to interpret and hence hinder the impact of a given result, but the actual effects being examined can be confused. For example, Peacor and Werner (2001) examined the relative influence of TMIEs (E4b) of a predator to the net indirect effect of the predator that includes the TMIE, the density-mediated indirect effect, and their interaction. While 8 of the 18 citations for this paper in 2018 correctly referenced the article as addressing TMIEs (E4), three citations referenced the paper as evidence for predation-risk effects on prey (E3, NCE). Similar incorrect reference to particular predation-risk effects can be seen in citations of review papers such as Werner and Peacor (2003). Further, searches based on terms like "landscape of fear" can yield results for any of the multiple effects of predation risk (E1–E4), which inhibits other researchers from determining which effect was actually studied.

Ultimately the most important benefit of establishing conceptual similarities in studies across systems is the discovery of transferrable insights, knowledge gaps, and methodologies. For instance, studies in freshwater systems have demonstrated a counterintuitive result in which risk-induced reduction in foraging (E1) by tadpoles (prey) has a net *positive* effect on tadpole growth rates (E4biii in Fig. 2; Peacor 2002). This result is theoretically predicted to occur on growth rates and abundances when resources display common density-dependent growth relationships (Abrams 1987). If empirical findings are more accessible across systems, which using this framework would promote, then practitioners in different systems will be more aware of such phenomena. Without standardized terminology, it would be nearly impossible for researchers to benefit from the perspectives and novel research tools now being used to study conceptually similar processes in different systems (Meadows et al. 2017). For example, the perspectives of researchers examining how lynx (predator) influence stress physiology of hare (prey; Sheriff et al. 2011) may benefit from clearly understanding the perspectives of those studying risk-induced changes in lipid content of zooplankton (prey; Bourdeau et al. 2016), and vice versa. With regards to research tools, practitioners in freshwater and marine systems may not be cognizant of the methodological uses of giving-up densities (GUDs; Jacob and Brown 2000, Brown 1988) that were developed in terrestrial mammalian systems to estimate perceived predation risk. Data analysis and modeling methods can also be transferred across systems, such as the application of neural nets and genetic algorithms applied to a freshwater system to model the effects of predation risk on prey behavior (Strand et al. 2002).

Using the framework and associated standardized terminology could be particularly useful in areas of research that have traditionally focused on predator-consumptive effects and that are only now beginning to give predation-risk effects more attention as in biological control and applied ecology (Vandermeer et al. 2010, Jandricic et al. 2016). The framework can help researchers recognize which aspect of predation-risk effects are being examined in the context of what has been done in other systems, facilitating the development of appropriate methodology and the communication of findings to the broader ecological community.

CONCLUSIONS

This literature review has led us to several recommendations on how to advance our understanding of predation-risk effects. First, researchers should strive to use terminology that is general to all ecological systems, which is possible due to the unifying ecological and evolutionary processes involved. Second, because there are multiple distinct effects in the overall process that is predation-risk effects, researchers must explicitly identify which effect is examined. Third, we advocate using "predation-risk effects" for the overall process, "risk-induced trait responses" for the flexible trait responses used by prey to reduce predation risk, "nonconsumptive effects" for the costs of trait responses to prey fitness measures and abundance, and "trait-mediated indirect effects" for ensuing indirect effects of the trait response on other species and community properties. While we acknowledge that researchers will also use terms that address more specific processes (e.g., behaviorally mediated trophic cascade, landscape of fear) for communication within disciplines and for attracting peer and public interest, we argue that it is essential to also reference the most general, unifying terms. We hope our framework and associated terminology help practitioners choose robust terminology to describe their study, assist them in identifying literature pertinent to their research, and, most importantly, facilitate a transfer of insights and methodologies across ecological systems. This will promote advancement in an exciting sub-field of ecology that has potentially significant applications to management and conservation challenges.

