Article title: Trophic Interaction Modifications: An empirical and theoretical framework

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Abstract

1 Consumer-resource interactions are often influenced by other species in the community. At present

2 these "trophic interaction modifications" are rarely included in ecological models despite

3 demonstrations that they can drive system dynamics. Here we advocate and extend an approach

4 that has the potential to unite and represent this key group of non-trophic interactions by

5 emphasising the change to trophic interactions induced by modifying species. We highlight the

6 opportunities this approach brings in comparison to frameworks that coerce trophic interaction

7 modifications into pairwise relationships. To establish common frames of reference and explore the

8 value of the approach, we set out a range of metrics for the 'strength' of an interaction modification

9 which incorporate increasing levels of contextual information about the system. Through

10 demonstrations in three-species model systems, we establish that these metrics capture

11 complimentary aspects of interaction modifications. We show how the approach can be used in a

12 range of empirical contexts; we identify as specific gaps in current understanding experiments with

13 multiple levels of modifier species and the distributions of modifications in networks. The trophic

14 interaction modification approach we propose can motivate and unite empirical and theoretical

15 studies of system dynamics, providing a route to confront ecological complexity.

Introduction

Trophic interactions between species are often affected by other species within the community (Abrams 1983; Werner & Peacor 2003). There have been growing calls to incorporate these processes into studies of system dynamics (Bolker *et al.* 2003; Ings *et al.* 2009; Fontaine *et al.* 2011; Kéfi *et al.* 2012; Ohgushi *et al.* 2012; Sanders *et al.* 2014) since these trophic interaction modifications (hereafter 'TIMs' (Wootton 1993; Golubski & Abrams 2011)) are often identified as the cause of unexpected responses to perturbations (Doak *et al.* 2008; Tack *et al.* 2011; Barbosa *et al.* 2017). Focussed, short-term, studies with small numbers of species have repeatedly demonstrated that TIMs have the capacity to drive population dynamics (Werner & Peacor 2003; Preisser *et al.* 2005) and there is growing impetus to test the potential role of modifications in more complex systems. A greater understanding of how they influence population dynamics will be a key part of improving our ability to forecast how ecosystems will respond to change (Kéfi *et al.* 2012).

A very wide range of ecological processes can cause TIMs and historically these have been studied independently within ecological sub-disciplines. While this breadth highlights the importance of interaction modifications and associated indirect effects, it may result in generalisations being missed and lost opportunities to draw inferences. Consistent and comparable quantification of TIMs that can be broadly applicable will be an essential tool to draw general conclusions regarding their impact (Abrams 1992, 2007; Okuyama & Bolker 2012). Whereas it can be comparatively clear which species are linked by trophic interactions, interaction modifications must be inferred from their effect upon the consumer and resource species. Furthermore, any species could hypothetically affect almost any interaction in a community to some degree. This potentially overwhelming complexity places great value on the ability to define when interaction modifications are 'large' enough to require consideration in order to understand the dynamics of a given system.

Here, we advocate extending our understanding of interaction modification effects beyond pairwise approaches through the use of an explicitly multi-species TIM approach. To establish common

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41 frames of reference and explore the value of this approach, we develop a set of metrics to show how

42 TIMs can be interpreted, quantified and linked to experimental data. We show that this TIM concept

43 offers a lens to unite a range of important processes that has the potential to greatly enhance our

44 understanding of these effects on both theoretical and empirical system dynamics.

45 *Delineating Trophic Interaction Modifications*

46 TIMs are defined as the modification of a consumer-resource interaction by a third species (Wootton

47 1993; Golubski & Abrams 2011). This common property can link a wide-range of important

48 ecological phenomena as modifications of functional responses and as such form a useful and

49 discrete subset of the wider field of 'non-trophic interactions' (Kéfi *et al.* 2012). Examples of sources

50 of TIMs include foraging choices (Abrams 2010a) and associational defences (Barbosa *et al.* 2009)

51 which act to cause non-trophic interactions such as ecosystem engineering impacts (Sanders *et al.*

52 2014), fear effects (Brown *et al.* 1999) and mutualistic relationships (Holland *et al.* 2005). By focusing

53 on effects that involve consumption, and not attempting to also include other processes that have

54 been grouped into the category of 'non-trophic effects' (such as reproductive interference,

55 migration effects and mutualistic impacts on survival), we believe this TIM framework strikes a

56 balance between grouping a wide range of ecological effects while still being able to examine

57 common dynamic consequences in depth. Nonetheless many of the concepts discussed in this paper

58 could also apply to non-trophic interaction modifications, such as modulation of competition for

59 space by a third species.

60 Two alternate concepts for the study of this same set of ecological phenomena have developed

61 (Table 1), which we will refer to here as the TIM approach and the trait-mediated indirect interaction

62 (TMII) approach, where 'trait' is broadly defined to include any property of an organism that affects

63 its functional response or that of its consumer (Bolker *et al.* 2003). The TIM approach conceptualises

64 the modification of the interaction as a distinct entity of study in itself, while the TMII approach

65 emphasises the pairwise consequences of the modification. The distinction between proximate

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66   cause (change in trait), dynamic (change to the interaction) and consequence (resultant effect

67   between species not otherwise linked) can be blurred and the terms conflated since the TIM and

68   TMII approaches attempt to represent the same underlying ecology (Fig. 1).

69   A pairwise TMII approach brings certain advantages, for example facilitating direct comparisons with

70   other classes of trophic and non-trophic interactions through established network metrics and

71   extensions into multi-layer networks (Kéfi *et al.* 2016). However, this coercion of a process involving

72   at least three species into an interaction between two species risks obscuring fundamental features

73   and mechanisms that differentiate these trait-mediated processes from other interactions (Golubski

74   *et al.* 2016). As a very direct example, if species B of the system depicted in Fig. 1 (a) is no longer

75   present, there should no longer be an A-C interaction, but the dependence on B is not included in

76   the specification of the A-C indirect pairwise link. In contrast, the TIM concept does not allow

77   conventional network analysis (Newman 2010), since that requires a distinct set of nodes and links

78   (edges). However, for this very reason a TIM framework is a more direct representation of the

79   process from a system dynamics perspective, in particular identifying the distinctive roles of the

80   species involved.

81   A third approach using the mathematical concept of 'hypergraphs' has recently been proposed by

82   Golubski *et al.* (2016). This framework represents interactions with 'hyperedges' that can link any

83   number of species, in contrast to conventional network links that each represent interactions

84   between exactly two species. This incorporates the multi-species nature of effects caused by

85   interaction modifications and allows the application of hyper-dimensional extensions of network

86   metrics. However, as Golubski *et al.* (2016) discuss, this approach is limited in its ability to represent

87   the underlying dynamics as it does not yet allow the specification of the identity of modifier and

88   interactors, or the directionality of the effect.

89   Opportunities of TIM approach

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90   Compared to pairwise TMII analyses, a TIM framework provides a practical approach to consider a

91   greater range of dynamic consequences from the same underlying ecology. TIMs provide a

92   mechanism to translate potentially disparate and complex underlying processes into an

93   understanding of how they lead to consequences at higher levels of organisation. To examine some

94   of these opportunities we first consider how the 'strength' of TIM effects can be defined. Here we

95   outline five aspects of interaction modifications that can be considered in metrics of their magnitude

96   to demonstrate the potential utility of the approach.

97   Firstly, the impact of an interaction modification can depend on the strength of the interaction being

98   modified - a large proportional effect on a weak interaction may be less likely to have a large effect

99   on the system as a whole. However, interaction strength has been specified by a host of different

100   complimentary approaches (Laska & Wootton 1998; Berlow *et al.* 2004), ranging from consumption

101   rate to response ratios. For simplicity, most simulation models seeking to evaluate the impact of

102   TIMs specify them as relative modifiers of interactions (Křivan & Schmitz 2004; Arditi *et al.* 2005;

103   Goudard & Loreau 2008). With the ability to consider explicitly the aspect of interaction strength

104   that is being modified, the dynamic impact of the modification under consideration can become

105   clearer.

106   Secondly, conceptions of TIM strength can consider the extent to which they incorporate indirect

107   effects of TIMs and resultant feedbacks, with important consequences for the interpretation of

108   experiments. The presence of a modifying species can change an interaction in three distinct ways,

109   which we define as direct, secondary and density-mediated TIMs (Fig. 2). As an example, consider a

110   three level (plant – herbivore - predator) food chain where higher densities of the predator cause

111   the herbivore to reduce its consumption rate of the plant. The TIM would reduce the herbivore-plant

112   interaction directly, but the interaction would also be affected by the reduced herbivore population

113   due to reduced food intake (secondary TIM) and because of predation losses (density-mediated

114   TIM). There is no guarantee that an indirect TIM would be in the same direction as, or of lesser

115   magnitude than, the direct TIM. Many verbal descriptions of interaction modifications include only

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116   direct TIMs and their effects, yet where populations vary secondary and density-mediated

117   mechanisms can play considerable roles in experimentally observed changes in interactions. A TIM

118   framework allows a more precise description of the scope of processes that are being described.

119   Thirdly, TIMs are inherently dynamic concepts and the full range of their impacts often only become

120   visible in non-equilibrial systems or after perturbations (Doak *et al.* 2008). If the modifying species is

121   at low or unvarying density there may be little observable modification effect, despite a large

122   potential to affect an interaction if the modifier's population was perturbed. Modifications can

123   obscure their own impact on dynamics if they lead to the stabilisation of systems (and hence reduce

124   the variation in interaction strength). There is therefore an important bi-directional link between

125   system dynamics and TIM strength, which pairwise approaches are unable to handle as easily.

126   Fourthly, modifications to interactions may occur only after a considerable time lag to changes in the

127   modifier population (Bolker *et al.* 2003) and such delays can have notable effects (Hastings *et al*.

128   2007). Delays could stem from the time taken to learn behavioural responses, time for genetic

129   selection to occur, or time taken for environmental changes to the ecosystem to develop. Multi-

130   scale models can incorporate delayed interaction modifications directly with a time lag, or more

131   commonly with an additional state variable representing an environmental cue or a trait. The trait

132   changes can be determined by adaptive considerations (Kondoh 2003; Valdovinos *et al*. 2010) or as a

133   direct function of the modifier (Garay-Narváez & Ramos-Jiliberto 2009). A dynamic-focused TIM

134   approach is amenable to studying system responses over different timescales. Transient dynamic

135   metrics can also be applied to investigate dynamics distinct to long-term asymptotic behaviour.

136   However, for the remainder of this paper, we will focus on the effect of changes that can be

137   reasonably be modelled as instantaneous.

138   Finally, multiple modifying species can exert simultaneous modifications upon a focal interaction

139   (Fig. 3a, Relyea 2003; Golubski & Abrams 2011). While it is possible to partition consumption directly

140   to particular species, partitioning effects of modifications poses a fundamentally challenging

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141   question since the process is not directly observable. Multiple modifying species can cause changes

142   in the same, opposite or a completely different direction in the trait-space of the interactors (also

143   described as functionally equivalent, functionally inverse or functionally diverse (Herzog & Laforsch

144   2013)). By focussing on the combined changes to interactions, the TIM framework aids the

145   generation of hypotheses for how modification effects combine (Golubski & Abrams 2011) and a

146   route to possible additional model structures, such as introducing cue variables (Fig. 3b, Garay-

147   Narváez & Ramos-Jiliberto 2009). Furthermore, the TIM framework allows a distinction between

148   multiple modifications acting simultaneously and the modulation of modifications where a TIM is

149   itself directly modified by a fourth species (Fig. 3c; for an example see Liere & Larsen 2010).

150   <u>Metrics</u>

151   Concepts of TIM strength are contingent on the extent to which information about the wider system

152   is incorporated. Table 2 outlines a set of TIM metrics, both longstanding and newly proposed, that

153   sequentially increase the amount of information incorporated about the system. TIM effects have

154   been studied in a wide range of theoretical frameworks (Peacor & Cressler 2012) including: network

155   re-wiring (Staniczenko *et al.* 2010), sign-only matrices (Dambacher & Ramos-Jiliberto 2007), fitness-

156   based models (Valdovinos *et al.* 2010), explicit cue-state variables (Garay-Narváez & Ramos-Jiliberto

157   2009) and individual-based models (Peacor *et al.* 2007; Railsback & Harvey 2013). Here we focus on

158   a common framework where sets of differential equations represent the rate of each population's

159   density change and the TIM is represented by additional functional response components (Arditi *et*

160   *al.* 2005; van Veen *et al.* 2005; Holt & Barfield 2013). This population-level representation abstracts

161   over individual variation and the underlying (often trait-based) causes of interaction modifications to

162   focus on resultant effects at the level of the species. Nevertheless, the distinctions between TIM

163   effects as measured by different metrics are not specific to this modelling approach.

