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Density-Mediated Interactions Are Stronger but More Variable Than Trait-Mediated Interactions in Predator–Prey Systems

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Density-Mediated Interactions Are Stronger but More Variable Than Trait-Mediated Interactions
in Predator–Prey Systems

by

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A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science
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ABSTRACT

Theoretical and empirical considerations of predator-prey dynamics have sought to determine the dominant of two effects exerted by predators onto prey: consumptive effects of predators and non-consumptive, or trait-mediated, effects. Many studies have identified trait-mediated interactions (TMIs) in diverse taxa, and meta-analyses of these studies found that prey population dynamics are as strongly – if not more strongly – affected by TMIs as density-mediated interactions (DMIs). Since then, there is now an expanded primary literature, and given this potential for new insight on the direct and indirect effect of predators on prey, the cost of traits involved in TMIs relative to the cost of consumption in DMIs should be revisited and reanalyzed with state-of-the-science research synthesis practices. Here we use a novel trivariate meta-analysis to jointly synthesize and model the multivariate effects of TMIs and DMIs on prey populations. We found that DMIs have twice the negative effects on prey populations than TMIs, but are more variable than TMIs, and that TMIs have the strongest effects in aquatic systems. Finally, we found that the model of total predator effects is not additive of DMIs and TMIs. Total predator effects were less than DMIs—which is biological intuitive given that prey should not initiate TMIs and therefore trait changes if it did not lessen total predator effects below that of DMIs. Gaps in the literature were detected, specifically that more experiments are needed that simultaneously assess TMIs and DMIs to a common control and that more studies are needed examining the demographic consequences of morphological TMIs. Our findings that DMIs are stronger than TMIs in affecting prey demographics suggests that DMIs are stronger regulators of

prey populations. Our findings also suggest that the total predator effect requires measuring the combination of DMIs and TMIs, and that TMIs should be researched within the context of how they reduce the impacts and cost of DMIs from predators.

CHAPTER ONE: INTRODUCTION

The fear caused by predation risk can negatively impact prey populations (Preisser et al. 2005, Werner and Peacor 2003, Schmitz et al. 2004) by shaping prey life history (Relyea and Werner 1999), physiology (MacLeod et al. 2017), behavior (Trussell et al. 2002), morphology (Relyea 2003, Relyea and Hovermann 2003), and survival (Pangle et al. 2007). These negative, non-consumptive effects (i.e. trait-mediated interactions or TMIs) differ from consumptive effects (i.e. density-mediated interactions or DMIs). Although DMIs are classically used to model predator–prey interactions, such as cyclical dynamics of populations over time (Norrdahl 1995, Abrams 2000, May 1972), an influential meta-analysis suggested that TMIs produce stronger effects on prey than DMIs (Preisser et al. 2005).

Non-consumptive effects could produce stronger effects than DMIs and constrain prey fitness through energy investments that are diverted away from reproduction or foraging, and these divestments impose biological tradeoffs. Tradeoffs occur when prey alter traits to lessen effects of predators, and trait alterations can include a variety of responses. One potential response of prey to predators within TMIs is to stimulate costly antipredator defenses—this is referred to as the inducible defense hypothesis (Bolnick and Preisser 2005, Preisser et al. 2005). Examples of TMIs and the tradeoffs of induced-defenses include lowered growth rates of bryozoans after developing defensive spines in response to predatory cues (Harvell 1986), snails adopting thicker shells in the presence of predators but suffering a tradeoff of reduced body size

(Trussell and Nicklin 2002), starved tadpoles increasing activity in the presence of alarm chemical cues of a predated conspecific (Carlson et al. 2015), tadpoles changing behavior relative to predation risk (Carlson and Langkilde 2014), and newt larvae having increased tail lengths in the presence of predatory chemical cues (Brossman et al. 2014). All of these studies suggest that inducible defenses have a biological trade-off due to their downstream constraints on growth rates, reproductive rates, or fecundity (Harvell 1990, Clark and Harvell 1992). Typically, ways to quantify the constraints of TMIs and DMIs is by comparing demographic changes in survival, fecundity, emigration, consumption over time, and time to metamorphosis/life history events. Evaluating demographic effects is key to distinguishing TMIs and DMIs effects on populations as it is a direct measure of the change in the prey population.

Here, we re-assess whether TMIs are a stronger force in predator-prey dynamics than DMIs—as implied by Preisser et al. (2005). By taking advantage of new synthesis techniques and a vastly updated and expanded literature, we apply a novel trivariate mixed-effects meta-analysis to model multivariate predator–prey dynamics and test whether the intense biological tradeoffs caused by trait-mediated interactions (TMIs) have greater demographic impacts than density-mediated interactions (DMIs). We also test: (1) whether induced-morphological changes, which require considerable energy investment (Fordyce 2006, Bennett et al. 2013, Teplitsky and Laurila 2007), are more costly than either behavioral or life history changes, and (2) whether ecosystems differ in the frequency and strength of effects produced from TMIs and DMIs due to the differences in ecosystem trophic structures, resource availability, and predator types across ecosystem (Schmitz et al. 2008, Schmitz et al. 2015, Schmitz et al. 2004). In ecosystems with more linear and less diverse trophic structures, prey may initiate TMIs that respond to single predators, whereas in systems with less linear dynamics, it is possible that prey initiate a variety

of simultaneous TMIs to maximize fitness to a host of potential predators. Finally, we test whether the TMIs and effects from invasive predator species differ from native predator species.

CHAPTER TWO: METHODS

Literature Search and Study Screening

Given that the terminology associated with TMIs and DMIs is inconsistent and has changed considerably over time (see Abrams 2007), and that we aimed to maximize representation of a diversity of TMI research, we developed a literature search that was inclusive to terminology use from the mid-1980s to present day. More specifically, on 13/6/2018, we performed a literature search on *Web of Science* (University of South Florida, Library subscription) with the following keyword string: (((((trait OR enemy OR parasite) NEAR/2 mediated) OR non-lethal OR non-addit*) AND (indirect* OR effect* OR modificat* OR facilitat* OR activit* OR intimidat* OR fear OR non-reciproc* OR induc* OR plastic*) AND (predator* OR prey OR herbivor* OR troph* OR resource* OR cascad* OR competition OR intraguild* OR consumpt* OR parasite* OR pathog* OR interact* OR emigrat*))).

This search returned bibliographic information on 3287 studies. The title and abstract of each study were screened for inclusion using a PDF-form generated by the package *metagear* for *R* (v. 0.5; Lajeunesse 2016). This PDF had the following keywords highlighted to optimize screening decisions: mediated, indirect, density, non-lethal, fear, apparent, predation, prey, herbivore, parasite, and interaction. Studies that fit the following inclusion criteria were identified during this screening: studies reporting indirect effects or TMI, experiments from systems with predator–prey–producer or consumer–producer dynamics (i.e., which is inclusive

to herbivore–plant, parasite–host dynamics). More elaborate trait mediated interactions were also included if they reported trophic extensions to predator–prey or herbivore–plant interaction (e.g., studies testing whether parasites/parasitoids/pathogens mediated changes in predator–prey TMIs or DMIs). Finally, we excluded pollinator–plant studies, as this dynamic lacks an equivalent to a density-mediated consumptive effect. In total, our screening process identified 664 candidate publications.

Candidate studies then had their full-text screened to determine whether they contained data on demographic variables (e.g., consumption, survival, changes in biomass of plants, population birth rates, percent alive at study termination, mortality, fecundity, dispersal). We followed Preisser et al. (2005) and Bolnick and Preisser (2005) in excluding studies that only reported data on growth rates, feeding success (i.e., prey efficiency), and changes in biomass of prey species (note: plant species with changes in biomass were still included, but animal prey species with changes in biomass were excluded). Similar to Pressier et al. (2005), we included studies reporting effects of TMI or DMI between predator and prey, and effects of predators on prey by contrasting prey demography in predator presence–absence experiments. However, we differed from Pressier et al. (2005) by including studies on herbivore–plant interactions that report demographic and TMI/indirect effects, and rather than inferring the strength of cascades based on the number of trophic links (as in Pressier et al. 2005), we explicitly include studies reporting indirect effects and trophic cascades mediated by TMIs and DMIs. For clarity, indirect effects caused by DMIs would include studies that examined predator consumption of prey (i.e. lethal exposure to predators or experimental hand-thinning) over time, and how that resulted in changes of prey resource levels/species. These studies were included so that the indirect effects from TMIs and DMIs relative to controls could be compared (i.e. comparing indirect effects

from trait changes/TMIs and indirect effects from trophic cascades via reduced densities/DMIs). Studies that simultaneously examined multiple predator effects on prey populations were also excluded—this was due to the lack of clarity regarding which effect is attributable to each predator and that combined effects may not be additive across predators. We also excluded studies testing effects of competitor species; unless TMIs and DMIs groups without competitors were reported. Finally, in order for studies to be included in our meta-analysis, studies must report at least two of the following experimental groups: a control (an unmanipulated group that lacked predator exposure), DMI (a manipulated group that exposed prey to a lethal and free-moving predator), and/or TMI (a manipulated group that exposed prey to a non-lethal predator, chemical cues from a predator, or alarm cues from crushed conspecifics to simulate predator presence) treatments.

