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2   Cascading diversity effects transmitted exclusively by behavioral interactions

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23   ABSTRACT

24   Consumer diversity generally increases resource consumption. Consumers can also impact other

25   species by altering their behavior, but it is unclear how such nonconsumptive effects scale with

26   diversity. We independently manipulated predator species richness, and the consumptive and

27   nonconsumptive effects of predator communities, to measure the role of each factor in protecting

28   *Brassica oleracea* plants from caterpillar herbivory. Plant biomass was greatest when diverse

29   predator assemblages induced antipredator behaviors in herbivores, an effect not further

30   strengthened when predators could also kill caterpillars. Predators within diverse communities

31   were more likely to forage on plants, and to disrupt herbivore feeding, reflecting greater aversion

32   to foraging among conspecific than heterospecific competitors. Predator diversity, therefore,

33   initiated behavioral changes at the predator and then herbivore trophic levels, both to the benefit

34   of plants. Our results indicate that strong, emergent species richness effects can be transmitted

35   entirely through behavioral interactions, independent of resource consumption.

36

37   *Keywords*: biodiversity, ecosystem function, interference competition, intraguild intimidation,

38   nontrophic interaction, predator-prey, trait-mediated, trophic cascade

39

40   INTRODUCTION

41   The degree of resource extraction by diverse communities generally exceeds that of species-

42   poor communities (Cardinale et al. 2006). In most cases this is attributed to niche partitioning

43   among species, or interspecific facilitation of resource capture (Hooper et al. 2005). In either

44   case, diversity effects are generally envisioned as operating through the consumption of

45   resources. However, multi-species interactions also may be mediated by changes in behavior,

46   which may be reflected in biomass changes that are one or more trophic levels removed from the

47   inciting species (Turner and Mittelbach 1990, Schmitz et al. 1997). For example, predator

48   avoidance behaviors by herbivores often come at the cost of lost feeding opportunities, leading to

49   reduced plant damage even when herbivore numbers do not change (Lima and Dill 1990, Werner

50   and Peacor 2003, Preisser et al. 2005). Such behaviorally-mediated indirect effects can be as

51   strong as those induced by the actual consumption of intermediary species (Schmitz et al. 2004).

52   Analyses confined to predator and prey demographics, therefore, may significantly

53   underestimate the effects of predators on community structure (Abrams 1995, Brown et al. 1999,

54   Byrnes et al. 2006, Goudard and Loreau 2008).

55   For predators, there is good reason to expect complex interactions between consumer

56   diversity and the relative strengths of nonconsumptive and consumptive effects (Schmitz 2007).

57   Behavioral interactions are particularly important in predator communities (Sih et al. 1998),

58   perhaps contributing to the widely varying diversity-consumption relationships observed at this

59   trophic level (Ives et al. 2005, Bruno and Cardinale 2008). Prey consumption can decline at

60   higher diversity levels when intraguild predation is common (Finke and Denno 2004), but

61   increase when predators partition prey (Wilby et al. 2005, Bruno and O'Connor 2005, Finke and

62   Snyder 2008) or facilitate one another's prey capture (Soluk and Collins 1988). Thus,

63   interactions between predator diversity and predator consumptive effects themselves often are

64   non-additive (Ives et al. 2005). Similarly, the consumptive and nonconsumptive effects of single

65   predators can be positively or negatively non-additive (Peacor and Werner 2001, Griffin and

66   Thaler 2006).

67   It is interesting that in terms of predator-predator intimidation, there is not a clear trend as to

68   whether interspecific interactions tend to differ from intraspecific interactions. Studies isolating

69   inter- and intraspecific competition among predators have shown that behavioral interference

70   between heterospecific predators can be more severe than that among conspecifics (e.g., Soluk

71   and Collins 1988, Peckarsky 1991, Wissinger and McGrady 1993); however, one study has

72   suggested the opposite (Björkman and Liman 2005) while still others found inter- and

73   intraspecific interference to be essentially equal (Evans 1991, Shaffer and Robinson 1996,

74   Vance-Chalcraft et al. 2004, Vance-Chalcraft and Soluk 2005). Thus, it may be difficult to

75   predict how changes in predator diversity will influence the nature and strength of predator-

76   predator intimidation. Consideration of the various habitat domains and foraging modes of

77   interacting predator species may provide a useful basis for predicting emergent diversity effects

78   (Schmitz 2007). However, these factors may be dependent on the predator and prey community

79   in which the species is embedded, necessitating natural history information on all potential

80   predator-predator and predator-prey interactions (Schmitz 2007).

81   In various terrestrial and aquatic systems, there is evidence to suggest that nonconsumptive

82   effects could largely underlie predator diversity effects (e.g., Sih et al. 1998, Byrnes et al. 2006,

83   Prasad and Snyder 2006, Schmitz 2007), but the relative scaling of nonconsumptive effects

84   across diversity levels has yet to be examined empirically (Borer et al. 2002, Goudard and

85   Loreau 2008). This omission is unfortunate given that in nature, higher-order consumers are

86   exerting both consumptive and nonconsumptive effects while imbedded in diverse communities

87   (Switalski 2003, Werner and Peacor 2003, Siddon and Witman 2004, Berger et al. 2008, Trussell

88   et al. 2008). Understanding the relationship between nonconsumptive effects and predator

89   diversity is of particular importance given global declines in biological diversity (Hooper et al.

90   2005) and the bias toward extirpation among higher-order consumers (Duffy 2002).

91   In the field within a community of predatory insects, we investigated how the consumptive

92   and nonconsumptive effects of predators scaled with predator diversity. We independently

93   manipulated consumptive and nonconsumptive predator effects, across two levels of predator

94   diversity, and within a fully-factorial design. We then measured the resulting effects on

95   predators, herbivores, and the basal resource of the system, *Brassica oleracea* L. plants.

96   Nonconsumptive effects were isolated by replacing caterpillars killed by predators, and

97   consumptive effects were isolated by hand-removing caterpillars in the absence of predators.

98   These manipulations were catered to reproduce the magnitude of these effects in predator

99   communities differing both in species richness and species composition, ensuring a factorial

100   manipulation of predator nonconsumptive, consumptive, and diversity effects. We found that

101   diverse predator communities promoted increased plant growth by reducing herbivory, but that

102   this emergent diversity effect was transmitted entirely through a chain of nonconsumptive

103   interactions at the predator and then herbivore trophic levels. Thus, when compared to species-

104   poor predator assemblages, the more diverse predator assemblages increased system productivity

105   without increasing herbivore mortality. Our results indicate that behaviorally-mediated effects

106   can be influenced by diversity quite differently than, and independent from, those due to resource

107   consumption. This supports the contention that nonconsumptive interactions warrant greater

108   attention in biodiversity studies (Borer et al. 2002, Schmitz et al. 2004, Bruno and Cardinale

109   2008, Goudard and Loreau 2008).