164   *Modification Parameter*

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165   With a functional response model that includes a TIM it is possible to identify a parameter that

166   specifies the strength and direction of the TIM influence on the interaction. These values can be

167   found by fitting models to experimental data (van Veen *et al.* 2005) and can be specified directly in

168   models (Křivan & Schmitz 2004; Goudard & Loreau 2008; Holt & Barfield 2013), thereby providing a

169   direct link between experiment and theory. A range of symbols have been used for the TIM

170   parameter in the literature, here we use c_{ijk} to represent the effect species *k* has on the

171   consumption of species *i* by species *j*. However, exactly how the resultant modification relates to this

172   parameter is critically dependent on the form of the functional response model used. While some

173   studies have used fully linear representations of TIMs (e.g. Bairey *et al.* 2016), non-linearities in

174   functional responses and the modification effect are likely to be prominent. It is possible for any

175   aspect of a non-linear functional response to be modified (Preisser & Bolnick 2008; Kéfi *et al.* 2012)

176   including consumption rate (Arditi *et al.* 2005; Goudard & Loreau 2008), handling time (Vos *et al.*

177   2004), sigmoidality (Alexander *et al.* 2013) or additional interference terms (Vos *et al.* 2001; van

178   Veen *et al.* 2005; Larsen 2012).

179   Given the huge diversity of possible models, it is useful to consider separately the underlying

180   functional response model, the choice of the affected parameter, and the sub-model linking the TIM

181   parameter to changes of the affected functional response parameter. Previous work has used a wide

182   variety of functions to link the density of the modifier to the modifier term, outlined in Supporting

183   Information 1, to introduce a variety of thresholds and non-linear relationships. So far, there has

184   been little theoretical comparison of different generic TIM functional responses (although see Holt &

185   Barfield 2013). With the exception of prey switching effects (Koen-Alonso 2007; Abrams 2010b), the

186   only class of TIM that are often implicitly included in population dynamic models, there is little

187   experimental data to inform the choice of TIM functional form. Until a significant body of data

188   develops, the choice of formulation will depend on fit to biologically informed criteria, such as those

189   suggested by Goudard & Loreau (2008).

190   *Modification Term*

191　　The term representing the effect of the TIM within the functional response model incorporates the

192　　density of the modifier species. This gives a measure of the modification at a particular system state.

193　　As it is a sub-element of the functional response model, the use of this term as a metric requires

194　　contextualisation within the wider model being used. The modification of different aspects of the

195　　functional response (such as handling time, attack rate or total consumption rate) can have very

196　　different effects on the change in consumption at different densities of interactors. This metric has

197　　had particular use in describing the combined effect of multiple modifications (Golubski & Abrams

198　　2011).

199　　*Change in flux*

200　　The most direct approach to incorporate the strength of the interaction being modified is to

201　　calculate the change in flux rate (biomass or energy) due to the modification. Either a ratio or an

202　　absolute flux difference can be considered. Indirect TIM effects (see Fig. 2) can lead to mixed

203　　responses to modifiers making it important to consider which effects are included in the

204　　measurement of flux change for comparisons to be meaningful.

205　　*Change in B_{CR}*

206　　The B_{CR} framework (Gilbert *et al.* 2014) proposes a metric of interaction strength that relates the

207　　energy flow between a consumer and a resource to static measures of the resource biomass in order

208　　to measure the biomass potential of the resource captured by the consumer. It can be calculated

209　　from the equilibrium biomass of the resource with and without the consumer being present, as well

210　　as directly from model parameters (Gilbert *et al.* 2014). As such it provides a way of linking empirical

211　　and theoretical studies and has been shown to be useful in relating interaction strength to stability

212　　(Nilsson & McCann 2016). Conveniently, as we show in Supporting Information 2, the relative change

213　　of this metric with and without the TIM can simplify to the relative density of the resource with and

214　　without the TIM. This is experimentally tractable compared to metrics that need to measure the flux

215   and the metric can also be defined from model parameters (for an example see Supporting

216   Information 2).

217   *Coefficient of variation of modification parameter or interaction strength metric*

218   TIMs are likely to be particularly critical in systems not at an equilibrium, but assessing the 'strength'

219   of TIMs in such cases poses challenges. Where a model of the system is available, the coefficient of

220   variation (the ratio of standard deviation to mean) of the modification parameter term can

221   represent the dynamic changes a TIM is exerting. However, a low degree of variation in parameter

222   modification does not necessarily mean the TIM is not having a significant impact since it is readily

223   possible to show TIM effects that lead to the stabilisation of cycling systems (Supporting Information

224   3). Measures such as coefficient of variation of flux or other interaction strength metrics can also be

225   derived from non-equilibrium systems. These can be considered with reference to the level of

226   environmental stochasticity underlying the system. There is considerable room within the TIM

227   framework for a more sophisticated understanding of how modification effects interact with system

228   variation to determine population dynamics (Peacor & Cressler 2012).

229   *Partial derivatives of Jacobian Matrix*

230   The metrics outlined above have represented a given TIM with a single value. An interaction is not

231   necessarily symmetric in its effect on the interactors which can result in a pair of values for each

232   TIM, representing the effect of the interaction modification on each species. Jacobian matrices of

233   community dynamics models are composed of the partial derivatives of each species' population

234   change functions with respect to each species in the community. Within a pairwise TMII framework

235   the elements from this matrix have been put forward as a metric of modification effect (Abrams

236   1984). These correspond to the effect of modifier density on the modified species population

237   growth. A development of this metric, taking the proportional change in growth rates with respect

238   to the modifier, has also been put forward (Abrams 2008; Okuyama & Bolker 2012) to compare trait-

239   and density-mediated indirect interactions at a particular community state. We propose here a

240   related metric aligned with the TIM concept that is able to distinguish TIM effects from direct

241   interactions linking the modifier and interactor. This can be computed by taking the partial

242   derivative with respect to the modifying species of the Jacobian matrix elements that specify the

243   modified interaction. This corresponds to the effect a modifier species has upon the direct

244   interaction. For simple models it is possible to calculate interpretable expressions for how this

245   metric responds to the system parameters. A significant feature of this metric is that it specifies the

246   dynamic relationship of modifier and the interaction for a particular community at a given state,

247   most likely an equilibrium. As with all Jacobian and gradient based metrics, it involves linearisation

248   and hence is only strictly valid for system states very close to that in which it was defined, which

249   could hinder direct experimental assessment.

250   *Partial derivatives of inverse negative Jacobian ('net-effects') matrix*

251   The previous metric can be extended to include indirect interactions between species. The inverse of

252   the negative Jacobian matrix $(-A^{-1})$ represents the combined direct and indirect interactions

253   between species (Levine 1976; Bender *et al.* 1984). Partial derivatives of elements of this 'net-

254   effects' matrix with respect to the modifier species density equate to the effect the modifier has on

255   the total effect of the interactors on each other. Such an approach may lead to a more thorough

256   understanding of the extent of impact that a TIM is having within a given system. However, there are

257   some significant difficulties. Expressions of the value of this metric in terms of model parameters can

258   be uninterpretably complex and numerical analysis can propagate errors due to the multiple

259   differentiation and whole matrix manipulation steps. More fundamentally, because indirect effects

260   are incorporated, values can be non-zero when no explicit TIM effect is included due to density-

261   mediated TIM effects (see Fig. 2 and Case & Bender 1981).

262   *Comparison of Metrics*

263   The need to differentiate between the diversity of potential approaches to TIMs is highlighted by a

264   lack of consistency in the concepts of TIM strength. To demonstrate this, we applied the different

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265   metrics to three model systems with TIMs (Fig. 4): a tri-trophic food chain with linear functional

266   responses and TIM, a tri-trophic system with non-linear functional responses and TIM, and the

267   experimentally parameterised aphid-parasitoid system described in van Veen *et al.* (2005). In each

268   case the strength of the model's TIM parameter was varied and the metric in question recalculated

269   at the resultant equilibrium densities. Full model details are given in Supporting Information 4.

270   There are notable quantitative and qualitative differences in how the strength of the TIM, as

271   measured by different metrics, responds to the changing underlying TIM parameter (Fig. 4). Since

272   they measure different properties it is not possible to propose one metric as universally superior.

273   Successfully applying TIM strength metrics to specific questions will require measures of 'strength'

274   that have tangible links to the theoretical concepts being considered, requiring a repertoire of

275   diverse approaches. Furthermore, many approaches require specific conditions (such as the system

276   being at equilibrium) that reduce their universality. Improving our understanding how different

277   aspects of interaction modifications relate to each other will be an important area for further

278   research. While 'lower-level' metrics are likely to be simpler to quantify, 'higher-level' metrics place

279   the modification in context and can provide more information on their role and impact in a dynamic

280   system.

281   With the exception of the modification parameter, the metrics represent the strength of the TIM at

282   a particular community state. These can provide considerable detail and insight about the process

283   occurring in the system, but extending conclusions to consider larger perturbations may be

284   challenging. This trade-off reflects the highly dynamic nature of interaction modifications where

285   taking a snapshot is essential to describe a system property concisely. For this reason, quantifying

286   model parameters has particular advantages for understanding the system dynamics. Combined

287   with a model specification they can describe the underlying process in a way that is not specific to a

288   given system state and can allow the derivation of other measures.

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289   Many of the apparently idiosyncratic relationships between the TIM parameter and the TIM strength

290   observable in Fig. 4 are caused by interactions via changing equilibrium densities, with significant

291   consequences for the interpretation of experimental data. Cascading effects of the changing link

292   strength can counter the naive expectation that increasing the magnitude of the TIM parameter

293   should lead to greater recorded 'strength' of the TIM. The capacity to explore the multi-facetted

294   nature of TIM effects is a significant advantage of this approach.

295   <u>Linking theory and experimental systems</u>

296   There is a significant gap between the concepts of interaction modifications that are used in

297   theoretical or simulation studies and the objectives of the majority of experimental work. Despite

298   repeated calls to try and close this gap (Bolker *et al.* 2003), a focussed program of work has yet to

299   emerge (Kéfi *et al.* 2012; Peacor & Cressler 2012). Key questions regarding the distribution,

300   functional form and impact of TIMs in natural systems are only starting to be addressed (Perfecto *et*

301   *al.* 2014; Kéfi *et al.* 2015; Suraci *et al.* 2016). The focus of a considerable number of experiments has

302   been to identify the relative roles of trait-mediated and density-mediated effect pathways in tri-

303   trophic systems (Peacor & Werner 2004; Bolnick & Preisser 2005; Preisser *et al.* 2005). These studies

304   have played a significant role in demonstrating that such effects can have major impacts, despite

305   issues with the interpretation and duration dependence of such experiments (Abrams 2001, 2008;

306   Okuyama & Bolker 2007). However, other experimental approaches will become necessary to

307   deepen our understanding of these processes both to understand the causal mechanisms underlying

308   TIMs and to quantify the modification.

309   A model-fitting approach is able to overcome some of the challenges involved in quantifying

310   modifications and their effects. Ideally, experiments seeking to investigate the effect a presumed

311   TIM is having on a system would use an experimental treatment where the putative modifying

312   species is present and trophically connected to the web, but the modifying effect is blocked.

313   However, there are few systems where this is feasible. Consequently, many studies have conducted

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314   the reverse experiment, introducing a modification without the modifier being trophically connected

315   to the system. A common experimental protocol has been to observe the effect of a single level of

316   disabled, fear-inducing, predator on the consumptive behaviour of another species (Werner &

317   Peacor 2003). The extent to which these studies can inform our understanding of system dynamics is

318   limited by the lack of information about the shape of the response and the lack of feedbacks to the

319   modifier species (Bolker *et al.* 2003; Abrams 2008; McCoy *et al.* 2012; Okuyama & Bolker 2012). A

320   shift in emphasis towards a TIM-centred approach based on functional responses, as we outline

321   here, rather than attempting to straightjacket such processes into an indirect-interaction framework,

322   will provide a profitable route of analysis. This would apply equally to modelling approaches at

323   either individual or population levels.

324   *Short-term experiments*

325   Ideally, experimental studies seeking to quantify TIMs would seek to parameterise a functional

326   response model by fitting a response surface of the strength of the interaction across multiple levels

327   of the modifier (Fig. 5; Denny & Benedetti-Cecchi 2012; Okuyama & Bolker 2012). While such studies

328   are inevitably more labour intensive than single-level studies, Okuyama & Bolker (2012) present

329   simulations that suggest even a low level of replication would provide useful results. Experimental

330   functional responses have been fitted at different levels of modifier (for example Kehoe *et al.* 2016;

331   Wasserman *et al.* 2016) and it would be a relatively small step for similar studies to define a single

332   functional response model. TIMs themselves can be context dependent, for example, depending on

333   prey hunger levels (Gravem & Morgan 2016) or temperature (Sentis *et al.* 2016). As it is well

334   established that TIM effects have the potential to be large (Werner & Peacor 2003), future studies

335   would be most valuable if they are as representative of natural conditions as possible rather than

336   being designed with the aim of demonstrating an effect.

