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SYNTHESIS

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A skewed literature: Few studies evaluate the contribution of predation-risk effects to natural field patterns

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Abstract

A narrative in ecology is that prey modify traits to reduce predation risk, and the trait modification has costs large enough to cause ensuing demographic, trophic and ecosystem consequences, with implications for conservation, management and agriculture. But ecology has a long history of emphasising that quantifying the importance of an ecological process ultimately requires evidence linking a process to unmanipulated field patterns. We suspected that such process-linked-to-pattern (PLP) studies were poorly represented in the predation risk literature, which conflicts with the confidence often given to the importance of risk effects. We reviewed 29 years of the ecological literature which revealed that there are well over 4000 articles on risk effects. Of those, 349 studies examined risk effects on prey fitness measures or abundance (i.e., non-consumptive effects) of which only 26 were PLP studies, while 275 studies examined effects on other interacting species (i.e., trait-mediated indirect effects) of which only 35 were PLP studies. PLP studies were narrowly focused taxonomically and included only three that examined unmanipulated patterns of prey abundance. Before concluding a widespread and influential role of predation-risk effects, more attention must be given to linking the process of risk effects to unmanipulated patterns observed across diverse ecosystems.

KEYWORDS
fear, natural experiment, non-consumptive, non-lethal, observational, plasticity, predation risk, process from pattern, trait mediated, trait response

INTRODUCTION

Over the past several decades a large literature has amassed that examines how predation-risk effects may influence predator–prey interactions that in turn affect the structure, composition and functioning of natural systems. Predation-risk effects include the risk-induced changes in plastic traits that prey adopt to reduce being eaten (a benefit), such as changes in behaviour, physiology, life history and morphology (Agrawal, 2001; Relyea, 2001; Stearns, 1989). Such risk-induced trait-responses (hereafter 'trait-responses' for brevity) cause non-consumptive effects (NCEs) on prey due to associated costs that affect prey fitness (Creel

& Christianson, 2008; Sheriff et al., 2020) as well as prey population growth rate and abundances (Peacor et al., 2011; Sheriff et al., 2020). For species interacting with the prey (e.g., their resources, competitors and other predators), their fitness or abundance can also be indirectly impacted by trait-responses, known as a trait-mediated indirect effects (TMIEs; Bolker et al., 2003; Ohgushi et al., 2012; Werner & Peacor, 2003). Risk effects are also predicted to cause higher-order interactions and altered functional relationships that can influence population dynamics (e.g., affect stability) and community properties that differ qualitatively from those resulting from consumptive effects of predators, i.e., those effects due to predators killing prey (Abrams, 2010; Levine et al., 2017; Peacor & Cressler, 2012).

A prevailing narrative in ecology is that NCEs and TMIEs have a profound influence on populations, communities and food webs that can rival or exceed that of consumptive effects. This narrative was presented by e.g., Peacor and Werner (2001) and Preisser et al. (2005), and can be seen in many recent publications citing these papers. A review of the literature showed that claims supporting the narrative, such as 'Evidence suggests that predators not only regulate animal populations through consumptive effects but also by the mere threat of predation…', are routinely repeated in the recent literature (Sheriff et al., 2020), highlighting both the acceptance and perpetuation of the prevailing narrative. The narrative has also been strengthened by researchers re-interpreting classic studies of predation in food webs as potentially being heavily influenced by risk effects (Peckarsky et al., 2008). Further, extensive experimental and theoretical literature on NCEs and TMIEs has given rise to numerous reviews in the general ecological literature (Ohgushi et al., 2012; Preisser et al., 2005; Werner & Peacor, 2003), in more specialised literatures on certain taxa or systems (e.g., Hermann & Landis, 2017; Mitchell & Harborne, 2020; Say-Sallaz et al., 2019), and on particular aspects such as context dependence [e.g., effect of prey density or environmental factors (Peacor et al., 2013; Wirsing et al., 2020)].

The intriguing trait-responses of prey are diverse, widely observed, and can be costly; therefore, the idea that consequent risk effects influence ecological communities seems an intuitive and compelling narrative. But has such influence been well established? The ecological literature is replete with arguments that to establish the relevance and importance of a process to an ecological community, it must ultimately be demonstrated to influence observed patterns, established through observational studies (i.e., surveys) of natural unmanipulated communities (Gotelli & Graves, 1996; Karban & Huntzinger, 2006; McIntire & Fajardo, 2009; Sagarin & Pauchard, 2010; Schoener & Spiller, 1987; Underwood et al., 2000; Vellend, 2016; Werner, 1998). For example, in his classic paper, Vellend (2010) articulated the ultimate goal of community ecology: 'perhaps the greatest challenge in community ecology is drawing the link between process and pattern'. As practitioners of the study of predation and risk effects in a diversity of natural and managed ecological systems, it was unclear to us if this bedrock requirement had been addressed for NCEs and TMIEs. In other words, have natural patterns of prey populations or communities (e.g., fitness measures, demographic rates or abundance) been demonstrated to be influenced by NCEs and TMIEs? And, if so, is it further well documented across diverse systems to justify a broad narrative about predation-risk effects?

At issue here is not *how* to establish that predation risk is influencing a field pattern (see Discussion) or even whether the research has revealed a strong influence of NCEs or TMIEs, but rather that to evaluate if a process is important in nature, we must ultimately examine its influence on an unmanipulated field pattern. In this paper, we denote studies that have as a *goal* to identify or parameterise the influence of a process on an unmanipulated field pattern as 'process linked to pattern' (PLP) studies. Given this paper's focus, the ecological patterns are those of species fitness measures, population growth rate or abundance, and the processes are NCEs or TMIEs which need to be differentiated from those resulting from predators killing prey. A justification for the use of the PLP term, and how it differs from many related terms, is given in Box 1.

Prior to our review we were aware of a few PLP risk-effect studies, and we use two here to illustrate their implementation (see Discussion for further examples). First, Marino et al. (2019) examined a 20-year time series of *Daphnia* density in Lake Michigan that was collected as part of a National Oceanic and Atmospheric Administration survey programme. They used state-space models with predator–prey equations that differentiated the consumptive effects and NCEs of the predatory cladoceran *Bythotrephes* on *Daphnia* population growth rate and abundance. NCEs were suspected based on laboratory results of *Daphnia* responses to *Bythotrephes* and from results of field surveys that indicated *Daphnia* migrated to deeper colder waters (and thus incurred a cost to growth rate) at higher *Bythotrephes* densities (Pangle et al., 2007; Pangle & Peacor, 2006). Second, experimental evaluations of TMIEs of fish predators in streams have shown how insect grazers can alter benthic algae by utilising different micro-habitats at higher fish densities (e.g., Peckarsky et al., 2002). Building on that work, Alvarez and Peckarsky (2014) conducted a PLP study that examined whether natural variation in composition of different benthic algae taxa was influenced by a TMIE. They examined variation in composition over an unmanipulated natural gradient of fish density to look for effects consistent with experimental TMIE findings. These are two examples of PLP risk-effect studies, one an NCE on a temporal field pattern, and the other a TMIE on a spatial field pattern.