Following this full-text screening, 163 of the 664 candidate studies reported at least one demographic variable for two of the three necessary experimental groups for effect size calculations (i.e., control, TMI, or DMI). Although our search was systematic and inclusion criteria broad, we were unable to replicate the original composition of studies synthesized by Preisser et al. (2005). A lack of clarity on how studies were found and screened in this meta-analysis significantly limits our ability to replicate their original search results. Preisser et al. (2005) generally described using several key words to search for papers in an exhaustive manner across multiple databases, and from there determined relevant papers from their screening process. We instead searched Web of Science with a systematic search string, and this likely explains why we could not replicate Preisser et al.'s (2005) search results. However, to address this gap, we used backward-inclusion to augment our dataset by adding studies reported in Preisser et al. (2005) that were not captured by our original search. This added 21 papers to the

existing 163, resulting in 184 studies available for data extraction and analysis. A summary of the entire screening and exclusion outcomes is summarized with a PRISMA diagram (Figure 1); this was generated by the *metagear* R package (Lajeunesse 2016).

Defining experimental outcomes and effects

In order to quantify experimental outcomes, and devise effect sizes for meta-analysis, it was necessary to distinguish between the types of DMI treatments reported: as either total predator effects or ‘true’ DMIs. True DMIs were defined as an experimental group that exposed prey to lethal predators on a timescale that would not result in trait-changes (TMIs). Here, consideration for what constituted a true DMI were experimental duration, the type of demographic variable, and the type of prey. Among invertebrates, DMIs were coded as true DMI treatments when the study-duration was 2 days or less (i.e., due to their rapid development and generation times, which can be less than 2-weeks). For vertebrates, true DMI treatments were coded when study duration was fewer than 7 days. This is due to many vertebrates having relatively longer durations to reach maturity than invertebrates, and that it is unlikely that a TMI would alter the vertebrate prey to cause death within a week. Experiments lasting over 7 days were coded as total predator effect treatments. Studies reporting plant–herbivore dynamics with 2 trophic links were coded as true DMI, given that the interaction between the plant and herbivore is almost entirely consumptive, regardless of the duration. However, these studies were few, as most report indirect effects caused by a TMII (trait-mediated indirect interaction). A TMII would constitute a change in foraging effort with increased predation risk resulting in the indirect effect of increased abundance of resource species. We also coded studies reporting experimental hand-thinning—which improves the accuracy of DMI effects (Relyea 2002), as

manual removal prey on scheduled intervals can help remove true predator effects since only consumptive effects of predators remains. Finally, when experimental duration was not reported, it was assumed that the total predator effect was present.

Demographic variables were grouped into seven categories: survival (e.g. abundance, change in abundance, density, consumption, herbivory, larval survival, mortality, prey cannabilized, survivorship, richness, pupae survival, and lifespan), trophic effects (e.g. ash-free dry mass (AFDM) periphyton, AFDM algae, algal biomass, algal biovolume, biomass, chlorophyll a, dry weight biomass, leaf mass loss, macrophyte biomass, periphyton chlorophyll a, periphyton mass, phytoplankton dry mass, plant biomass, and primary production of resource species), reproduction (e.g. age at first reproduction, average seeds produced, eggs, eggs and larvae, emerging adults, fecundity, and larval chambers, new recruits, offspring emerged, and reproductive investment), development (e.g. development rate, hatching time, larval duration, larval period, length of larval period, metamorphosis, number of metamorphs, pupation, and settlement success), behavioral (e.g. dispersal and emigration), pathogens (e.g. viremia and infection), and fitness (e.g. rate of increase). Behavioral demographics are less obvious, but behaviors such as emigration and dispersal of prey directly change the population densities, and therefore the composition of the prey demography. Pathogens may also be less clear in how they relate to demographics, but infection status changes the reproductive and behavioral profiles of prey and how they interact with predators. Finally, the predator/consumer species were classified according to their Linnaean taxonomic Class. Taxonomic ranking was done as an exploratory method to elucidate any potential patterns and effects produced from differing predator classes. Taxonomic class was favored due to it being a finer-scale category for analysis than kingdom and phylum but was also coarser-scale than genus (which would require a phylogenetic

approach). Phylogenetic meta-analysis (Lajeunesse 2009) was not possible due to single effects representing pairwise interaction outcomes between predator and prey species.

Data extraction protocol

Data that were targeted for data extraction were demographic data contained within figures, tables, or text of papers that included one or more of the following: a DMI experimental group with a paired control, a TMI experimental group with a paired control, or TMI and DMI experimental groups that shared a common control in the same figure or table. If tables were used from papers for extraction, the numbers reported in the table were directly extracted. Data were extracted from relevant figures by using DataThief III version 1.7 software (B. Tummings, DataThief III. 2006) by reverse engineering the figures to calculate the mean and standard error or standard deviation. The sample size was found by reading the methods section, unless it was directly reported within the figure or figure caption. The sample size that was used was the number of experimental replicates, and this was held consistent throughout the entirety of the data extraction process. If the number of replicates was not reported, the paper was not used for data extraction and was rejected. If the standard error was reported, this was extracted and later converted to the standard deviation. Papers that reported 95% confidence intervals were also extracted and then converted to the standard deviation.

A single effect was extracted per row of data in our database, meaning that one row would not contain more than one of a DMI – Control, TMI – Control, or TMI – DMI. Common control identifiers were assigned to figures and their extracted data in order to produce the correct number of effects for analysis and to not overestimate single effects from each figure and paper. Aggregate identifiers were also assigned to each row of data in the event that differences

were absent between the moderator variables in a figure's extracted data (i.e. the only difference was accounted for in our notes, but was not captured by the moderator variables we determined a priori for our analysis and extraction process). The resulting effects from extracted data that were converted to Hedge's D were DMI – Control, TMI – Control, and TMI – DMI where a common control was shared between the two experimental groups.

Effect sizes and multivariate meta-analyses

One-thousand and thirty-one effect sizes were extracted from 183 studies that reported demographic characters of prey with predators (DMI – Control group, which were studies that exposed prey to lethal predator exposure and compared to a control group) and indirectly with predators (TMI – Control group, which were studies that exposed prey to non-lethal predator exposure such as a caged predator, predatory chemical cues, alarm cues from digested or crushed conspecifics), and compared these with a control group (Control groups were unmanipulated such that prey were left free of any and all predator exposure). Some studies reported both DMIs and TMIs but compared these effects to a single control group (N = 32 studies). Hedge's D effect size was justified for this analysis since we used a multivariate model with 3 effects that incorporated homogenizing variances across the trivariate effects. Calculating effect sizes with a single (common) control group introduces statistical dependencies among effects and increases the type II errors of meta-analysis (Lajeunesse 2011). Therefore, following Olkin and Gleser (2009) and Brace et al. (2017), we modeled the variance ($\hat{\varphi}_{ii}$) and covariance ($\hat{\varphi}_{ij}$) of a multi-treatment common-control (\bar{Y}_C) Hedges' \hat{d} as:

$$\hat{\varphi}_{ii} = \frac{1}{n_i} + \frac{1}{n_c} + \frac{\hat{d}_i^2}{2n^*} \quad \text{and} \quad \hat{\varphi}_{ij} = \frac{1}{n_c} + \frac{\hat{d}_i \hat{d}_j}{2n^*},$$

where $n^* = n_C + \sum_{i=1}^m n_i$, m is the number of non-control treatments (i.e., the \bar{Y} of DMI and TMI groups), and i and j designate the multiple treatment effects that share \bar{Y}_C . Finally, the multi-treatment Hedges' \hat{d} uses the pooled variances from all m treatment groups such that

$$\hat{d}_i = \frac{\bar{Y}_i - \bar{Y}_C}{S_C} \left[1 - \frac{3}{4(n^* - m)} \right],$$

which has a pooled standard deviation (S_C) of:

$$S_C = \sqrt{\frac{(n_C - 1)SD_C^2 + \sum_{i=1}^m (n_i - 1)SD_i^2}{n_C - 1 + \sum_{i=1}^m (n_i - 1)}}.$$

Note that when $m = 1$, there is no covariance ($\hat{\phi}_{ij} = 0$), and \hat{d} and $\hat{\phi}_{ii}$ simplify to the original formulation of Hedges' d (Hedges 1981).

In matrix notation, our trivariate mixed-effects meta-analysis can be described with this regression model, referred to as equation 1 (eq.1):

$$d = MW\beta + \varepsilon + Mu + \gamma^2 + \tau^2,$$

where d denotes a $(k \times 1)$ column vector containing all of the k number of effect sizes. For each i^{th} of m number of studies, there can be three Hedges' \hat{d} effect sizes: the standardized difference between DMI and a control group ($\hat{d}_{\text{DMI-CONTROL}}$, or $\hat{d}_{\text{D-C}}$), the standardized difference between TMI and a control group ($\hat{d}_{\text{TMI-CONTROL}}$, or $\hat{d}_{\text{T-C}}$), and finally the standardized difference between TMI and DMI ($\hat{d}_{\text{TMI-DMI}}$, or $\hat{d}_{\text{T-D}}$). Therefore \hat{d} can have length $k = m \times 3$. However, some studies only report either $\hat{d}_{\text{DMI-CONTROL}}$ or $\hat{d}_{\text{TMI-CONTROL}}$. The indicator matrix M models this availability of effect sizes among studies. It has a block diagonal design with its main diagonal defined by I_i ; a vector whose i^{th} elements are either a 3×3 Identity matrix when the 3 effect sizes are available or a 1×1 Identity matrix when otherwise (e.g., coding studies with only $\hat{d}_{\text{D-C}}$ or $\hat{d}_{\text{T-C}}$ available). The second matrix in eq. 1 (W) is the regression design

matrix of $m \times (p + 1)$ size, with p number of covariates, and where the first column of W contains only ones (e.g., the model intercept). The regression coefficients of this model is defined by β which is a column vector of size $(p + 1) \times 3$. Since covariates (predictors) are included in our model and are treated as fixed effects, our meta-analysis model can also be described as a trivariate mixed-effects meta-regression.

