1 **Intraguild aggressiveness between an alien and a native predatory mite**
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14 **Abstract**

15 The predatory mite *Amblydromalus limonicus*, non-native in Europe, can be used
16 legally in several European countries as greenhouse biocontrol agent against thrips
17 species, although this species is also able to feed on whiteflies and gall mites. The first
18 record of the unintended occurrence of *A. limonicus* in apple orchards in Europe comes
19 from Catalonia (Spain), where *A. limonicus* is well established in the native predatory
20 mite community since 2011. The dominant species in this community is *Amblyseius*
21 *andersoni*, which has a similar life-style as *A. limonicus* (large, aggressive predator with
22 broad diet range) making intraguild (IG) interactions between the two predators likely.
23 Thus, we tested the IG aggressiveness of native and alien female predators, when
24 provided with IG prey (larvae). Alien females of *A. limonicus* proved to be highly
25 aggressive IG predators against native larvae of *A. andersoni*, which were attacked
26 earlier and more frequently than alien larvae by the native predator. Nearly all attacks
27 by the alien predator resulted in the death of native IG prey, whereas about 10% of the
28 alien intraguild prey escaped the attacks of the native predator. Additionally, native IG
29 prey is smaller than alien prey, which should facilitate the overwhelming by the alien
30 predator. We argue that the strong aggressive intraguild behavior of *A. limonicus* is
31 contributing to its establishment success in the native predatory mite community.
32
33 **Keywords**: Biological control, *Amblydromalus limonicus*, *Amblyseius andersoni*,
34 intraguild predation, invasive species, Phytoseiidae

Introduction

Life-history traits, habitat and diet range of alien species are commonly used to predict their establishment opportunities in novel environments (Kolar and Lodge 2001; Colautti *et al.* 2006; Hayes and Barry 2008), whereas behavioral traits have been seldom considered (Chapple *et al.* 2011). Behavior, however, mediates how an alien species interact with novel resources and native species and should therefore play a pivotal role in the establishment opportunities of alien species (Holway and Suarez 1999; Chapple *et al.* 2011). A characteristic feature of successful established alien species is their highly aggressive behavior against native species (Chapple *et al.* 2011) resulting in the superiority of alien species in competitive interactions such as resource competition [alien Argentine ant *Linepithema humile* Mayr versus native tyrant ant *Iridomyrmex bicknelli* Emery (Rowles and O'Dowd 2007; Carpintero and Reyes-López 2008)], shelter competition [alien crayfish *Pacifastacus leniusculus* Dana versus native crayfish *Cambaroides japonicus* (De Haan) (Usio *et al.* 2001)], and nest site competition [alien European starling *Sturnus vulgaris* Linnaeus versus native house wrens *Troglodytes aedon* (Vieillot) (Weitzel 1988)].

When an alien predator encounters a native predator guild sharing similar prey resources, intraguild (IG) aggressiveness among the invader and its native opponents is a frequent observed event. The degree of IG aggressiveness strongly influences not only the outcome of resource competition, but also the strength and direction of intraguild predation (IGP) (Polis *et al.* 1989; Snyder and Evans 2006; Wang *et al.* 2013). For example, the Asian ladybeetle *Harmonia axyridis* Pallas, initially used as alien biological control agent control agent against greenhouse aphids in France, has immigrated and established in native European ladybeetle communities (Slogett 2012). The alien ladybeetle exhibited high IG aggressiveness against the native ladybeetles *Coccinella septempuncata* (Linnaeus) and *Adalia bipunctata* (Linnaeus). Therefore, *H. axyridis* was also superior in IGP, which is assumed a major cause for the successful establishment of *H. axyridis* in European ladybeetle communities (Raak-van den Berg *et al.* 2012).