BOX 1 Process linked to pattern (PLP) studies: Term justification and concept explanation

Based on the conceptualisation of Vellend (2010), we denote studies that pursue the goal of determining the influence of a process on an unmanipulated field pattern as 'process linked to pattern (PLP)' studies. A PLP study requires some form of a quantification of variation over space and/or time of species fitness measures, demographic rates or abundance, and a means (based on e.g., experimental results, modelling or statistical analyses) of linking the process of interest to that pattern. The term PLP study describes both 'pattern first' and 'process first' approaches (Vellend, 2010). In other words, PLP studies may have either a primary interest in the process itself, with research also being conducted to identify and quantify the influence of that process on an observed pattern, or may have as a main goal of explaining an established pattern, with research being conducted on characterising potential processes that could underly the pattern.

Differentiation of goal and implementation

It is well beyond the scope of this paper to review the advantages and disadvantages of the different approaches used in ecology to link process with pattern. Instead, we emphasise that PLP studies are identified by their *goal* to link a process to a pattern, not by how (i.e., method/approach) the study is implemented.

Differentiation of PLP studies and strictly manipulative experiments

A PLP study is to be differentiated from other field studies that rely on a manipulative experiment to examine a process (e.g., competition or predation), but lack an observational component that quantifies a pattern somehow linked with the process. For example, a classic paper by Schoener and Spiller (1987) manipulated the presence of predatory lizards on islands to examine their effects on spider prey and surveyed unmanipulated distributions of lizards and spiders. They employed the former experiment to help understand the processes that influenced patterns observed in the latter. We therefore categorise the study of Schoener and Spiller to be a PLP study because it seeks to explain a process' influence on an observed unmanipulated pattern. We note that the lizard field manipulation alone, in the absence of the link to an observational pattern, would be a powerful experiment elucidating a process, but would not constitute a PLP study.

Inclusion of studies without experiments

While the interplay of modelling, experiment and observational studies is a powerful approach to understand ecological processes, PLP studies do not fundamentally depend on manipulative experiments being a component of the study. Indeed, for some processes, the literature is replete with studies that seek to explain process from pattern in the absence of experimental studies (Larsen et al., 2019; McIntire & Fajardo, 2009).

Relationship with other terms

Various partially overlapping terms have been used to describe this type of investigation.

Natural experiments

The term natural experiment has been used in ecology for targeted studies of recently perturbed ecosystems, by either humans (e.g., new roads) or natural causes (e.g., hurricanes), to examine how given factors influence ecological communities. For example, Rogers et al. (2012) examined the influence of trophic interactions by studying the natural experiment of insectivorous bird extirpation by invasive snakes. An older and different description of natural experiments are those that analyse a series of observations across a gradient of a variable of interest in the absence of any perturbation (Côté et al., 2004; Diamond, 1983; Schoener & Spiller, 1987). The different usages of the term natural experiment and focus on implementation rather than goal of a study, make it less suitable for our purposes.

Mensurative experiments

The term mensurative experiment has been used similarly as natural experiment (Underwood et al., 2000; Watt & Scrosati, 2013) to examine a process through examination of unmanipulated patterns in combination with experiments to elucidate mechanism. The term deviates from our usage of PLP study because it can be used for studies with intentional manipulations that introduce subjects over a gradient of a variable of interest.

Observational studies

The term 'observational studies' (Binning et al., 2022; Underwood et al., 2000; Vellend, 2016) and related terms such as 'strictly observational approaches' (Sagarin & Pauchard, 2010), are sometimes used to describe studies that include observing unmanipulated patterns of variables across space and/or time to contribute to the study of a process. The term observational study is too vague for our purposes.

Though experiments over a controlled set of conditions, ranging from laboratory studies to field manipulations, are a powerful way to evaluate mechanisms, they are insufficient to characterise (Côté et al., 2004; Mielke et al., 2022; Underwood et al., 2000; Vellend, 2010) and may even mischaracterise (Rogers et al., 2012; Sagarin & Pauchard, 2010; Schoener & Spiller, 1987; Werner, 1998) the influence of a process on natural patterns. For example, Sagarin and Pauchard (2010) argued that manipulations of predators by Paine (1966) to examine effects of competitive relationships on species diversity were not capable, as presented, of estimating parameters and accurately depicting the examined processes in the natural, unmanipulated system. There are several broad causes of the limitations. First, experiments are necessarily short term and therefore do not capture the influence of feedbacks (Diamond, 1983; Rogers et al., 2012; Schoener & Spiller, 1987) nor the interaction of multiple direct and indirect effects that operate on different time scales (Bender et al., 1984; Werner, 1998). Second, natural patterns are affected by processes over multiple spatial scales including those much larger than can typically be manipulated (Levin, 1992; Madin et al., 2019; Sagarin et al., 2006). Lastly, manipulative experiments (even field-based) can only test a limited number of interacting variables and thus cannot capture the full interaction complexity inherent in natural systems (Li et al., 2019; Vellend, 2016; Werner, 1998). Note that the argument made here does not diminish the power and importance of experimental work, nor diminish the large tradition in ecology as to the power of integrating experiments and observational studies (Côté et al., 2004; Schoener & Spiller, 1987; Werner, 1998). Rather, the argument emphasises the need for a PLP component in a research programme to fully address the influence of a process given the limitations of experimental work conducted in isolation.

Some of the limitations raised generally about experiments have been raised specifically about risk effect studies. It has been suggested that inferences made from experiments on risk effects, using standard designs, exaggerate the magnitude of NCEs and TMIEs, provide conflicting results depending on the duration of the experiment and fail to provide critical information for assessing NCE and TMIEs (Abrams, 2008; Prugh et al., 2019; Weissburg et al., 2014). It has further been argued that the complexity of natural systems include feedbacks and compensatory mechanisms that may reduce the contribution of NCEs and TMIEs found in experiments (Abrams, 2008, 2010; Hoverman & Relyea, 2012; Luttbeg et al., 2003). For example, Persson and de Roos (2003) argued that models of NCEs and TMIEs that leave out key components of stage structure could also neglect compensatory mechanisms that reduce the influence of NCEs and TMIEs.