337   *Long-term experiments*

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338   Model selection and parameter fitting with time series can give powerful insights into system

339   dynamics (Mueller & Joshi 2000). Studying populations displaying natural dynamics can avoid the

340   problems of contextualisation with short-term experiments. Several studies have experimentally

341   introduced a modification to a system, such as a predator cue, and studied the resulting dynamics

342   (Peacor *et al.* 2012; Frago & Godfray 2014; Suraci *et al.* 2016). However, to our knowledge, as yet

343   only one study has included the modifier species treatment as a dynamic part of the system and

344   gathered time series data to fit a mechanistic model (van Veen *et al.* 2005). Where the modifier is

345   not a dynamic part of the system, cue-based studies risk making an assessment of the effect of an

346   altered parameter, rather than the effect of the dynamic nature of the TIM, as discussed further

347   below.

348   Unfortunately, the difficulties commonly encountered when fitting models to time series could be

349   exacerbated when studying interaction modifications. In order to detect changes to interactions the

350   unmodified pairwise relationships must be well characterised. Furthermore, for robust model

351   selection it is necessary for the populations to vary sufficiently for the system to traverse a

352   significant part of the multi-dimensional space specified by the modifiers and the interactors. In

353   many systems experimental perturbations would be necessary for this to occur in a reasonable

354   period of time. Tight correlations between the modifier and either of the species involved in the

355   interaction may hinder accurate parameterisation. Characterisation of the model structure is likely

356   to have to remain the domain of short-term studies since model selection in addition to model

357   fitting is likely to require data beyond most available or feasible datasets. Because of the high level

358   of experimental effort necessary, preliminary analysis using detailed models would be of value to

359   examine the potential impacts of TIMs and aid the design of appropriate experiments.

360   Using time series methods to detect TIMs *de novo* is challenging because of the large potential

361   number of modifications and hence a high risk of identifying artefacts. Nonetheless, it may be

362   possible to directly calculate Jacobian-based metrics from reconstructed manifolds based on long

363   time series (Deyle *et al.* 2016). Well-studied systems with existing time series also offer a wide scope

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364   to investigate TIM effects (Peckarsky *et al.* 2008) and would reduce the need to conduct new TIM-

365   specific time series experiments.

366   <u>Outlook</u>

367   The stronger conception of interaction modifications we suggest here will allow new analyses and

368   perspectives. One such area is highlighting TIMs that exert dynamic influences, compared to those

369   emanating from species with comparatively fixed densities that may exert a strong, but unvarying

370   influence. While stable equilibria may be a consequence of TIMs, modifications within systems at

371   equilibrium introduce a constant change and the risk of examining the effect of a changed trait, not

372   an additional dynamic property. For example, the stabilising effect of a TIM in three-species model

373   food chains (Křivan & Schmitz 2004; Holt & Barfield 2013) can be almost completely replicated by

374   directly changing the model parameters to represent the modification without introducing a

375   dynamic TIM (Supporting Information 5). It is important to consider the situations for which

376   specifically introducing the added complexity of TIMs is valuable. For example, many plants have

377   been shown to release volatiles to attract enemies of their herbivores (van Veen 2015). Where the

378   trait modification is unrelated to the plant population density this could be represented by a

379   statically changed functional response. This would be a more parsimonious representation of the

380   process than introducing a dynamic TIM from the plant population to the herbivore-enemy

381   interaction. However, where the attractant effect is dependent on other herbivores (for example

382   Vos *et al.* 2001) the TIM framework has much to offer by representing the relationship between the

383   other herbivore and the enemy-herbivore interaction.

384   This paper has largely discussed modelling at a population level, making the simplifying assumption

385   that populations are homogenous and that their dynamics are tightly coupled. There is a body of

386   evidence that intra-species behavioural syndromes can exert a strong impact on ecological processes

387   (Sih *et al.* 2012) and it has been demonstrated that some individuals consistently exhibit bolder

388   behaviours in response to predation threat (Griffen *et al.* 2012). Even without a diversity of

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389 behavioural syndromes, environmental heterogeneities can create differences in how interactions of

390 individuals are modified. For example, it has been shown that hunger-level can determine whether

391 individuals respond to predator cues by reducing their foraging (Gravem & Morgan 2016). One route

392 to address the effects of intra-specific diversity (Bolnick *et al.* 2011) would be individual-based

393 modelling approaches (Peacor *et al.* 2007; Railsback & Harvey 2013). In principle, it would be

394 possible to build up from individual measurements of response to modifiers to create individual

395 based models (DeAngelis & Mooij 2005), although the demands on data would be high. Additionally,

396 relatively abstract population-level models cannot easily provide a causal explanation for the

397 modification to interactions. 'Bottom-up' approaches would supplement the population dynamic

398 approach that has been principally discussed in this paper, in particular for their potential to show

399 how individual behavioural optimisation in response to the trade-offs involved in foraging choices

400 leads to interaction modifications (Werner 1992).

401 While their ubiquity has been well established (Werner & Peacor 2003), the distribution of TIMs in

402 empirical networks is a major unknown that will need to be addressed. There is every reason to

403 expect that non-random distributions will impact how TIMs influence community dynamics.

404 Nonetheless, simulation studies using random networks of TIMs can still provide useful insights –

405 much useful work was done with random trophic networks (May 1973; Allesina & Tang 2015) before

406 and since detailed experimental data on trophic webs was developed. However, theoretical

407 simulation studies must carefully consider the consequences of their choices of inter-TIM

408 relationships. If TIMs combine non-additively, introducing a balanced distribution of positive and

409 negative TIM parameters can shift average interaction strength, a key determinant of food-web

410 properties (Berlow *et al.* 2004). Goudard and Loreau (2008, 2012) suggest that such shifts in

411 interaction strength may have contributed to the relationship between TIM connectance and

412 ecosystem functioning they found in their simulation study. Calibrating modifications to maintain

413 the average interaction strength may be challenging for complex communities. A profitable route

414   may be to compare results to matched simulations that vary average interaction strength to identify

415   where results can be attributed specifically to dynamic effects of TIMs.

416   There is currently only one study that attempts to represent the distribution of non-trophic

417   interactions in a whole natural community (Kéfi *et al.* 2015). It is highly unlikely that TIMs will be

418   distributed randomly as current models (Arditi *et al.* 2005; Goudard & Loreau 2008; Lin & Sutherland

419   2014; Bairey *et al.* 2016) have assumed (Golubski & Abrams 2011). In particular, there is likely to be

420   a tight relationship between the TIM topology and the underlying trophic network. For instance, it

421   would be reasonable to expect that TIMs are more prevalent between species that are closely

422   trophically connected. Despite the large challenges, there are reasons to be optimistic that

423   significant progress can be made in empirically determining the distributions of TIMs in more

424   systems. Mayfield & Stouffer (2017) demonstrate a model selection framework to identify TIM

425   effects in a community of plants. There is also the opportunity to make use of allometric scaling

426   relationships to make pattern based models for the distribution of modifications in a system (Krenek

427   & Rudolf 2014).

428   *Conclusion*

429   The field of non-trophic interactions is poised to build upon demonstrations of possible effects

430   towards an understanding of their role in the dynamics of natural systems. Trophic interaction

431   modifications are a key set of processes where there is particular potential for progress. Theoretical

432   work demonstrates that almost any set of dynamics can be generated from a model incorporating

433   TIMs, necessitating communication between theory, laboratory experiment and field work to

434   constrain possibilities (Bolker *et al.* 2003). Here we have put forward specific examples of the

435   additional perspectives and depth that a TIM framework can bring and hope this encourages those

436   planning experiments to take advantage of the opportunities. As with estimates of interaction

437   strength (Laska & Wootton 1998), there is a benefit to identifying diverse perspectives for the

438   strength of interaction modifications to understand and improve the links between theory and

439   experiment. With a shift towards a focus on the modification itself as a discrete entity we believe

440   there are many exciting prospects to improve our understanding of ecosystem dynamics.

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743 **Tables**

744 Table 1. Terminology used to describe approaches focussing on pairwise effects and changes to

745 interactions. Note that 'higher-order interaction' has been used for both concepts.

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Process	Terminology	Reference
Pairwise effect		
	trait-mediated indirect interaction	Werner & Peacor (2003); Abrams (2007)
	functional indirect interaction	Janssen *et al.* (1998)
	trait-mediated biotic indirect effect	Goudard & Loreau (2012)
	trait-initiated indirect effect	Abrams (2004)
	trait-transmitted indirect effects	Abrams (1995)
	behavioural indirect effect	Miller & Kerfoot (1987)
	chemical response indirect effect	Miller & Kerfoot (1987)
	non-consumptive predator effect	Preisser & Bolnick (2008)
	non-trophic interaction	Kéfi *et al.* (2015)
	risk effect	Creel & Christianson (2008)
	emergent multi-predator effects	Sih *et al.* (1998)
	higher-order interaction	Vandermeer (1969)
Change to Interaction		
	trophic interaction modification	Golubski & Abrams (2011)
	interaction modification	Wootton (1993)
	rheagogy	Arditi *et al.* (2005)
	environment-mediated interaction modification	Wootton (2002)
	associational resistance / susceptibility	Barbosa *et al.* (2009)
	resource choice	Abrams (2010b)
	prey switching	Koen-Alonso (2007)
	higher-order interaction	Billick & Case (1994)

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Table 2. Metrics of TIM strength, discussed in more detail in the main text. Indices: i = prey, j =

predator, k = modifier species.

Metric	Composition	Explanation
Modification Parameter	c_{ijk}	Parameter in function that links modifier species density to consumption rate in the functional response model (van Veen *et al.* 2005).
Modification Term	$f(c_{ijk}, k)$	The term by which a functional response parameter, such as attack rate, is modified. It incorporates modifier density and TIM model structure (Golubski & Abrams 2011).
Flux Change	$$\Delta_{rel} = \frac{f(i,j,k_{=0})}{f(i,j,k)}$$ $$\Delta_{abs} = f(i,j,k_{=0}) - f(i,j,k)$$	The difference in the interaction strength (as measured by biomass or energy flux) due to the modifier, as either a raw difference or a ratio (Peacor & Werner 2004).
Change in B_{CR}	$$\frac{I^*}{I^*_{c_{ijk}=0}}$$	The relative B_{CR} (biomass potential of the resource consumed, computed from the relative change in equilibrium density of the resource in the presence of the consumer (Gilbert *et al.* 2014)) change due to a TIM as the ratio of the equilibrium value of the prey with and without the TIM.
Coefficient of Variation of Modification	$$\frac{\sigma_{f(k)}}{\mu_{f(k)}}$$	For non-stationary systems, the ratio of the standard deviation of the interaction

		strength modification divided by the mean modification over a period of time.
Elements of Jacobian Matrix	$\dfrac{\partial \dot{\imath}}{\partial K}, \dfrac{\partial \dot{\jmath}}{\partial K}$	TMII-framework metric representing the direct effects of the modifier species on each interactor (Abrams 2008; Okuyama & Bolker 2012).
Partial derivatives of Jacobian Matrix	$\dfrac{\partial}{\partial K} A_{ij}, \ \dfrac{\partial}{\partial K} A_{ji}$	The change in direct interaction strengths between the interactors with respect to modifier density.
Partial derivatives of inverse negative Jacobian Matrix	$\dfrac{\partial}{\partial K}(-A^{-1})_{ij}, \ \dfrac{\partial}{\partial K}(-A^{-1})_{ji}$	The change in total (indirect and direct) interaction strength between the interactors with respect to modifier density.

754

755

756

Figure Legends

758

759 Figure 1. Illustration of the distinction between different frameworks that can represent the impact

760 of the influence of third species on trophic interactions. A trait-mediated indirect interaction

761 approach (a) represents the resultant link between A and C, a trophic interaction modification

762 approach (b) represents the change in the interaction strength, while an undirected hypergraph

763 approach (c) represents a relationship between all three species.

764

765 Figure 2. Illustration of distinction between direct and indirect trophic interaction modifications

766 (TIM). The red arrows show the proximate driver of the change to the interaction. For the indirect

767 cases the grey arrows depict the process by which the interaction was modified.

768

769 Figure 3. Illustration of how multiple modifying species can act on an interaction. Dotted lines

770 indicate interaction modifications; dashed lines indicate other processes related to interaction

771 modifications: increase in 'cue' in (b) and a modification of a modification in (c).