110

111   METHODS

112   *Natural history*

113   Our study focused on the diverse community of predators attacking *Plutella xylostella* L.

114   caterpillars on *B. oleracea* plants. These caterpillars are the dominant chewing herbivore on *B.*

115   *oleracea* in the northwestern region of the United States (Biever et al. 1992). When threatened

116   by a predator, *P. xylostella* caterpillars drop from the plant, anchored by a silk thread affixed to

117   the leaf underside (Wang and Keller 2002). This behavior is readily observed, and the larvae

118   may remain suspended for minutes to hours on this thread before climbing back up to the plant

119   (Wang and Keller 2002). Since they cannot feed while dangling from the plant, deployment of

120   this antipredator behavior likely carries a fitness cost.

121   Locally common predators attacking these caterpillars include the ladybird beetle

122   *Hippodamia convergens* Guérin-Méneville, the predatory bugs *Geocoris pallens* Stål and *Nabis*

123   *alternatus* Parshley, the golden-eyed lacewing *Chrysopa oculata* Say, and the specialist

124   endoparasitoid *Diadegma insulare* (Cresson). This predator community encompasses a wide

125   variety of body sizes, feeding rates, hunting modes, and foraging domains, of the type that has

126   been demonstrated to yield complementary impacts on shared prey (Snyder et al. 2006, Straub

127   and Snyder 2006, 2008, Preisser et al. 2007). At the same time, intraguild predation has been

128   documented among several community members: lacewing larvae may succumb to *Geocoris* and

129   *Nabis* attacks (Rosenheim et al. 1999), and *Geocoris* and *Nabis* prey upon one another (Snyder et

130 al. 2006). Further, prey may stand to benefit from various manifestations of intraguild

131 intimidation among predators in more diverse communities (Sih et al. 1998, Berger et al. 2008).

132 Assemblages of heterospecific predators, therefore, would be expected to endure antagonism yet

133 also benefit from a degree of complementarity among their constituent species.

134   Our experiments included green peach aphids, *Myzus persicae* (Sulzer) (Hemiptera:

135 Aphididae), as these aphids are nearly always present on *B. oleracea* plants at our study site and

136 serve as an important prey for many of the predators (Snyder et al. 2006). In a survey of insect

137 communities on *B. oleracea* plants conducted the same year as the field experiment, we found

138 that 98.33% of caterpillar-infested plants also had aphids ($N = 120$ plants sampled; S. A. Steffan,

139 unpublished data). Predators, therefore, would nearly always encounter aphids when hunting for

140 caterpillars in nature, and thus the inclusion of aphid prey provided a more accurate reproduction

141 of the *B. oleracea* insect community than would caterpillars alone. If some predator species are

142 drawn to plants primarily to feed on aphids and, once there, feed opportunistically on

143 caterpillars, this too would be a naturally occurring phenomenon, again justifying the inclusion

144 of aphids.

145

146   *Experimental design*

147   In the field, four factors— predator diversity (*Low*, *High*), predator nonconsumptive

148 effects (*Fear+*, *Fear−*), predator consumptive effects (*Lethal+*, *Lethal−*), and temporal block (1,

149 2) —were manipulated within a fully crossed, $2 \times 2 \times 2 \times 2$ factorial design, yielding 16 unique

150 treatment combinations, each of which was replicated five times (total $N = 80$; Fig. 1). Our

151 independent manipulation of these factors allowed us to calculate all main effects and

152   interactions. Experimental units were 60 × 60 × 60-cm field cages (BugDorm-3120, MegaView

153   Science Education Services Co., Taiwan), enclosed on three sides by polyester netting (96 × 26

154   threads per cm mesh) and on the fourth with a clear plastic panel that allowed easy viewing of

155   cage occupants. In the middle of the clear front panel, a mesh sleeve allowed access to the

156   interior of the cage. Each cage housed, in addition to predators, two *B. oleracea* plants, 20 *P.*

157   *xylostella* caterpillars, and 40 *M. persicae* aphids (see *Methodological details* below). The

158   bottom edge of each cage was buried under 5-10 cm of packed soil to block arthropod

159   movement.

160

161   *Manipulation of predator diversity*

162   Replicates of the *Low Diversity* treatment consisted of one species each (drawn from the

163   pool of five predator species) in separate monocultures, while the *High Diversity* treatment

164   included each of the unique draws of four species from our pool of five predator species (i.e., one

165   species was absent from each polyculture) (Snyder et al. 2006). This design controls for the

166   effects of species composition and identity by ensuring that no single composition or species was

167   over- or underrepresented (Tilman 1997, Straub and Snyder 2006). Each of these species

168   compositions was included once at each level of consumptive/nonconsumptive effect

169   manipulation (Fig. 1). Predator diversity was manipulated within a substitutive design, with *Low*

170   *Diversity* cages receiving four individuals of the same species, and *High Diversity* cages

171   receiving one individual of each of four species.

172

173   *Manipulation of nonconsumptive predator effects*

174   We isolated nonconsumptive predator effects by systematically replacing caterpillars that

175   had been killed. Each cage in this treatment (*Fear+*, *Lethal−*) included predators, assembled

176   according to diversity level and species composition, that were allowed to forage freely. Each of

177   these cages was randomly paired with a no-predator control (*Fear−*, *Lethal−*) cage, and every

178   day, caterpillar densities in the *Fear+*, *Lethal−* cages were restored to no-predator levels by

179   replacing any dead or missing caterpillars. This system of prey replacement allowed us to

180   virtually eliminate prey losses in excess of background mortality, thereby neutralizing the effect

181   of predator lethality in these cages. Every replaced larva was ensured to be the equivalent instar

182   as that of its corresponding control cage, and all replacement larvae were chosen randomly from

183   the same cohort used to originally populate the cages. Our methods obviated the need for

184   physical manipulation of predators or the confinement of un-manipulated predators, and by

185   allowing predators to kill prey, the system preserved the cues associated with predation, such as

186   tactile vibration signatures (Castellanos and Barbosa 2006) and substrate-borne residues

187   (Magalhães et al. 2005). Such cues have been shown to initiate antipredator behaviors in

188   terrestrial communities.

189   Further, we attempted to minimize any disturbance to caterpillars during the transfer

190   process by never physically grasping or handling the caterpillars. Using a fine camel-hair brush,

191   we would gently touch a caterpillar with the brush tip to initiate a silk-drop. We then rolled this

192   silk thread onto the brush, and with the caterpillar suspended in mid-air, transferred it to a new

193   plant. This methodology allowed us to move caterpillars without risking handling trauma, and

194   also allowed us to deposit caterpillars into cages without touching plant foliage (other than the

195   caterpillar itself touching down on the leaf). Caterpillar transfers were quick, taking less than 1

196   min to release a caterpillar into a cage.