The within-study sampling error and sampling covariances (e.g., $\hat{\phi}_{ii}$ and $\hat{\phi}_{ij}$ defined earlier) among the effect sizes is modeled as a block diagonal matrix ε which on its main diagonal contains the elements of an $m \times 1$ column vector of sampling variance-covariance matrices. The ε matrix models the weighting of effect sizes based on their sampling error, and models the non-independence of the trivariate effects that share common dependent variables. The multivariate (trivariate) component of our model is achieved by modelling three variance components (as well as covariance) for each of the three main underlying effects (u from eq. 1). For simplicity, it is assumed that these main effects have the following multivariate Normal (MVN) between-study random-effects distribution:

$$\begin{bmatrix} u_{D-C} \\ u_{T-C} \\ u_{T-D} \end{bmatrix} \sim MVN \left(0 = \begin{bmatrix} 0 \\ 0 \\ 0 \end{bmatrix}, u = \begin{bmatrix} \tau_{D-C}^2 & \tau_{(D-C),(T-C)} & \tau_{(D-C),(T-D)} \\ & \tau_{T-C}^2 & \tau_{(T-C),(T-D)} \\ sym & & \tau_{T-D}^2 \end{bmatrix} \right).$$

In addition to this multivariate between-study random effects, we include a second random-effects (γ^2) that models the over-representation of effects derived from multiple or repeated measure outcomes (e.g., time series, multiple populations; see Lajeunesse 2011). Finally, we include a third random effect (τ^2) that models the conventional between-study variance component of all random-effects meta-analysis (see Hedges and Olkin 1986).

This model (eq. 1) was implemented assuming unstructured trivariate random effects estimated via restricted maximum likelihood using the `rma.mv()` function of the *metafor* package

(v. 1.9-9; Viechtbauer 2010) in *R* (v. 3.3.3; R Core Team 2017). For all pooled effects (with k number of effect sizes), confidence intervals (CI) not overlapping with zero indicate significant effects, pairwise differences between pooled effect groups were evaluated using Wald-type z -tests, and multi-group differences were evaluated using Q_b tests (akin to omnibus ANOVA; Hedges and Olkin 1986). Forest and meta-regression plots, as well as the calculation of common control variable-covariance matrices, were completed using the *metagear* R package (v. 0.5; Lajeunesse 2016). Intra-class correlation coefficients (ICC), which estimates the between-study correlation among were \hat{d}_{D-C} and \hat{d}_{T-C} was estimated from the trivariate random-effects models from *metafor*'s `rma.mv()` function (termed rho within model outputs). Finally, Egger's tests for publication bias (Egger et al. 1997) was applied with the `regtest()` function for $\hat{d}_{DMI-CONTROL}$ ($k = 411$), $\hat{d}_{TMI-CONTROL}$ ($k = 486$), and $\hat{d}_{TMI-DMI}$ ($k = 104$)

CHAPTER THREE: RESULTS

Study composition and bias

One-hundred and eighty-three studies comprised our database following data extraction. From these 183 studies, 411 effects for the DMI – Control groups were obtained, 486 effects were obtained from the TMI – Control groups, and 104 effects were obtained from the TMI – DMI groups. This produced a total of 1031 effects from the 183 studies. Nineteen different predatory taxonomic classes were present in our database and diversity of classes ranged from Actinopterygii to Turbellaria. However, many taxonomic classes lacked sufficient sample sizes, and Actinopterygii (N = 47 studies), Arachnida (N = 19 studies), Insecta (N = 69 studies), and Malacostraca (N = 34 studies) were the predominant classes that represented our database. These 4 classes composed 91.8% of the predator taxonomic classes from studies included in data extraction.

Ecosystems were grouped into their type (aquatic, marine, terrestrial). Aquatic ecosystems were best represented in our database (N = 78 studies), followed by terrestrial ecosystems (N = 66 studies), and marine ecosystems were the least represented (N = 39 studies). Experiment type was also considered for each study included in data extraction, and laboratory experiments were slightly more prevalent (N = 96 studies) than field experiments (N = 93 studies). Behavioral TMIs were more represented (N = 80 studies) opposed to life history TMIs (N = 48) and morphological TMIs (N = 14 studies). Indirect effects were also examined in our

database, and studies including indirect effects from TMIs or DMIs were less prevalent ($N = 90$ studies) than studies lacking data on indirect effects ($N = 118$ studies). Demographic variables were separated into similar categories (see Methods). Survival category had the most representation in our database ($N = 116$ studies), trophic effects were the second most prevalent ($N = 74$ studies), and then reproductive category ($N = 20$ studies), followed by behavioral ($N = 7$ studies) and pathogens ($N = 2$ studies). Note that not all categories and their factors summate to 183 studies, which is because some studies reported more than one of each. For example, indirect effects had a total of 214 when the sample sizes of those with indirect effects ($N = 96$) and those without indirect effects ($N = 118$) are summed, and this is because some studies included multiple figures, some of which included data on indirect effects while other figures from the same study did not.

Egger's test was performed across the trivariate effects (DMI – Control, TMI – Control, and TMI – DMI). DMI – Control, TMI – Control, and TMI – DMI were determined to contain publication bias, respectively (DMI – CONTROL: $z = -13.5$, $p < 0.001$, $k = 442$, TMI – CONTROL: $z = 2.7$, $p = 0.006$, $k = 485$, and TMI – DMI: $z = 10.2$, $p < 0.001$, $k = 105$). This indicates that studies with small sample sizes (and therefore lesser precision) contributed larger effect sizes (see Appendix A, Supplemental Figure 6). There are numerous reasons why publication bias was detected. First, we used the number of experimental replicates as the sample size, and many studies had small numbers of replicates. Furthermore, there are violations of assumptions from our model with respect to the Egger's test. The first is that our model assumed random effects within the trivariate effects model. Second, dataset had too much heterogeneity to not violate the assumptions of Egger's test for publication bias. Finally, there was not enough variability amongst the weights of our studies, as most studies had similar sample sizes due to

experimental replicates being fairly homogenous. These violations of assumptions from our data and model make the test much less reliable and interpretable. We decided that a fail-safe test was inappropriate for our synthesis because all studies had relatively low power (which was underpinned by the smaller number of experimental replicates that were used as the sample size).

Overall effects

Density-mediated interactions (DMIs) have stronger, more negative effects on prey populations than trait-mediated interactions, or TMIs (see Figure 2); a difference that remains when DMI and TMI effects are contrasted directly within studies (TMI – DMI: $z = 2.75$, $p = 0.006$), and indirectly among studies (contrast between DMI – CONTROL and TMI – CONTROL groups: $z = 2.65$, $p = 0.0081$). However, both DMIs and TMIs produce non-zero negative effects on population demographics (DMI – CONTROL: $z = -3.78$, $p < 0.01$, TMI – CONTROL: $z = 2.39$, $p = 0.01$). Further, our joint synthesis of these two effects reveals a strong positive correlation between DMIs and TMIs (between-study correlation between DMI – CONTROL and TMI – CONTROL: $ICC = 0.575$), but DMI effects are considerably more heterogeneous than TMIs (DMI – CONTROL: $\tau^2 = 3.314$; TMI – CONTROL: $\tau^2 = 0.596$). Finally, there were no differences between indirect effects caused by reductions in prey density (DMIs) and TMIs relative to controls ($z = 0.51$, $p = 0.613$; see Appendix A), and total predator effects are not an additive model of $TMI + DMI = \text{Total effect}$ (Figure 2)—where DMIs produced stronger, more negative effects on prey than the total predator effect.

Predictors of DMI and TMI effects

Aquatic ecosystems had DMIs with significantly stronger, more negative effects than TMIs (Figure 3; $z = 2.55$, $p = 0.01$). TMIs between ecosystems did not significantly differ (Figure 3). However, DMIs from aquatic ecosystems had a marginally significant difference between DMIs in terrestrial ecosystems (Figure 3; $z = 1.78$, $p = 0.075$), but not between marine ecosystems (Figure 3; $z = -0.92$, $p = 0.360$). Morphological TMI effects had large variability and overlapped zero, so a reliable, definitive result is difficult to interpret or assert (Figure 2). Furthermore, no significant differences were found between the 3 types of TMIs (morphological, life history, and behavioral; see Figure 2).

DMIs from laboratory experiments had stronger, more negative effects on prey populations than DMIs from field experiments ($z = -1.98$, $p = 0.048$; see Appendix A) but the effects of TMIs from laboratory experiments did not significantly differ from TMIs from field experiments ($z = -1.01$, $p = 0.311$; see Appendix A). Demographic category (see Methods) revealed that effects measuring survival of prey over time were significantly different between DMIs and TMIs ($z = -4.39$, $p < 0.001$). All other demographic categories (trophic effects, reproductive, developmental, behavioral, and pathogens) were non-significant.

TMIs produced from invertebrate and vertebrate predators did not differ in their effects (Figure 4; $z = 0.20$, $p = 0.842$). However, DMIs from invertebrate predators had more negative effects than DMIs from vertebrate predators (Figure 4; $z = -2.01$, $p = 0.045$). Predator taxonomic class revealed that Insecta and Malacostraca had significant differences in effects between their DMIs and TMIs, respectively ($z = -3.75$, $p < 0.001$, $z = -1.98$, $p = 0.048$). No other significant differences were found between well-represented predator taxonomic classes.

DMIs from experiments with 2 trophic links had significantly stronger, more negative effects than TMIs (Figure 5; $z = 3.68$, $p < 0.001$). There were no significant differences in effect sizes between DMIs and TMI in experiments with 3 trophic links (Figure 5; $z = -0.64$, $p = 0.524$), 4 trophic links (Figure 5; $z = 0.34$, $p = 0.731$), and 5 trophic links (Figure 5; $z = 0.14$, $p = 0.889$). We did not find any trends or significant results with the type of indirect effect, the number of predators, the number of prey, invasive or native predators, and the duration of experiments (See Appendix A, Supplemental Figures).

