

Invasion success in communities with reciprocal intraguild predation depends on the stage structure of the resident population

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The probability of individuals being targeted as prey often decreases as they grow in size. Such size-dependent predation risk is very common in systems with intraguild predation (IGP), i.e. when predatory species interact through predation and competition. Theory on IGP predicts that community composition depends on productivity. When recently testing this prediction using a terrestrial experimental system consisting of two phytoseiid mite species, *Iphiseius degenerans* as the IG-predator and *Neoseiulus cucumeris* as the IG-prey, and pollen (*Typha latifolia*) as the shared resource, we could not find the predicted community shift. Instead, we observed that IG-prey excluded IG-predators when the initial IG-prey/IG-predator ratio was high, whereas the opposite held when the initial ratio was low, which is also not predicted by theory. We therefore hypothesized that the existence of vulnerable and invulnerable stages in the two populations could be an important driver of the community composition. To test this, we first demonstrate that IG-prey adults indeed attacked IG-predator juveniles in the presence of the shared resource. Second, we show that the invasion capacity of IG-predators at high productivity levels indeed depended on the structure of resident IG-prey populations. Third, we further confirmed our hypothesis by mimicking successive invasion events of IG-predators into an established population of IG-prey at high productivity levels, which consistently failed. Our results show that the interplay between stage structure of populations and reciprocal intraguild predation is decisive at determining the species composition of communities with intraguild predation.

Intraguild predation (IGP hereafter, Polis et al. 1989, Polis and Holt 1992) is a predator–prey interaction among potential competitors (Holt and Huxel 2008) where the intensity of predation is usually highly dependent on the presence of the shared resource and on the difference in size between the competitors. Indeed, several intraguild predators (IG-predators, hereafter) tend to reduce attacks on the intraguild prey (IG-prey, hereafter) when other food sources are present (Hatherly et al. 2005, Onzo et al. 2005, Zannou et al. 2005, Çakmak et al. 2006), and IG-predators tend to prey preferentially on young, small stages of IG-prey (Polis et al. 1989, Magalhães et al. 2005a, Rudolf and Armstrong 2008). Theoretical models of IGP usually consider three species (the shared resource, the IG-prey and the IG-predator). Models of IGP that consider individuals within a population to be identical predict different stable communities depending on environmental productivity: coexistence of resource and IG-prey is predicted at low productivity levels; coexistence of resource, IG-prey, and IG-predator is predicted at intermediate productivity levels; and coexistence of resource and IG-predator is predicted at high productivity levels (Polis and Holt 1992, Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001). All models predict that the region of coexistence of the three species is restricted to a narrow range of productivity,

which profoundly contradicts the ubiquity of IGP observed in natural communities (Polis et al. 1989, Rosenheim et al. 1995, Polis and Winemiller 1996, Holyoak and Sachdev 1998, Arim and Marquet 2004).

A scenario that better complies with what is observed in nature is that of populations with individuals of different sizes (stages) interacting with each other. In the course of their development, animals increase in size and the probability to fall prey to larger individuals consequently decreases. Such ontogeny-dependent predation risk can occur when contestants are of the same species (i.e. cannibalism – Fox 1975, Polis et al. 1989) or of different species. In the latter case, the predator can belong to a higher trophic level (i.e. predation – Byström et al. 2003, Nomikou et al. 2004) or to a lower trophic level (e.g. role reversals in predator–prey systems – Saito 1986, Polis et al. 1989, Palomares and Caro 1999, Janssen et al. 2002, Magalhães et al. 2005a). Alternatively, the two interacting species can belong to the same trophic level, in which case they are involved in IGP. Stage (size) structure has been included in a few models of IGP, and different consequences for the coexistence of the whole community have been found. Mylius et al. (2001) included size (stage) structure in either the IG-prey or the IG-predator, but predictions did not vary much from those of models without size (stage)

structure, i.e. elimination of the intermediate species by the top species was more likely than coexistence. Rudolf (2007) incorporated stages in either the IG-prey or the IG-predator, which consumed smaller juvenile conspecifics. He found that cannibalism in the IG-predator significantly increased the region of coexistence of the three species. Furthermore, when cannibalism was high enough, it facilitated invasion of IG-prey at higher productivity levels, and IG-predators never drove IG-prey to extinction. van de Wolfshaar et al. (2006) studied a model with life-history omnivory, in which the IG-predators shifted their diet during ontogeny, acting only as competitors of the IG-prey as juveniles, and only as predators after reaching a given size. In this model, the likelihood for coexistence between IG-predators and IG-prey decreased drastically, and alternative states, with either IG-prey and resource or IG-predator and resource, appeared likely to occur. Such limitation for IG-predator and IG-prey to coexist was further empirically shown in invasion experiments carried out in lakes (Person et al. 2007) and aquaria (Schröder et al. 2009).

In systems with IGP, size (stage) structure in both IG-prey and IG-predator populations can result in ontogenetic role-reversals with vulnerable and invulnerable stages of IG-predator and IG-prey acting as prey and predator, respectively. Therefore, in reciprocal intraguild predation (RIGP hereafter) the terms intraguild prey and intraguild predator become somewhat confusing. Here, we refer to the species that is the superior competitor but a relatively weak intraguild predator as the intraguild prey, to retain the terminology of models without reciprocal intraguild predation, in which the intraguild prey is assumed the superior competitor. Reciprocal intraguild predation is known to be common in many systems of true predators (Polis et al. 1989, Wissinger 1992, Woodward and Hildrew 2002, Omori et al. 2006), but less so among herbivores involved in intraguild predation (Camus et al. 2008). Theoretical models that incorporate mutual predation in systems with IGP are scarce. All of them show that the inclusion of mutual predation results in a dramatic reduction of the parameter space where three-species coexistence is possible (HilleRisLambers and Dieckmann 2003, HilleRisLambers and de Roos 2005, HilleRisLambers et al. 2005). Instead, models predict alternative stable states where either one or the other species would persist alone with the resource at intermediate to high productivity levels.