197

198   *Manipulation of consumptive predator effects*

199   To isolate consumptive effects, a system of manual prey culling was employed in cages

200   where predators were absent (as in Griffin and Thaler 2006). Each replicate of the *Fear−*,

201   *Lethal+* treatment (predators absent) was paired with the *Fear+*, *Lethal+* replicate (predators

202   present) with the same predator species composition. Each day of the experiment, we recorded

203   caterpillar densities within *Fear+*, *Lethal+* cages and then duplicated these densities within their

204   corresponding *Fear−*, *Lethal+* cages by manually removing caterpillars. Because the *Fear−*,

205   *Lethal+* cages did not contain predators, the prey experienced density reductions in the absence

206   of any predation cues. To ensure that the culling of prey accurately mimicked predation in the

207   *Fear+*, *Lethal+* treatment (as suggested by Okuyama and Bolker 2007), the developmental

208   stages (instars) of surviving larvae were recorded as well, allowing us to not only duplicate the

209   population trajectory of the prey, but also the particular age structure of the survivors.

210   We again attempted to minimize disturbance to other cage occupants when removing a

211   caterpillar. The caterpillar selected for removal was gently touched with a fine camel-hair brush

212   to initiate a silk drop. Then, the silk thread was wound onto the brush and the suspended

213   caterpillar lifted out of the cage. Thus, we were able to remove caterpillars without ever touching

214   the plant foliage, and removals could be accomplished quickly (less than 1 minute per caterpillar

215   being removed).

216

217   *Methodological details*

218   Experiments were conducted at the Washington State University Tukey Horticulture Orchard

219 in Pullman, WA. Block 1 was initiated 27 July 2007, and Block 2 was initiated 25 August 2007.

220 First, two *c.* 16-cm-tall *B. oleracea* plants (3-4 unfurled true leaves) were planted in each cage.

221 We released 20 green peach aphids, *M. persicae*, onto each plant and allowed three days for the

222 plants and aphids to establish. We then released 10 *P. xylostella* caterpillars (3rd instars, reared on

223 *B. oleracea* under the same greenhouse conditions) onto each plant in each cage (= 20

224 caterpillars per cage). This is well within the historical range of *P. xylostella* densities locally

225 under open-field conditions (Biever et al. 1992), and 2007 surveys of local *B. oleracea* fields

226 confirmed this, with per-plant densities ranging from 0 to 23 and averaging 11 caterpillars/plant

227 (S.A. Steffan, unpublished data). On the same day, all enemy treatments were randomly applied

228 to the cages, and the predators released. *Hippodamia*, *Geocoris*, and *Nabis* individuals were

229 collected on adjacent vegetation within 48 h of the experiment's start, and only adult females

230 were used. *Diadegma* females and larval *Chrysopa* were collected from greenhouse colonies.

231   Three response variables were measured every day, in each cage, during the course of this

232 experiment: the number of surviving caterpillars, the number of caterpillars displaced from

233 plants (i.e., silk-drops or otherwise displaced from plants), and the number of each predator

234 species present on the plants. To minimize disturbance to cage occupants, insect counts were

235 accomplished using small hand mirrors that allowed the observer to find insects on all plant and

236 cage surfaces without ever touching plant foliage. Both caterpillars and predators were easily

237 found using this method, such that counting these insects in each cage took only 2-3 minutes per

238 cage per day. At this time, any missing predator was replaced in order to maintain predator

239   density and diversity levels. Caterpillars were exposed to the predator treatments for 4 days, at

240   which time the caterpillars began spinning cocoons, and the experiment had to be concluded (as

241   pupae, diamondback moths no longer feed and thus no longer transmit the predators' effects to

242   the plant). Despite the relatively short trial duration necessitated by the caterpillar's rapid

243   development, our study captured the majority of the diamondback moth's herbivory potential by

244   spanning the last two of its four instars, during which caterpillars are known to do 90% of their

245   feeding (Boldt et al. 1975). First- and second-instar diamondback moth caterpillars are

246   exceedingly small, and as first-instars, they feed entirely within the leaf (as leaf miners),

247   emerging to feed on external leaf surfaces as second-instars (Wang and Keller 2002). At the

248   conclusion of the experiment, cages were carefully searched and all remaining arthropods

249   collected. Aphids were counted and removed from plants. Finally, the leaves (including petioles)

250   were harvested, dried for at least 4 d at 90° C, and weighed.

251

252   *Data analyses*

253   Final plant biomass and the total number of caterpillars observed off of plants were analyzed

254   as 2 x 2 x 2 x 2 fully-factorial ANOVAs, including the factors species richness (high, low),

255   nonconsumptive effects (*Fear+*, *Fear−*), consumptive effects (*Lethal+*, *Lethal−*), and temporal

256   block (1, 2). Total numbers of predators observed on plants was analyzed as a three-way

257   ANOVA including the factors diversity treatment, species identity, and block. Caterpillar

258   densities across the four days of each trial were analyzed using repeated measures MANOVA

259   including the factors block (1, 2) and predators (absent, low diversity, high diversity). Here, only

260 *Fear+, Lethal+* and *Fear−, Lethal−* cages were included in the analysis because caterpillar

261 densities were directly manipulated in the other treatment combinations.

262   We tested for emergent biodiversity effects (overyielding) in the plant biomass and herbivore

263 data, as transmitted through either consumptive or nonconsumptive channels. We calculated D_T,

264 a metric of polyculture performance relative to the average of its constituent species in

265 monoculture, and D_{max}, a metric of polyculture performance relative to that of the single most

266 effective species in monoculture (Petchey 2003). For the jth polyculture, the D_T value was

267 calculated as $D_{Tj} = (O_j - E_j)/E_j$, where O_j = observed effect of the jth polyculture, and E_j =

268 expected effect of the jth polyculture; E_j = summed per-capita performances in monoculture of

269 the species in the jth polyculture (see Appendix C). For each polyculture, a D_{max} value was

270 calculated; here, $D_{max} = (O_j - M_{max})/M_{max}$, where M_{max} was the single "best" performance

271 (greatest consumptive or nonconsumptive effect) of predators in monoculture, and again, O_j =

272 observed effect of the jth polyculture. One-sample *t*-tests were used to determine whether the

273 respective D_T and D_{max} means differed significantly from zero. In the analyses, values

274 significantly different than zero were taken as evidence of emergent diversity effects. All

275 analyses were conducted in SYSTAT (Systat Software, Richmond, CA, USA) (SPSS 1999).

276

277   RESULTS

278   Because effects on plants of our predator manipulations represented the sum of direct and

279 indirect effects through all channels, we first present the plant biomass data. We then work our

280 way up through the other two trophic levels, presenting behavioral and density data for

281 herbivores and then predators.