Figures

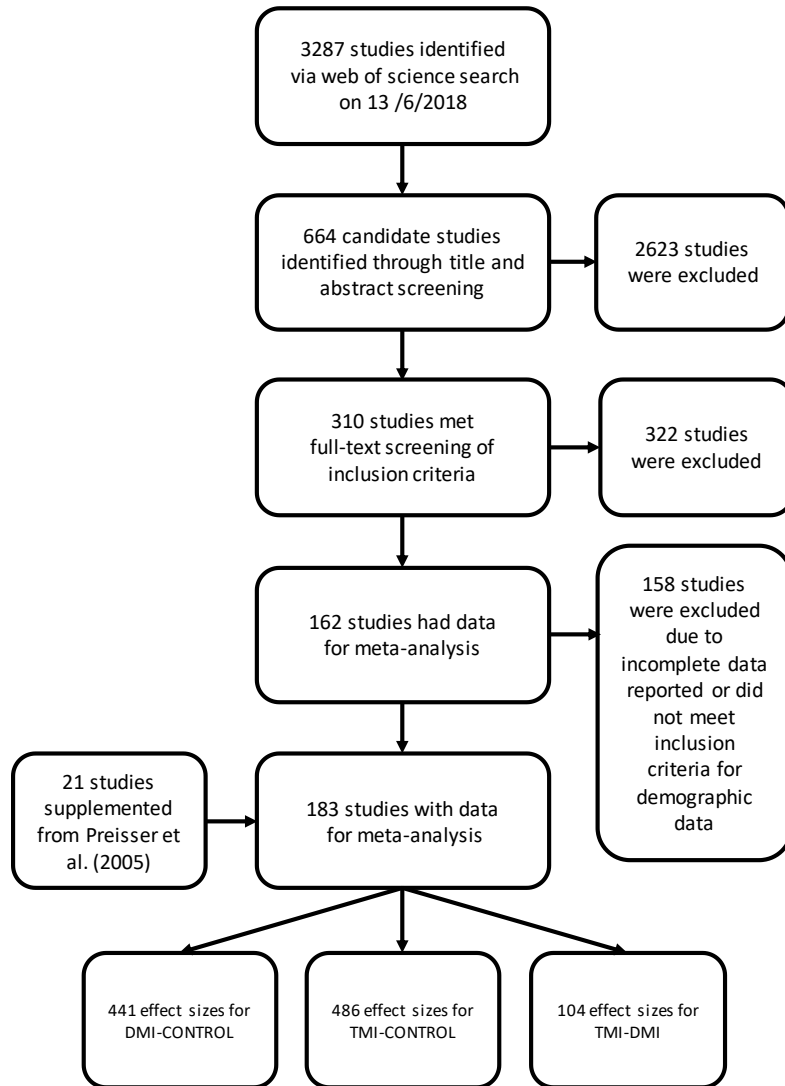


FIGURE 1. PRISMA plot that summarizes the results from the search string, screening process, inclusion criteria and elimination of studies until we arrived at our final number of studies that met our inclusion criteria for the meta-analysis. 21 supplemental studies were added from Preisser et al. 2005’s original list of papers.

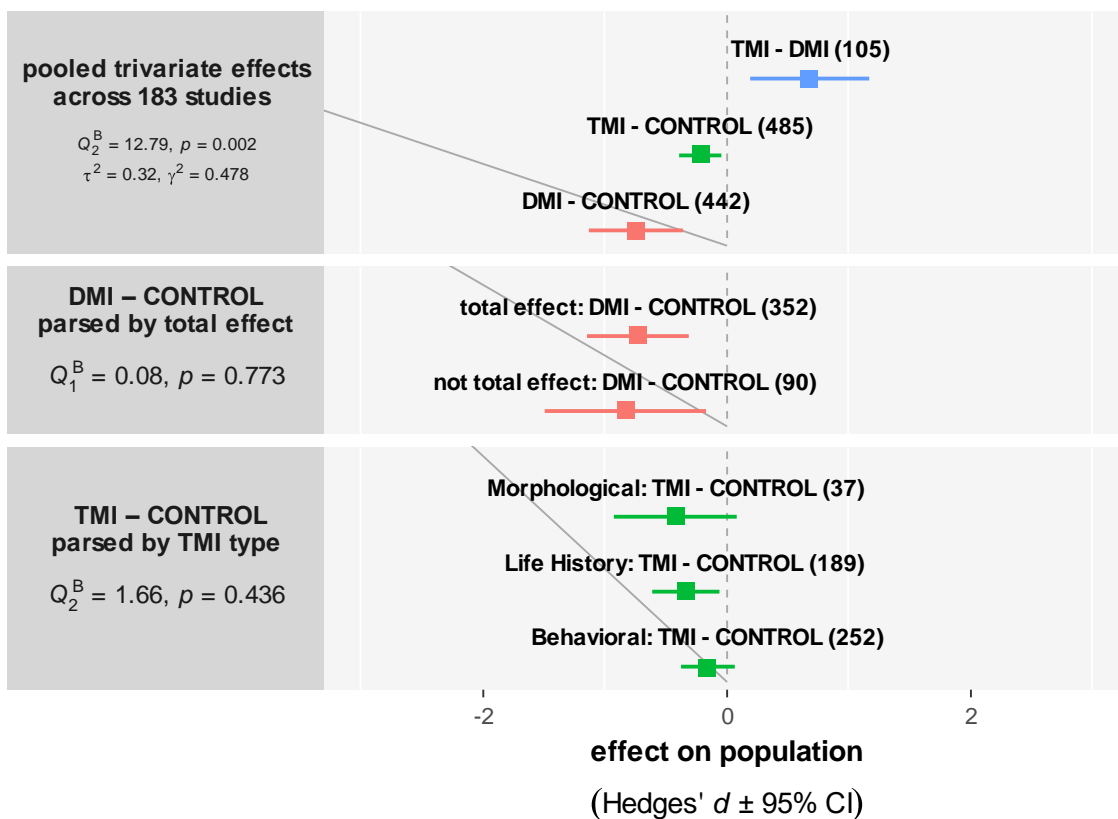


FIGURE 2. Main trivariate effects (DMI – CONTROL, TMI – CONTROL, AND TMI – DMI) across the 183 studies that were included for the meta-analysis. DMIs produced significant, negative effects relative to controls, and TMIs also produced negative effects relative to controls, but not to the same extent as DMIs. When TMIs and DMIs were directly contrasted (TMI – DMI), the overall effect size was positive. This is because both TMIs and DMIs were producing negative effects, but the effects from DMIs when directly contrasted were still more negative than those from TMIs, therefore a smaller negative effect size (TMI) being subtracted by a larger negative effect size (DMI) will mathematically produce a positive number, and that is why the TMI – DMI group has a positive effect size as depicted in the figure. The total predator effect and true DMI effects are also illustrated. A DMI – CONTROL labeled as the total effect included data that was from the total predator effect (meaning that the predator was able to kill prey and also was able to induce TMIs in prey over a sufficient duration), and a DMI – CONTROL without the total effect was solely the consumptive effect from the predator on the prey. The final illustration in this figure is TMI – CONTROL effects parsed by TMI type (behavioral, morphological, life history). No significant trends or results were obtained from TMI types. In the figure, Q_2^B represents test for between-group heterogeneity of effect sizes and τ^2 represents the random between-study variance from the effect size parameters and reflects the variance of the true effect sizes. γ^2 represent the random variation associated with effects derived from multiple or repeated measure outcomes. P value represents the significance of the associated heterogeneity with Q^B for each test from the Q test (Q^B).