We recently tested for the existence of regions of coexistence of IG-prey and IG-predators, depending on the level of environmental productivity, which was determined by the amount of available food to IG-prey and IG-predators. Despite our experimental system (Material and methods) fulfilling the prerequisites for coexistence of all three species (i.e. the IG-prey was superior at exploitative competition for the shared resource, and the IG-predator preyed on both the IG-prey and the shared resource – Montserrat et al. 2008), the results did not support model predictions: the IG-prey sometimes excluded the IG-predator at high resource levels and the IG-predator excluded the IG-prey at resource levels at which it could not persist on the resource alone. Although we could not find a community shift as resource levels were increased, we observed that the IG-prey excluded the IG-predator when the initial IG-prey/IG-predator ratio was high, whereas the opposite held when the initial ratio was

low. We therefore hypothesized that the existence of vulnerable and invulnerable stages in the two populations could be an important driver of species composition in our system. More specifically, we hypothesized that reciprocal predation of IG-prey on vulnerable IG-predators could hamper invasion of the IG-predator population into populations of IG-prey, even when coexistence of the IG-predator with the shared resource would be possible. This would occur specifically at intermediate and high productivity levels, when densities of reciprocal IG-prey are high relative to those of invading IG-predators. These high IG-prey densities would result in high predation rates on the IG-predator, even with the per capita reciprocal predation of the IG-prey on juvenile IG-predators being low. Hence, RIGP would result in mutual exclusion, as predicted in HilleRisLambers and Dieckmann (2003), HilleRisLambers and de Roos (2005), and HilleRisLambers et al. (2005).

Here, we aimed at testing the hypothesis that the interplay between initial stage structure of populations and reciprocal intraguild predation is decisive at determining the species composition of communities with IGP. Specifically, we tested one of the predictions from models with RIGP (HilleRisLambers et al. 2005), which is that the presence of reciprocal IG-prey stages hampers invasion of IG-predators into a population of IG-prey, even at levels of productivity where classical IGP theory predicts either coexistence or exclusion of IG-prey by IG-predators. We chose to carry out the experiments at high resource levels because 1) it is the resource level at which theory predicts that IG-predators will exclude IG-prey independently of initial conditions (Holt and Polis 1997, Mylius et al. 2001), 2) it is the resource level at which the IG-predator (*I. degenerans*) persisted when alone (Montserrat et al. 2008). Therefore, high resource levels reflect the conditions under which the effect of stage structure on invasion can be more readily detected. We first carried out laboratory experiments to determine whether IG-prey adults indeed attacked IG-predator juveniles, even in the presence of the shared resource. Second, we manipulated the structure of resident IG-prey populations to evaluate the effect of stage-structure on the invasion capacity of IG-predators at high productivity levels. Third, we mimicked successive invasion events of IG-predators into an established population of IG-prey at high resource levels, to account for failures of establishment due to stochastic events.

Material and methods

The experimental system consisted of two phytoseiid mite species, *Iphiseius degenerans* (the IG-predator) and *Neoseiulus cucumeris* (the IG-prey), and pollen (*Typha latifolia*) as the shared resource. Phytoseiid mites commonly engage in intraguild predation (Hatherly et al. 2005, Montserrat et al. 2006, Seelmann et al. 2007, Ferreira et al. 2008), and many species can feed and reproduce on pollen (Ferragut et al. 1987, McMurtry and Croft 1997, van Rijn and Tanigoshi 1999). Phytoseiid mites have five developmental stages: egg, larva, protonymph, deutonymph and adult. In our system, adults and eggs of the IG-predator and the IG-prey are largely invulnerable to predation by both co- and heterospecifics (DeCourcy-Williams et al. 2004, Montserrat et al. 2007). The IG-prey,

N. cucumeris, is superior to the IG-predator, *I. degenerans*, at exploitative competition for the shared resource (Montserrat et al. 2008). Predation of IG-predator on IG-prey juveniles is high both in the absence and in the presence of the shared prey (Montserrat et al. 2008). The occurrence of reciprocal IGP of IG-prey on vulnerable IG-predators was tested here. Cannibalism of adult IG-prey on juveniles is rare, both in absence and in the presence of shared prey (De Courcy-Williams et al. 2004, Montserrat et al. 2008). Cannibalism of IG-predator adults and juveniles is high in the absence of shared prey (pollen) or intraguild prey, but rare in its presence (Montserrat et al. 2006, this study). The egg-to-egg period in the two species is 7–8 days (van Rijn and Tanigoshi 1999). Stage-dependent trophic and competitive interactions between IG-predator and IG-prey in the presence of the shared prey (pollen) are summarized in Figure 1.