282

283   *Plants*

284   Final plant biomass was greatest where diverse predator communities initiated predator-

285   avoidance behavior by caterpillars (predator diversity × nonconsumptive effects interaction, $F_{1,64}$

286   = 6.88, P = 0.011; Fig. 2a). Consumption of prey also increased plant biomass (predator

287   consumptive main effect, $F_{1,64}$ = 20.44, $P < 0.001$; Fig. 2a), but this effect was not further

288   strengthened with either greater predator diversity or the co-occurrence of nonconsumptive

289   effects (all interactive consumptive effects $P > 0.05$; Appendix A1; Fig. 2a). Nonconsumptive

290   effects were stronger in *Block 2* than *Block 1* (nonconsumptive × block interaction, $F_{1,64}$ = 10.12,

291   P = 0.002), but block effects otherwise did not interact with other model terms (Appendix A1,

292   Appendix B1).

293   For plants, only the nonconsumptive effects of predators in high diversity assemblages

294   significantly exceeded expectations, based on the summed per-capita performances of the

295   constituent predator species in monoculture: the mean D_T value for the indirect, nonconsumptive

296   effect channel was significantly greater than zero (t = 7.43, df = 9, $P < 0.001$; Appendix C; Fig.

297   3a), while that of the consumptive (lethal) effect channel was not significantly different from

298   zero (t = 0.157, df = 9, P = 0.878). The mean D_{max} values for the indirect consumptive and

299   nonconsumptive effect channels did not differ from zero (consumptive: t = -1.614, df = 9, P =

300   0.141; nonconsumptive: t = -0.069, df = 9, P = 0.946), suggesting that in terms of either

301   consumptive or nonconsumptive effects, the average performance of polycultures did not exceed

302   that of the single most effective predator species (Fig. 3a; Appendix C).

303

304   *Herbivores*

305   Mirroring the results for plant biomass, herbivore displacement from the host plant was

306   greater among treatments coupling nonconsumptive effects with diverse predator communities

307   (diversity × nonconsumptive effects interaction, $F_{1,64}$ = 8.51, P = 0.005; Fig. 2b). Again,

308   nonconsumptive predator effects were stronger in *Block 2* than *Block 1* ($F_{1,64}$ = 5.30, P = 0.025;

309   Appendix A2, Appendix B2), though the relationship between diversity and caterpillar behavior

310   did not change across blocks (diversity × nonconsumptive × block interaction, $F_{1,64}$ = 0.212, P =

311   0.647; Appendix A2). Displaced caterpillars were observed almost exclusively in cages bearing

312   predators, indicating that the caterpillars generally did not stray from their host plants unless

313   induced by predators (Fig. 2b).

314   The magnitude of predator-induced mortality grew through time (predator × time interaction;

315   $F_{3,108}$ = 29.65, P < 0.001; Appendix A3; Appendix D), but caterpillar suppression was not further

316   strengthened with greater predator diversity (Appendix A4; Appendix D). Overall caterpillar

317   mortality was significantly higher in *Block 1* than *Block 2* (Appendix A3).

318   The consumptive effects of predators in polyculture did not exceed what would be expected

319   based on the summed per-capita performances of their constituent species in monoculture: the

320   mean D_T value for the direct consumptive effect channel was not significantly greater than zero (t

321   = 1.788, df = 9, P = 0.107; Appendix C; Fig. 3b). Conversely, the mean D_T value for direct

322   nonconsumptive predator effects was significantly greater than zero (t = 2.67; df = 9, P = 0.026;

323   Fig. 3b), providing evidence of consistent overyielding among predator polycultures. The mean

324   D_{max} value for the direct consumptive effect channel was significantly less than zero (t = -4.047,

325   df = 9, P = 0.003; Appendix C; Fig. 3b), while that of the nonconsumptive effect channel was

326   not significantly different from zero ($t = -1.781$, df $= 9$, $P = 0.109$). This indicates that the

327   consumptive effects of predators in polyculture were significantly less than, and nonconsumptive

328   effects no different than, the single most voracious or intimidating predator species in

329   monoculture (Fig. 3b).

330   Aphid densities were reduced in cages including predators (nonconsumptive main effect:

331    $F_{1,64} = 42.06$, $P < 0.001$; Appendix A5; Appendix E1). However, unlike plant biomass and

332   caterpillar silk-drop behaviors, aphid density was not impacted by an interaction between

333   predator diversity and nonconsumptive effects (diversity × nonconsumptive interaction: $F_{1,64} =$

334   0.25, $P = 0.621$; Appendix A5). A significant interaction between predator diversity and block

335   (diversity × block: $F_{1,64} = 5.719$, $P = 0.020$) appeared to reflect somewhat lower aphid densities

336   in diverse predator communities in *Block 1*, but somewhat higher aphid densities in diverse

337   predator communities in *Block 2* (Appendix E2).

338

339   *Predators*

340   Predator species differed in how diversity impacted their likelihood to forage on plants

341   (predator diversity × species identity interaction; $F_{4,20} = 3.80$, $P = 0.019$; Fig. 4a; Appendix A6).

342   This interaction appeared to be driven by the responses of two species, the lady beetle

343   *Hippodamia* and the parasitoid *Diadegma*, both of which exhibited higher per-capita visitation of

344   plants when foraging within diverse communities (Fig. 4a); plant visitation by the other predators

345   was unaffected by diversity treatment. Overall, plant-visitation by predators was significantly

346   higher in polyculture than in monoculture ($F_{4,20} = 8.33$, $P = 0.009$; Appendix A6).

347   Predator species differed in their likelihood of dying during the experiment ($F_{4,20} = 7.14$, $P =$

348   0.001; Fig. 4b), but there was no difference in mortality, for any species, between *Low* and *High*

349   *Diversity* treatments (diversity × species identity interaction, $F_{4,20} = 1.91$, $P = 0.147$; Fig. 4b

350   Appendix A7). Thus, there was no evidence that predator diversity influenced predator mortality

351   rates.

352   When in monoculture, predator species differed both in their likelihood of triggering

353   caterpillar displacements ($F_{4,15} = 4.71$, $P = 0.012$; Fig. 4c) and in the total caterpillar mortality

354   that they exerted ($F_{4,15} = 4.74$, $P = 0.011$; Fig. 4d). The lady beetle *Hippodamia* and the

355   parasitoid *Diadegma* were most likely to evoke displacement (Fig. 4c), while the lacewing

356   *Chrysopa* was the most lethal predator (Fig. 4d). In diverse predator communities, displaced and

357   dead caterpillars could not be attributed to a particular predator species.

358

359   DISCUSSION

360   Nonconsumptive interactions are increasingly recognized as ubiquitous and important

361   ecological phenomena, influencing not only how species interact but also how communities

362   function (Lima and Dill 1990, Sih et al. 1998, Schmitz et al. 2004, Preisser et al. 2005).