The plant-inhabiting predatory mite *Amblydromalus limonicus* (Garman and McGregor) (Acari: Phytoseiidae), alien in Europe, is used in some European countries such as Belgium, France, Germany, The Netherlands, Poland and Austria, as natural enemy against greenhouse thrips species (Garman and McGregor 1956; Moraes *et al.* 1994; Chant and McMurtry 2005; Knapp *et al.* 2013). In 2011, the alien predator was detected for the first time on apple trees in Catalonia (Spain) (Escudero-Colomar and Chorąży 2012), where the commercial use of *A. limonicus* as biocontrol agent is not permitted. In this region the native predatory mite guild in apple orchards frequently consists of the species *Amblyseius andersoni* (Chant), *Neoseiulus californicus* McGregor and *Euseius stipulatus* (Athias-Henriot) (Acari: Phytoseiidae) sharing herbivorous mites, small insects and pollen as food resource (Costa-Comelles et al. 1986, Costa-Comelles et al. 1990, Avilla et al. 1993). These native predators provide an important ecosystem service by the natural control of pest species such as spider mites (*Tetranychus urticae* Koch, *T. turkestani* Ugarov y Nikolski, *Panonychus ulmi* (Koch)) (Costa-Comelles et al. 1994,) and gall mites (*Aculus schlechtendali* (Nalepa)) (Duso C and Pasini M 2003). Although all three species are able to use a broad range of food items allowing development, reproduction and survival, their different feeding preferences result in resource partitioning and reduce intraguild aggression among them. *Neoseiulus californicus* is a selective predator of spider mites producing dense webbing, which can also serve as shelter against IG predators. Euseius *stipulatus* is a pollen-

feeding generalist predator, whereas *A. andersoni* is a generalist predator, feeding and reproducing on a wide range of animal and non-animal food without specific preferences (McMurtry *et al.* 2013).The numerical dominant species in this guild on apple trees is *A. andersoni*, a large, aggressive predator (Walzer and Schausberger 2011a, b, 2013), which is responsible for the successful suppression of the spider mite *Panonychus ulmi* (Koch) (Vilajeliu et al, 1994). The now established alien predator *A. limonicus*, however, has a very similar life-style as the native predator *A. andersoni* (McMurtry *et al.* 2013). Thus, the two predator species are currently sharing both space and prey increasing the likelihood of aggressive IG encounters. Consequently, the objective of this study is to evaluate the IG aggressiveness potential between them. These data should provide first indications, whether the native or alien predator is superior in IGP over the other.

Material and methods

Mite cultures
The predatory mites were collected in September 2015 from apple leaves of organically managed orchards located at the Mas Badia Experimental Station, in La Tallada d'Emporda (42.0541°N, 3.0614°E), near Girona, Spain. About 100 specimens of *Amblydromalus limonicus* and *Amblyseius andersoni* were used to initiate lab populations, which were reared on separate arenas consisting of plastic tiles (13 cm x 13 cm) resting on water-saturated foam cubes (14 cm x 14 cm x 3.5 cm) in plastic boxes (20 cm x 20 cm x 4 cm) half-filled with water. The edges of the arenas were covered with filter paper strips. Stripes of cloth of 1 cm width were placed on the filter paper in such a way that they had in direct contact with the water of the plastic box to keep the filter paper moisturized. A barrier of fruit tree grease (Vitax Ltd, Leicestershire, UK) was placed around the complete perimeter of the arena. Consequently, the mites were provided with access to water without a risk of escaping from the arena. Small, transparent plastic pieces and cotton wool threads were distributed on the surface of the arena to provide shelter and egg deposition sites for the predatory mites. The predatory mites were fed with a mix of stages of *T. urticae* and *Typha latifolia* pollen ad libitum three times per week. Rearings of *A. limonicus* and *A. andersoni* were kept in climatic chambers at 25°C±1°C, 70±10% RH and 16:8 L:D (Light:Dark).

Experimental units
The experiment was conducted using lockable cages consisting of acrylic plates (80 x 35 x 3 mm) with a 15 mm diameter hole. Each hole was closed in one side with a fine mesh screen at the bottom, which provided mites with adequate ventilation. The other side of the cage was covered with a microscope slide secured with rubber bands (Schausberger 1997). Cages were kept in a climatic chamber SANYO at 25°C ± 1°C, 70 ± 10% RH and a photoperiod of 16:8 L:D (Light:Dark).