Stock cultures

Iphiseius degenerans (the IG-predator) and *Neoseiulus cucumeris* (the IG-prey) were reared on plastic arenas placed on top of sponges in water-containing trays. The edges of the arenas were covered with tissue paper in contact with the water, thereby serving both as barrier and water source. *Iphiseius degenerans* was fed with birch pollen *Betula pubescens*, and *N. cucumeris* with cattail (*Typha* sp.) pollen. Both types of pollen were collected on the campus of the Univ. of Amsterdam. Male flowers were dried in a stove at 45°C for 24 h, then sieved (350 µm). The pollen was subsequently stored in a freezer (−10°C) until use. In the experiments, we used *Typha* pollen as the shared resource because it is a suitable food source for both mite species, whereas *N. cucumeris* does not oviposit when fed birch pollen (van Rijn and Tanigoshi 1999).

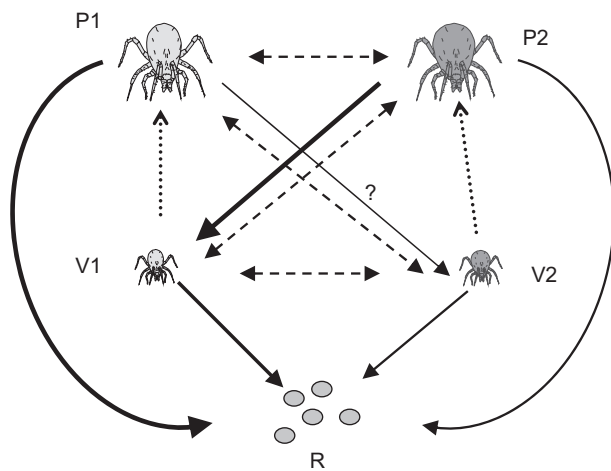


Figure 1. Stage/size dependent trophic and competitive interactions between the IG-prey *N. cucumeris* and the IG-predator *I. degenerans*. P1 are the invulnerable stages of the IG-prey, i.e. adults and eggs. P2 are the invulnerable stages of the IG-predator, i.e. eggs, adults and older juveniles. V1 are the vulnerable stages of IG-prey, i.e. all mobile juvenile stages. V2 are the vulnerable stages of IG-predator, i.e. larvae. The question mark above the trophic link between P1 and V2 indicates that predation of P1 on V2 was unknown before. R is the shared resource, i.e. pollen. Solid arrows indicate 'who eats whom' interactions, dashed arrows indicate indirect predator–predator (competition) interactions, and dotted lines indicate life-history transitions.

Reciprocal intraguild predation (RIGP)

Experiments were designed to determine whether reciprocal IGP occurred between the IG-prey (*N. cucumeris*) and the IG-predator (*I. degenerans*) in the presence and absence of the shared resource (pollen). Predation rates (averages ± SE) of the IG-predator on IG-prey juveniles in the absence and presence of the shared resource were determined in Montserrat et al. (2008) (11.6 ± 0.86 vs 13.7 ± 1.05 IG-prey juveniles per day, respectively). The experiment was carried out on plastic arenas (7.5×7.5 cm) similar to the arenas used for rearing. Either 30 protonymphs (three to four days old since egg deposition) or 30 larvae (two to three days since egg deposition) of the IG-predator were added to each arena, either with or without cattail pollen, which was supplied ad libitum. One gravid female of IG-prey (9–11 days old since egg deposition) was introduced onto the arena. After 24 h, the number of IG-predator juveniles eaten and the number of eggs laid by the IG-prey female were counted, they were removed from the arenas together with the remaining juveniles, and either 30 new IG-predator protonymphs or 30 IG-predator larvae were added to the arenas. Twenty four hours later, the number of eaten juveniles and eggs laid by females were counted again. Predatory mites suck out the body fluids of their prey and the empty or partially empty prey corpse remains. Therefore, eaten individuals can be easily recognized. A total of eight and ten replicates were done for the larvae and protonymph treatments, respectively. *Iphiseius degenerans*, the IG-predator, is a species that, in absence of other food, is extremely cannibalistic, to the point that cannibalism may drive its populations to extinction (Montserrat unpubl.). To assess mortality due to cannibalism or starvation, arenas with 30 IG-predator protonymphs or 30 IG-predator larvae without the IG-prey females, and with or without pollen, were used as control; Controls for oviposition rates consisted of arenas with one IG-prey female with pollen only. Because the first egg laid by females during the first 24 h of the experiment could still be produced from food ingested prior to the experiment, only data of the second day were analyzed to ensure that only the treatment effect was measured. The number of replicates ranged from eight to ten. The number of eaten/dead IG-predator protonymphs and number of eaten/dead IG-predator larvae (log transformed) were analysed with two separate two-factor ANOVA, with presence of the IG-prey female and presence of pollen as main factors. The number of eggs laid by the female predatory mites were analysed with a one-factor ANOVA, with type of diet as factor. Means were separated by the Tukey least-squares-difference (LSD) test.

Invasion of IG-predators in IG-prey populations

This experiment served to evaluate the effect of stage structure of the resident IG-prey population on invasion by the IG-predator at high productivity levels. We expected the IG-predator to be able to invade a resident population initially composed of only IG-prey juveniles, whereas invasion should be impossible into a resident population with adult female IG-prey, because recruitment of the IG-predator population would be hampered by predation of IG-prey on the vulnerable stages of the IG-predator. Given that the predation rate of adult stages of IG-prey on small and young stages

of IG-predators in the presence of the resource was low (Results), high numbers of adult IG-prey relative to that of IG-predators should be necessary to impede invasion.