363   However, it has yet to be resolved how the effects of behavioral interactions scale with changes

364   in species diversity. Our fully-factorial manipulation of predator diversity and predator impacts

365   operating through nonconsumptive (behavioral) and consumptive (lethal) channels, allowed us to

366   explore the independent and interactive effects of these factors. We found that trophic cascades

367   were strengthened significantly through an interaction between predator diversity and the

368   nonconsumptive component of the predator effect, with caterpillars significantly more likely to

369   engage in antipredator behavior, both eating less (Fig. 2a) and dropping from the plant more

370   often (Fig. 2b), when facing diverse than single-species predator communities. While predators

371   also protected plants by killing caterpillars (Fig 2a; Appendix D), predator effects through the

372   consumptive channel were not influenced by predator diversity or the occurrence of antipredator

373   behavior. In monoculture, two predator species were particularly strong disruptors of caterpillar

374   feeding, the parasitoid *Diadegma* and the lady beetle *Hippodamia* (Fig. 4c), and these same two

375   predator species were more likely to forage on plants when embedded within diverse

376   communities (Fig. 4a). Together, these results suggest that predator diversity effects were

377   conducted through a chain of behavioral interactions, with the most intimidating predators more

378   likely to occur on plants, and thus to disrupt herbivore feeding, when within diverse

379   communities.

380   The cascading diversity effects we observed appear to have been initiated by a reduction in

381   the degree of interference among predators in the diverse communities. In our system, plant-

382   visitation by predators served as an indicator of predator-predator interactions. Given that

383   caterpillars (and aphids) remained on their host plant until confronted by a threat (Fig. 2b),

384   predators were generally forced to converge on the plants in order to locate food. Our finding

385   that plant-visitation was greater in the high diversity treatment (Appendix A6) suggests that

386   interference was relaxed to some extent among predators in the multi-species communities. In

387   our low diversity arenas, predators interacted only with conspecifics, whereas in diverse arenas

388   predators interacted only with heterospecifics. Thus, intraspecific competition among predators

389   was entirely eliminated within the diverse communities. To the extent that intraspecific

390   competition may exceed interspecific competition for some species, relief from intraspecific

391 interactions may facilitate greater foraging efficiency. It was evident in our study that the

392 predators *Diadegma* and *Hippodamia* were much more likely to forage for prey within cages

393 housing heterospecific than conspecific competitors (Fig. 4a), suggesting that the release from

394 intraspecific interference in diverse communities allowed these species to forage more

395 effectively. There is good evidence in the literature of strong intraspecific interference among

396 arthropod predators (Sih et al. 1998), including for many of the predators used in this study when

397 foraging on *B. oleracea* plants (Northfield et al., in revision). Both lady beetles and parasitoids

398 have the ability to recognize and respond to cues left by earlier-arriving conspecific competitors

399 (Rosenheim 1998, Hodek and Michaud 2008), which is thought to be adaptive because of the

400 high risk of cannibalism for progeny oviposited where conspecifics already occur. In our

401 experiments predator mortality was rare overall, and we saw no evidence that intraguild

402 predation exceeded mortality (if any) due to cannibalism (Fig. 4b). This strengthens our

403 argument that predator-predator interactions were primarily behavioral in nature. At least one

404 other study has provided theoretical evidence that relief from intraspecific competition can

405 generate positive diversity effects (Weis et al. 2007); the mechanism in that case was the

406 reduction of exploitative competition with increasing diversity, rather than the reduction of

407 intraspecific interference.

408   Nonetheless, we were curious whether higher plant-visitation rates by *Diadegma* and

409 *Hippodamia* could entirely explain the behaviorally-mediated diversity cascade that we

410 observed. We can examine this quantitatively by calculating an "expected" number of

411 displacements for each polyculture replicate, under the simplifying assumption that a plant visit

412 by a predator incites the same level of intimidation regardless of diversity treatment. We first

413   calculate the number of caterpillar displacements per predator, per plant-visit for each species in

414   monoculture (displacements could not be attributed to particular predator species in the

415   polycultures). Then, multiplying this value by the observed plant visitation rate of each predator

416   species in a given polyculture, and summing these values across all species in that polyculture,

417   yields the expected number of caterpillar displacements for that replicate. Intriguingly, observed

418   caterpillar displacement per-visit in polyculture was greater than predicted by this calculation (t

419    $= 2.41$, df $= 19$, $P = 0.026$; Fig. 5). Thus, accounting for higher per-capita visitation rates by the

420   two most intimidating predator species does not entirely explain the greater nonconsumptive

421   effects of diverse predator assemblages, suggesting that another factor was also at work. One

422   possibility is that predator consumptive and nonconsumptive effects scale differently with

423   predator density. Behaviorally-mediated effects could remain relatively intense as the density of

424   particular predator species declined, as happens at higher diversity levels within substitutive

425   designs. This could occur, for example, because a predator can simultaneously intimidate many

426   prey individuals but kill only one at a time (Peacor and Werner 2001). Consistent with this

427   explanation, in our experiments nonconsumptive effects were similar to those of the single most

428   intimidating predator species, whereas consumptive effects reflected the average predation rates

429   across species (Fig. 3). A relative insensitivity of nonconsumptive effects to predator density

430   would allow these effects to remain consistently intense in diverse communities, even when

431   greater diversity dilutes densities of the more intimidating predator species. This points to the

432   possibility that a highly intimidating species may effectively saturate a system with fear,

433   rendering other predators variously redundant. If predators' nonconsumptive effects were indeed

434   partially redundant in both monoculture and polyculture, then our finding that D_T values were

435   significantly greater than zero (in terms of nonconsumptive effects; Fig. 3) indicates that the

436   more intimidating predator species were less redundant in polyculture than in monoculture. So,

437   not only did *Diadegma* and *Hippodamia* spend more time on plants when embedded in diverse

438   communities, but their nonconsumptive effects on caterpillars and plants were, to some extent,

439   complementary.

440   More generally, dissimilarity in hunting domain and foraging mode decreases the probability

441   of predator-predator encounters and thereby may reduce interference competition (Björkman and

442   Liman 2005, Preisser et al. 2007, Schmitz 2007). Interference can be direct, manifesting as

443   aggressive or despotic behavior among predators (Shaffer and Robinson 1996, Switalski 2003),

444   or indirect, with intraguild prey assessing their surroundings for evidence of intraguild predators

445   and actively avoiding encounters (Soluk and Collins 1988, Siddon and Witman 2004, Vance-

446   Chalcraft and Soluk 2005, Berger et al. 2008). Given that conspecific predators would be

447   expected to be more similar than heterospecifics, intraspecific competition should be greater than

448   interspecific competition (MacArthur 1958). Hence, if foraging in a more diverse predator

449   community can spare an actively hunting species from frequent encounters with conspecifics

450   (e.g., Björkman and Liman 2005), then such predators should be more efficient in polyculture.