IG predator and prey behavior
IGP is a common interaction among phytoseiid mites, which is asymmetric with respect to size. Small/younger juveniles are usually preyed upon by larger/older juveniles and/or adult females, whereas adult females and eggs are relatively invulnerable to IGP (Walzer and Schausberger 2011a). Consequently, large females and small larvae were used as IG predators and IG prey, respectively.
Single IG predator females of *A. limonicus* and *A. andersoni* were isolated and starved for 24 hours in the lockable cages. Only females that laid eggs during this period were

135   used in the experiments. A single IG prey was placed in the cage together with a single
136   IG predator. 67 to 71 replicates per treatment were conducted. The behavior of IGP
137   predator and IGP prey was observed and recorded every 10 minutes for 6 hours (360
138   minutes in total) using a chronometer Fisherbrand™ (Fisher Scientific SL, Madrid) to
139   evaluate the following parameters: (1) attack time of the IG predator, (2) the attack
140   success (if the attack results in the death of the prey or not), (3) activity of the IG
141   predator and IG prey (moving or not).
142
143   *IG predator and prey body sizes*
144   All females used in the experiment were measured and 50 larvae of each species were
145   randomly caught from the rearing boxes. Females and larvae were mounted on
146   microscopic slides using Heinze polyvinyl alcohol (PVA Heinze) (Heinze 1952; Colloff
147   2009). The distances between the bases of eight and six setae, i.e. j3, s4, S4, Z5 and j3,
148   s4 and Z5 at both sides of the dorsal shield were measured for IG predator females and
149   IG prey larvae of both predatory mites, respectively (Croft *et al.* 1999) (Fig. 1). The
150   calculated perimeter is a suitable approximation to body size, because it integrates both
151   body length and width and corresponds to 85- 90% of the total perimeter of the dorsal
152   shield.   The pictures of the figures were taken using a Leica DMRXA Direct
153   microscope equiped with a digital camera Pointgrey Flea3 of 12MPx. The
154   measurements were done using the Nikon Eclipse 50i microscpe using the software
155   NIS-D Elements 3.20 (Nikon Corporation, Japan).
156
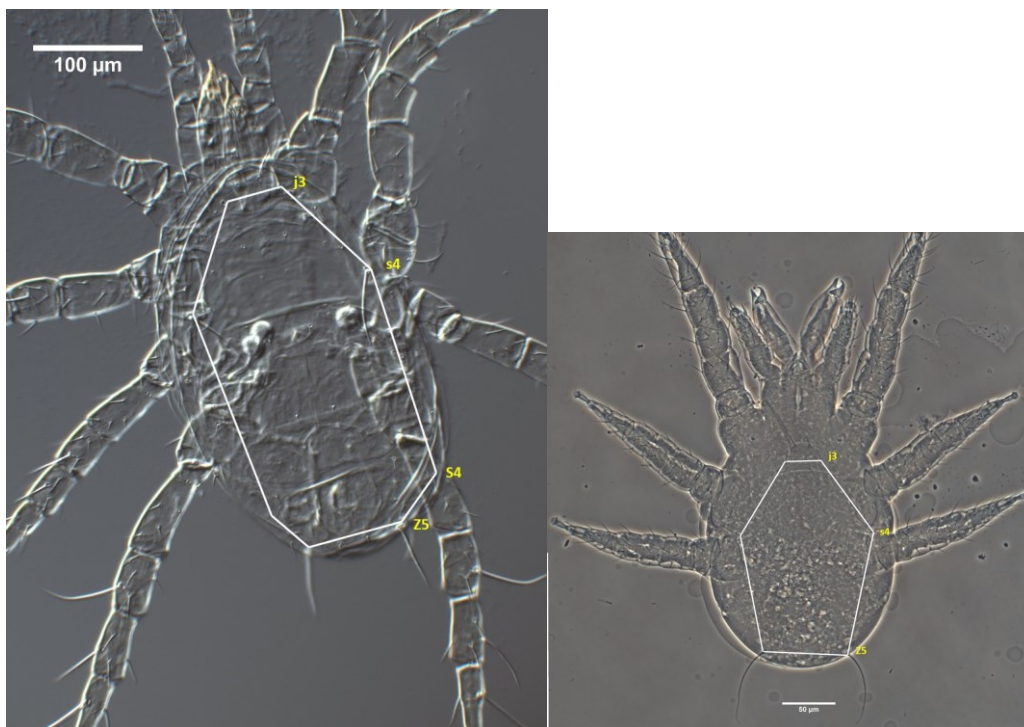
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159   **Fig 1** Body size measurements a) females (*A. limonicus*) and b) larvae (*A. andersoni*).
160   The distances between the bases of eight (j3-j3, j3-s4, s4-S4, S4-Z5, Z5-Z5) and six (j3-
161   j3, j3-s4, s4-Z5, Z5-Z5) setae on the dorsal shield were measured for the females (IG
162   predators) and larvae (IG prey), respectively. The calculated perimeter of the dorsal
163   shields was used as proxy for body size
164
165
166