Experiments were carried out on arenas similar to those described previously, but bigger (i.e. plastic arenas of 15×7.5 cm). Two sets of replicates were performed at the same time, one with a resident population consisting of both juveniles and adults, and another with a resident population of initially only juveniles. To gain time in the preparation of a resident IG-prey population close to equilibrium levels, we started with numbers (250–300 individuals per arena) and an age distribution ($27.5 \pm 2.6\%$ adult females; $18.1 \pm 1.5\%$ protonymphs, deutonymphs and males; $7.1 \pm 0.6\%$ larvae; and $47 \pm 2.4\%$ eggs) similar to those found in previous population dynamics experiments at high productivity levels, when numbers were at plateau levels (Montserrat et al. (2008) and unpublished data on population dynamics with only the IG-prey). Then we allowed these populations to settle for two weeks. All individuals were then counted, and while the structure of the population of one of the replicates was left intact, the adult females were replaced by the same number of juveniles in the other replicate. Subsequently, three gravid IG-predator females were introduced as invaders onto the arenas. The number and stages (adult females, juveniles, larvae, eggs) of the two species were counted twice a week until one of the two populations went extinct. Eaten corpses of both IG-predator and IG-prey juveniles (it is not possible to distinguish between species when bodies have been preyed on) were counted and removed from the arenas. During the whole process, arenas were provided twice a week with 4.8×10^{-3} g of *Typha* pollen, the highest supply rate used in the experiments of Montserrat et al. (2008), after removal of old pollen with a wet brush, to mimic chemostat dynamics at the resource level (Mylius et al. 2001). The experiment was repeated three times. Numbers of IG-predator and IG-prey through time were analysed using generalized linear mixed models (SAS, Proc GLIMMIX), which allow for non-linearity and heteroscedasticity in data. The analysis was done assuming a binomial error structure of data and a logit relationship (i.e. link function) between the mean of the response variable (numbers of IG-predator or numbers of IG-prey) and the linear combination of the two explanatory variables (initial condition, i.e. with or without stage structure of IG-prey, and 'time' as the random variable). Only data points with three replicates still running were included in the analysis, i.e. eight levels for the random variable 'time'.

Another series of invasion experiments was carried out on arenas similar to those described above. These experiments were designed to mimic successive invasion events of IG-predators into an established population of IG-prey at high resource levels (4.8×10^{-3} g), to account for failures of establishment due to stochastic events. IG-prey populations were started with 30 females and were allowed to establish and reach equilibrium densities for three weeks prior to the introduction of IG-predators. Three females of the IG-predator were then introduced, and numbers and stages of the two species were counted twice per week. When IG-predators failed to establish, three more females were introduced.

Results

Reciprocal intraguild predation (RIGP)

The presence of pollen and of IG-prey females affected the mortality rate of IG-predator larvae (main factors: $F_{1,34} = 16.10$, $p = 0.0003$, and $F_{1,34} = 65.52$, $p = < 0.0001$, respectively). Mortality of IG-predator larvae in the absence of IG-prey females was negligible, and female IG-prey predation rates on IG-predator larvae was four times higher in the absence of pollen than in its presence (Interaction term: $F_{1,34} = 16.45$, $p = 0.0003$; Fig. 2a). Mortality rates of IG-predator protonymphs were also affected by the presence of pollen ($F_{1,36} = 140.89$, $p < 0.0001$), but not by the presence of females of the IG-prey (main factor: $F_{1,36} = 3.07$, $p = 0.09$; interaction term: $F_{1,36} = 0.46$, $p = 0.50$). The presence of pollen reduced protonymph mortality by more than six-fold (Fig. 2b, compare first and third bars with second and fourth bars). As mortality rates of IG-predator protonymphs were not influenced by the presence of the female IG-prey (compare first bar with third bar, and second bar with fourth bar, in Fig. 2b) our results indicate that IG-prey females only killed and preyed on the most vulnerable stage, i.e. IG-predator larvae. This suggests that cannibalism, scavenging, or starvation rather than reciprocal intraguild predation was the most probable cause of mortality of IG-predator protonymphs. Cannibalism, scavenging and starvation can be excluded as mortality factors in larvae of the IG-predator because survival in the absence of female IG-prey was high. Indeed, larvae of *I. degenerans*, the IG-predator, tend to remain still and close to the hatching site, and they do not eat until moulting to the protonymph stage (Montserrat and Janssen unpubl.), which occurs ca 24 h after egg-hatching (van Rijn and Tanigoshi 1999).

Oviposition rates of IG-prey were influenced by the presence of pollen and by the stage of the IG-predator that was present in the arena ($F_{4,37} = 12.78$, $p < 0.0001$). The highest oviposition rate was obtained when IG-prey were provided with only pollen or with pollen and IG-predator larvae (Fig. 2c, first and second bar). Intermediate oviposition rates were reached when IG-prey was supplied with IG-predator larvae, and when they could consume IG-predator protonymphs and pollen (Fig. 2c, third and fourth bar). The lowest oviposition rate was observed when IG-prey had access to IG-predator protonymphs only (Fig. 2c, fifth bar).

