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Cascading diversity effects transmitted exclusively by behavioral interactions

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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

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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).

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METHODS

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Natural history

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Our study focused on the diverse community of predators attacking *Plutella xylostella* L. caterpillars on *B. oleracea* plants. These caterpillars are the dominant chewing herbivore on *B. oleracea* in the northwestern region of the United States (Biever et al. 1992). When threatened by a predator, *P. xylostella* caterpillars drop from the plant, anchored by a silk thread affixed to the leaf underside (Wang and Keller 2002). This behavior is readily observed, and the larvae may remain suspended for minutes to hours on this thread before climbing back up to the plant (Wang and Keller 2002). Since they cannot feed while dangling from the plant, deployment of this antipredator behavior likely carries a fitness cost.

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Locally common predators attacking these caterpillars include the ladybird beetle *Hippodamia convergens* Guérin-Ménéville, the predatory bugs *Geocoris pallens* Stål and *Nabis alternatus* Parshley, the golden-eyed lacewing *Chrysopa oculata* Say, and the specialist endoparasitoid *Diadegma insulare* (Cresson). This predator community encompasses a wide variety of body sizes, feeding rates, hunting modes, and foraging domains, of the type that has been demonstrated to yield complementary impacts on shared prey (Snyder et al. 2006, Straub and Snyder 2006, 2008, Preisser et al. 2007). At the same time, intraguild predation has been documented among several community members: lacewing larvae may succumb to *Geocoris* and *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 j^{th} polyculture, the D_T value was
267 calculated as $D_{Tj} = (O_j - E_j)/E_j$, where O_j = observed effect of the j^{th} polyculture, and E_j =
268 expected effect of the j^{th} polyculture; E_j = summed per-capita performances in monoculture of
269 the species in the j^{th} 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 j^{th} 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.

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Plants

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Final plant biomass was greatest where diverse predator communities initiated predator-avoidance behavior by caterpillars (predator diversity \times nonconsumptive effects interaction, $F_{1,64} = 6.88$, $P = 0.011$; Fig. 2a). Consumption of prey also increased plant biomass (predator consumptive main effect, $F_{1,64} = 20.44$, $P < 0.001$; Fig. 2a), but this effect was not further strengthened with either greater predator diversity or the co-occurrence of nonconsumptive effects (all interactive consumptive effects $P > 0.05$; Appendix A1; Fig. 2a). Nonconsumptive effects were stronger in *Block 2* than *Block 1* (nonconsumptive \times block interaction, $F_{1,64} = 10.12$, $P = 0.002$), but block effects otherwise did not interact with other model terms (Appendix A1, Appendix B1).

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For plants, only the nonconsumptive effects of predators in high diversity assemblages significantly exceeded expectations, based on the summed per-capita performances of the constituent predator species in monoculture: the mean D_T value for the indirect, nonconsumptive effect channel was significantly greater than zero ($t = 7.43$, $df = 9$, $P < 0.001$; Appendix C; Fig. 3a), while that of the consumptive (lethal) effect channel was not significantly different from zero ($t = 0.157$, $df = 9$, $P = 0.878$). The mean D_{max} values for the indirect consumptive and nonconsumptive effect channels did not differ from zero (consumptive: $t = -1.614$, $df = 9$, $P = 0.141$; nonconsumptive: $t = -0.069$, $df = 9$, $P = 0.946$), suggesting that in terms of either consumptive or nonconsumptive effects, the average performance of polycultures did not exceed that of the single most effective predator species (Fig. 3a; Appendix C).

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 \times 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 \times nonconsumptive \times 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 \times 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 \times nonconsumptive interaction: $F_{1,64} =$
334 0.25 , $P = 0.621$; Appendix A5). A significant interaction between predator diversity and block
335 (diversity \times 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 \times 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 \times 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.

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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 effects 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).

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FIGURE LEGENDS

Fig. 1 Factorial structure of the experiment: predator diversity (*Low, High*) × consumptive effects (*Lethal+*, *Lethal-*) × nonconsumptive effects (*Fear+*, *Fear-*) × temporal block (1, 2). All factors were fully-crossed, achieving a complete $2 \times 2 \times 2 \times 2$ factorial design.

Fig. 2 (a) Final plant biomass and (b) Total number of caterpillars observed off of plants, for three factors: predator diversity (*Low, High*), predator nonconsumptive effects (*Fear+*, *Fear-*), and predator consumptive effects (*Lethal+*, *Lethal-*). Data are shown averaged across the two temporal blocks; data are presented separately by block in Appendix B. Data are means \pm 1SE.