167 *Data analysis*
168 SPSS 21.0.1 (SPSS Inc., 2012) was used for all statistical analyses. Kaplan-Meier
169 analysis with successive Breslow tests was used to compare the IG aggressiveness
170 functions of the predators (combination of cumulative attacks and attack time) (Bewick
171 et al. 2004). Generalized linear models (GLMs) with chi-square statistics (Wald-tests)
172 were used to analyze the effects of IG predator species on the predator activity, prey
173 activity (moving or not), IGP success (prey killed or not), IG prey survival (yes/no)
174 (binomial distribution, logit link function). Additionally, the differences between the
175 two species with respect to the predator body size (females), the prey body size (larvae)
176 and the IG predator/prey body size ratio were analyzed using GLM's (normal
177 distribution, identity link function).
178
179
180 **Results**
181
182 *IG predator and prey behavior*
183 The IG aggressiveness functions of the IG predators differed significantly between the
184 two predator species (Kaplan-Meier analysis, Breslow tests: $\chi^2_1 = 10.834$, p = 0.001).
185 The alien IG predator *A. limonicus* was more aggressive than the native predator *A.*
186 *andersoni*, which was reflected in earlier attacks (mean attack times of *A. limonicus*:
187 48.31 min ± 5.55 SE versus *A. andersoni*: 103.78 ± 5.55) and more frequent attacks on
188 IG prey larvae (Fig. 2).
189   Both IG predator ($\chi^2_1 = 0.142$, p = 0.706) and prey activity ($\chi^2_1 = 0.723$, p =
190 0.395) were not influenced by species affiliation (Fig. 3). Contrary, IGP success ($\chi^2_1 =$
191 4.569, p = 0.033) of the alien predator was higher than for the native predator. First,
192 almost all alien IG predators were observed to attack the IG prey within 360 min in