772

773 Figure 4. Demonstration that TIM metrics display different qualitative and quantitative responses to

774 changing the underlying parameter representing the TIM strength. Full model structures and

775 parameters are given in supporting information. Note that the aphid-parasitoid system population

776 densities are on a log-scale.

777

778 Figure 5. Illustration of how the results of multi-level experiments can be used to specify a response

779 surface that is of value for understanding system dynamics. Short-term functional response

780 experiments that include multiple levels of both prey and modifier can be used to define a function

781 corresponding to a response surface, either by fitting parameters of a mechanistic model or with a

782   regression based spline model. Such a function can then be used as part of models of the population

783   dynamics of the system.

a) Trait-Mediated Indirect Interaction
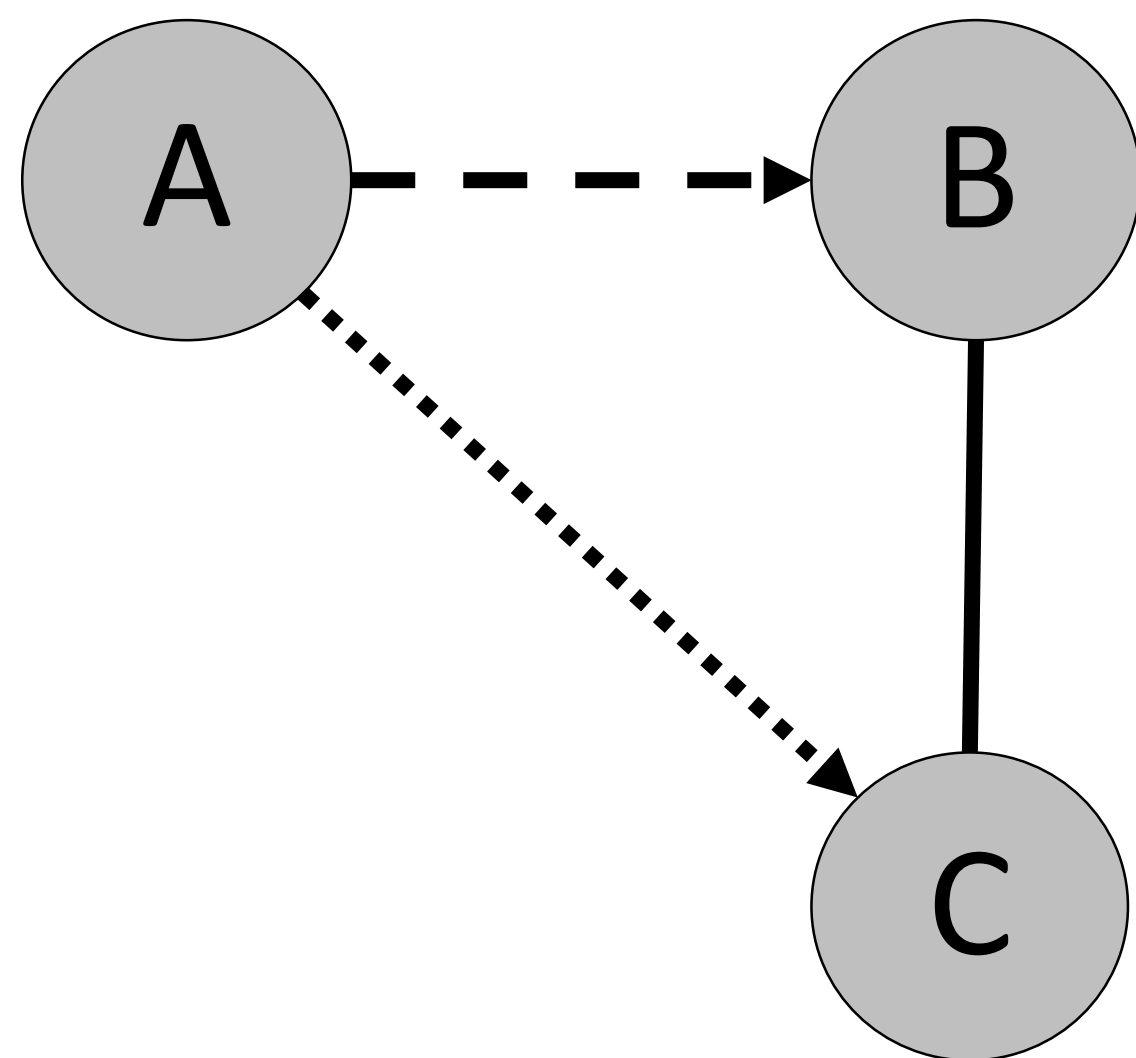
b) Trophic Interaction Modification
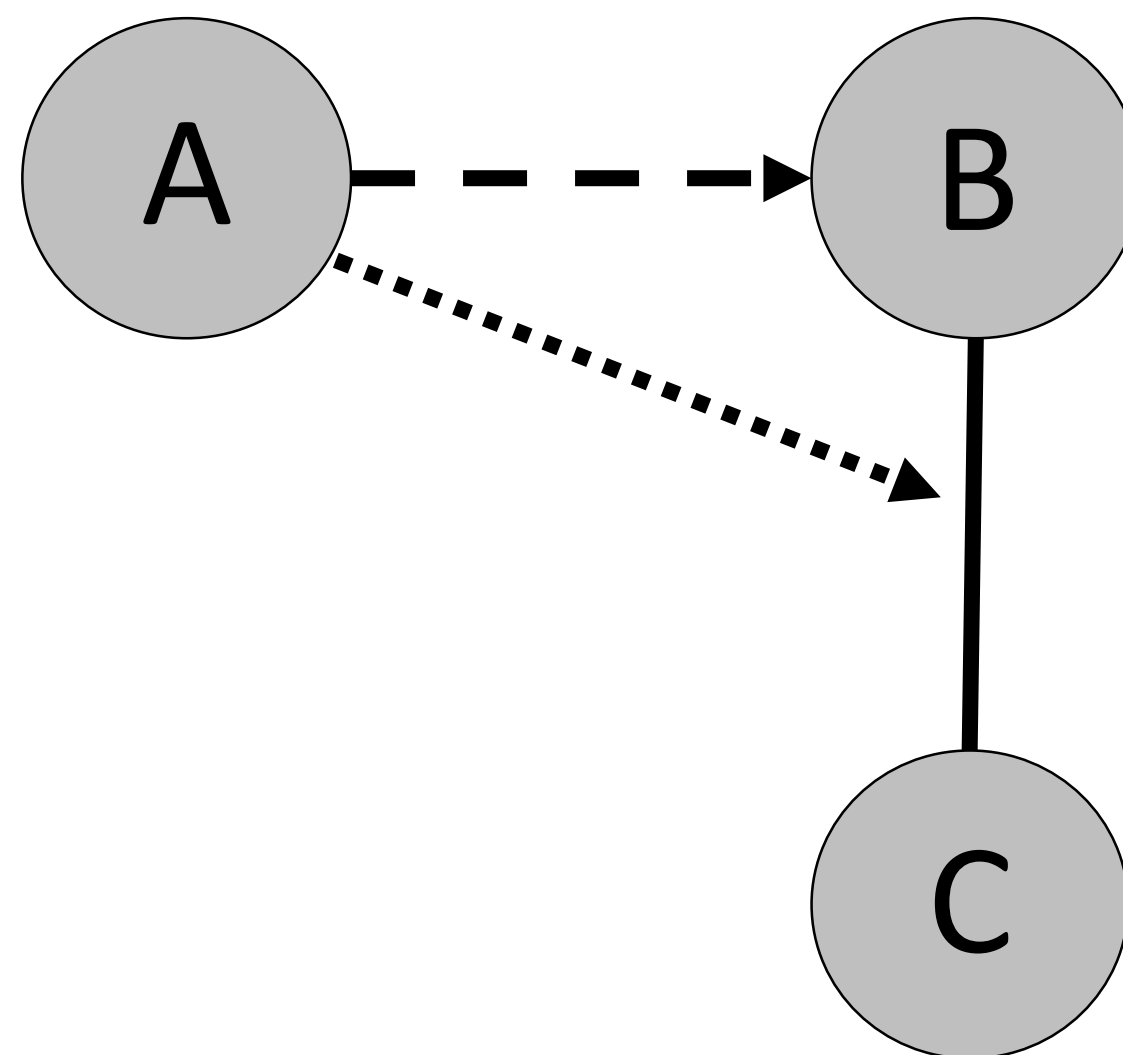
c) Undirected Hypergraph
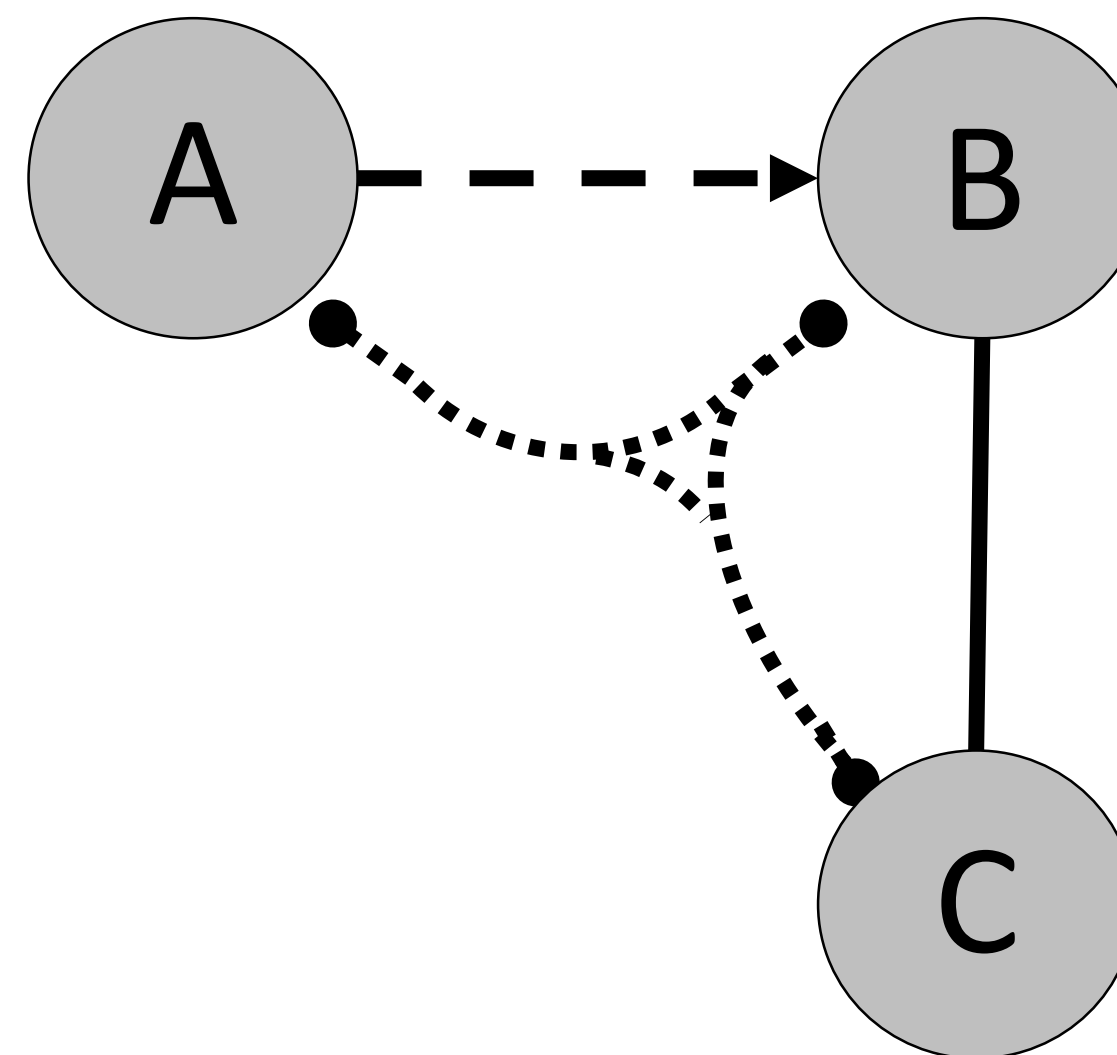
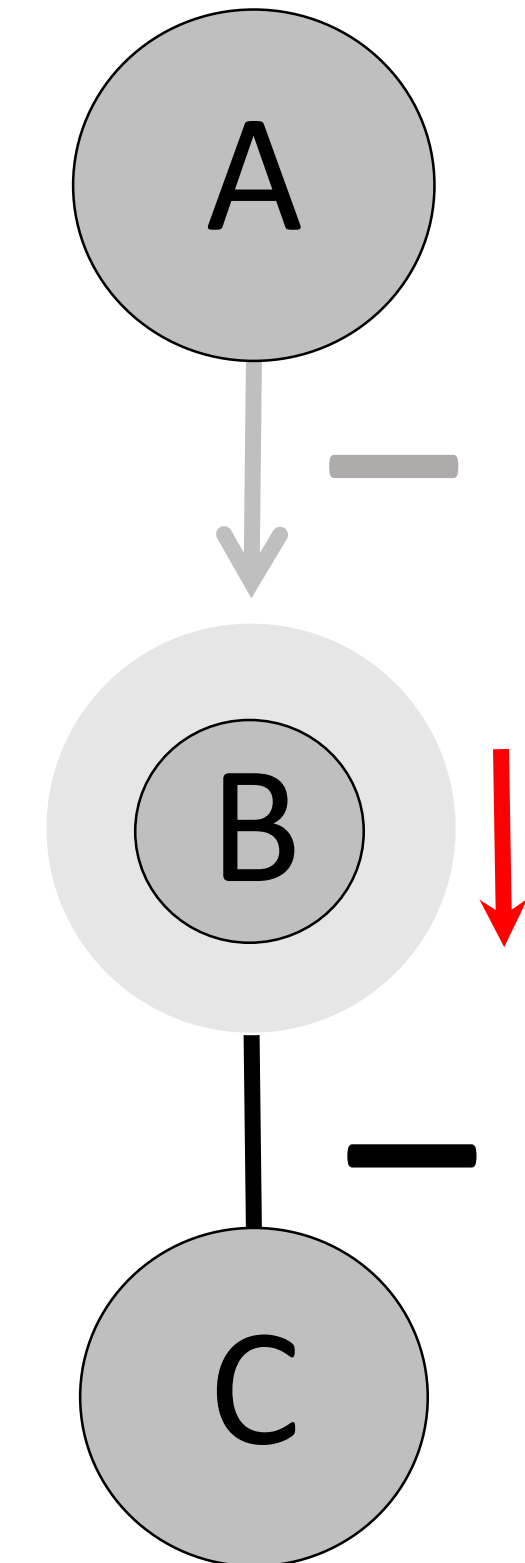Change in trait
Trophic interaction
Framework