451   Our results are consistent with this expectation, yet our data also represent a departure from

452   studies isolating the cascading effects of diversity. Predator diversity effects have been shown to

453   cascade via lethal predator-prey interactions (Bruno and Cardinale 2008), as well as by lethal

454   predator-predator interactions (Finke and Denno 2004). Our data suggest that cascading diversity

455   effects can also be initiated by nonconsumptive interactions among predators, which dovetails

456   well with recent work investigating how the effects of complementary predator-prey

457   relationships may cascade via nonconsumptive channels (Byrnes et al. 2006).

458   Our experimental arenas included green peach aphids as a second, non-focal herbivore

459   species because caterpillars nearly always co-occur with aphids on *B. oleracea* plants at our

460   study site and are common prey of the predators (Snyder et al. 2006, Straub and Snyder 2006,

461   2008). Although the magnitude of the difference is relatively small (Appendix E), predators

462   significantly reduced aphid densities in *Fear+* cages because these were the only cages that

463   included predators. These lower aphid densities may have reinforced the strength of the

464   significant trophic cascade that we observed in these cages (see nonconsumptive main effect for

465   plant biomass, Appendix A1). However, in contrast to the plant biomass (Appendix A1) and

466   caterpillar displacement findings (Appendix A2), the aphid data showed no evidence of an

467   interaction between predator diversity and nonconsumptive effects (Appendix A5), suggesting

468   that the significant diversity effects we observed were unlikely to have been mediated by aphid

469   densities. For aphids, a significant interaction between Diversity and Block appeared to result

470   from aphid densities being slightly lower in diverse predator communities in *Block 1*, but slightly

471   higher in diverse predator communities in *Block 2* (Appendix A5). So, there was no consistent

472   predator diversity main effect influencing aphids, and there were no significant interactions

473   between Diversity and any other factor. Since aphid densities were similar everywhere predators

474   foraged, any impact of aphid density on predator foraging behavior would be similar across all

475   treatments. Thus, it does not appear that the direct or indirect effects of aphids could explain the

476   strong interaction between predator diversity and nonconsumptive effects that impacted our

477   trophic cascades (Fig. 2).

478   We used removals and replacements of herbivores to isolate predator trophic versus

479   nontrophic effects. This precluded the need to render predators nonlethal and thereby avoided

480   many of the potential problems resulting from such manipulations (e.g., altered predator

481   behavior, absence of substrate-borne cues associated with prey capture). However, there are

482   limitations to what can be achieved using our techniques. When removing prey from no-predator

483   cages to isolate lethal (consumptive) predator effects, there is always a short lag between when

484   predation events occur and when the prey are removed to mimic predation (Griffin and Thaler

485   2006). As a result, prey culling techniques slightly underestimate the true strength of

486   consumptive effects, as prey that should be "dead" continue feeding until the daily predation

487   simulation can be levied. Similarly, when adding prey to isolate nonconsumptive effects, there is

488   a lag between the moment a prey individual is killed and when it is replaced, leading to an

489   overestimation of the strength of nonconsumptive predator effects. These biases heighten the

490   importance of frequently censusing herbivores such that lag times are minimized (< 1 day), and

491   suggest caution in placing too much weight in estimates of the relative strengths of consumptive

492   versus nonconsumptive effects. Despite these limitations, our methodology can be particularly

493   useful when looking for interactions between these two effects and other factors (e.g., predator

494   diversity), where it is less important to precisely reproduce the magnitudes of

495   consumptive/nonconsumptive effects, but more important to isolate them from each other.

496   To our knowledge, no previous studies have isolated nonconsumptive from consumptive

497   effects while also manipulating consumer diversity. Theoretical and empirical evidence suggest

498   that consumer species richness may commonly influence the nature and magnitude of nontrophic

499   interactions between predators and prey, as well as among predators (Sih et al. 1998, Borer et al.

500   2002, Byrnes et al. 2006, Schmitz 2007, Goudard and Loreau 2008). It is striking how often

501   behavioral interactions underlie emergent diversity effects for predators and other animal

502   consumers. For example, inherent differences in foraging behavior and/or prey choice can lead to

503   a positive relationship between predator diversity and herbivore exploitation (Preisser et al. 2007,

504   Finke and Snyder 2008). Similarly, prey species may exhibit predator-specific antipredator

505   behavior, modulated to reflect the differing risks posed by different predator species (Shaffer and

506   Robinson 1996, Byrnes et al. 2006, Castellanos and Barbosa 2006). This suggests that behavioral

507   interactions may mediate diversity effects to the same degree that consumptive interactions may,

508   as has been found when looking at simpler subsets of consumer communities (Preisser et al.

509   2005).

510   Our results bring us to several conclusions. First, behaviorally-mediated diversity affects can

511   cascade across multiple trophic levels, as do density-mediated effects (Ives et al. 2005, Duffy et

512   al. 2007). This reinforces suggestions that nonconsumptive interactions warrant greater attention

513   in ecological research (Peckarsky et al. 1991, Brown et al. 1999, Borer et al. 2002), and that it

514   may be unwise to rely entirely on abundance or biomass metrics when quantifying diversity

515   effects (Byrnes et al. 2006, Goudard and Loreau 2008). Second, consumer effects operating via

516   nonconsumptive channels might act quite differently than, and in our study were independent

517   from, those due to resource consumption. This raises the possibility that diversity effects

518   attributed to consumptive interactions may instead be partially, or entirely, due to

519   nonconsumptive interactions. It appears that many cases of consumptive diversity effects in

520   animal communities have complex behavioral underpinnings (Bruno and Cardinale 2008), and

521 only a more consistent consideration of how behavior influences diversity effects will allow

522 incorporation of these effects into theory (Borer et al. 2002, Goudard and Loreau 2008).

523

533

534   REFERENCES

535 Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and

536   measuring direct and indirect effects in ecological communities. American Naturalist

537   146:112-134.

538 Berger, K. M., E. M. Gese, and J. Berger. 2008. Indirect effects and traditional trophic cascades:

539   A test involving wolves, coyotes, and pronghorn. Ecology 89:818-828.

540   Biever, K. D., R. L. Chauvin, G. L. Reed, and R. C. Wilson. 1992. Seasonal occurrence and

541   abundance of lepidopterous pests and associated parasitoids in the northwestern United

542   States. Journal of Entomological Science 27:5-18.

543   Björkman, C., and A. -S. Liman. 2005. Foraging behavior influences the outcome of predator-

544   predator interactions. Ecological Entomology 30:164-169.

545   Boldt, P. E., K. D. Biever, and C. M. Ignoffo. 1975. Consumption of soybean foliage and pods

546   and development time. Journal of Economic Entomology 68:480-482.

547   Borer, E. T., K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, B.S. Halpern, E. W.

548   Seabloom, and J. B. Shurin. 2002. Topological approaches to food web analyses: a few

549   modifications may improve our insights. Oikos 99:397-401.

550   Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game

551   theory, and trophic interactions. Journal of Mammalogy 80:385-399.