193 contrast to the native IG predators (alien *A. limonicus*: 69 out of 71; native *A. andersoni*:
194 58 out of 67). Second, nearly all attacked native IG prey larvae were killed by the alien
195 predator females, whereas about 10% of the alien IG prey larvae survived the attacks of
196 the native IG predator females. Thus, the survival probabilities of the native IG prey
197 were negligible in contrast to the alien IG prey ($\chi^2_1 = 9.500$, p = 0.002) (Fig. 3).
198
199 *IG predator and prey body sizes*
200 The IG predator females of *A. limonicus* and *A. andersoni* were similarly sized ($\chi^2_1 =$
201 0.402, p = 0.526); however, IG larval prey sizes differed between the alien and native
202 species ($\chi^2_1 = 13.343$, p < 0.001). The alien IG prey was larger than the native IG prey
203 (Fig. 3). Consequently, also the IG predator/prey body size ratio of the alien predator
204 and native prey was larger than the corresponding data of the native predator and alien
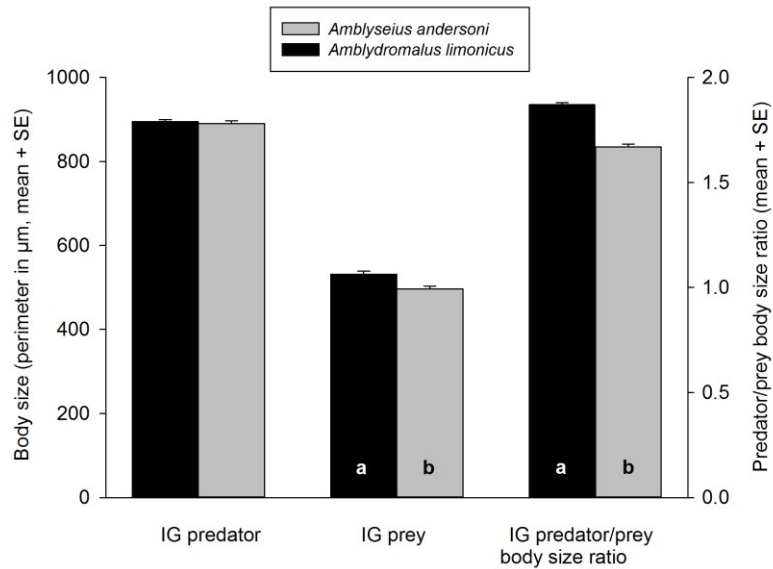205 prey (Fig. 4).
206
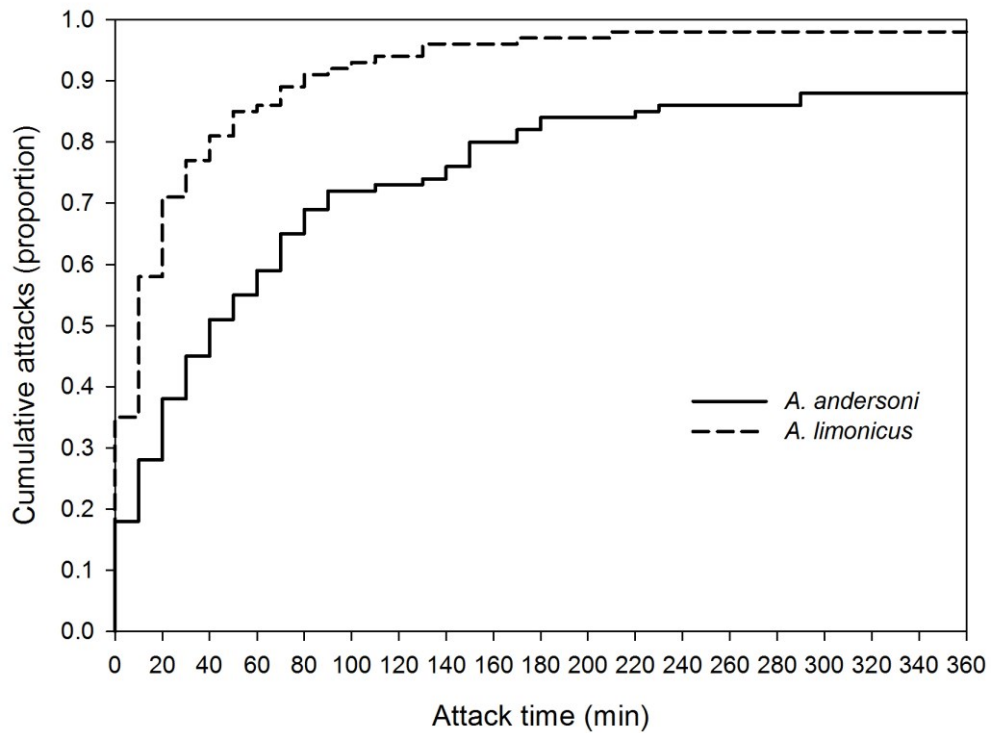
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209 **Fig 2** Attack functions (combination of the proportion of attacking predators and the
210 time elapsed until an attack occurred) of singly caged native IG predators females of *A.*
211 *limonicus* (black line) and *A. andersoni* (grey line), when offered single IG prey larvae
212 over 360 min
213
214
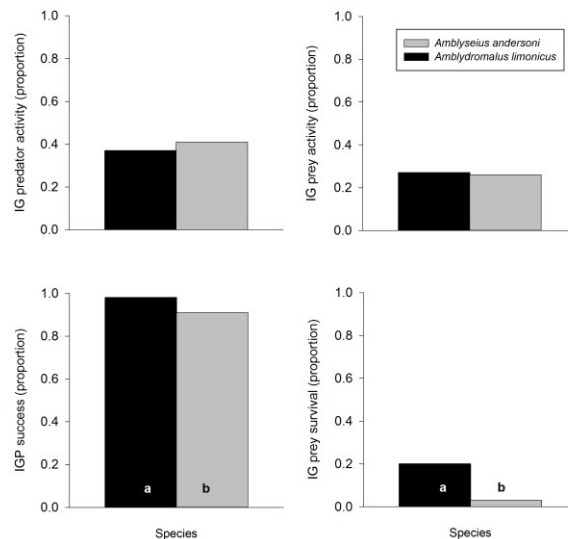
215
216 **Fig 3** IG predator activity (A), IG prey activity (B), IG predation success (C) and IG
217 prey survival (D) of *A. limonicus* (black bars) and *A. andersoni* (grey bars), when acting
218 as IG predator (female) or IG prey (larva) over 360 min. Different lower-case indicate
219 significant effects between the species based on pairwise LSD-tests