ACKNOWLEDGMENTS

We thank P. Abrams, B. Peckarsky, O. Schmitz, and D. MacNulty for input on an early draft of this paper. The ideas in this paper were developed through conversations with M. Cherry, N. Dorn, and J. Smith during a literature review on predation-risk effects. We thank Tanya Rogers for artwork and assistance with formulation of figures. S. D. Peacor acknowledges support from AgBioResearch of Michigan State University. Funding for this paper was provided by the National Science Foundation DEB-1145808 to S. D. Peacor and OCE-1736943 to D. L. Kimbro.

LITERATURE CITED

Abrams, P. A. 1983. Arguments in favor of higher-order interactions. American Naturalist 120:382–390.

Abrams, P. A. 1984. Foraging time optimization and interactions in food webs. American Naturalist 124:80–96.

Abrams, P. A. 1987. Indirect interactions between species that share a predator: Varieties of indirect effects. Pages 38–54 *in* W. C. Kerfoot and Sih, A., editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Abrams, P. A. 2007. Defining and measuring the impact of dynamic traits on interspecific interactions. Ecology 88: 2555–2562.

Abrams, P. A. 2010. Implications of flexible foraging for interspecific interactions: Lessons from simple models. Function Ecology 24:7–17.

Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 *in* G. Polis and Winemiller, K., editors. Food webs: dynamics and structure. Chapman and Hall, New York, New York, USA.

Billick, I., and T. J. Case. 1994. Higher order interactions in ecological communities: What are they and how can they be detected? Ecology 75:1529–1543.

Boonstra, R. 2013. Reality as the leading cause of stress: Rethinking the impact of chronic stress in nature. Functional Ecology 27:11–23.

Bourdeau, P. E. 2009. Prioritized phenotypic responses to combined predators in a marine snail. Ecology 90:1659–1669.

Bourdeau, P. E., M. T. Bach, and S. D. Peacor. 2016. Predator presence dramatically reduces copepod abundance through condition-mediated non-consumptive effects. Freshwater Ecology 61:1020–1031.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk and competition. Behavioral Ecology and Sociobiology 22:37–47.

Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: Optimal foraging, game theory, and trophic interactions. Journal of Mammalogy 80:385–399.

Carter, A. J., W. E. Feeney, H. H. Marshall, G. Cowlishaw, and R. Heinsohn. 2013. Animal personality: what are behavioural ecologists measuring? Biological Reviews 88:465–475.

Clinchy, M., M. J. Sheriff, and L. Y. Zanette. 2011. Predator-induced stress and the ecology of fear. Functional Ecology 27:55–65.

Creel, S., and S. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194–201.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

Dill, L. M., M. R. Heithaus, and C. J. Walters. 2003. Behaviorally mediated indirect interactions in marine communities and their conservation implications. Ecology 84:1151–1157.

Fauth, J. E., J. Bernardo, M. Camara, W. J. Resetarits, J. Van Buskirk, and S. A. McCollum. 1996. Simplifying the jargon of community ecology: A conceptual approach. American Naturalist 147:282–286.

Gaynor, K. M., J. S. Brown, A. D. Middleton, M. E. Power, and J. S. Brashares. 2019. Landscapes of fear: spatial patterns of risk perception and response. Trends in Ecology and Evolution 34:355–368.

Harvell, C. D. 1992. Inducible defenses and allocation shifts in a marine bryozoan. Ecology 73:1567–1576.

Heithaus, M., A. Frid, A. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. Trends in Ecology and Evolution 11:69–73.

Houston, A. I., J. M. Mcnamara, and J. M. C. Hutchinson. 1993. General results concerning the trade-off between gaining energy and avoiding predation. Philosophical Transactions of the Royal Society B 341:375–397.

Jacob, J., and J. S. Brown. 2000. Microhabitat use, giving-up densities and temporal activity as short- and long-term antipredator behaviors in common voles. Oikos 91:131–138.

Jandricic, S. E., D. Schmidt, G. Bryant, and S. D. Frank. 2016. Non-consumptive predator effects on a primary greenhouse pest: Predatory mite harassment reduces western flower thrips abundance and plant damage. Biological Control 95: 5–12.