We also perceived a disconnect in the literature about the prevailing narrative of NCEs and TMIEs in natural communities. As stated above, the study of NCEs and TMIEs is so vast that it already contains a large literature of review papers, and reiterations in recent articles about the importance of NCEs and TMIEs in structuring communities are common. In contrast, we have observed that NCEs and TMIEs have been almost universally omitted in ecological theoretical studies except for those studies specifically examining them. This suggests a broader population of ecologists appear sufficiently conflicted or unconvinced about NCEs or TMIEs such that they have not incorporated them into models used to address conservation and societal needs. We conjectured that a lack of PLP studies, or lack of knowledge of them, if they actually do exist in high numbers, could underlie this apparent disconnect; i.e., a literature replete with PLP studies that illustrates and elucidates how predation risk influences the abundance and population growth rate of prey and other species would surely obviate the disconnect. We suspected PLP studies were rare, but until this review there had been no quantitative examination of the *types of evidence* undergirding this narrative.

We performed a comprehensive literature review to quantify the growth of the literature on risk effects and identify the types of evidence provided for risk effects over 29 years. We identified and categorised the studies of NCEs and TMIEs with particular attention to the approaches used to identify the influence of these risk effects. We differentiated risk-effect studies that only examined trait-responses from those that examined NCEs and TMIEs (i.e., the consequence of trait-responses). For NCE and TMIE studies only, we identified if there was a field component and, if so, if it was a PLP study (Figure 1). We catalogued study taxa in order to identify differences in attention across study systems. Our intent was to quantify the research approaches used by ecologists, rather than evaluate the results such as the magnitude of the NCEs and TMIEs. If the state of the field were heavily skewed towards controlled laboratory or field experiments versus PLP studies, or if studies have only been conducted in a narrow range of systems, then we would conclude that broad statements about the influence of NCEs and TMIEs on natural populations should be reserved until direct evaluations of unmanipulated, natural populations have been more widely performed.

METHODS

Overview

We developed a decision tree to categorise risk-effect papers. The diversity of approaches used to study risk effects and the aspects studied are numerous and thus considerable deliberation was required to differentiate well-defined categories. The following sections explain the categories, the decision tree, and the criteria and methodology used to identify and categorise the papers.

Categories and decision tree

We subdivided studies into independent, and increasingly restrictive, categories using a decision tree. First, we identified if the study was in fact a predation risk study. Risk studies encompass all categories in Figure 1 (Group A). The second division, based on ecological theory (Abrams, 1984, 1991) and associated conceptual frameworks (Peacor et al., 2013; Sheriff et al., 2020), is a sequence of risk effects (columns in Figure 1); we determined if the study only examined a trait-response (risk-induced trait-response column, Figure 1), or went to a level beyond (Group B, Figure 1), i.e., examined consequences to the fitness component, population growth rate or abundance of the prey (NCEs) or of a species the prey interacts with (TMIEs). Third, we subdivided studies that went beyond the trait-response (Group B) according to broad categories based on the role of the field component in the research: those which were laboratory/mesocosm based with no field component, those having any field component (whether a small or large contribution), but not being a PLP study or those that were a PLP study. Fourth, for PLP studies only (Group C), we subdivided studies by whether they examined a fitness component (Group D1), population growth rate (Group D2) or abundance (Group D3) of the focal organism. For studies that examined a fitness component, the specific component was recorded.

Also indicated in Figure 1 is the type of study examined in the risk-effect literature review of Sheriff et al., 2020. As that paper also highlights a shortcoming in the literature on risk effects, we differentiate our review for clarity. The Sheriff et al. paper walks through predation risk effects step-by-step and then argues that we do not have sufficient evidence to support the contention that predation risk can alter population abundance, and then provides arguments for reasons why predation risk may or may not alter population abundance. Sheriff et al. identified NCE studies in the literature that examined NCEs on prey abundance regardless of study approach (i.e., field or lab based, dashed group in Figure 1). The current review was, in contrast, motivated by the type of studies performed to examine risk effects, and in particular a perceived imbalance due to a lack of PLP studies. Further, it was more extensive by enumerating all risk

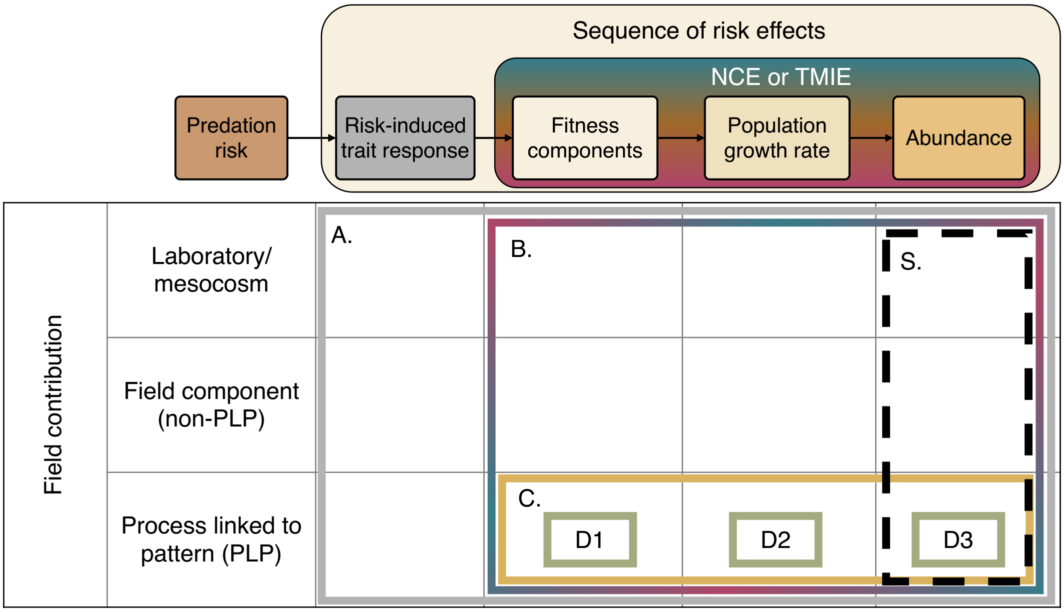

FIGURE 1 Our survey was conducted as a series of decision points which distinguished different experiments as they relate to field contribution (rows), and a sequence of risk effects (columns). In regards to the risk effects (columns), an increase in risk leads to a risk-induced trait-response of the prey, which can affect a fitness component, then population growth rate, and then abundance of prey (NCE) or indirectly that of another species such as the prey's resource (TMIE). Nested groups (a–d) correspond to the categorical divisions described in the text. Group S is shown to highlight the difference between our review and that of Sheriff et al. (2020, see text).

effects (Figure 1, Group A) and NCEs and TMIEs on fitness components and population growth rate in addition to abundance (Figure 1, Group B), allowing the evaluation of not only the number of a given type of study, but the relative proportion.