7

220
Fig 4 Body size of *A. limonicus* (black bars) and *A. andersoni* (grey bars) as IG predator
(females) or IG prey (larvae), and the predator/prey body size ratios. Different lower-
case indicate significant effects between the species based on pairwise LSD-tests

Discussion

Alien females of *A. limonicus* proved to be highly aggressive IG predators against
native larvae of *A. andersoni*, which were attacked earlier and more frequently than
alien IG prey by the native predators. Additionally, nearly all attacks by the alien
predator resulted in the death of native IG prey, whereas about 20% of the alien IG prey
survived in the presence of native predators.

    Both predator and prey traits may explain the proximate reasons for these

234 results. A specific feature of *A. limonicus* females, not known for *A. andersoni* females,
235 is their capability to overwhelm and kill 2nd instar thrips larvae (Van Houten *et al.*
236 1993), which are about double as large as the predator (Schuster and Pritchard 1963;
237 Van Houten *et al.* 1993). In concert with our results, these findings indicate that alien *A.*
238 *limonicus* females have a higher tendency to attack heterospecific individuals than
239 native *A. andersoni* females. Second, the IG predators are similarly sized, but not IG
240 prey. The native IG larval prey is smaller than the alien IG prey, which facilitates the
241 overwhelming of the former by the alien predator. Additionally, the alien larvae are
242 obligatory feeders (Walzer, personal observation), whereas native larvae are facultative
243 feeders (Schausberger and Croft 1999a). Thus, alien *A. limonicus* larvae might be more
244 successful in defending themselves against IG predator attacks than the native *A.*
245 *andersoni* larvae.
246   High interspecific aggressiveness is often correlated with foraging behavior (Sih
247 *et al.* 2004), whereas more aggressive species are strong food competitors or superior
248 IG predators compared to less aggressive species (Schausberger and Croft 1999b,
249 2000a; Drescher *et al.* 2011). Dominance in IGP offers three adaptive benefits for the
250 alien *A. limonicus*: (1) the killing of juvenile native IG prey reduces the number of
251 potential adult IG predators and consequently increases the survival probabilities of
252 alien offspring; (2) the consumption of native predatory mites probably offers an
253 additional high-quality food resource for the generalist predator in the novel habitat
254 (Schausberger and Croft 2000b); and (3) the decimation of a native food competitor
255 alleviates the access to extraguild prey.
256   We assume that the implications of the high interspecific aggressiveness of *A.*
257 *limonicus* are strongly dependent on the context. For example, acting as biocontrol
258 agent against greenhouse thrips species, the aggressive predation behavior of *A.*
259 *limonicus* observed in the present study should have benefits, because *A. limonicus* can
260 kill a higher proportion and larger individuals of the target pest than other phytoseiid
261 mites (Van Houten *et al.* 1995). However, when acting as alien IG predator in the case
262 of escape from greenhouses to novel environments, high IG aggressiveness may allow
263 *A. limonicus* to become established in native predatory mite communities. Additionally,
264 the capacity for population increase of *A. limonicus* is among the highest values
265 reported for phytoseiid mites (Sabelis 1985; Steiner *et al.* 2003) and clearly exceeds the
266 corresponding values of *A. andersoni* (Lorenzon *et al.* 2012). Nonetheless, so far the
267 alien predator *A. limonicus* was not able to eliminate the native predator *A. andersoni* on
268 apple trees in Catalonia. In contrast, alien and native predatory mites still co-exist since
269 the detection of *A. limonicus* in 2011. Five non-mutually exclusive causes may be put
270 forward to explain these findings. First, the availability of alternative food resources and
271 high structural habitat complexity may lower the potential detrimental effects of IGP on
272 the native species, as it was demonstrated in two other phytoseiid mite species
273 (Pozzebon *et al.* 2015). Second, strong egg cannibalism of the alien predator species is a
274 well-documented phenomenon, which seems not dependent on the quality of available
275 food resources (Vangansbeke *et al.* 2014). Such a behavior should reduce the capacity
276 for population increase, so that *A. limonicus* is not able to build up sufficient high
277 population densities to outcompete native species. Third, the local climatic conditions
278 may negatively influence the population growth and dispersal abilities of the alien
279 predator. The relative humidity can be very low during the vegetation period in the
280 apple producing area of the extreme NE of Catalonia (Ninyerola *et al.* 2001).
281 *Amblydromalus limonicus* is a species with high moisture requirements, being a
282 determining factor for the hatching success of their larvae (Bakker *et al.* 1993; Van
283 Houten *et al.* 1995). For example, in contrast to *A. andersoni,* the densities of *A.*