Direct TIM
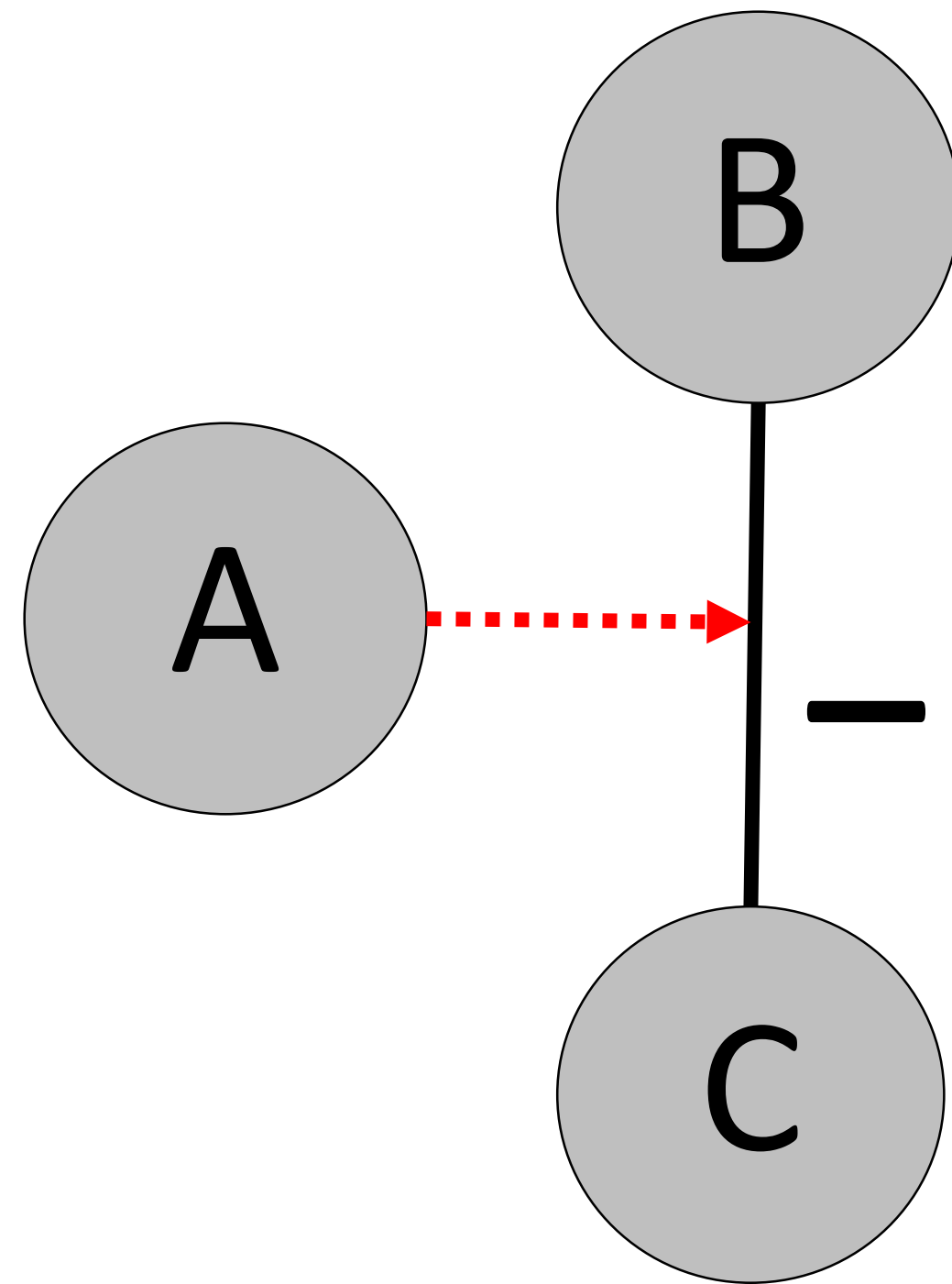
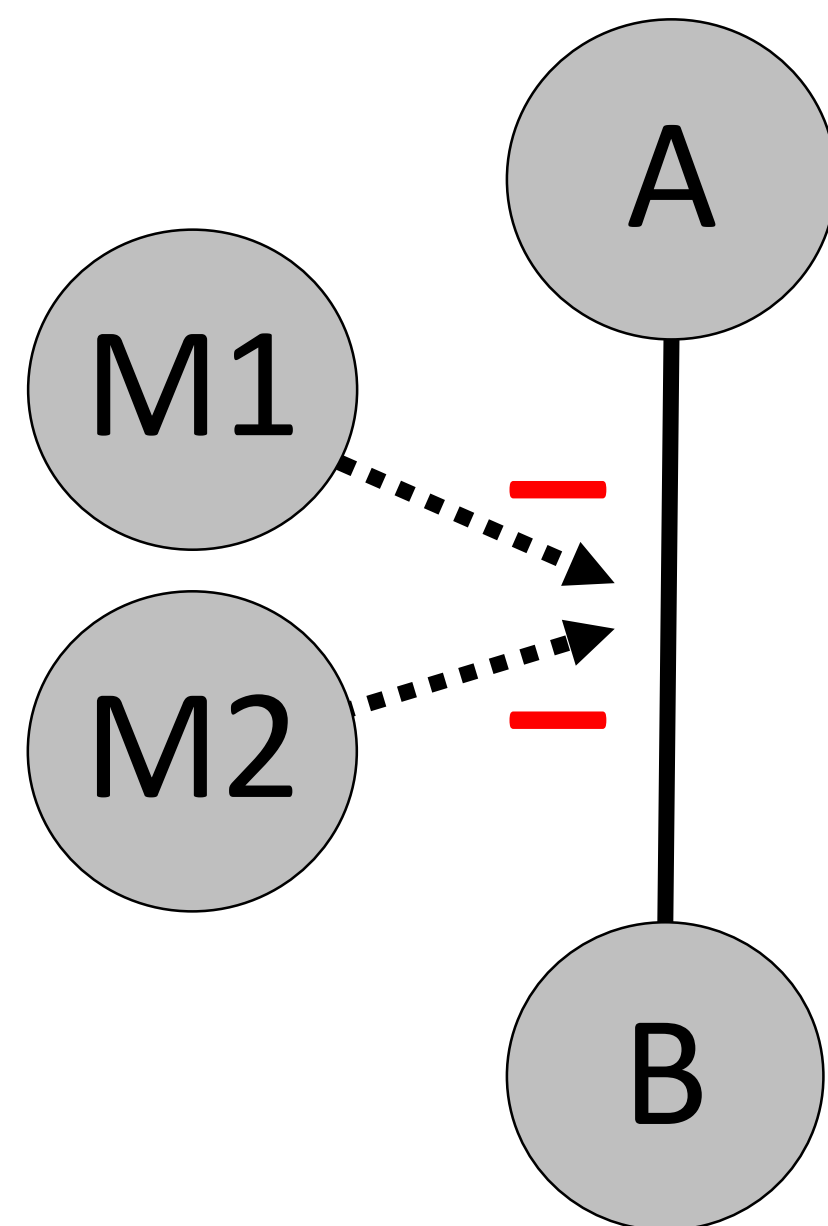Alteration of B-C interaction via change in a trait of either consumer or resource

Secondary TIM
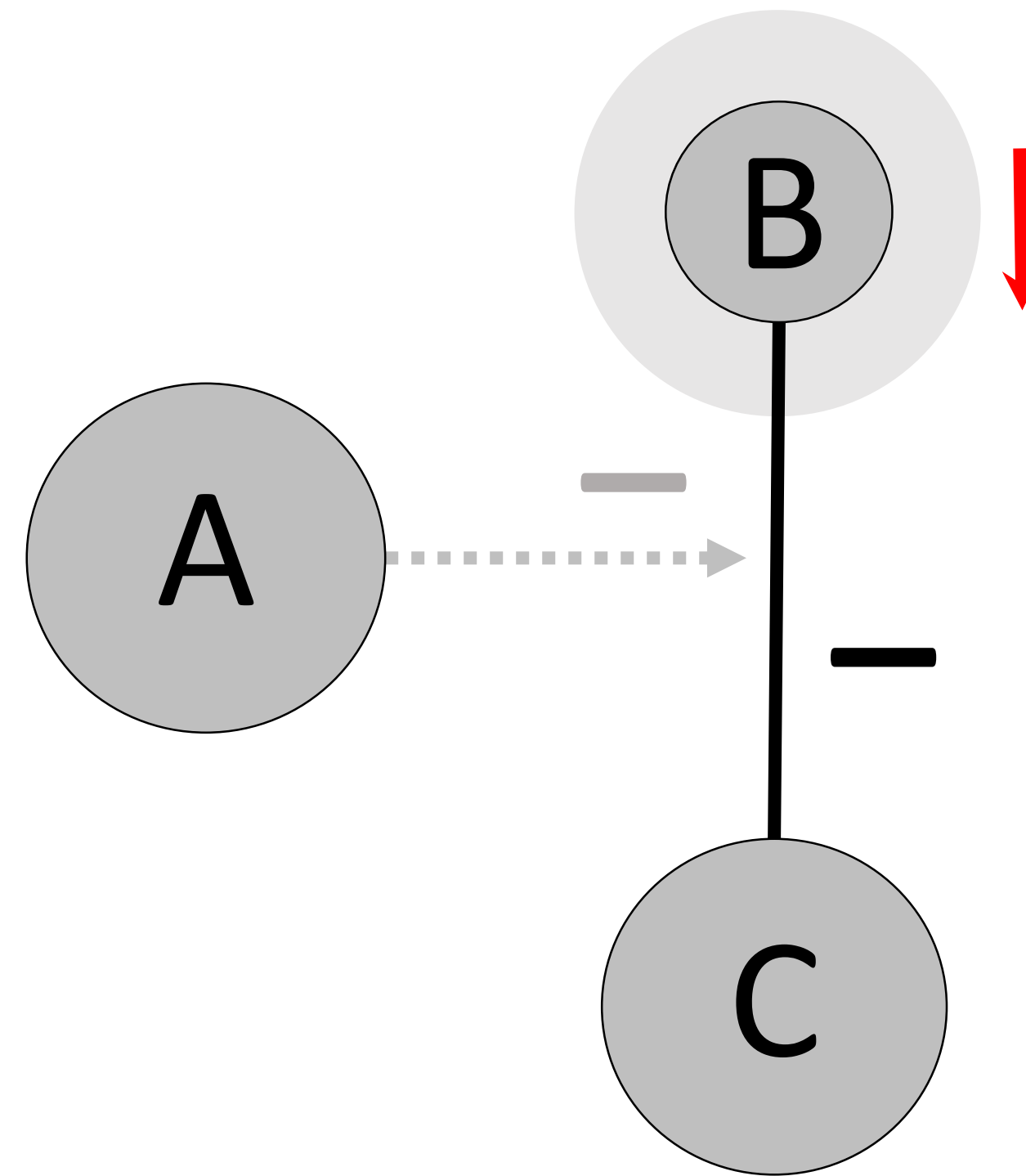
Further changes to B-C interaction caused by population changes in B and/or C stemming from the direct modification