Invasion of IG-predators in IG-prey populations

Numbers of IG-predator and IG-prey differed through time depending on whether the initial population of IG-prey consisted on all developmental stages or only juvenile stages (Wald statistic for interaction between initial condition \times days = 201.91, DF = 7, $p < 0.001$). When the resident IG-prey population consisted of all developmental stages, IG-predators consistently failed to invade (Fig. 3, upper panel). In contrast, when the resident population consisted of only juvenile stages of the IG-prey, the population of IG predators increased and the population of IG-prey went extinct (Fig. 3, lower panel). High numbers of eaten corpses were consistently found on all the arenas at the beginning of the experiments, (Fig. 4, all the panels, see grey triangles),

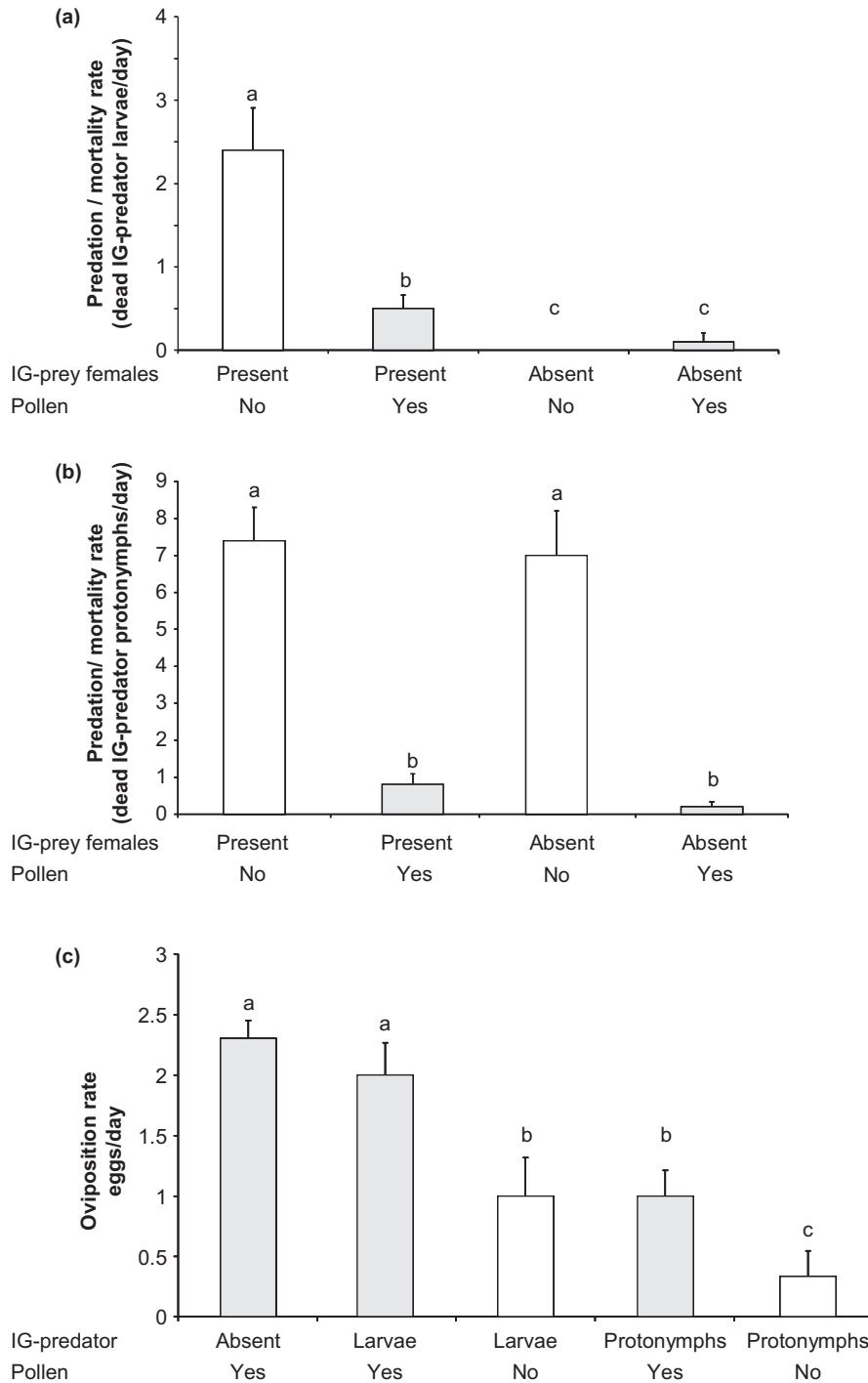


Figure 2. Predation/mortality rates (mean \pm SE) of (a) larvae and (b) protonymphs of IG-predators in the presence (grey bars) or absence (white bars) of pollen and in the presence or absence of adult IG- prey. (c) Oviposition rates (mean \pm SE) of the IG-prey for the same treatments as in (a) and (b). Different letters above bars indicate significant differences among the treatments.

which is consistent with high predation rates of IG-predators on IG-prey juveniles in the presence of the shared resource (Montserrat et al. 2008), i.e. 13.7 ± 1.05 IG-prey juveniles day^{-1} . Also, numbers of female IG-prey, the reciprocal predatory stage, were high enough to prevent IG-predator populations from growing, even when the reciprocal predation rate was 0.5 vulnerable IG-predator stages / female \times day. Indeed, because the average number of IG-prey females through time in the replicates with

stage structure was between 40 and 65 individuals (Fig. 4, left panels, see crosses), and female IG-predators lay an average of two eggs per day when fed on *Typha* pollen and IG-prey juveniles (Montserrat et al. 2008), total reciprocal predation was sufficient to kill all juvenile IG-predators.