284 *limonicus* were very low on apple trees in the dry-hot summer 2012 in Catalonia
285 (Escudero-Colomar, personal observation), which could be caused by high egg
286 mortality of the alien predator. In California, native *A. limonicus* populations were
287 found only along the shore, but not in the drier inland regions (McMurtry and Scriven
288 1965; McMurtry *et al.* 1971). Along the same line, alien *A. limonicus* populations were
289 only sampled in high densities near to the seacoast in Catalonia (Chorąży *et al.* 2016).
290 Thus, the sensitivity of *A. limonicus* against dry-hot conditions may restrict its dispersal
291 potential to the coastal areas in Mediterranean countries. Fourth, the leaf morphology of
292 plants shared by *A. limonicus* and the native predatory mites may affect the strength of
293 their IG interactions (Seelmann *et al.* 2007). The alien predator *A. limonicus* is known to
294 avoid pubescent leaves (Lee and Zhang 2018), whereas *A. andersoni* is often found on
295 pubescent leaves (Overmeer and Van Zon 1984; Duso and Pasini 2003). Such
296 differential habitat selection should reduce encounters between the native and alien
297 predator. Finally, our results suggest that potential IG interactions between the alien
298 predator *A. limonicus* and the native predator *A. andersoni* could be mainly
299 unidirectional with *A. limonicus* as predator and *A. andersoni* as prey. Thus, the
300 selection pressure to cope with IG interactions should be lower on predator than on
301 prey, because it is less costly to miss a meal (in the case of the predator) as to be one (in
302 the case of the prey). Therefore, the native predator *A. andersoni* may have evolved
303 adaptive anti-predator strategies to cope with the presence of the aggressive alien IG
304 predator. A common behavior in predatory mites is the spatiotemporal avoidance of
305 leaves occupied by high-risk IG predators (Walzer *et al.* 2006; Walzer *et al.* 2009),
306 which is often optimized by learning (Walzer and Schausberger 2011a, 2012). It
307 remains an open question, whether experienced *A. andersoni* females respond in a
308 similar manner to alien IG predator cues.
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