Density-mediated TIM

Changes to the B-C interaction caused by population changes in B and/or C derived from trophic links with A

a) Multiple Modifications
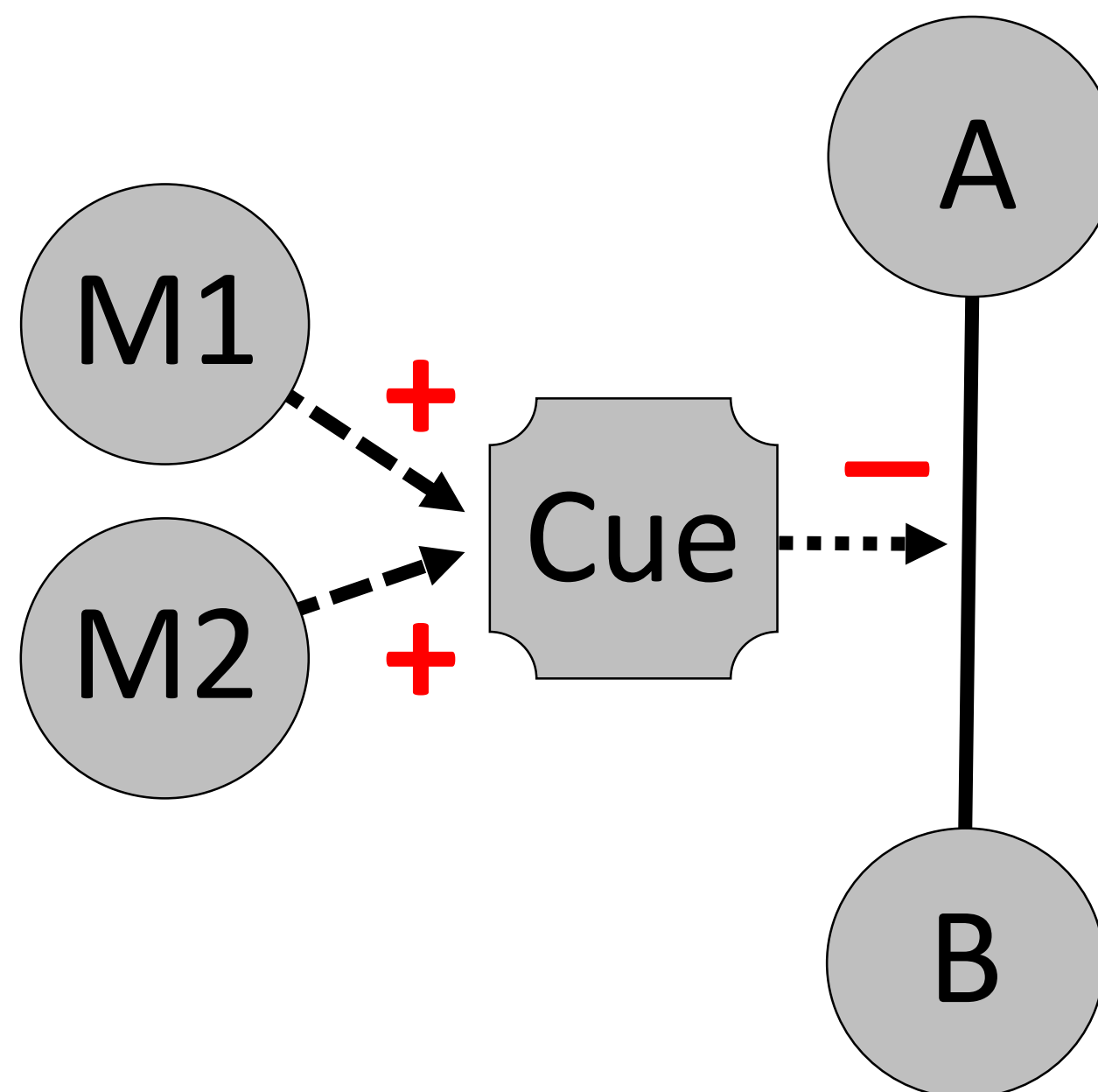
b) Cue-mediated Modification
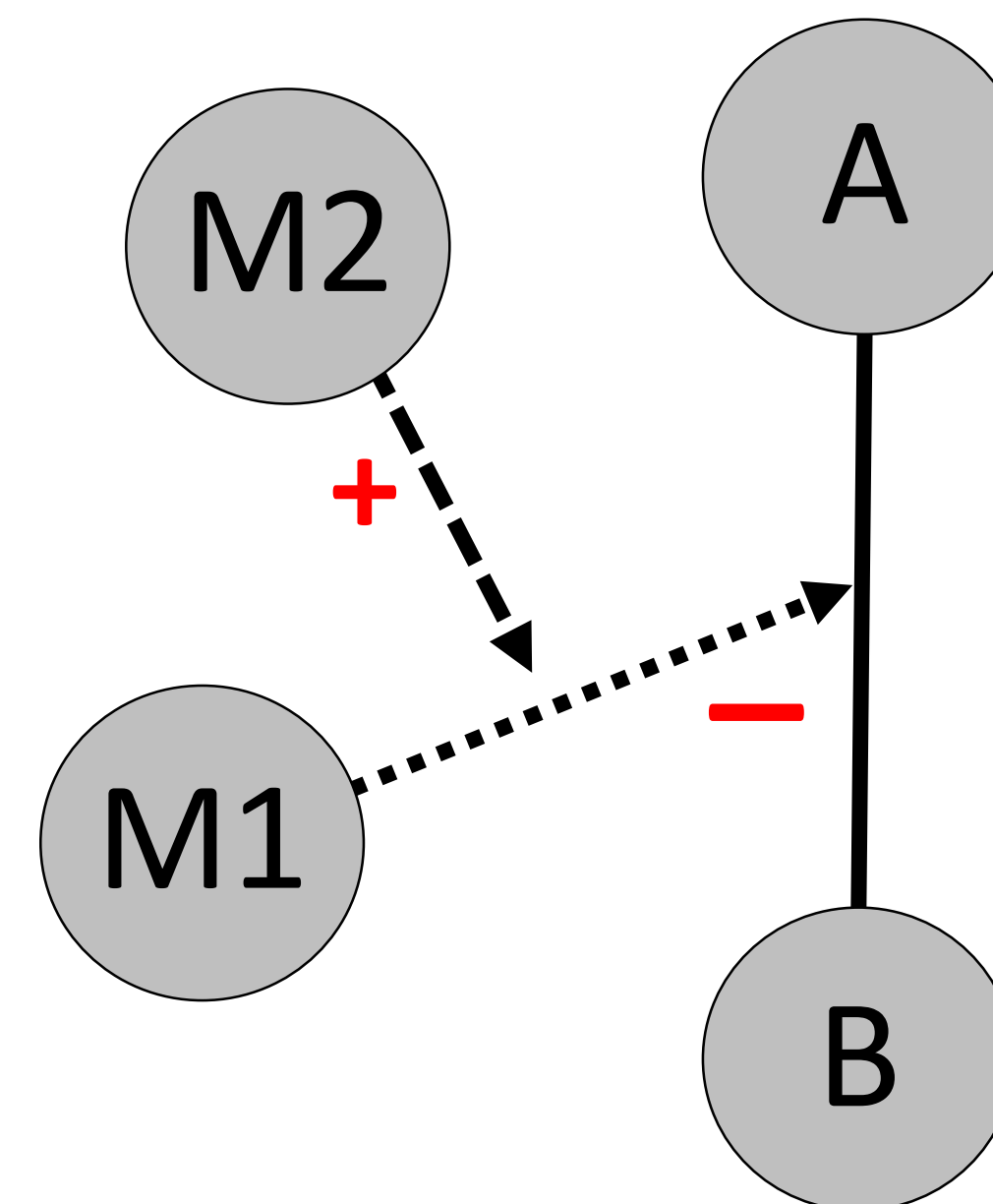
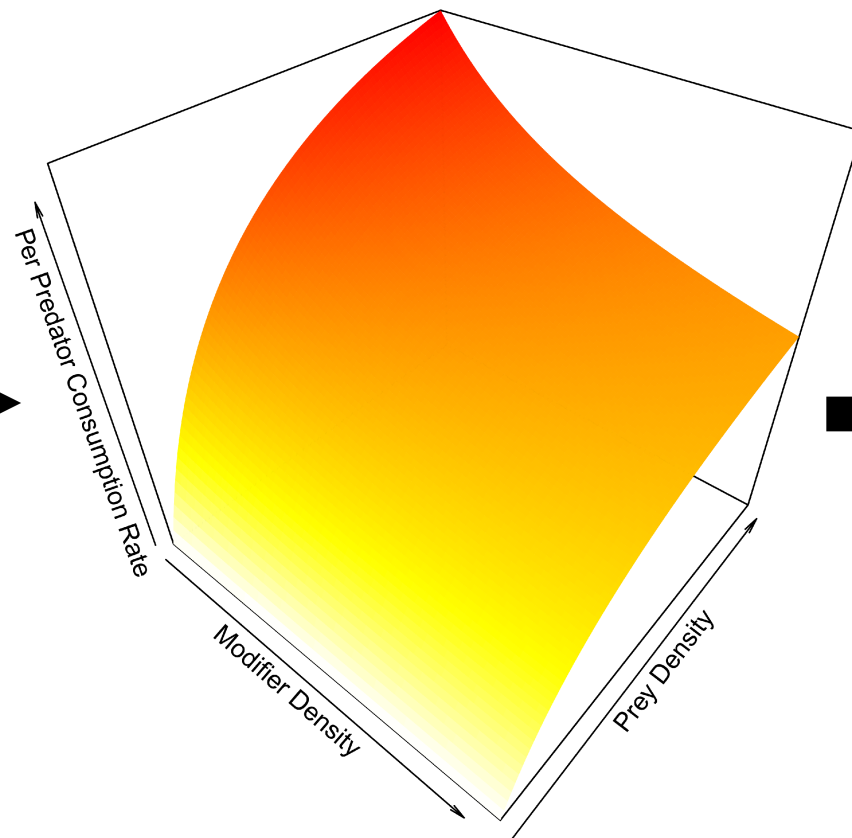c) Modulation of Modifications

Linear
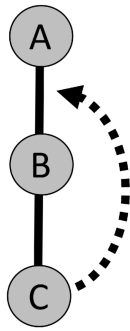
Non-Linear
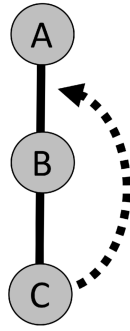
Aphid-Parasitoid

(van Veen *et al* 2005)

Population
- A
- B
- C

Metric
- μ
- Absolute Flux Change
- Relative Flux Change
- B_{CR} Ratio
- J_{AC}
- J_{BC}
- $\dfrac{\delta J_{AB}}{\delta C}$
- $\dfrac{\delta J_{BA}}{\delta C}$
- $\dfrac{\delta -J^{-1}_{AB}}{\delta C}$
- $\dfrac{\delta -J^{-1}_{BA}}{\delta C}$