Two consecutive invasion attempts of three IG-predator females at high levels of productivity always failed (Fig. 5). Together, these results show that IG-predators were not

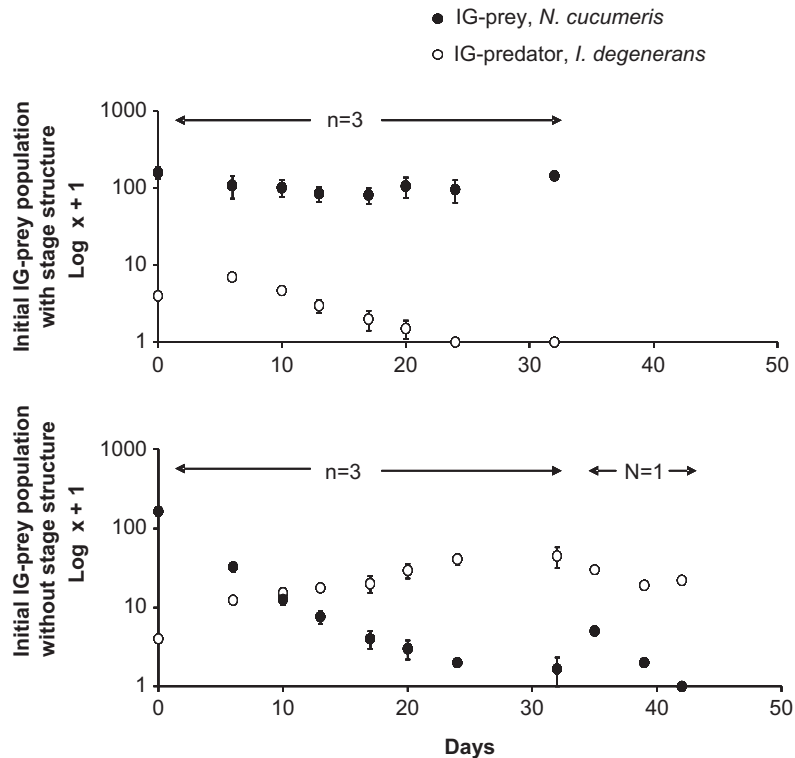


Figure 3. Invasion dynamics (average number \pm SE, $n = 3$, except indicated otherwise) of the IG-predator (*Iphiseius degenerans*, white dots, all stages, i.e. females, males, juveniles and eggs, included) into a resident population of IG-prey (*Neoseiulus cucumeris*, black dots, all stages, i.e. females, males, juveniles and eggs, included) when the structure of IG-prey populations was left intact (upper graph), and when the structure of IG-prey populations was manipulated so that only juveniles were present at the moment of the IG-predator introduction (lower graph).

capable of invading a population of IG-prey that is capable of feeding on juveniles of the IG-predator, even when this reciprocal intraguild predation affects only a small fraction of the IG-predator population.

Discussion

Mutual exclusion in systems with RIGP

We showed that reciprocal intraguild predation occurred in our system in the presence of pollen as alternative food, mainly through IG-prey attacking IG-predator larvae, the most vulnerable stage in phytoseiid mites (Schausberger 1999, Walzer and Schausberger 1999, Abad-Moyano et al. 2010), but that the level of RIGP was very low (an average of 0.5 ± 0.19 IG-predator larvae \times adult IG-prey $^{-1}$ day $^{-1}$). Nonetheless, IG-predators consistently failed at invading stage-structured populations of the IG-prey. When we created an artificial environment with the stage structure of the IG-prey being manipulated so that all the reciprocal predators (IG-prey adults) were removed prior to the introduction of the IG-predators, all the invasion attempts succeeded. We therefore conclude that IG-predators are not able to invade a resident population of reciprocal IG-prey because of the stage structure. Extinction of IG-prey in the stage-unstructured treatments was caused by the high predation pressure imposed by IG-predators (Fig. 5, eaten corpses), which prevented IG-prey recruitment. Indeed, predation rate of *I. degenerans* on *N. cucumeris* juveniles in the presence of pollen is 13.7 ± 1.05 individuals per female and day (Montserrat et al. 2008).

When the initial IG-prey population was stage-structured, extinction of IG-prey was prevented by the abundant presence of ovipositing IG-prey females, despite the mortality of IG-prey juveniles being high when IG-predators were present (Fig. 5, eaten corpses). Therefore, our results suggest that the invasion of IG-predators failed because adult IG-prey fed on vulnerable IG-predator stages at the start of the invasion process, when numbers of adult IG-prey were much higher than those of the invading IG-predator (15–20 times – Fig. 5). This would be the likely scenario in patches where the IG-prey was the resident population. During an invasion event, the population of IG-predators would have been prevented from growing as long as the difference in numbers between the two species was large enough for the total reciprocal predation rate to be higher than the IG-predator population growth rate. Hence, even weak reciprocal intraguild predation can result in priority effects, given that the population of IG-prey has reached sufficiently high densities, i.e. at high productivity levels.