Note that our categorisation was more refined for studies that proceeded further in the sequence of risk effects, especially PLP studies, as depicted in Figure 1, with consecutively smaller groups from A to D. For example, studies that examine the trait-response only are not categorised with regard to study type. Explanations of criteria used are given in the next section, and further in the Supporting Information S1 for more detailed criteria.

Explanations of search criteria used

Criteria for risk-effect study

A risk effect study was defined as those studies that examined prey trait-responses and/or NCEs and TMIEs. A trait-response as defined here occurs when plastic traits (i.e., phenotypes) vary in response to the level of perceived predation risk (Agrawal, 2001; Brönmark & Miner, 1992; Lima & Dill, 1990). Thus, whereas prey may have baseline constitutive traits (i.e., inflexible; Sih, 1987) that serve as defences against predation (such as vigilance levels, spatial or temporal habitat preference, or shell thickness), it is the plastic nature of such traits that underlie risk effects. For example, Stephenson et al. (2015) examined differences in life-history traits in Trinidadian guppies under different predation risk levels. As their paper examined effects due to differences in the constitutive aspect of the trait (Stephenson, personal communication) we did not categorise it as a risk-effect study.

Criteria for fitness component categorisation

We clarify our criteria of fitness components, the importance of which is highlighted by the potential categorisation of a some responses, such as growth rate, fecundity and condition, as either a trait-response or a fitness component. We designated a change in growth rate, fecundity or condition as a trait-response when change in that trait was described as being a plastic response to risk, i.e., prey adaptively changed allocation of resources to that trait as a function of risk. For example, the observation that *Daphnia* zooplankton grew to a larger size in the presence of invertebrate *Chaoborus* predators was presented as a protective plastic allocation of resources (i.e., a trait) by Liu and Steiner (2017). In contrast, we categorised effects on growth rate, fecundity or condition as effects on fitness components when they resulted from a trait-response, such as behavioural change, to reduce predation risk. For example, if a change in habitat preference in response to an increase in predation risk resulted in poorer environmental conditions or resources, a resultant reduction in growth rate, fecundity or condition was categorised as an NCE on the prey. For responses that could be either classified as a trait-response or a fitness component response, we referred to the expertise and explanation of the authors.

Criteria for fitness component type category

We grouped studies that examined fitness components of the prey (in NCE studies) or resources (in TMIE studies) into six broad categories. Mortality (often reported as survival) included starvation or death due to predators other than the focal predator. Condition, which was only reported for animals, included responses such as % fat content, body condition index (i.e., mass/length) and nutritional status. Growth was used to describe a change in size of individuals (including mass or height in the case of plant resources in TMIE studies), while biomass was used as a proxy to describe population size (in all cases resources). Tissue loss, which was only used for plant resources, described herbivory on parts of a resource such as partial or whole leaf herbivory. Reproduction included a wide range of responses that affected reproductive success or recruitment, including clutch or seedling number, birth rate or proportion of a clutch that was viable. Survival or growth of young was categorised as reproduction since they were used as a measure of reproduction success.

The TMIE term is used to describe the interaction in which a focal predator causes a trait-response in prey that in turn affects the foraging rate by a second predator on that prey, but a fitness consequence to the second predator was not examined. Because our focus was on studies that examined fitness consequences and abundance of the affected species, we did not include such interactions in our enumeration of TMIE studies. As there were only approximately 20 such studies in our review, not including these studies had negligible influence on our results.

Criteria for process linked to pattern (PLP) studies

PLP studies were those that examined whether the unmanipulated natural distribution (i.e., a field pattern) of a species' fitness component, population growth rate or abundance was influenced by risk effects (the process, Box 1). For example, a PLP study could include a survey of predation risk in different spatial regions, and then perform a statistical analysis (which considers confounding factors) to evaluate if predation risk differences among the regions influenced a risk-induced fitness component (not direct mortality from predation) or abundance of the prey (an NCE) or its resources (a TMIE). Such a study would be strengthened by laboratory and field experiments that elucidate the risk-effect process; i.e., determine the magnitude of the trait-response(s) of the prey to the predator and how that trait-response is manifested in costs to fitness components. However, cost extrapolations from lab measurements to field patterns alone do not constitute a PLP study. Although a potentially powerful approach to elucidate risk effects, field studies that manipulated predation risk, prey number or the environment did not meet the criteria for a PLP study (see Discussion).

A number of studies showed a relationship between predator abundance and prey or prey resource abundance in the field, and separately demonstrated that predation-risk effects could influence prey traits or fitness component in experiments. An inference might then be made, typically in the Discussion of a paper, that the field pattern was influenced by risk effects. However, if there was no direct assessment of risk affecting a field pattern (e.g., to distinguish from effects of consumption), but only a conjectured relationship was provided, we did not categorise the study as a PLP study.

Paper search method

Our search was composed of three sub-searches encompassing 1990–2018 (29 years). In the first sub-search, we scoured the literature using prominent risk-effect terms in Web of Science (All Databases; Supporting Information S2) which yielded 4013 publications. One author made a first pass through the papers by reading the titles, and abstracts if necessary, to eliminate papers that clearly did not meet the criteria; many were not ecological or were using the search terms to describe different processes (as in Box 2 in Peacor et al., 2020). From the reduced list, pairs of authors reviewed each paper independently according to the decision rules, and thereafter met to reconcile their scores. Disagreements were passed along and considered by a third member of the team. Finally, the lead author, SDP, reviewed all results with special attention to any that had disagreements or flagged concerns. In this final scoring, difficult papers were discussed among everybody that had reviewed the paper. For approximately 20 papers, when there was a clear question on methodology that we could not discern in the paper, we sought input from the authors of the reviewed paper for clarification. In the end, each paper in the reduced list was examined by three to four authors with closer examination given to papers that made it further along the decision tree.

We cannot overstate the effort required to accurately categorise many of the papers. We encountered a large diversity of approaches used to study risk effects, terminology used in contrasting ways (Peacor et al., 2020) and huge variation in the aspects studied (e.g., risk effects may be the focus of a study, or only one aspect of a larger study). These differences, and the complexity of risk effects, combined with our rigorous approach that used multiple reviewers, led to at each branch in the decision tree needing considerable attention for many papers.