Densities

Metric Values

TIM Parameter

Multi-level Experiments

Per Predator Consumption Rate

Modifier Density

Prey Density

Response Surface

Per Predator Consumption Rate

Modifier Density

Prey Density

System Dynamics

Populations

Time
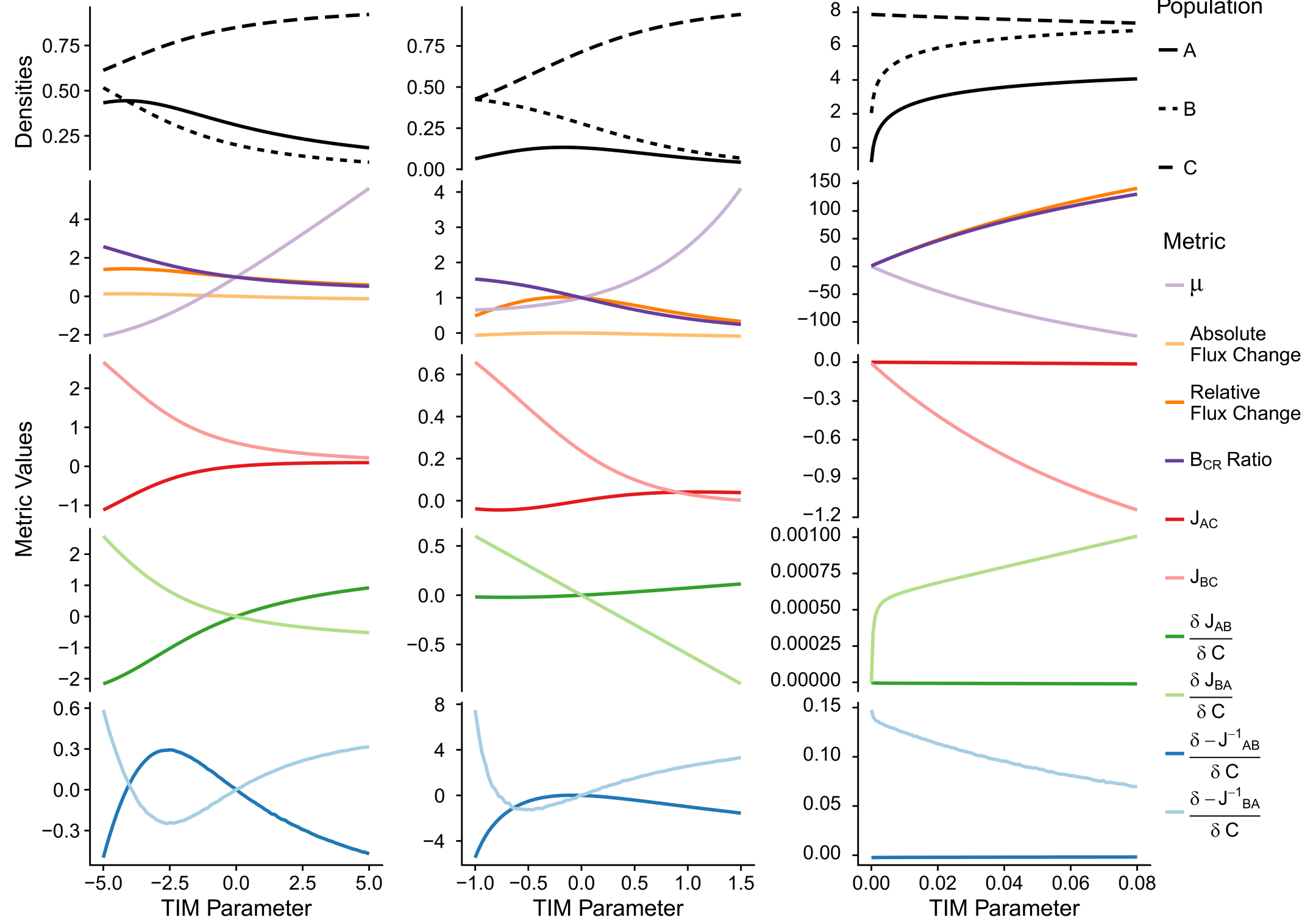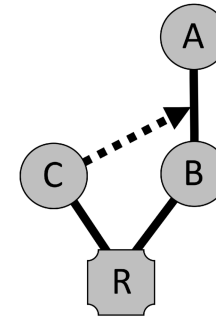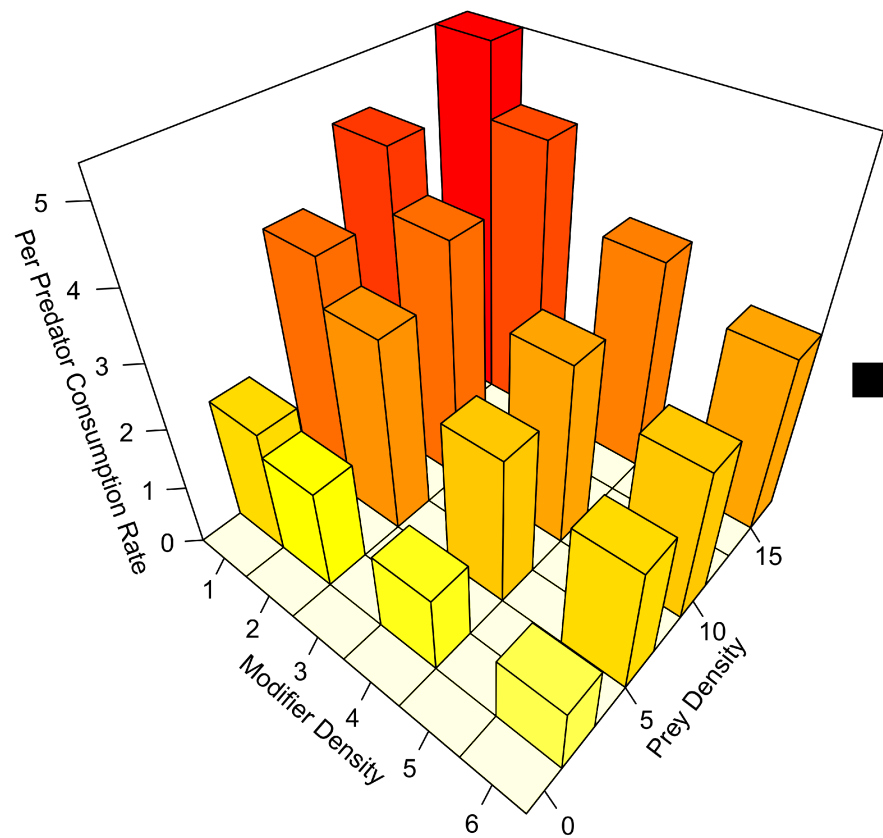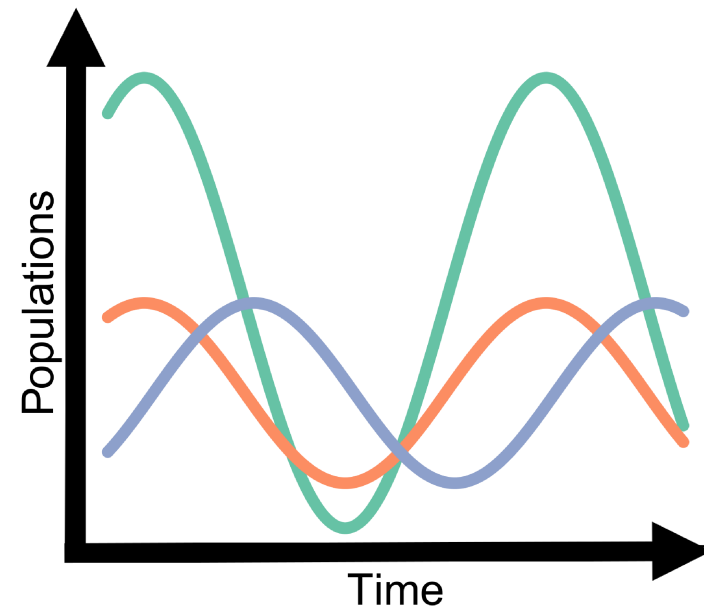
Appendices

2 Appendix 1. Functions used to describe relationship between modifier species
3 density and functional response parameter.

| Name	Examples of Use	Function	Lower Bounded above 0?	Upper Bounded?	Contains threshold?	Number of free parameters
Linear	Arditi et al. (2005)	$\max\{0, 1 + X_k c_{ijk}\}$	N	N	N	1
Exponential	Křivan & Schmitz (2004) Okuyama & Bolker (2012)	$exp(c_{ijk} X_k)$	N	N	N	1
Power Law	Goudard & Loreau (2008) Lin & Sutherland (2014)	$(1 + X_k)^{c_{ijk}}$	N	Y	N	1
Interference	Paixão et al. (2014)	$\dfrac{1}{1 - c_{ijk} X_k}$	N	N	N	1
Saturating	Kéfi et al. (2012) Sanders et al. (2014)	$\dfrac{exp(c_{ijk}) \times X_k + T_0}{X_k + T_0}$	Y	Y	N	2
Logistic	Kéfi et al. (2012)	$\dfrac{M_{nti} - M_0}{1 + e^{a(X_k - d)}} + M_0$	Y	Y	Y	3
Dose Response	Ramos-Jiliberto et al. (2008)	$1 + \dfrac{c_{ijk}(X_k)^v}{(X_k)^v + u^v}$	Y (if c_{ijk} > -1)	Y	Y	3

Table S1. Expressions that have been suggested or used for the modification of functional response parameters. c_{ijk} = Modification Parameter (k's effect on the consumption of i by j), X_k = Modifier Density, T_0 = Half-Saturation Density of Modification, a = plays role in determining steepness of threshold, direction of effect and intercept, d= point of inflection, also affects intercept. M_{nti}= value when X_k tends to infinity, M_0 = baseline value, v = curve abruptness, u = modifier density when μ (modification effect) = 0.5. Some models have been adapted from the original source for consistency in the table. Note that the large number of expressions for predators adaptively foraging between multiple prey that have been put forward but not in a TIM context have not been included in this table.

4

5

Negative Modifications

6

Positive Modifications
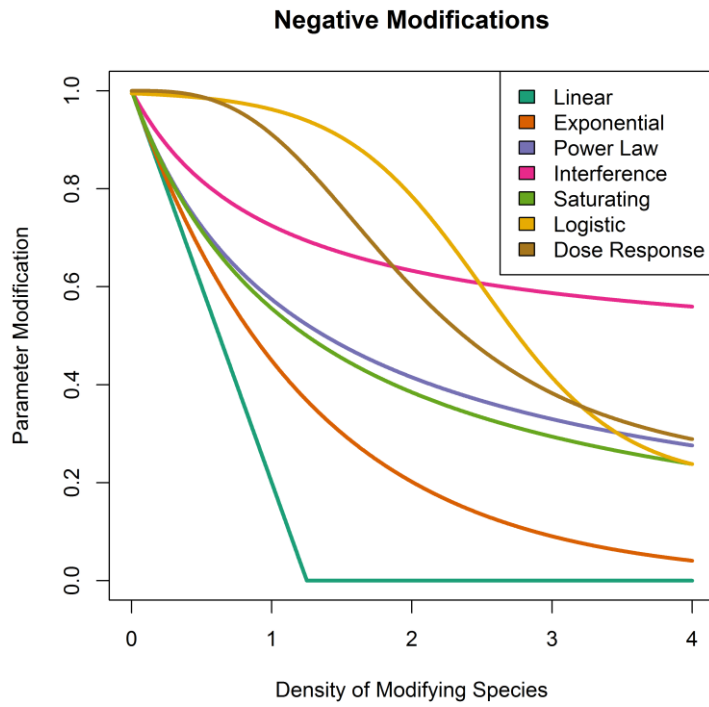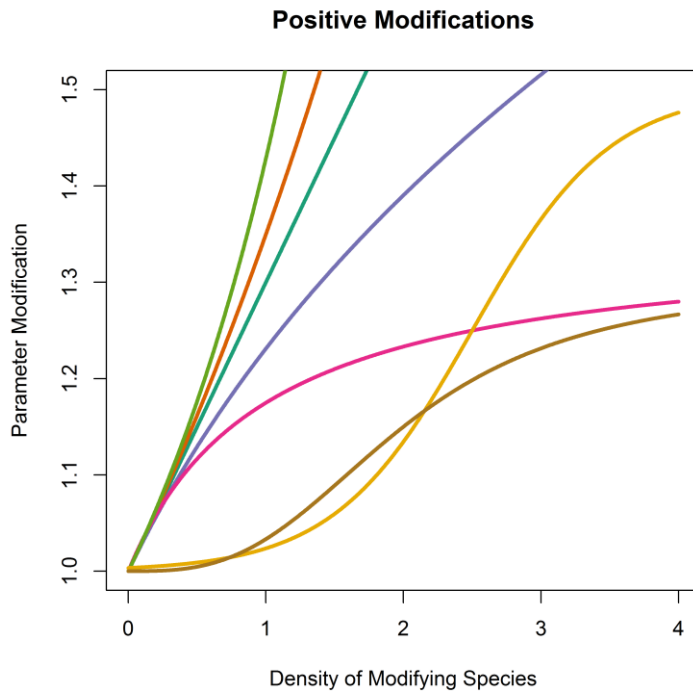
7

8 Figure S1. Graphical depictions of example modification functions in Table 1. For the negative modifications T_0 =
9 1, M_{nti} = 0.2, M_0 = 1, d = 2.5, u=2, v=3, c_{ijk} = -0.8, a= -2. For positive modifications values are the same
10 except: c_{ijk} = 0.3, M_{nti} = 1.5.