552   Bruno, J. F., and B. J. Cardinale. 2008. Cascading effects of predator richness. Frontiers in

553   Ecology and the Environment 6:539-546.

554   Bruno, J. F., and M. I. O'Connor. 2005. Cascading effects of predator diversity and omnivory in

555   a marine food web. Ecology Letters 8:1048-1056.

556   Byrnes, J., J. J. Stachowicz, K. M. Hultgren, A. R. Hughes, S. V. Olyarnik, and C. S. Thornbert.

557   2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore

558   behavior. Ecology Letters 9:61-71.

559   Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C.

560   Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems.

561   Nature 443:989-992.

562   Castellanos, I., and P. Barbosa. 2006. Evaluation of predation risk by a caterpillar using

563   substrate-borne vibrations. Animal Behaviour 72:461-469.

564   Duffy, J. E. 2002. Biodiversity and ecosystem function: the consumer connection. Oikos 99:201-

565   219.

566   Duffy, J. E., B. J. Cardinale, K. E. France, P. B. McIntyre, E. Thebault, and M. Loreau. 2007.

567   The functional role of biodiversity in ecosystems: incorporating trophic complexity. Ecology

568   Letters 10:522-538.

569   Evans, E. W. 1991. Intra versus interspecific interactions of ladybeetles (Coleoptera:

570   Coccinellidae) attacking aphids. Oecologia 87:401-408.

571   Finke, D. L., and R. F. Denno. 2004. Predator diversity dampens trophic cascades. Nature

572   429:407-410.

573   Finke, D. L., and W. E. Snyder. 2008. Niche partitioning increases resource exploitation by

574   diverse communities. Science 321:1488-1490.

575   Goudard, A., and M. Loreau. 2008. Nontrophic interactions, biodiversity, and ecosystem

576   functioning: an interaction web model. American Naturalist 171:91-106.

577   Griffin, C. A. M., and J. S. Thaler. 2006. Insect predators affect plant resistance via density- and

578   trait-mediated indirect interactions. Ecology Letters 9:335-343.

579   Hodek, I., and J. P. Michaud. 2008. Why is *Coccinella septempunctata* so successful? European

580   Journal of Entomology 105:1-12.

581   Hooper, D. U., F. S. Chapin, III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, D.

582   M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A. J. Symstad, J. Vandermeer, and D.

583   A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current

584   knowledge. Ecological Monographs 75:3-35.

585   Ives, A. R., B. J. Cardinale, and W. E. Snyder. 2005. A synthesis of subdisciplines: predator-prey

586   interactions, and biodiversity and ecosystem functioning. Ecology Letters 8:102-116.

587   Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: A

588   review and prospectus. Canadian Journal of Zoology 68:619-640.

589   MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests.

590   Ecology 39:599-619.

591   Magalhães, S., C. Tudorache, M. Montserrat, R. van Maanen, and M. W. Sabelis. 2005. Diet of

592   intraguild predators affects antipredator behavior in intraguild prey. Behavioral Ecology

593   16:364-370.

594   Northfield, T. D., G. B. Snyder, A. R. Ives and W. E. Snyder. (In revision). Niche saturation

595   reveals resource-use differences among consumers. Ecology Letters.

596   Okuyama, T., and B. M. Bolker. 2007. On quantitative measures of indirect interactions.

597   Ecology Letters 10:264-271.

598   Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the

599   net effects of a predator. Proceedings of the National Academy of Sciences (USA) 98:3904-

600   3908.

601   Peckarsky, B. L. 1991. Mechanisms of intra- and interspecific interference between larval

602   stoneflies. Oecologia 85:521-529.

603   Petchey, O. L. 2003. Integrating methods that investigate how complementarity influences

604   ecosystem functioning. Oikos 101:323-330.

605   Prasad, R. P., and W. E. Snyder. 2006. Diverse trait-mediated interactions in a multi-predator,

606   multi-prey community. Ecology 87:1131-1137.

607   Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of

608   intimidation and consumption on predator-prey interactions. Ecology 86:501-509.

609   Preisser, E. L., J. L. Orrock, and O. J. Schmitz. 2007. Predator hunting mode and habitat domain

610   alter nonconsumptive effects in predator-prey interactions. Ecology 88:2744-2755.

611   Rosenheim, J. A. 1998. Higher-order predators and the regulation of insect herbivore

612   populations. Annual Review of Entomology 43:421-447.

613   Rosenheim, J. A., D. D. Limburg, and R. G. Colfer. 1999. Impact of generalist predators on a

614   biological control agent, *Chrysoperla carnea*: direct observations. Ecological Applications

615   9:409-417.

616   Schmitz, O. J. 2007. Predator diversity and trophic interactions. Ecology 88:2415-2426.

617   Schmitz, O. J., A. Beckerman, and K. M. O'Brien. 1997. Behaviorally-mediated trophic

618   cascades: effects of predation risk on food web interactions. Ecology 78:1388-1399.

619   Schmitz, O. J., V. Krivan, and O. Ovadia. 2004. Trophic cascades: the primacy of trait-mediated

620   interactions. Ecology Letters 7:153-163.

621   Shaffer, L. R., and J. V. Robinson. 1996. Do damselfly larvae recognize and differentially

622   respond to distinct categories of macroinvertebrates? Journal of Insect Behavior 9:407-419.

623   Siddon, C. E., and J. D. Witman. 2004. Behavioral indirect interactions: multiple predator effects

624   and prey switching in the rocky subtidal. Ecology 85:2938-2945.

625   Sih, A., G. Englund, and D. Wooster. 1998. Emergent impacts of multiple predators on prey.

626   Trends in Ecology and Evolution 13:350-355.

627 Snyder, W. E., G. B. Snyder, D. L. Finke, and C. S. Straub. 2006. Predator biodiversity

628   strengthens herbivore suppression. Ecology Letters 9:789-796.

629 Soluk, D. A., and N. C. Collins. 1988. Synergistic interactions between fish and stoneflies:

630   facilitation and interference among stream predators. Oikos 52:94-100.

631 Straub, C. S., and W. E. Snyder. 2006. Species identity dominates the relationship between

632   predator biodiversity and herbivore suppression. Ecology 87:277-282.

633 Straub, C. S., and W. E. Snyder. 2008. Increasing enemy biodiversity strengthens herbivore

634   suppression on two plant species. Ecology 89:1605-1615.

635 Switalski, T. A. 2003. Coyote foraging ecology and vigilance in response to gray wolf

636   reintroduction in Yellowstone National Park. Canadian Journal of Zoology 81:985-993.

637 Tilman, D. 1997. Distinguishing between the effects of species diversity and species

638   composition. Oikos 80:185.

639 Trussell, G. C., P. J. Ewanchuck, and C. M. Matassa. 2008. Resource identity modifies the

640   influence of predation risk on ecosystem function. Ecology 89:2798-2807.

641 Turner, A. M., and G. G. Mittelbach. 1990. Predator avoidance and community structure:

642   interactions among piscivores, planktivores, and plankton. Ecology 71:2241-2254.