The interplay between initial conditions and reciprocal intraguild predation is an important driver of communities with RIGP. Indeed, the presence of stages of the IG-predator that are susceptible to predation by IG-prey can prevent IG-predator populations from increasing as long as reciprocal IG-prey stages are abundant enough. If they are not, this results in the interesting phenomenon that IG-predators can invade populations of IG-prey when productivity of the environment is low (i.e. densities of IG-prey are low), can wipe out populations of IG-prey, and subsequently go extinct because persistence of IG-predators is impossible at low environmental productivity levels. This phenomenon was observed in

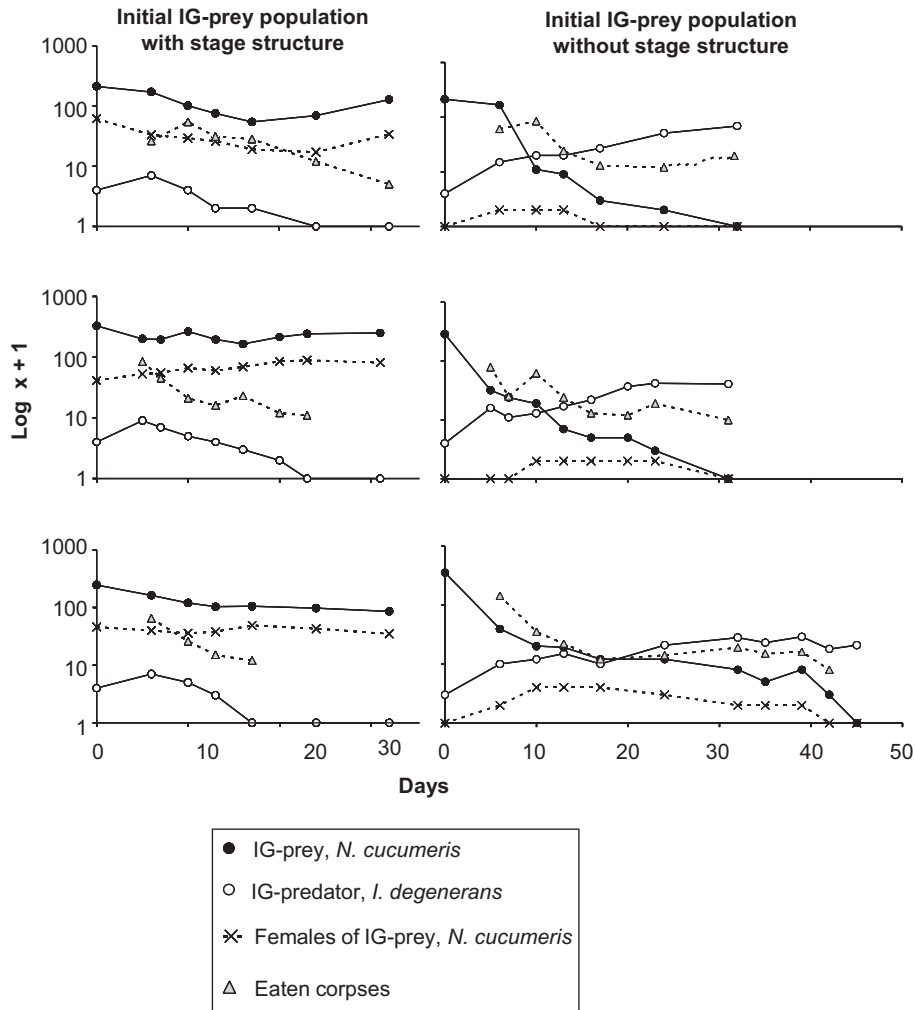


Figure 4. Invasion dynamics of IG-predators into a resident population of IG-prey, for each of the replicates separately. The IG-predator (*Iphiseius degenerans*, all stages, i.e. females, males, juveniles and eggs, included) is depicted in white dots. The IG-prey (*Neoseiulus cucumeris*, all stages, i.e. females, males, juveniles and eggs, included) is depicted in black dots. In the left panels, the structure of IG-prey populations was left intact; and in the right panels, the structure of IG-prey populations was manipulated so that only juveniles were present at the moment of the IG-predator introduction. Crosses indicate the number of IG-prey females present in the arena, and grey triangles are the number of eaten corpses of both IG-predator and IG-prey juveniles (it is not possible to distinguish between species when bodies have been preyed on) found in the arena, which were removed after counting them. Replicates next to each other were carried out at the same time.

Montserrat et al. (2008). Conversely, at high productivity levels IG-predators are capable of invading populations of IG-prey only when densities of the latter are low and when the IG-prey population has not yet reached a stable age distribution, i.e. when the IG-prey has recently arrived on the patch. Once settled, IG-prey populations become invulnerable to invasion. Similar phenomena were recently described in a fish life-history omnivory system (Schröder et al. 2009). In their experiments, Schröder et al. (2009) found that invasion success of IG-predators into a resident population of IG-prey was size-dependent, with large IG-predators driving IG-prey populations to extinction because of high predation pressure, and with small IG-predators being unable to invade because of their competitive inferiority. Interestingly, such an outcome was independent of the level of the environmental productivity, as it is in our mite system (Montserrat et al. 2008). However, at low environmental productivity levels, Schröder et al. (2009) did not observe that the population

of (large) IG-predators went extinct after excluding the IG-prey, indicating that the lowest productivity level tested by these authors was still high enough to allow IG-predators to persist on the resource alone. Indeed, the range of environmental productivity in Schröder et al. (2009) was narrower than that used in Montserrat et al. (2008) (four- fold and 48-fold difference between the lowest and the highest level of environmental productivity, respectively).