Unfortunately, many papers do not use common terminology to describe risk effects even in the keywords section and therefore were not found with our first sub-search. For example, some papers may misuse ‘indirect effect’ to describe NCEs (Peacor et al., 2020) and searches using such non-descript and general terms yield too many results to effectively review. To locate the missed papers, the second sub-search examined all papers that referenced ten classic and heavily cited papers on risk effects that were chosen to span a range of taxa and study systems (Supporting Information S3). This yielded 2358 papers after removing duplicates with the first sub-search. They were reviewed with the same methodology as the first sub-search.

For the third sub-search, we examined citations of the classic behavioural ecology publication by Lima and Dill (1990). We found 3891 citing papers after removing duplicates with the first and second sub-searches. Due to this large number, we evaluated the benefit of reviewing those citations using the search method of the first sub-search by first doing so for 330 citing papers randomly sorted by date. This analysis revealed that the missed risk papers citing Lima and Dill (1990) were overwhelmingly studies of trait-responses only (not making it to Group B in Figure 1), with a much smaller percentage of studies examining NCEs, TMIEs, and especially, PLP studies (for which there was only 1 paper). Given the lower numbers and estimated effort required to fully review the remaining 3561 papers, we used a sub-sample methodology; we used the percentages from the 330-paper sub-search to estimate the number of papers that cited Lima and Dill (1990) in the categories of risk effect (Group A), and consequences of risk effects (i.e., NCEs and TMIEs [Group B] as a group). This third sub-search therefore provides sub-sampled data to estimate the number of papers in broad categories and was not used in the in-depth analysis using the decision tree to identify NCE, TMIEs and PLP studies.

For comparison of temporal trends in the sub-field of predation risk and the field of ecology, ecology publication numbers from 1990 to 2018 were derived from Web of Science publication records within the designated Web of Science Category ‘Ecology’.

RESULTS

From 1990 to 2018 the number of papers published per year on NCEs and TMIEs increased at a rate higher than that of total ecology publications (Figure 2a). The rate was approximately 21% per year from 1995 to 2005, after which the rate decreased to approximately 8% per year (inset, Figure 2a).

For the 29-year period our search yielded 3945 risk-effect papers (Figure 2b). Of these, 81% examined only the trait-response of the prey while 19% examined the consequences of the trait-response to fitness components or abundance of the prey (NCEs) or other species (TMIEs; Figure 2b). We therefore estimate that there have been >4000 studies of risk effects, as the 3945 studies identified in our search represents a lower limit since some risk effect studies were not captured in our three sub-searches. These results are from all three sub-searches, including the third sub-search, which used a subsample method for estimation (Methods). The remaining results are from the first and second sub-searches.

Of 349 NCE studies found, 26 (7%) were PLP studies (Figure 2c). The majority of the NCE studies did not have a field component (220, 63%). Of 275 TMIE studies found, 35 (13%) were PLP studies (Figure 2d). In contrast to NCEs, the majority of the TMIE studies (162, 59%) had some type of a field component. A table of PLP papers is provided in Supporting Information S4, with an associated bibliography in Supporting Information S5.

Of the PLP NCE studies, three examined the abundance of the prey, while 23 examined fitness components (Figure 2c). One PLP study quantified risk effects on population growth rate, an NCE study which also examined abundance. For PLP TMIEs studies, 16 examined abundance of the resource and 21 examined a fitness component (Figure 2d).

When measured, the most common fitness component examined in PLP studies of NCEs was reproduction, followed by somatic growth rate, body condition and mortality due to causes other than consumption by the focal predator (Figure 3). For TMIEs on the prey's resource, reproduction was also the most common, followed by