643 Vance-Chalcraft, H. D., and D. A. Soluk. 2005. Multiple predator effects result in risk reduction

644   for prey across multiple prey densities. Oecologia 144:472-480.

645 Vance-Chalcraft, H. D., D. A. Soluk, and N. Ozburn. 2004. Is prey predation risk influenced

646   more by increasing predator density or predator species richness in stream enclosures?

647   Oecologia 139:117-122.

648   Wang, X. -G., and M. A. Keller. 2002. A comparison of the host-searching efficiency of two

649   larval parasitoids of *Plutella xylostella*. Ecological Entomology 27:105-114.

650   Weis, J. J., B. J. Cardinale, K. J. Forshay, and A. R. Ives. 2007. Effects of species diversity on

651   community biomass production change over the course of succession. Ecology 88:929-939.

652   Werner, E. E., and S. D. Peacor. 2003. A review of trait-mediated indirect interactions in

653   ecological communities. Ecology 84:1083-1100.

654   Wilby, A., S. C. Villareal, L. P. Lan, K. L. Heong, and M. B. Thomas. 2005. Functional benefits

655   of predator species diversity depend on prey identity. Ecological Entomology 30:497-501.

656   Wissinger, S., and J. McGrady. 1993. Intraguild predation and competition between larval

657   dragonflies: direct and indirect effects on shared prey. Ecology 74:207-218.

658

659

660 FIGURE LEGENDS

661 **Fig. 1** Factorial structure of the experiment: predator diversity (*Low*, *High*) × consumptive

662 effects (*Lethal+*, *Lethal−*) × nonconsumptive effects (*Fear+*, *Fear−*) × temporal block (*1*, *2*).

663 All factors were fully-crossed, achieving a complete 2 × 2 × 2 × 2 factorial design.

664

665 **Fig. 2** (a) Final plant biomass and (b) Total number of caterpillars observed off of plants, for

666 three factors: predator diversity (*Low*, *High*), predator nonconsumptive effects (*Fear+*, *Fear−*),

667 and predator consumptive effects (*Lethal+*, *Lethal−*). Data are shown averaged across the two

668 temporal blocks; data are presented separately by block in Appendix B. Data are means ± 1SE.

669

670 **Fig. 3** Two measures of overyielding, D_T and D_{max}, for consumptive and nonconsumptive

671 predator effects on (a) plant biomass and (b) herbivore density (Lethal channel) and behavior

672 (Fear channel). See Appendix C (*Ecological Archives*) for calculations of D_T and D_{max} values

673 (data are means ± 95% CI).

674

675 **Fig. 4** Occurrences, per-capita, of each predator species (a) observed foraging on plants, and (b)

676 dying during the course of the experiment in high and low diversity compositions. Total number

677 of caterpillars (c) displaced and (d) killed by each predator species when in monoculture. Data

678 are for the predator species *Hippodamia* (Hip), *Diadegma* (Dia), *Chrysopa* (Chr), *Nabis* (Nab),

679 and *Geocoris* (Geo). Data are means ± 1 SE.

680

681 **Fig. 5** Predicted and observed caterpillar displacements in high diversity species compositions.

682 Predicted displacement for a given polyculture was calculated by summing the predicted

683 displacements generated by each species constituting the polyculture: $\sum[$(observed

684 displacements)$_i$/(observed visits)$_i$](observed visits)$_{ij}$, for the ith species in monoculture, and the ith

685 species within the jth polyculture. Data are means ± 1 SE

686

687

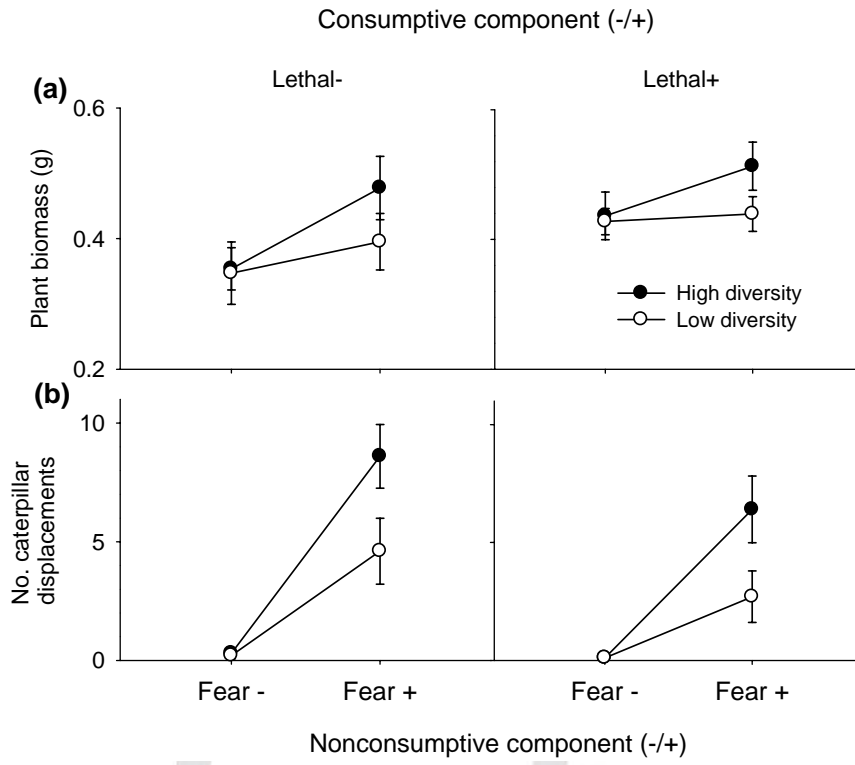688

689 FIGURES

690

691 Figure 1

692

693

694

695 × Predator Diversity × Temporal Block
(High, Low) (1, 2)

696

697

698

	Consumptive	
	−	+
Non-consumptive −	Control	Lethality
Non-consumptive +	Fear	Lethality + Fear

699

700   Figure 2

Consumptive component (-/+)

701   Nonconsumptive component (-/+)
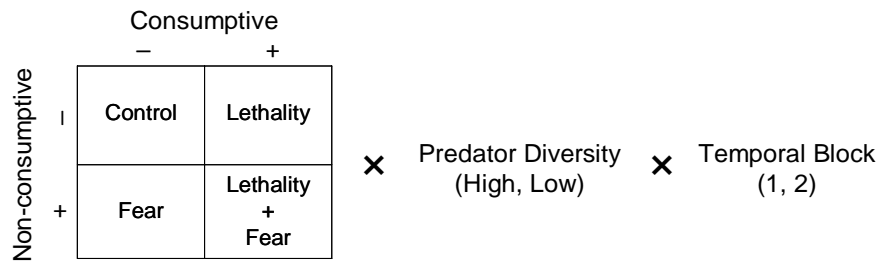
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704   Figure 3

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711 Figure 4

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725   Figure 5

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