Jones, C. G., and J. L. Gutiérrez. 2007. On the purpose, meaning, and usage of the physical ecosystem engineering concept. Pages 3–24 *in* K. Cuddington, J. Byers, W. Wilson, and A. Hastings, editors. Ecosystem engineers: plants to protists. Volume 4. Academic Press, Brultington, Massachusetts, USA.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Ecosystem engineering by organisms: Why semantics matters. Trends in Ecology and Evolution 12:275.

Kauffman, M. J., J. F. Brodie, and E. S. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91:2742–2755.

Kotler, B. P., J. S. Brown, and O. Hasson. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecology 72:2249–2260.

LaManna, J. A., and T. E. Martin. 2017. Seasonal fecundity and costs to lambda are more strongly affected by direct than indirect predation effects across species. Ecology 98: 1829–1838.

Laundre, J. W., L. Hernandez, and K. B. Altendorf. 2001. Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology 79:1401–1409.

Lima, S. L. 1998*a*. Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. Advances in the Study of Behavior 27:215–290.

Lima, S. L. 1998*b*. Nonlethal effects in the ecology of predator-prey interactions—What are the ecological effects of anti-predator decision-making? BioScience 48:25–34.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology 68:619–640.

Macleod, K. J., C. J. Krebs, R. Boonstra, and M. J. Sheriff. 2018. Fear and lethality in snowshoe hares: the deadly effects of non-consumptive predation risk. Oikos 127:375–380.

Maher, J. M., E. E. Werner, and R. J. Denver. 2013. Stress hormones mediate predator-induced phenotypic plasticity in amphibian tadpoles. Proceedings of the Royal Society B 280 (1758):20123075.

Martin, T. E., and J. J. Roper. 1988. Nest predation and nest-site selection of a western population of the Hermit Thrush. Condor 90:51–57.

McCauley, S. J., L. Rowe, and M.-J. Fortin. 2011. The deadly effects of "nonlethal" predators. Ecology 92:2043–2048.

Meadows, A. J., D. W. Crowder, and W. E. Snyder. 2017. Are wolves just wasps with teeth? What invertebrates can teach us about mammal top predators. Food Webs 12:40–48.

Miller, T. E., and W. C. Kerfoot. 1987. Redefining indirect effects. Pages 33–37 *in* W. C. Kerfoot and Sih, A., editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire, USA.

Mills, L. S., M. E. Soulé, and D. F. Doak. 1993. The keystone-species concept in ecology and conservation. BioScience 43:219–224.

Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. Trends in Ecology and Evolution 20:685–692.

Ohgushi, T., O. J. Schmitz, and R. D. Holt. 2012. Introduction. Pages 1–6 *in* T. Ohgushi, T. O. Schmitz, and R. D. Holt, editors. Trait-mediated indirect interactions: ecological and evolutionary perspectives. Cambridge University Press, New York, New York, USA.

Pangle, K. L., S. D. Peacor, and O. Johannsson. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology 88:402–412.

Peacor, S. D. 2002. Positive effect of predators on prey growth rate through induced modifications of prey behaviour. Ecology Letters 5:77–85.

Peacor, S. D., and C. E. Cressler. 2012. The implications of adaptive prey behavior for ecological communities: A review of current theory. Pages 131–160 *in* T. Ohgushi, O. Schmitz and R. D. Holt, editors. Trait-mediated indirect interactions: ecological and evolutionary perspectives. Cambridge University Press, Cambridge, UK.

Peacor, S. D., and E. E. Werner. 1997. Trait-mediated indirect interactions in a simple aquatic food web. Ecology 78:1146–1156.

Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. Proceedings of the National Academy of Sciences USA 98:3904–3908.

Peckarsky, B. L., D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. L. Luttbeg, J. L. Orrock, S. D. Peacor, E. L. Preisser, O. L. Schmitz, and G. C. Trussell. 2008. Rewriting the textbooks: Considering non-consumptive effects in classic studies of predator–prey interactions. Ecology 89:2416–2425.