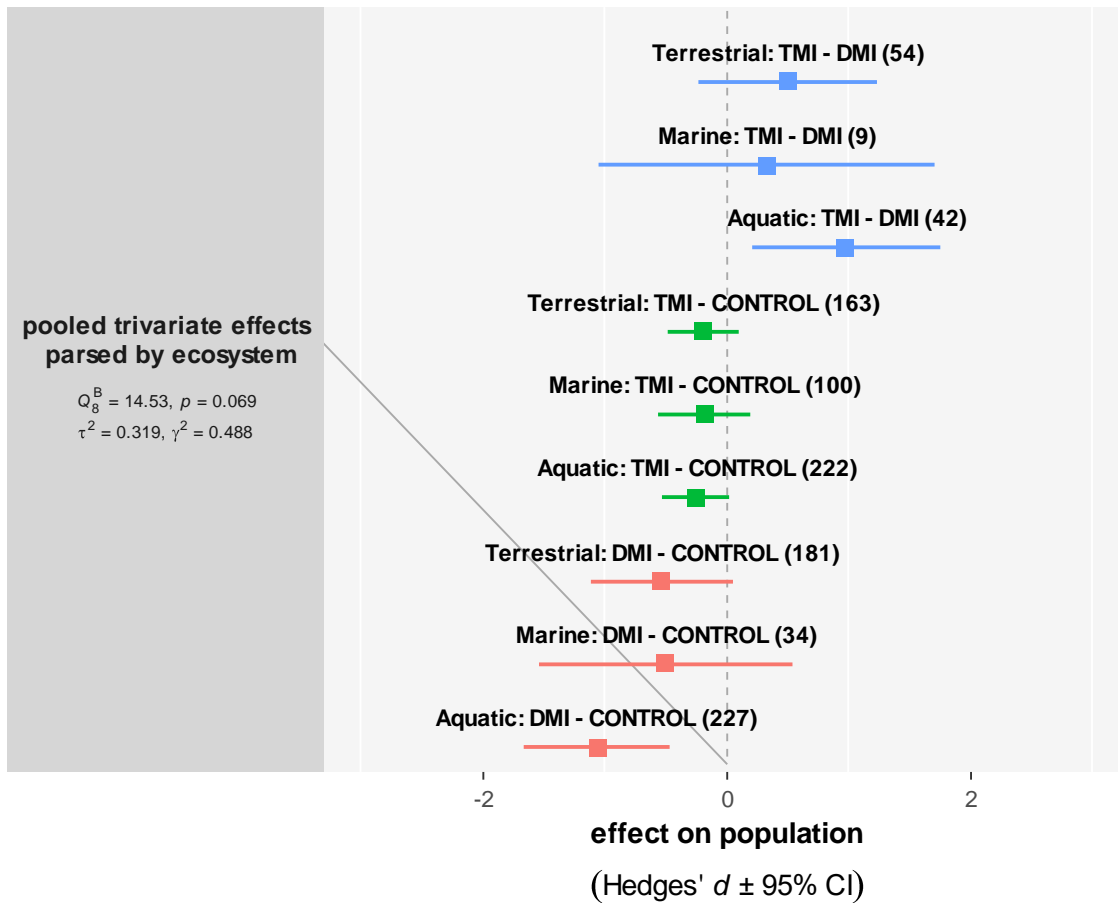


FIGURE 3. Trivariate effects for ecosystem type for comparisons between the effects of DMIs and TMIs. Aquatic ecosystems represent freshwater systems. Significant differences existed between DMI effects in terrestrial and aquatic ecosystems. In the figure, Q^B represents test for between-group heterogeneity of effect sizes and τ^2 represents the random between-study variance from the effect size parameters and reflects the variance of the true effect sizes. γ^2 represent the random variation associated with effects derived from multiple or repeated measure outcomes. P value represents the significance of the associated heterogeneity from the Q test (Q^B).

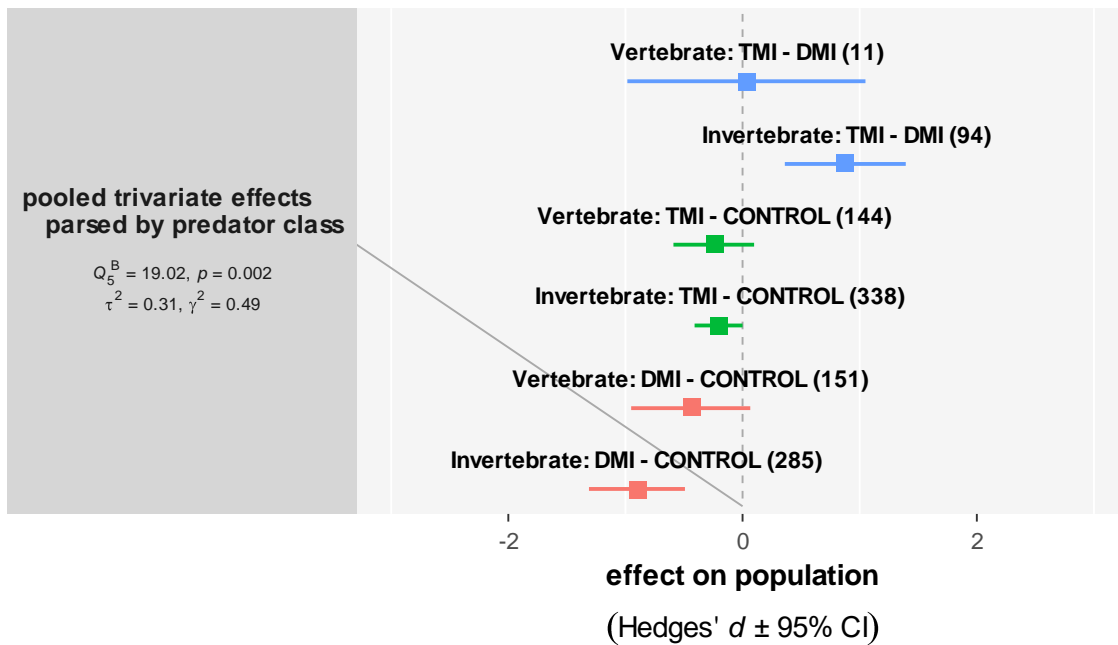


FIGURE 4. Trivariate effects with the predator type moderator with the factors of invertebrate or vertebrate predator. There was no trend or significant effect between DMIs and TMIs produced by invertebrate or vertebrate predators. In the figure, Q^B represents test for between-group heterogeneity of effect sizes and τ^2 represents the random between-study variance from the effect size parameters and reflects the variance of the true effect sizes. γ^2 represent the random variation associated with effects derived from multiple or repeated measure outcomes. P values represent the significance of the associated heterogeneity from the Q test (Q^B).

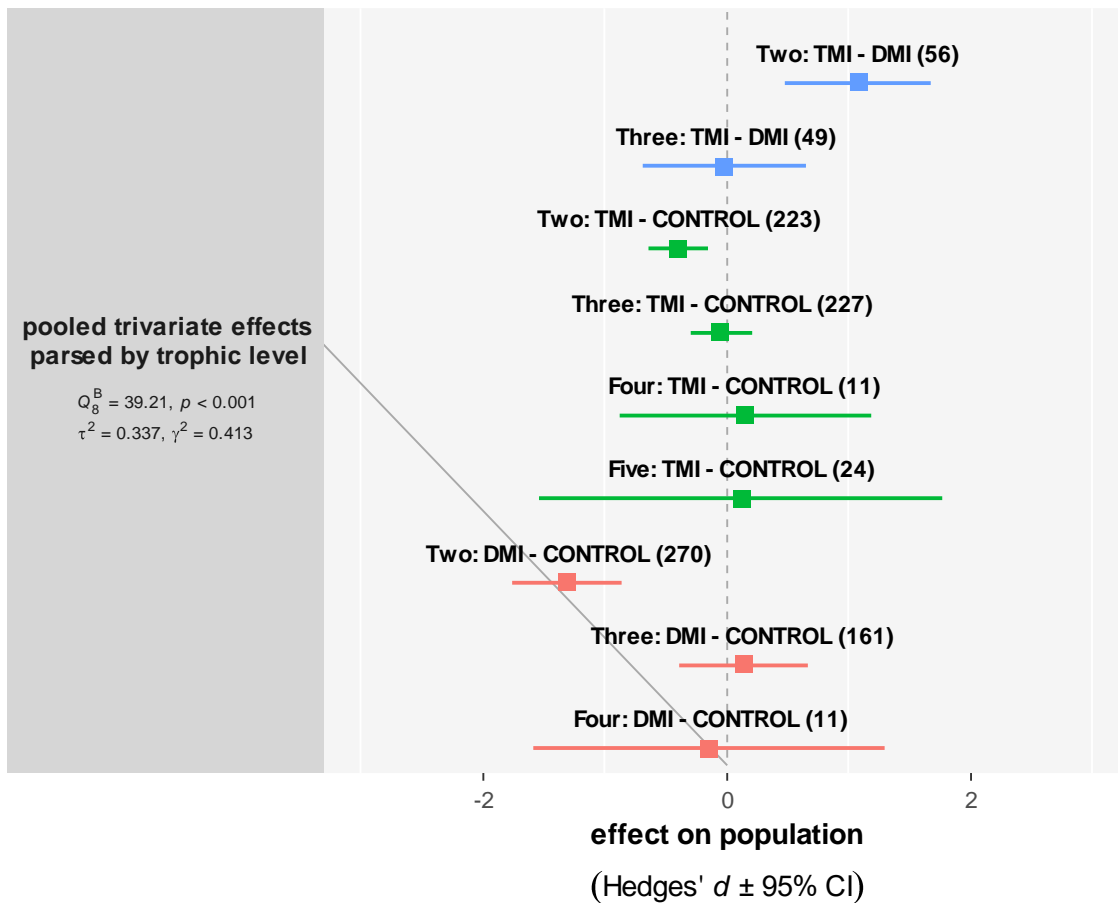


FIGURE 5. Trivariate effects with the number of trophic links moderator. The factors were 2, 3, 4, and 5 trophic links. Effects produced from 2 trophic links systems were stronger than effects from other linkages and is suggestive that effects from TMIs and DMIs lessen with increasing number of trophic linkages. In the figure, Q^B represents test for between-group heterogeneity of effect sizes and τ^2 represents the random between-study variance from the effect size parameters and reflects the variance of the true effect sizes. γ^2 represents the random variation associated with effects derived from multiple or repeated measure outcomes. P values represent the significance of the associated heterogeneity from the Q test (Q^B).

CHAPTER FOUR: DISCUSSION

We found that the total predator effect is less than the effects produced by DMIs alone. This is biologically intuitive. The predator effect encapsulates both the DMI effects and the TMI effects, and prey initiate TMIs and corresponding trait changes in order to reduce the risk of predation and increase fitness via trait changes (Fordyce 2006, Peacor et al. 2006, Inouye and Stinchcombe 2003). If prey experienced an additive model of DMIs and TMIs that created equal effects as the total predator effect, and thus did not reduce the total predator effect, then it makes little biological sense for prey to initiate a TMI, since it would not reduce the total predator effect.

We also found that although TMIs have negative effects on prey populations, DMIs nearly have twice this negative impact. These findings contrast with Preisser et al. (2005) original findings that TMIs/non-consumptive effects contributed more to predator effects on prey than DMIs/consumptive effects, and that TMI effects are generally equal to or stronger than DMIs. Our findings are a more robust evaluation of the overall effects of DMIs and TMIs in prey populations given that we: (1) synthesized significantly more studies across a broader range of experimental systems and taxonomic classes, (2) used a more systematic approach to find studies, (3) jointly modelled DMI and TMI effects using a multivariate model to directly and indirectly compare the effect sizes of TMIs and DMIs relative to controls, (4) used a more appropriate effect size in Hedge's *D*, and (5) used more inclusive criteria.