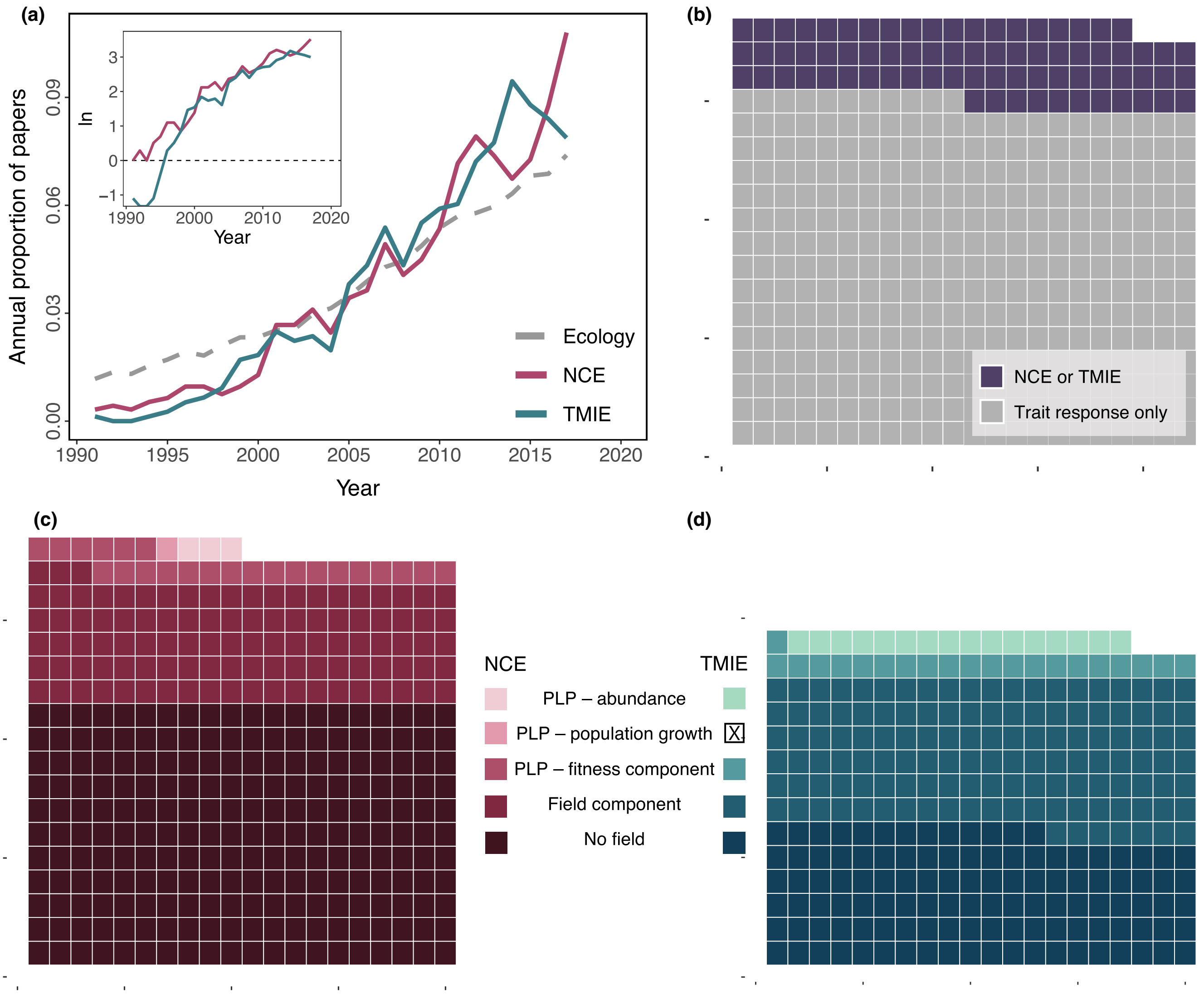

FIGURE 2 (a) Three-year running average of papers that examined NCEs, TMIEs and all ecology papers shown as a proportion of the total number of papers in each of the three categories over the 29-year period (inset provides natural logarithm of the data to facilitate visualisation of relative changes through time). (b) Composition of risk effect papers from 1990 to 2018 using all three sub-searches ($n = 3945$ total papers). Each square represents ten papers. NCE (c) and TMIE (d) papers categorised by field component metrics. Each square represents one paper (except for one paper that is represented twice having a PLP study of abundance and growth rate). Though PLP studies include a field component, the field component category in the figure does not include PLP studies as to not double count.

studies that examined somatic growth, tissue loss and biomass change (Figure 3).

There was a marked difference in the composition of prey taxa examined in all NCE and TMIE studies relative to PLP studies (Figure 4; numbers and proportions for all taxa provided in Supporting Information S6). Across all NCE studies, the number of vertebrate and invertebrate studies were similar (169 and 182, respectively), but the ratio was highly skewed for PLP studies, with far fewer invertebrate studies (1 and 25 for invertebrate and vertebrate, respectively). The ratios were markedly different for TMIEs studies relative to NCE studies. For TMIE studies, there were far fewer vertebrate than invertebrate studies (81 and 194, respectively). And while there were proportionally fewer invertebrate than vertebrate TMIE PLP studies (11 and 24, respectively), the compositional skew was much smaller than that seen among NCE studies. The differences in representation were also great for more specified taxa. For example, exceedingly few of the PLP NCE studies had insect (0 of 94), crustacean (1 of 32) and amphibian (1 of 81) prey. In contrast, a relatively high proportion of PLP NCE studies had mammal (12 of 29, 41%) and bird (6 of 21, 29%) prey. Similar large differences in taxonomic representation existed for TMIE studies (Figure 4, Supporting Information S6).

DISCUSSION

Our literature review revealed that predation-risk effects are a prominent topic in the ecological literature with well over 4000 studies. The overwhelming majority of such studies were of the trait-response alone (i.e., risk-induced trait-responses). Nevertheless, the study of NCEs and TMIEs has remained high after rapidly increasing since the early 1990s (Figure 2a), cumulatively producing hundreds of studies in each category (Figure 2c,d). In fact, the rate of increase in studies of NCEs and TMIEs exceeds that of ecological studies in general (Figure 2a). A noteworthy fraction of these studies included field components (Figure 2c,d). Although some taxa were more highly represented (e.g., insects and amphibians), studies of both NCEs and TMIEs were represented by a broad taxonomic diversity (Figure 4). Attention to NCEs and TMIEs thus remains high and spans different study approaches, taxa and systems.

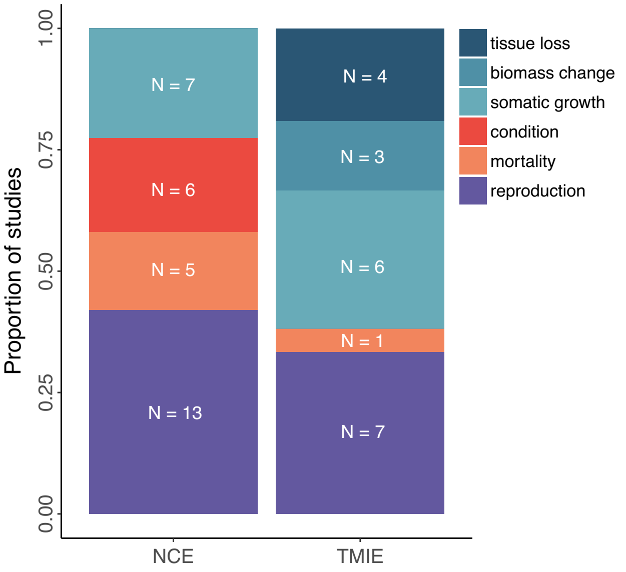

FIGURE 3 Proportion (y-axis) and number (indicated) of responses in PLP studies categorised by the fitness component of the prey measured in NCE studies, and the fitness component of the resource measured in TMIE studies. Multiple rates were included for studies that measured 2 (six studies) or 3 (1 study) different fitness components (fitness component categorisation described in methods).

The review unveiled an enormous heterogeneity across the sequence of risk effects (i.e., on trait-responses that influence prey fitness components, population growth rate and abundance; Figure 1), with a greatly reduced number of studies at each transition. Our review places a lower limit on the number or risk effect studies at 4000 publications. As we move through the sequence of risk effects, only 19% (Figure 2b) of risk effect studies examined NCEs or TMIEs, with the great majority examining the trait-response but not ensuing consequences. In fact, our estimated total number of risk effect studies and the corresponding fractional estimate of the 'trait-response only' studies remain conservative; we sought to find the full literature of NCEs and TMIEs and for that reason the fraction of the risk-effect studies that were only examining trait-responses could only possibly be larger (i.e., the exact fraction of studies going beyond a trait-response is less than 19%) if we had conducted a search to enumerate the complete literature on trait-responses. Of the 19% of studies going beyond traits, only 7% of NCE studies and 13% of TMIE studies were PLP studies. Of the PLP studies, most investigated effects on components of fitness, and far fewer investigated effects on population growth rate or abundance. In fact, for NCEs there were only three PLP studies that quantified abundance (Figure 2c, Supplementary Information S1), one of which that also examined population growth rate (Supplementary Information S1). The result of these consecutive drops in representation across the sequence of risk effects is that less than 0.7% of all risk-effect studies were PLP studies of NCEs on fitness components (0.6%), population growth rate (0.03%) and abundance (0.08%), and less than 0.9% of risk effect studies were PLP studies of TMIEs on fitness components (0.5%), population growth rate (0%) and abundance (0.4%).