Fig. 3 Two measures of overyielding, D_T and D_{max} , for consumptive and nonconsumptive predator effects on (a) plant biomass and (b) herbivore density (Lethal channel) and behavior (Fear channel). See Appendix C (*Ecological Archives*) for calculations of D_T and D_{max} values (data are means \pm 95% CI).

Fig. 4 Occurrences, per-capita, of each predator species (a) observed foraging on plants, and (b) dying during the course of the experiment in high and low diversity compositions. Total number of caterpillars (c) displaced and (d) killed by each predator species when in monoculture. Data are for the predator species *Hippodamia* (Hip), *Diadegma* (Dia), *Chrysopa* (Chr), *Nabis* (Nab), and *Geocoris* (Geo). Data are means \pm 1 SE.

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: $\sum[(\text{observed}$
684 $\text{displacements})_i / (\text{observed visits})_i] (\text{observed visits})_{ij}$, for the i^{th} species in monoculture, and the i^{th}
685 species within the j^{th} polyculture. Data are means \pm 1 SE

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691 Figure 1

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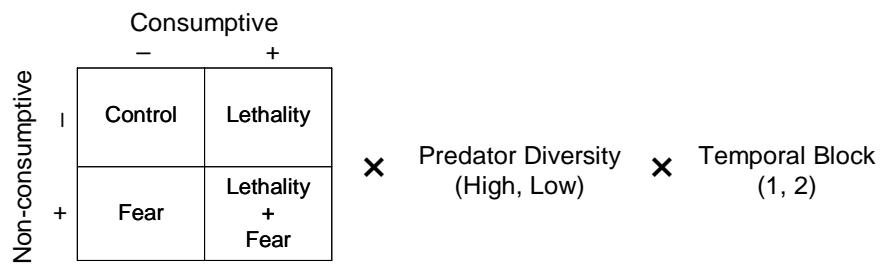
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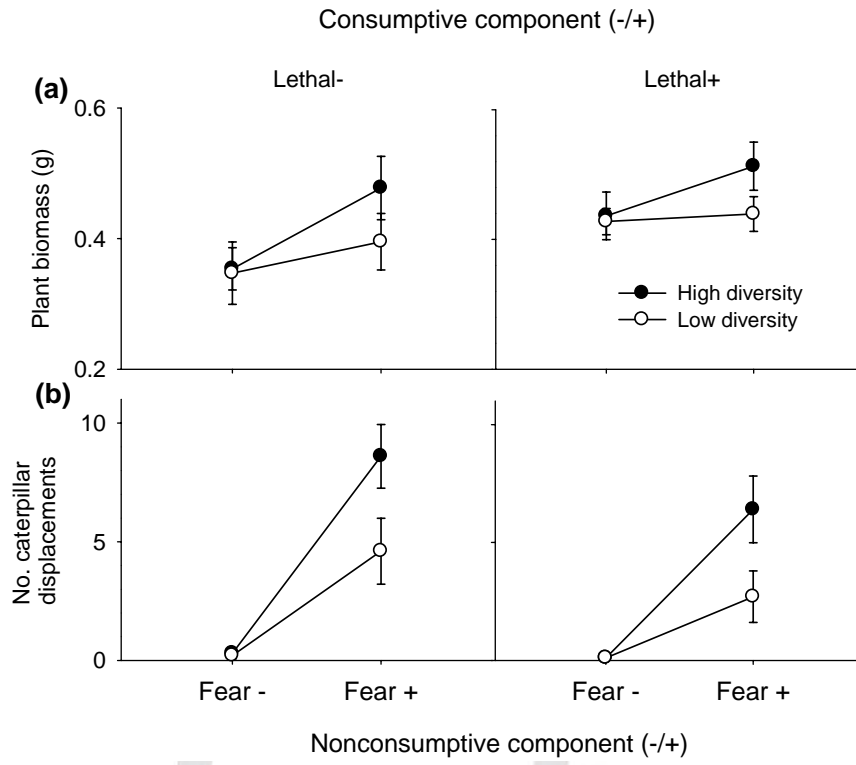
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FIGURES