11

2

Appendix 2. Derivation of Relative Change in B_{CR} TIM Metric

B_{CR} is an interaction strength metric that represents the biomass potential of the resource that is captured by the consumer. It was originally put forward by Gilbert *et al* (2014) in their study of the effect of temperature on interaction strength given temperature affects multiple parameters simultaneously. It has been used by Nilsson & McCann (2016) to show that this metric (which they term *'New IS'*) relates in a straightforward and meaningful way to stability. It uses resource biomass accumulation and consumer relative growth to define B_{CR} in terms of biomass flow through the consumer- resource system. This flow is related to static measures of the resource biomass (K/R*) and has the advantage of being interpretable both experimentally and theoretically. K in this context is seen as an aggregate of supply rate and resource loss rate.

B_{CR} is defined (Gilbert et al 2014, Eq 3.) where both resource and consumer are able to coexist as:

$$B_{CR} \propto \frac{[Consumption\ Efficency][R\ Biomass\ Accumulation]}{[ConsumerLoss]} = \frac{[ef(R)][K]}{[m(C)]} = \frac{K}{R^*}$$

$$= \frac{R\ without\ consumer}{R\ with\ consumer}$$

B_{CR} measures can be represented by aggregates of parameters. Both papers present how these values can be derived from parameter sets for different models with different functional responses. It can be used for higher trophic levels using appropriate measures of equilibrium biomasses of prey in place of K. Eg: Type I functional response (Gilbert et al 2014, Eq 5.):

$$B_{CR} \propto \frac{R^*\ without\ consumer}{R^*\ with\ consumer} = \frac{K}{m/ea} = \frac{eaK}{m}$$

In a system where a modifier species affects how a consumer affects a resource it is possible to use this measure of interaction strength in a measure of interaction strength change. Using the definition of:

$$B_{CR} \propto \frac{R\ without\ consumer}{R\ with\ consumer}$$

We suggest a metric of the strength of a TIM could be the ratio of this new metric with and without the TIM:

$$\Delta B_{CR} = \frac{B_{CR} + TIM}{B_{CR}\ 0\ TIM} = \frac{\frac{R\ without\ consumer + TIM}{R\ with\ consumer + TIM}}{\frac{R\ without\ consumer\ 0\ TIM}{R\ with\ consumer\ 0\ TIM}}$$

Since the TIM would not be having an effect when there is no consumer this can be simplified twice:

$$TIM = \frac{\frac{R\ without\ consumer}{R\ with\ consumer + TIM}}{\frac{R\ without\ consumer}{R\ with\ consumer\ 0\ TIM}} = \frac{R\ with\ consumer + TIM}{R\ with\ consumer\ 0\ TIM}$$

This gives some stronger justification for using this otherwise quite simple metric of TIMs, the change in equilibrium density of the resource caused when the TIM is present. It has the advantage of being composed of calculable parameters.

3

42   As an example, here we calculate the change in B_{CR} in a minimal three species Lotka-Volterra with
43   logistic growth and a TIM from modifier species M denoted by $f(M)$:

44    $\delta M/dt = eaMC - nM$

45    $\delta C/dt = ef(M)aCR - aMC - mC$

46    $\delta R/dt = r(1 - R/K)R - f(M)aCR$

47   The effect of the TIM could be defined from the non-zero equilibria, showing that in this case the
48   strength of the TIM depends on a particular subset of parameters and the magnitude of ΔB_{CR} is not
49   directly related to f(M) due to the 1- term.

50    $C^* = n/ea$

51    $R^* = K(1 - \dfrac{af(M)C^*}{r}) = K(1 - \dfrac{f(M)n}{er})$

52    $M^* = ef(m)R^* - m/a) = ef(m)K(1 - \dfrac{f(m)n}{er}) - m/a)$

53    $$\Delta B_{CR} = \frac{R \text{ with consumer} + TIM}{R \text{ with consumer } 0 \text{ } TIM} = \frac{K(1 - \dfrac{f(M)n}{er})}{K(1 - \dfrac{n}{er})} = \frac{1 - \dfrac{f(M)n}{er}}{1 - \dfrac{n}{er}}$$

54

4

Appendix 3. Measuring TIMs in cycling systems.

One approach to quantify the impact of a TIM on the dynamics of a particular system would be to measure the coefficient of variation (CV) of key values such as μ or biomass flux. This approach is not always straightforward as fluctuations in biomass flux that would be present in the system without the TIM would need to be taken into account.

As an example system, the non-linear tri-trophic system detailed below can be parameterised to give stable cycles, as indicated by the positive CV of predator density in Fig S4a when c = 0.
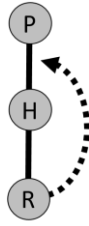
$$\frac{dP}{dt} = \frac{\mu e_p a_p HP}{1 + \mu h_p a_p H} - m_p P$$

$$\frac{dH}{dt} = \frac{e_h a_h RH}{1 + h_h a_h R} - \frac{\mu a_p HP}{1 + \mu h_p a_p H} - m_h H$$

$$\frac{dR}{dt} = GR\left(1 - \frac{R}{k}\right) - \frac{a_h RH}{1 + h_h a_h R}$$

$$\mu = \exp(c_{ijk} R)$$

a_h = 5, h_h = 1.24, m_h= 0.4, e_h = 1, a_p =0.8, h_p = 2.5, m_p = 0.08, e_p = 1, c_{ijk} = 0, G = 1, K= 0.58

 When an exponential TIM from the resource onto the predator-herbivore interaction is included, it can be seen that initially moving c_{ijk} above or below 0 leads to an increase in the CV of the parameter modification (μ) (Fig S2b). With larger positive values of c, the values for CV of μ continue to rise. However, in this model a negative TIM is stabilising (Fig S2a) and past a point (marked '*') the CV of μ starts to decline to 0 as the system is forced towards an equilibrium (Fig S2b). A strongly negative TIM has in this case had a strong effect on the macro-dynamics of the system, but in doing so has masked its own dynamic effect.
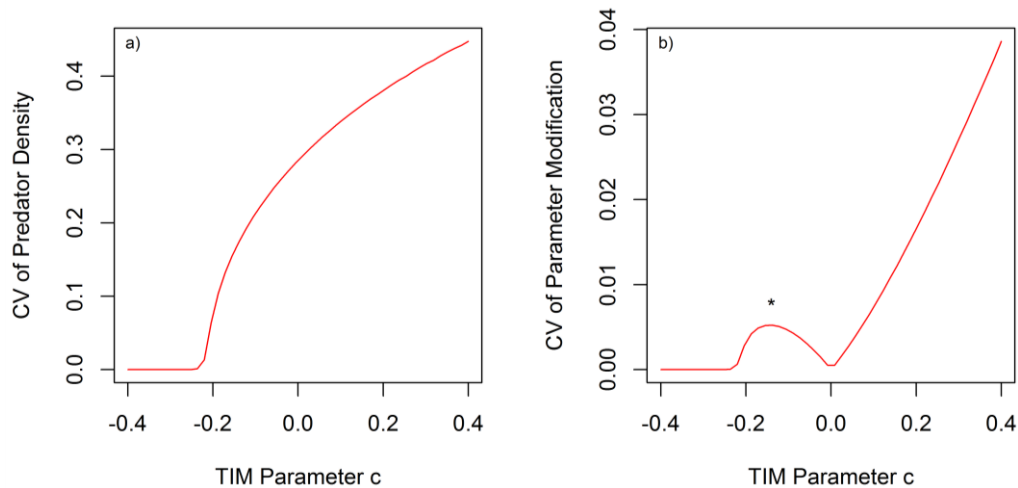

Figure S2. Plots of metrics for TIMs in a cycling system. A) coefficient of variation (CV) of the predator population density, b) CV of the parameter modification term (μ)

5

94   # Appendix 4. Model details for metric comparisons.

95   Model structures and parameters used in the Figure 3 of the main text.
96
97   **'Linear' Model:**

$$\frac{dA}{dt} = a'AB - mA$$

$$\frac{dB}{dt} = bBC - a'AB - nB$$

$$\frac{dC}{dt} = rC\left(1 - \left(\frac{C}{K}\right)\right) - bBC$$

$$a' = a + cC$$

98
99   *a = 5, b = 3, r = 4, c = 0, m = 1, n = 1, K = 1*

100   **'Non-linear' Model:**

$$\frac{dA}{dt} = \frac{a'AB}{1 + a'hB} - mA$$

$$\frac{dB}{dt} = \frac{bBC}{1 + bhC} - \frac{a'AB}{1 + a'hB} - nB$$

$$\frac{dC}{dt} = rC\left(1 - \frac{C}{K}\right) - \frac{bBC}{1 + bhC}$$

$$a' = ae^{cR}$$

101
102   *a = 6, b = 5, r = 2, c = 0, m = 1, n = 1, h = 0.4, K = 1*

103

104   **'Aphid-Parasitoid' Model** of van Veen *et al* (2005):

$$\frac{dA}{dt} = \frac{saAB}{1 + bB + cC + dA} - mA$$

$$\frac{dB}{dt} = r_B B(1 - \alpha_{BB}B - \alpha_{BC}C) - \frac{aAB}{1 + bB + cC + dA}$$

$$\frac{dC}{dt} = r_C C(1 - \alpha_{CC}C - \alpha_{CB}C)$$

105
106   Parameters have been renamed for consistency with the other models. In order to fit the
107   populations on the same scale, the population densities of the aphids and parasitoids are
108   displayed on a log-scale.

109   A = Parasitoid wasp, (*A. ervi*), B = Host aphid (*A. pisum*), C= Competitor aphid (*M. viciae*).
110   *a =0.000382, α_{BC}=0.00037, α_{CB}=0.000397, r_B =3.22, r_C =2.82, a_A =0.281, s =0.5, d =1.26, b =0.0233,*
111   *m =0.634.* Fitted value of *c=0.043*
112

Appendix 5. Comparison of TIMs with direct parameter changes

In stable systems, the introduction of a TIM can have equivalent effects to directly changing TIM parameters. As a demonstration, we examine the tri-trophic system detailed in Appendix 3 above, with a TIM introduced using an exponential link function and a standard set of parameters where the producer modifies the top predator-consumer interaction.

Stability is calculated from eigenvalues of the Jacobian at the system roots. A system with parameters that would lead to a cycling system can be stabilised either by reducing the attack rate of the predator directly (Fig S3a), or by increasing the negative effect of the TIM (Fig S3b). The stabilising effect of the TIM cannot therefore be directly attributed to the extra dynamic components of the TIM. For this an additional step is necessary, for example a close examination of the point at which the stability is attained. It is possible to infer the resultant post-modification attack rate and compare to direct modification diagram. Here the system with direct change becomes unstable at an attack rate of approximately 0.66. With the TIM the equivalent boundary between stability and instability occurs at c_{ijk} = -0.267, which is equivalent in this model to a µ of 0.876 and hence a predator attack rate of 0.7. This means that this system with a resultant attack rate of 0.68 would be stable when produced by this TIM, but unstable in a system with fixed parameter values, demonstrating an additional role for the dynamic processes. Note that towards the left of the diagrams in this system there is a very strong divergence between the impact of lower fixed attack rates (which do not permit even unstable systems to exist) and large negative effects of the modification, which can lead to persistent (albeit very large) cycles.
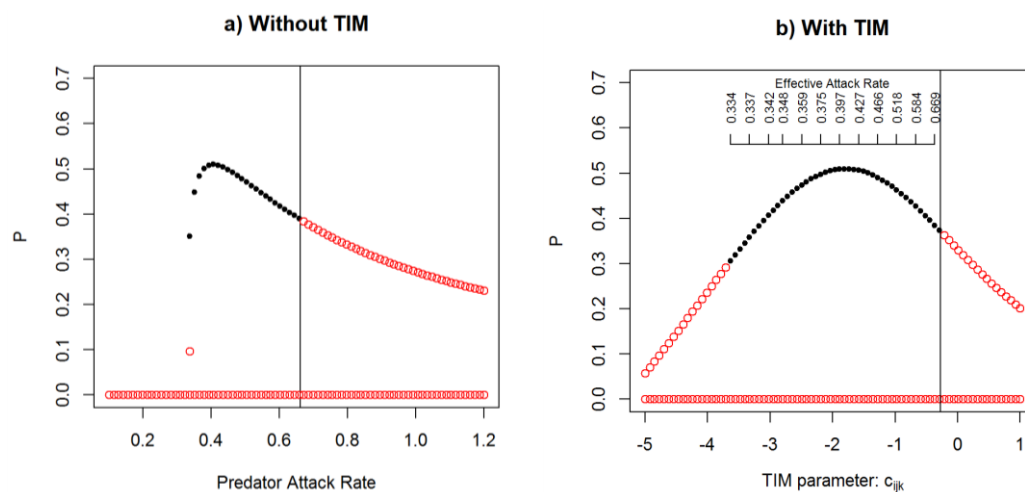

Figure S3. Stability diagrams comparing direct modification of attack rates (a) to the introduction of a TIM (b). Stable roots are shown as black dots, unstable with red circles.

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