Peckarsky, B. L., C. A. Cowan, M. A. Penton, and C. Anderson. 1993. Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. Ecology 74:1836–1846.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509.

Relyea, R. A. 2001. Morphological and behavioral plasticity of larval anurans in response to different predators. Ecology 82:523–540.

Schmitz, O. J., A. P. Beckerman, and K. M. O'Brien. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. Ecology 78:1388–1399.

Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: The primacy of trait-mediated indirect interactions. Ecology Letters 7:153–163.

Sheriff, M. J., C. J. Krebs, and R. Boonstra. 2011. From process to pattern: How fluctuating predation risk impacts the stress axis of snowshoe hares during the 10-year cycle. Oecologia 166:593–605.

Sheriff, M. J., E. K. McMahon, C. J. Krebs, and R. Boonstra. 2015. Predator-induced maternal stress and population demography in snowshoe hares: the more severe the risk, the longer the generational effect. Journal of Zoology 296:305–310.

Sheriff, M. J., S. D. Peacor, D. Halena, and M. Thaker. 2020. Non-consumptive predator effects on prey population size: a dearth of evidence. Journal of Animal Ecology 89:1302–1316.

Sih, A. 1987. Predators and prey lifestyles: An evolutionary and ecological overview. Pages 203–224 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University of New England Press, Hanover, New Hampshire, USA.

Sih, A., D. I. Bolnick, B. Luttbeg, J. L. Orrock, S. D. Peacor, L. M. Pintor, E. Preisser, J. S. Rehage, and J. R. Vonesh. 2010. Predator-prey naivete, antipredator behavior, and the ecology of predator invasions. Oikos 119:610–621.

Sih, A., G. Enlund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey. Trends in Ecology and Evolution 13:350–355.

Sih, A., J. Krupa, and S. Travers. 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. American Naturalist 135:284–290.

Strand, E., G. Huse, and J. Giske. 2002. Artificial evolution of life history and Behavior. American Naturalist 159:624–644.

Tollrian, R. 1995. Predator-induced morphological defenses: costs, life history shifts, and maternal effects in *Daphnia pulex*. Ecology 76:1691–1705.

Trussell, G. C., P. J. Ewanchuk, and C. M. Matassa. 2006. The fear of being eaten reduces energy transfer in a simple food chain. Ecology 87:2979–2984.

Trussell, G. C., C. M. Matassa, and P. J. Ewanchuk. 2017. Moving beyond linear food chains: trait-mediated indirect interactions in a rocky intertidal food web. Proceedings of the Royal Society B 284:20162590.

Vandermeer, J. 1969. Competitive structure of communities: an experimental approach with protozoa. Ecology 50: 362–370.

Vandermeer, J., I. Perfecto, and S. Philpott. 2010. Ecological complexity and pest control in organic coffee production: Uncovering an autonomous ecosystem service. BioScience 60:527–537.

Velland, M. 2010. Computational synthesis in community ecology. Quarterly Review of Biology 85:183–206.

Vilhena, D. A., G. J. Foster, M. Rosvall, J. D. West, J. Evans, and C. T. Bergstrom. 2014. Finding cultural holes: How structure and culture diverge in networks of scholarly communication. Sociological Science 1:221–238.

Werner, E. E., and B. R. Anholt. 1996. Predator-induced behavioral indirect effects: Consequences to competitive interactions in anuran larvae. Ecology 77:157–169.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64:1540–1548.

Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions. Ecology 84:1083–1100.

Werner, E. E., and S. D. Peacor. 2006. Interaction of lethal and non-lethal effects of a predator on a guild of herbivores mediated by system productivity. Ecology 87:347–361.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist 141:71–89.

Zanette, L. Y., M. Clinchy, and J. P. Suraci. 2014. Diagnosing predation risk effects on demography: can measuring physiology provide the means? Oecologia 176:637–651.

Zanette, L. Y., A. F. White, M. C. Allen, and M. Clinchy. 2011. Perceived predation risk reduced the number of offspring songbirds produce per year. Science 334:1398–1401.