Because linking processes to pattern is an enduring goal of ecology, the paucity of PLP studies of TMIEs, and especially NCEs, indicates that the evidence for the importance of these effects is insufficient to support the general narratives being used concerning predator impacts through risk effects. Neither the existence of

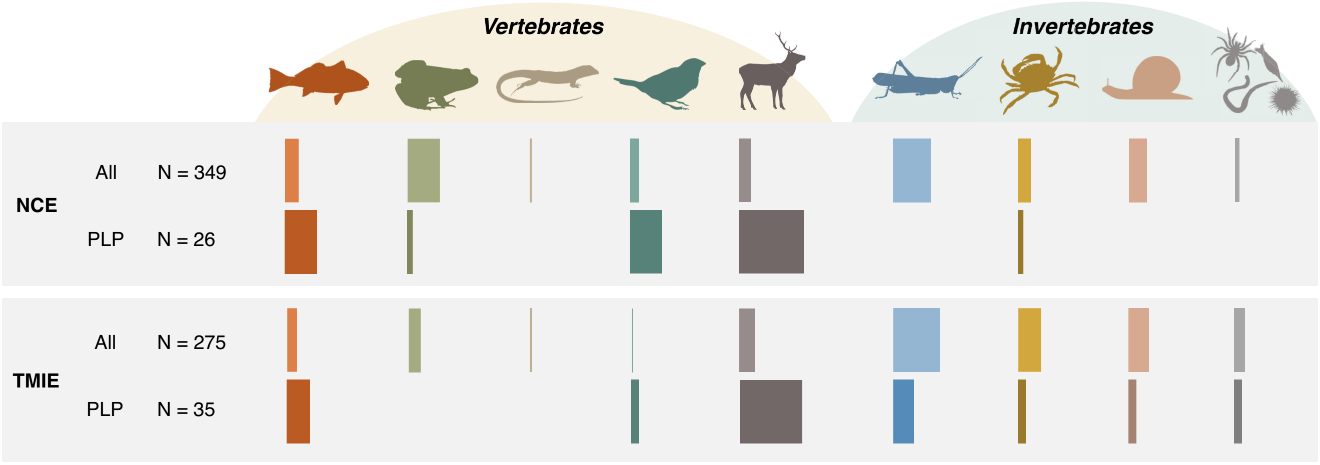

FIGURE 4 Proportion (width of a bar) of a given prey taxon for NCE and TMIE studies, with the sum of the widths being equal across rows. Four taxa of invertebrates were combined into one group (echinoderms, rotifers, annelids and arachnids). The 'all' category includes PLP studies; e.g., of 29 mammal NCE studies, 12 were PLP studies. The total number of studies for each category is given.

reviews (Introduction) and meta-analyses of the current literature on risk effect (e.g., Preisser et al., 2005), nor the wealth of risk-induced trait-response studies, can affect this conclusion; this evaluation is not premised upon the intuitive nature of the mechanisms nor the experimental demonstration of effect sizes. Rather, it is based on the critical need to link process to field patterns to support such narratives in general (Diamond, 1983; Levin, 1992; Sagarin & Pauchard, 2010; Schoener & Spiller, 1987; Underwood et al., 2000; Vellend, 2010; Werner, 1998) and that some of the reasons underlying that general need have been made specifically concerning risk effects (Abrams, 2008, 2010; Luttbeg et al., 2003; Prugh et al., 2019). These arguments do not diminish the role of experimental studies to understand the role of processes, but rather reflect contentions that an observational (i.e., natural survey) component of a study is an essential component of a research programme designed to evaluate the influence of a process (Côté et al., 2004; Gotelli & Graves, 1996; Karban & Huntzinger 2006; Rogers et al., 2012; Sagarin & Pauchard, 2010; Vellend, 2016).

Whereas an in-depth review of diverse methodologies used in PLP studies is beyond the scope of this article, we illustrate them by highlighting several studies that varied in a number of aspects (see also two other examples summarised in the Introduction). As a first example, Schmitz et al. (2017) demonstrated that observed differences in the abundance of *Solidago* plants across 15 fields was influenced by TMIEs of predator spiders. Experiments in complementary studies elucidated the risk-effect process. During short-term (40 day) enclosure experiments, the cues of sit-and-wait predatory spiders consistently caused grasshopper prey to relocate from nutritious grasses to safer and less nutritious forbs, resulting in vegetation dominated by grasses rather than by competitive dominant forbs (Schmitz et al., 1997). The same pattern and process was observed in subsequent field experiments that were longer (3 years) and less controlled, which experimentally enclosed (Schmitz, 2009) or excluded spider assemblages (Schmitz, 2003). Consequently, when observed differences in forb and grass abundance across 15 fields were best explained by spatial variation in spider identity (hunting versus sit-and-wait), the mechanistic TMIE was linked to an observed spatial pattern in vegetation abundance (Schmitz et al., 2017). This inferential link between mechanism and pattern was strengthened by both the absence of a similar spatial pattern in grasshopper biomass and by a paired experiment at each of the 15 old-field sites that further supported the proposed mechanism.

As a second PLP study example, Zanette et al. (2006) demonstrated that NCEs affect a natural pattern of egg production by song sparrows (*Melospiza melodia*). Zanette et al. (2006) quantified annual clutch number, egg per clutch and total egg production for sparrows nesting in independently determined, and replicated unmanipulated low predator and high predator habitats. The habitats differed in loss to predation (consumptive effects) and diversity and abundance of predators, and the authors ruled out effects of potentially co-varying environmental factors. Subsequent, experimental studies of predator playback calls (i.e., simulated risk) have elucidated the risk effect process by demonstrated large NCEs on sparrow egg laying, hatching and fledging (e.g., Zanette et al., 2011). By carefully following the progression of the nesting, they demonstrated that natural variation in predation risk affected clutch number (i.e., re-nesting) and size, but not the total egg production, because an increase in clutch number at high predation sites correlated with a decline in average clutch size.

Many of the PLP studies we identified were from research groups that had a well-established research programme on risk effects, but this is not required for PLP studies, as illustrated by some of the identified PLP studies. For example, as a new postdoctoral research fellow establishing a research project in a system not directly examined by his new research lab home, Kimbro (2012) examined whether trait-responses of snails to predatory crabs led to a TMIE on the natural spatial variation in the biomass of cordgrass observed in a marine intertidal system. Using information on the risk mechanism ascertained from laboratory and field experiments, he was able to differentiate indirect effects due to induced behavioural changes in the snails from those due to consumption of the snails on the natural cordgrass biomass pattern. Consider also the PLP study summarised in the introduction by Marino et al. (2019). Analysis of the risk effects on temporal patterns observed in the long-term survey data could have been performed without accompanying experiments. The supporting experiment strengthened inferences in that study, but they were not essential. Indeed, research on other ecological processes in which experiments are not possible is prominent in ecology with a large literature espousing the improvements in survey methods and statistical methods to find 'causality' in observational patterns (Larsen et al., 2019; McIntire & Fajardo, 2009). And, of course, in some academic disciplines, such as astronomy and history, scientific inquiries must depend on non-experimental approaches no matter how difficult the enterprise is. Decades of experience in a system, paired with extensive experimental work on risk effects, will facilitate and strengthen the ability to perform PLP studies on risk effects, but a PLP study is distinguished by the goal to link process with pattern, and approaches, responses measured and robustness of findings, will vary greatly.