DMIs being twice as large in effects as TMIs is highly suggestive that predator-prey dynamics are strongly regulated and shaped by consumptive effects. Furthermore, predators are regulators of ecosystem nutrient cycles and abundance (Schmitz 2006, Schmitz et al. 2010), and therefore this regulation is also likely mediated by consumptive effects as opposed to non-consumptive effects. Consumptive effects of predators and DMIs regulating prey abundance and recruitment are ubiquitous (Weinstein 1977, Dorn 2013, Kellogg and Dorn 2012) and our synthesis supports that the consumptive effects from predators are much stronger regulators of predator-prey dynamics than non-consumptive effects.

DMIs were found to be more heterogenous than TMIs, and this could be due to differences in predatory hunting strategies producing much more variable consumptive effects. For example, sit-and-pursue predators were found to elicit stronger non-consumptive effects than sit-and-wait predators (Preisser et al. 2007), and similar processes may be true for consumptive effects. We also posit that the variability associated with DMIs could be due to other factors such as the body size ratios between the respective predator and prey, the type of feeding strategy utilized by the predator, and the satiation limits to the predator. For example, in systems where the prey is order of magnitudes smaller than the predator (such as in lacewing-aphid predator-prey dynamics), it is highly likely the predator will be able to consume a greater number of prey while hunting. Furthermore, the satiation limit of the predator is a consideration to explain the variation of DMIs, as some predators are voracious and continually consume prey at higher rates, whereas other predators may consume prey at a lower frequency and the prey they do consume at a lower frequency could be relatively larger in body size than predators who feed at more regular intervals. We also found a strong correlation between DMIs and TMIs, and suggest this correlation means that predators that exert large DMI effects also exert large TMI effects on prey

species. This is biologically intuitive. For example, the more lethal and therefore stronger DMI a predator imposes upon prey species, then it follows that the prey should make a larger effort to avoid this more lethal predator as opposed to other, less lethal potential predator. This is also consistent with natural selection, as the greater intensity of predation and therefore risk from a predator would result in a greater intensity of responses in prey to maximize fitness. Therefore, a highly lethal predator (which imposes relatively large DMIs) would be expected to impose relatively large TMIs since the intensity of selection of the prey to avoid predation via trait modifications would also be large. This is a possible explanation for the biological underpinning of the correlation between DMIs and TMIs that was observed from our analysis. Also, this could suggest that certain predators disproportionately regulate lower level trophic guilds via their large, combined effects from TMIs and DMIs. In marine systems, apex predators are known to mediate significant changes in resource and prey abundance via consumption and behaviorally induced TMIs (Heithaus et al. 2007, Wirsing et al. 2007).

Our findings agree with Preisser et al (2005) that aquatic systems produced more costly TMIs and DMIs than terrestrial ecosystems, however only DMIs were significantly different between aquatic and terrestrial ecosystems. This could be that aquatic ecosystems contain prey that are more adept at detecting predator cues (Brown 2003, Ferrari et al. 2010) and therefore initiate TMIs at greater frequencies. It has been suggested that aquatic ecosystems have more trophic levels and interactions (Hairston and Hairston 1993) and this could explain why these systems have stronger, more negative DMI effects than terrestrial ecosystems. Furthermore, with more trophic links and predator types, it is likely there is a greater diversity of hunting modes by predators in aquatic systems, and hunting mode has been suggested to be important for evaluating the consumptive and non-consumptive effects of predators (Preisser et al. 2007).

Alternative explanations for why aquatic ecosystems have stronger DMIs and TMIs than terrestrial ecosystems could be due aquatic systems, on average, being more constrained in elemental nutrient composition ratios (Elser et al. 2000) and in their physical boundaries. Boundaries are more constrained in aquatic systems as dispersal is highly limited. For example, an aquatic species can only disperse as far as the system is in size, meaning that the size of the puddle, pond, or lake is a physical constraint for movement and dispersal from predation risk. In terrestrial systems, prey are able to disperse much further distances in order to find microhabitats that have lower predation risk yet are still energetically profitable. Another caveat to aquatic ecosystems is that they appear to be driving the overall effects from DMIs being twice as large as TMIs (see Figure 3). The effect sizes from the overall model (see Figure 2) show DMI – CONTROL effects being much more negative than TMI – CONTROL, and this pattern is also true within aquatic ecosystems but not terrestrial or marine ecosystems (see Figure 3). Furthermore, the sample sizes for aquatic ecosystems were greater than those from terrestrial and marine ecosystems for both the TMI – CONTROL and DMI – CONTROL groups. The variability associated with the 95% confidence interval within marine and terrestrial ecosystems from the DMI – CONTROL is also suggestive that we are not able to determine significant effects from controls as the 95CIs overlapped zero (see Figure 3), but this was not true of aquatic ecosystems, giving further support that aquatic ecosystems could be the overall driver of our trivariate effects model revealing that DMIs are nearly twice as strong and negative in effects relative to TMIs.

There were no significant differences found amongst the types of TMIs described within our analysis (which were behavioral, morphological, and life history), and we suggest that many TMIs may come with relatively equal trade-offs. However, this could be biased due to more

studies in our database that examined behavioral and life history TMIs than morphological TMIs. Invasive predator species did not show effects that were significantly different than native predator species. This was true for both DMIs and TMIs. We suggest that the lack of co-evolutionary history relative to invasive species and native prey is not an important consideration for the cost of TMIs initiated by prey species. Examples of invasive predators causing TMIs and non-consumptive effects in native prey are ubiquitous across a variety of predator-prey dynamics (Pangle and Peacor 2006, Pangle et al. 2007, Griffen and Byers 2009). Furthermore, examples of invasive prey species initiating TMIs to native predators are rife (O'Neill et al. 2014, Naddafi et al. 2007, Naddafi and Rudstam 2013). With this, we assert the lack of co-evolutionary history is not an important consideration for TMIs in native and non-native species, and results from our analysis support that native species will respond in similar manners to invasive species as they would native species when initiating TMIs.

We found that indirect effects had no significant differences whether caused by DMIs or TMIs. Our results are suggestive that indirect effects and trophic cascades are equally affected by TMIs and DMIs, and that both processes are important considerations for top-down control of ecosystems and trophic cascades.

Laboratory experiments produced stronger magnitudes of effect sizes than field experiments, and this was true for both DMIs and TMIs. However, only DMIs significantly differed between field and lab results (see Results section). This could be due to laboratory conditions being highly controlled and optimal for predator-prey interactions (examples being temperature, lighting, food availability, lack of inter-specific competition, lack of weather), and lacking the confounding nature of field experiments. For example, in aquatic field experiments that seek to enclose prey and expose them to chemical predatory cues and determine the effect of

a TMI, there remains the issue of all other, potential predatory cues being experienced by prey species from other alarm, kairomone, or chemical cues from predators that were not the target of the experiment. These simultaneous cues from multiple predators in field experiments could dampen the specific TMI response of prey, and thus produce smaller effects than the more controlled laboratory experiments.

We did not find significant differences between TMIs initiated by invertebrate or vertebrate predators. Prey may respond in similar ways to increase vigilance and predator avoidance regardless of whether it is a vertebrate or invertebrate predator. Our analysis only contained 4 studies that examined the effects of an invertebrate and vertebrate predator on the same prey species, thus making it impossible to determine if one predator type elicited larger TMIs on the shared prey. This is a gap in the literature that could be a fruitful avenue for future research.

The number of prey, number of predators, and experimental duration did not produce meaningful or significant results when analyzed under meta-regression for DMIs and TMIs (See Appendix A). Previous meta-analysis determined that resource availability and competition are influential in determining the strength of TMIs (Bolnick and Preisser 2005), however, our analysis suggests that the degree of competition as determined by the number of prey was not a significant predictor for TMI effect size. We also found that prey respond to predators regardless of how many predators are present in the system: the risk of predation (TMI effects) does not appear to be modified depending on how many predators are present. This suggests prey may only have a threshold of detection for predators, and a single predator may be enough to initiate a TMI in prey.

Future directions for research should examine the role of simultaneous predator effects on prey with multiple predators, as this is more representative of ecosystems and reality.

Furthermore, multiple predator effects are more representative of field experiments, and we suggest these experiments be conducted in the field and laboratory so that the results can be compared across these two systems. Further directions for research should also examine the role of competitor or companion species and how their presence alters TMI and DMI dynamics. These types of studies are most common in agricultural systems aimed at controlling pest presence and herbivore damage. Another direction for research is to design more experiments that examine both TMIs and DMIs simultaneously, relative to a common control, as we found a relatively low number of studies that reported both. Publication bias was detected in our analysis, but this is a minor cause for concern because most studies had smaller numbers of experimental replicates. Also, the sample size in our analysis was not the effective sample size, and our data and trivariate model violated many of the assumptions of Egger's test (see Results section). Future research should work to address increasing their number of replications, as this will increase the power of future studies as well as allowing for more power in future meta-analyses on this subject.

With DMIs being twice as large as TMIs, being highly correlated with each other, and DMIs being more variable than TMIs, we suggest future research should evaluate the effects of TMIs within the context of how it relates to the DMI, as there does not appear to be a clear reason to study TMIs without also evaluating DMIs as TMIs appear to be used to lessen the DMIs from predators.. Furthermore, we did not find any differences between indirect effects caused from DMIs or TMIs and suggest that trophic cascades should be equally evaluated under

both processes to arrive at more complete and complex understandings of ecosystems and the processes that alter them.