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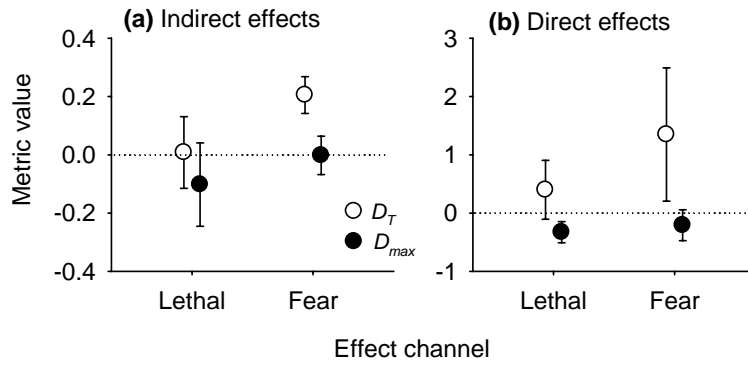
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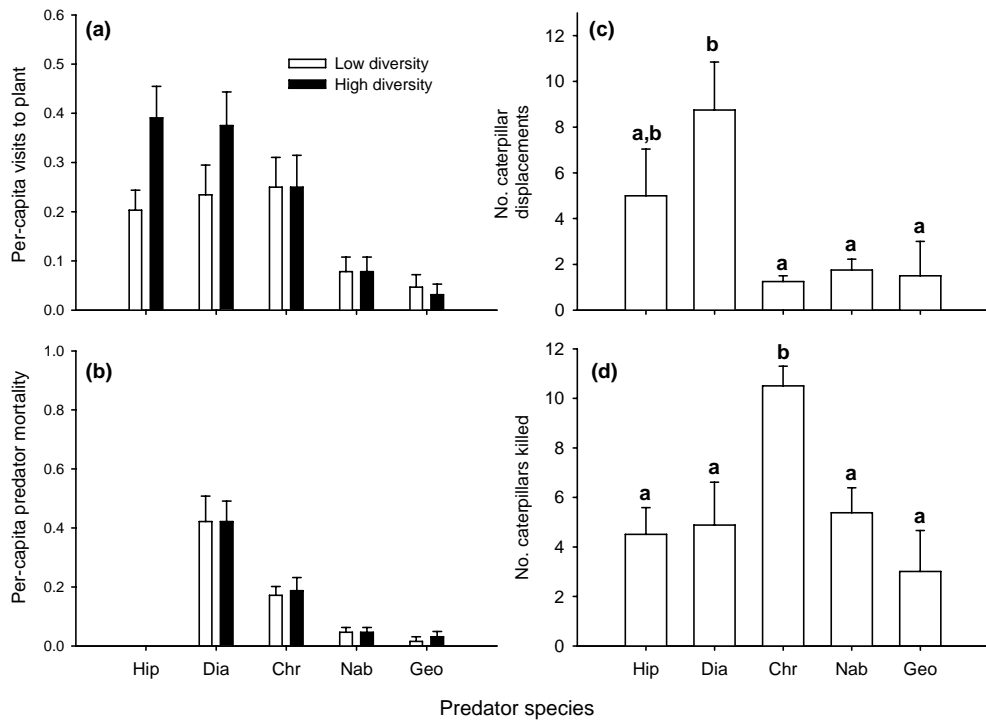
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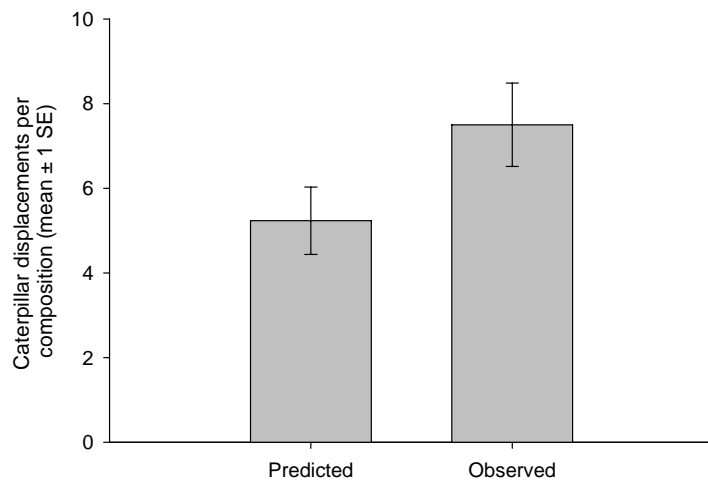
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725 Figure 5



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