In addition to PLP studies, we also found a diversity of other strong approaches that included field components. At one end of the spectrum, there was the category of papers with field components and high levels of experimental manipulation. For instance, an experiment with cages in a field that had prey added at prescribed densities, but uncontrolled colonisation by alternative prey resources and/or perhaps some natural variation (unstandardised) in habitat structure. At the other end of the spectrum, there were studies with little manipulation. For example, a number of experimental studies manipulated predator presence in an otherwise natural setting (Cherry et al., 2016; Peckarsky et al., 2002; Zanette et al., 2011). In one such study, Schoener et al. (2002) added large lizards to a series of islands and estimated the contribution of their risk effects to the abundance of *Anolis* lizards (the prey) and their resources. Other studies manipulated prey (in NCE studies; Thomson et al., 2012) or resources (for TMIE studies; Witman et al., 2017) in a controlled manner across gradients of predation risk. For example, Thomson et al. (2012) examined reproductive performance of flycatchers in nest boxes that were moved during incubation to different distances from predatory sparrowhawk nests. The study of predation risk would benefit from a quantitative review that examines how the manipulative approaches across this continuum help inform and interpret PLP studies, with attention also to the difficulty and resources required to carry out different approaches.

Our survey revealed that there was considerable heterogeneity in the taxa represented in NCE and TMIE studies, and a marked compositional shift in PLP studies (Figure 4, Supporting Information S6) further challenging the narrative of risk effects being influential generally. Several taxa exemplify this heterogeneity. Insects and amphibians dominated all NCE studies (50% combined), but made up a small percentage of PLP studies of NCEs (4% combined). In contrast, bird and mammal studies represented a small percentage of all NCE studies (14% combined), but dominated NCE PLP studies (69% combined). Similar heterogeneity exists in TMIE studies (Figure 4, Supporting Information S6). Thus, while there is marked heterogeneity in the taxa representation, there is also a disconnect in the proportion of studies that examine the risk effect's influence on natural field patterns (PLP studies). It is beyond the scope of this paper to investigate this heterogeneity, but one reason for the discrepancy may be the ease of performing laboratory, highly controlled or small-scale experiments with insects and amphibians relative to birds and mammals. Nevertheless, there have been field experiments that explore mechanism in which the prey are birds (Kobiela et al., 2015; Zanette et al., 2011) and mammals (Cherry et al., 2016; MacLeod et al., 2018). Further, we see no system-specific reason that it would be more difficult to perform PLP studies in insect systems. Therefore, we suspect the heterogeneity in taxa representation is at least in part due to differences in the motivation and goals of researchers studying different systems. Given that some broad taxonomic groups (such as amphibians, reptiles and invertebrates, Figure 4) had exceedingly few examples of risk influencing a natural pattern of species fitness measures, population growth rate or abundance, a narrative of the generality of NCEs and TMIEs being widespread must be recognised as hypothetical as opposed to established.

The paucity of PLP studies of NCEs and TMIEs, plus the selective treatment of PLP studies in some systems, is significant to the applied ecological disciplines including agriculture, conservation and management. Research over the last 30 years has been guided by a repeatedly published claim that predation risk is an equivalent or more important driver of prey populations and their resources than are the consumptive effects of predators (Sheriff et al., 2020). Consequently, for example, agricultural ecology is being shaped by reviews suggesting that predation risk can be used as a tool in arthropod pest management (Culshaw-Maurer et al., 2020). Meanwhile, support for large carnivore restoration depends upon an accurate assessment of the role predators play in ecosystems including through predation, NCEs and TMIEs. For example, in conservation biology there are ongoing and extensive debates about the role of wolves as fear-inducers, with ascertained effects on elk demographics (pro: Creel et al., 2007; con: Middleton et al., 2013) and vegetation recovery (pro: Ripple & Beschta, 2007; con: Brice et al., 2022). While our study does not diminish the widespread support for trophic interactions in causing empirically observed system-wide changes (e.g., Estes et al., 1998), it does suggest that conclusions about the role of predation risk needs further empirical evidence pertaining to the magnitude of predation-risk effects and how they are maintained across spatial and temporal scales. Thus, while there is good support that predation-risk effects, via NCEs and TMIEs, may have important implications to applied ecological disciplines, we require better and ultimately consistent evidence from PLP studies so that appropriate management actions and strategies can be taken.

In conclusion, a goal of the study of predation-risk effects is to determine if, to what degree, and under what circumstances, they influence species demographic rates and abundance, and community attributes. A prevailing narrative in the literature that this is well established, and that predation risk influences prey abundance and dynamics as much, or even more than, direct consumption, is often used to justify proposed research. Our review of the literature indicates we need to flip this reasoning around: more PLP studies of NCEs and TMIEs are needed that examine the influence of risk effects on natural patterns of species' fitness components, population growth rate and abundance. We predict that this will address a disconnect in the literature, in which practitioners promote their influence, but where a broader population of ecologists appear sufficiently conflicted or unconvinced about NCEs or TMIEs such that they have not incorporated them into models used to address conservation and societal needs. Our call is ultimately a request to researchers, reviewers, editors and granting institutions to carefully consider the sequence of risk effects (Figure 1) and the differential attention that they have been given. We hope that our results provide justification and motivation for PLP studies, especially if it is perceived that they are too difficult, or such work is already well established. PLP studies may be challenging, but they are a crucial component of a well-balanced portfolio of risk effect and predation studies.

AUTHORSHIP

SP, ND and DK conceived the study, with input from other coauthors. All authors performed a substantial portion of the comprehensive review with DK leading the search and SP leading the reconciliation stage. All authors contributed to results interpretation. SP enumerated the review results. Figures were conceptually developed by DK, SP and JS and produced by JS. SP wrote the first draft of the paper, with all coauthors contributing substantially to the early and the final versions.

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The data supporting the results can be accessed at doi: 10.5061/dryad.ffbg79cxt

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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