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APPENDIX A: Supplemental Figures

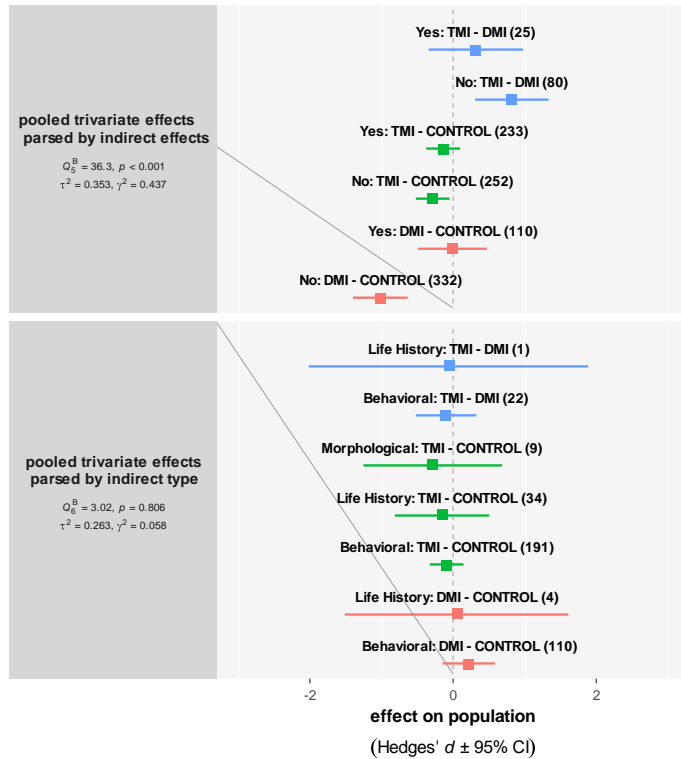


FIGURE A1. Trivariate effects plot for the indirect effects and type of indirect effects moderator variables. Indirect effects mediated by TMIs and DMIs in the top portion of the figure, and the lower portion illustrates how the type of indirect effect (behavioral, life history, or morphological) alter the strength of indirect effects produced from TMIs and DMIs from our database. Effect sizes for indirect effects caused by reductions in prey density (DMIs – CONTROL) did not significantly differ from effect sizes caused by changes in prey traits (TMIs). Furthermore, the type traits causing indirect effects within DMI – CONTROL and TMI – CONTROL groups did not result in significant differences. In the figure, Q^B represents test for between-group heterogeneity of effect sizes and τ^2 represents the random between-study variance from the effect size parameters and reflects the variance of the true effect sizes. γ^2 represent the random variation associated with effects derived from multiple or repeated measure outcomes. P values represent the significance of the associated heterogeneity from the Q test (Q^B).

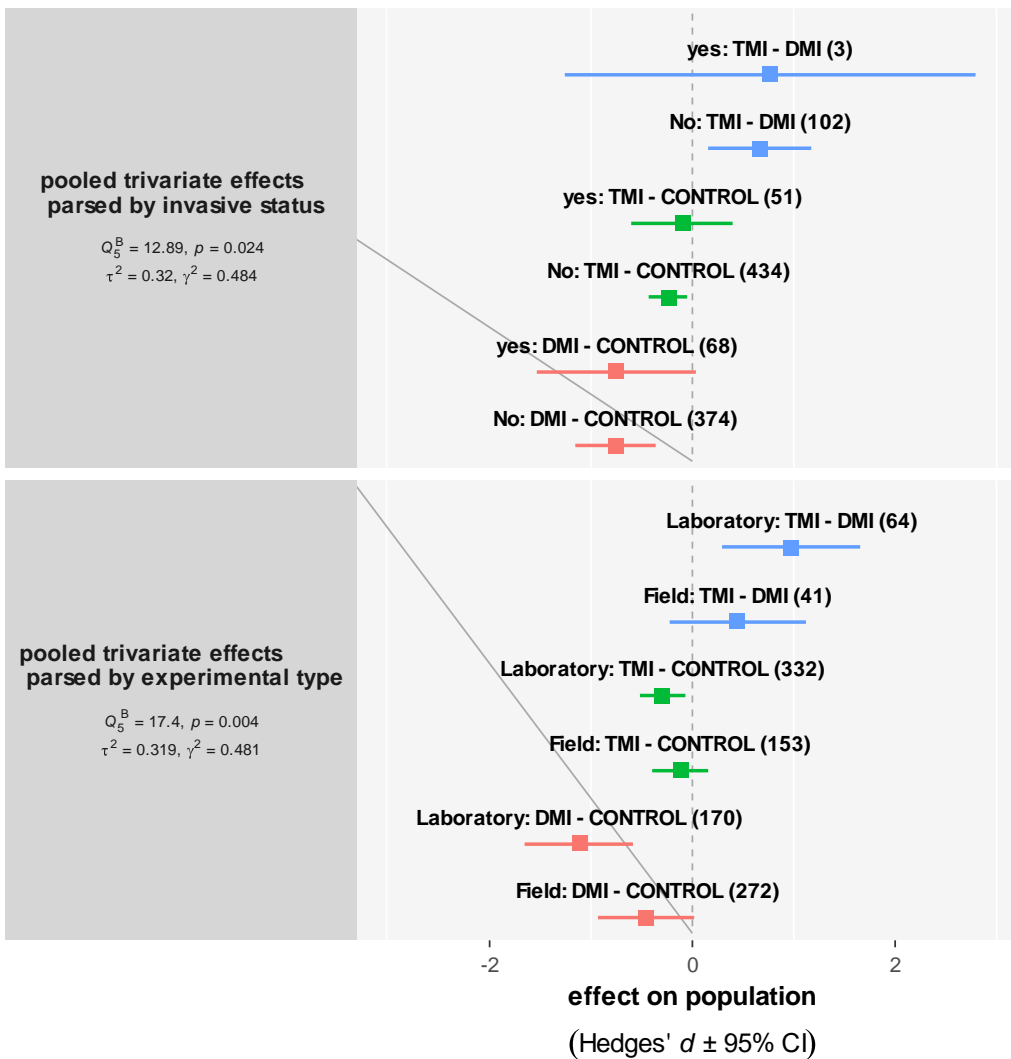


FIGURE A2. Trivariate effects moderator plot for the invasive species and experiment type variables. Invasive species status alters the effect sizes of DMIs and TMI relative to control groups, and in the lower portion illustrates how effect sizes within and between TMIs and DMIs relative to control groups differ in studies from laboratory or field conditions. Invasive species are represented by effect sizes in the plot with ‘yes’ and native are labeled with ‘no.’ Invasive species status did not significantly alter effect sizes within any of the trivariate effects we modeled and analyzed. Within the type of experiment, there were significant differences between effects sizes between laboratory and field experiments within DMI - CONTROL effect sizes. However, there was not a significant difference between effect sizes from laboratory and field experiments within TMI – CONTROL. In the figure, Q^B represents test for between-group heterogeneity of effect sizes and τ^2 represents the random between-study variance from the effect size parameters and reflects the variance of the true effect sizes. γ^2 represent the random variation associated with effects derived from multiple or repeated measure outcomes. P values represent the significance of the associated heterogeneity from the Q test (Q^B).

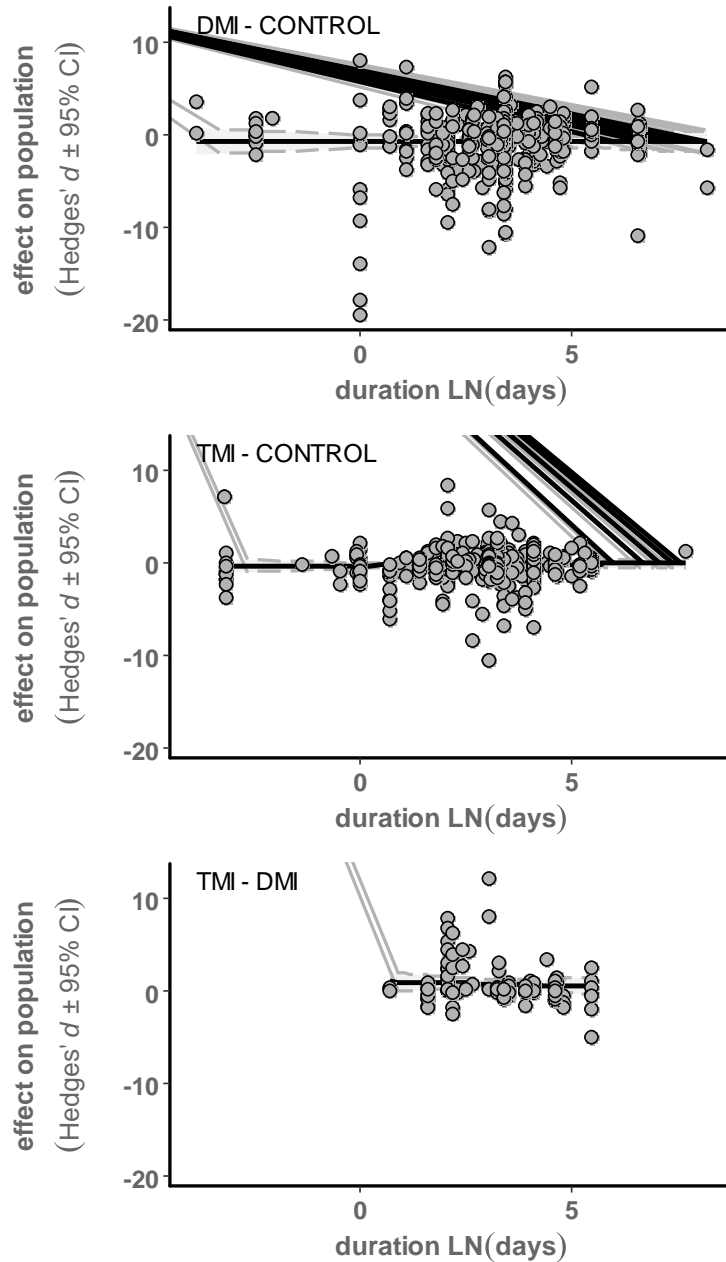


FIGURE A3. Results from the meta-regression plot for the trivariate effects with respect to the duration of experiments in days. Experimental duration was natural log transformed. There were no significant directionalities or correlations within any of the trivariate effect sizes when regressed with the number of days for the experiment duration. This suggests that experimental duration does not correlate to the effect sizes produced from TMI – DMI, TMI – CONTROL, or DMI – CONTROL.

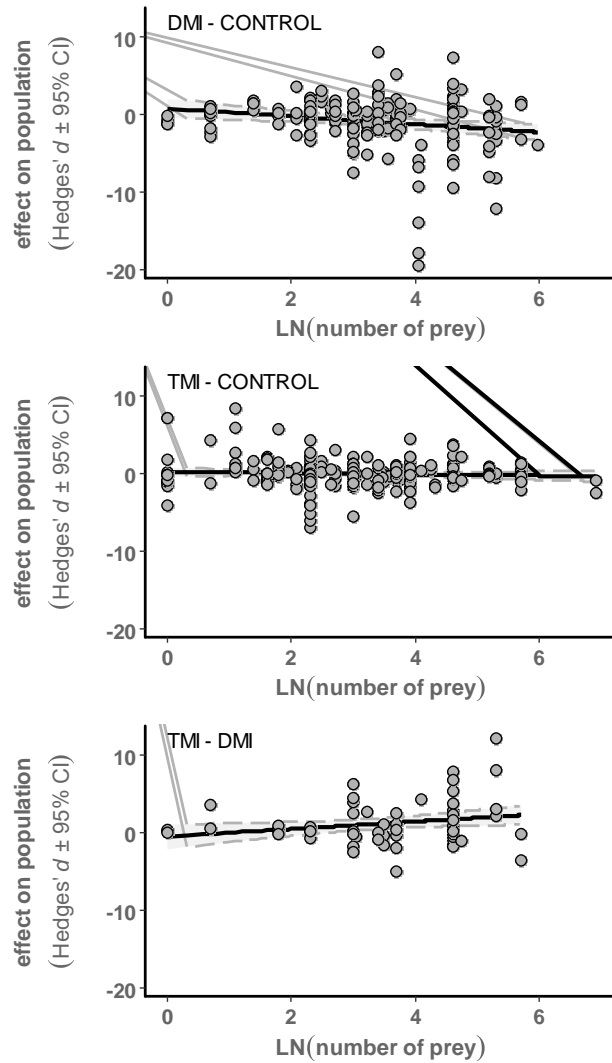


FIGURE A4. Results from the meta-regression plot for the trivariate effects with respect to the number of prey in each experimental design. The number of prey in each experiment were natural log transformed. There were no significant or obvious directionalities or correlations within any of the trivariate effect sizes when regressed against the number of prey. This suggests that intraspecific competition does not significantly alter the effect sizes for TMI – DMI, TMI – CONTROL, or DMI – CONTROL. The solid line represents the correlation, and the dashed lines represent the 95% confidence intervals of the correlation.

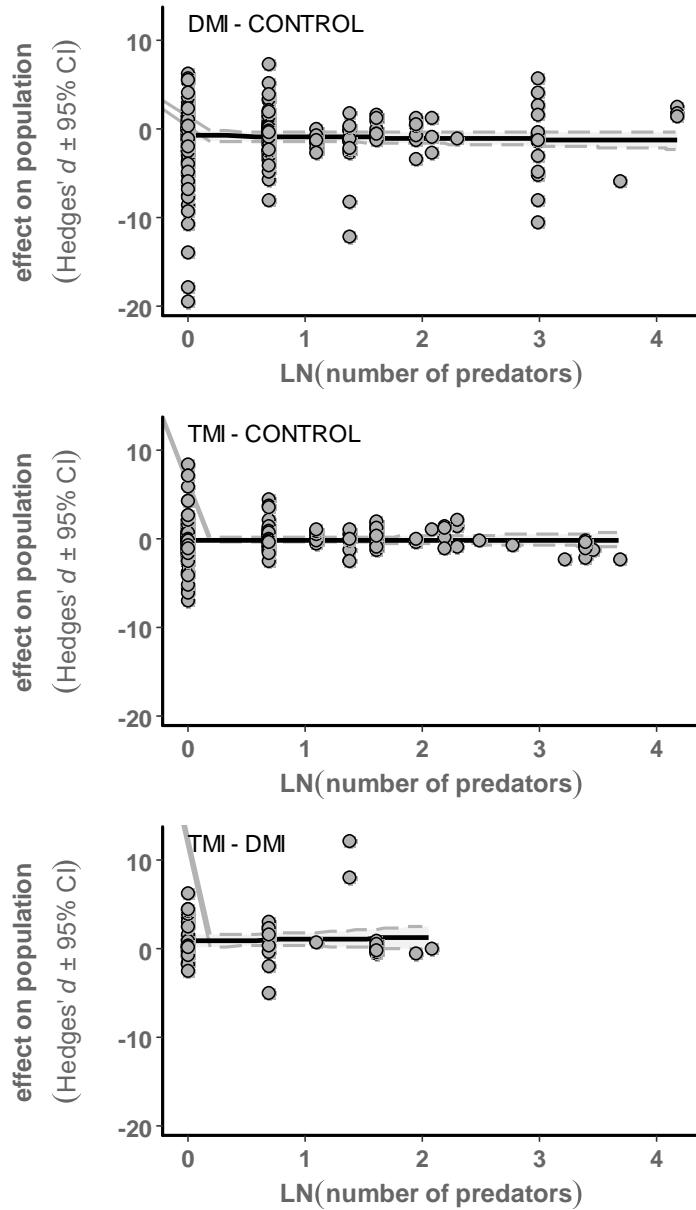


FIGURE A5. Results from the meta-regression plot for the trivariate effects with respect to the number of predators that prey were exposed to. The number of predators in each experiment were natural log transformed. There were no significant directionalities or correlations found within any of the trivariate effects when regressed against the number of predators. This suggests that prey respond to predators in a more binary manner, as opposed to altering responses depending upon the intensity of predation risk. The solid line represents the correlation, and the dashed lines represent the 95% confidence intervals of the correlation.

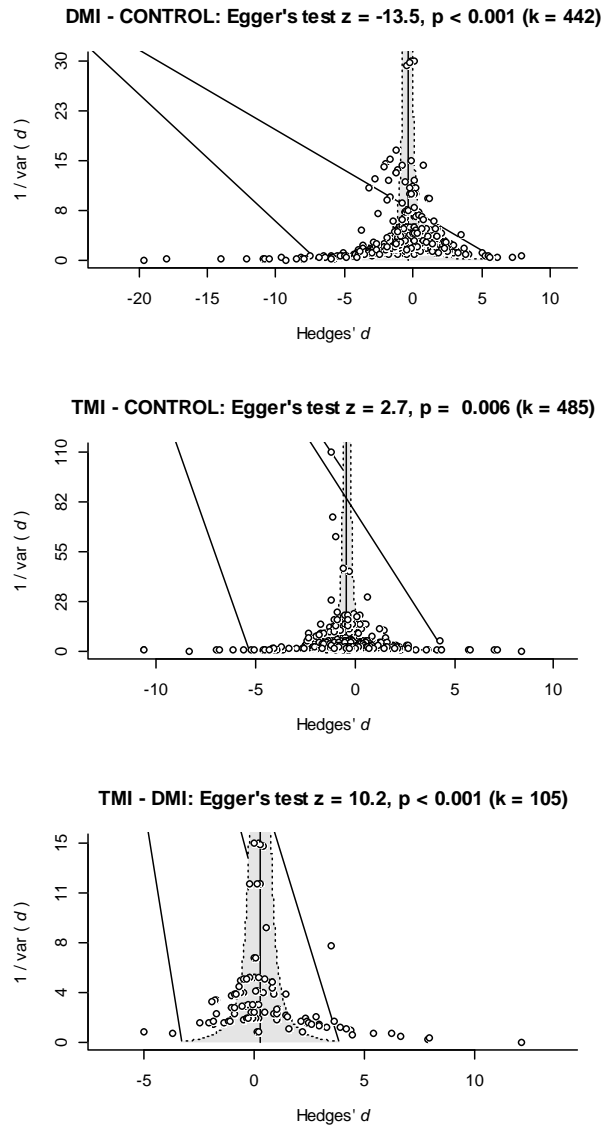


FIGURE A6. Egger's test for publication bias across the trivariate effects that were used for the meta-analysis. Within each effect type in our trivariate model (TMI – DMI, TMI – CONTROL, and DMI – CONTROL) publication bias was detected. There are numerous reasons why publication bias was detected. First, we used the number of experimental replicates as the sample size, and many studies had replication below $N = 30$. This is likely due to constraints on designing mesocosms with more than 30 replicates per treatment. Furthermore, there are violations of assumptions from our model with respect to the Egger's test. The first is that our model assumed random effects within the trivariate effects model. Second, dataset had too much heterogeneity to not violate the assumptions of Egger's test for publication bias. Finally, there was not enough variability amongst the weights of our studies, as most studies had similar sample sizes due to experimental replicates being fairly homogenous. These violations of assumptions make the test much less reliable and interpretable.