Mortality rates of IG-predator protonymphs were not dependent on the presence of adult females of the IG-prey (Fig. 2b, compare first and third bar). This indicates that cannibalism rather than IG-predation was the probable cause for most of the mortality of IG-predator protonymphs. Death because of starvation is not likely because mortality of protonymphs in the absence of food is negligible during the two first days of starvation (Montserrat et al. 2006). Cannibalism in communities with intraguild predation can promote species coexistence, mainly when the cannibal is the IG-

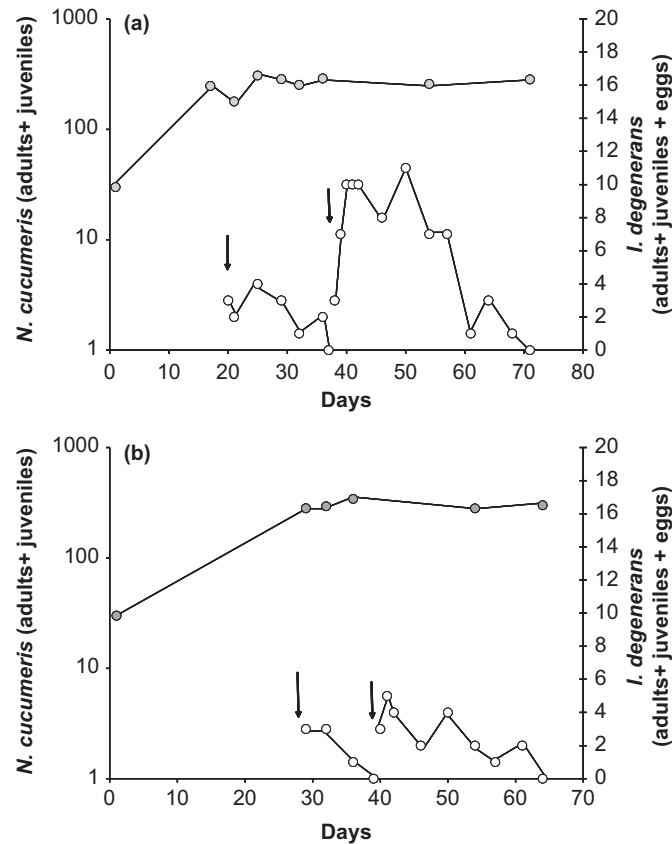


Figure 5. Invasion dynamics of the intraguild (IG)-predator (*Iphiseius degenerans*, white dots, all stages, i.e. females, males, juveniles and eggs, included) into a population of IG-prey (*Neoseiulus cucumeris*, grey dots, mobile stages, i.e. females, males, and juveniles, included) at high resource (pollen) density. Arrows indicate successive introductions of three females of IG-predator, to account for failures of establishment due to stochastic events.

predator and cannibalism rates are high (Rudolf 2007). However, effects of cannibalism on community dynamics are likely less important when rates of cannibalism depend on the presence of alternative prey, or on food being limiting, a pattern which is commonly observed in many cannibalistic species (Polis 1981, Elgar and Crespi 1992), including phytoseiid mites (Schausberger and Croft 2000, 2001). Rates of cannibalism in *I. degenerans*, the IG-predator used here, strongly depend on the presence of heterospecific prey; when intraguild or shared prey are present, cannibalism rates are negligible (Montserrat et al. 2006, Fig. 2a). Therefore, cannibalism is not likely to promote coexistence in our experimental system, which agrees with previous results (Montserrat et al. 2008).

Using the same two species as here, Montserrat et al. (2008) found that the invasion of a resident population of IG-predators by IG-prey was also not possible at high productivity levels. Hence, it is expected that with reciprocal IGP, IG-predators and IG-prey will show mutual exclusion at high productivity levels, with the resident population always preventing the invasion of the other species, a result that is in agreement with predictions of RIGP theory (HilleRisLambers and de Roos 2005, HilleRis Lambers et al. 2005). The results in Montserrat et al. (2008) and those shown here provide experimental evidence of the existence of a bistable outcome of invasion experiment.

The ubiquity of IGP and RIGP

When compared with models that consider a resource, a consumer, and a predator engaged in predatory interactions only (i.e. trophic chains), models with IGP predict that intraguild predation is detrimental to species coexistence (Oksanen et al. 1981 vs Polis and Holt 1992, Holt and Polis 1997, Diehl and Feissel 2000, 2001, Mylius et al. 2001). Incorporating mutual predation into models of IGP promotes alternative states and further limits the persistence of these communities (HilleRisLambers 2005). Yet, communities with IGP and RIGP are common in nature. It is clear, therefore, that the effects of omnivory on the persistence of food webs needs further studies to reveal which factors are essential in promoting their persistence. Our results agree with model predictions in that RIGP promotes mutual exclusion, thereby making persistence of RIGP communities impossible. The experimental set-up was designed to comply with theoretical models that consider well-mixed populations in unstructured habitats. Recently, however, it has been shown that habitat structure can reduce the effects of intraguild predation (Janssen et al. 2007) by reducing the strength of IG-predator and IG-prey interactions (Harvey and Eubanks 2005, Finke and Denno 2006, Griffen and Byers 2006). For instance, the presence of structure in a habitat can amplify the positive effects of anti-predator behaviour (e.g. escaping from predators or refuge use) on IG-prey (Persson and Eklöv 1995), promoting

the persistence of communities with RIGP through species spatial segregation (Heithaus 2001). Spatial segregation of IG-prey and predator can be promoted if IG-prey are able to avoid patches occupied by IG-predators (Magalhães et al. 2005b) or when they move to safer sites when perceiving IG-predators (Moran and Hurd 1994, Finke and Denno 2002). In our study system, we know that the presence of adult females of *I. degenerans*, the IG-predator, induces egg-retention in *N. cucumeris*, the IG-prey (Montserrat et al. 2007). We hypothesized that this behaviour served to win the mothers time to find a predator-free oviposition site, and thus a safer place for the juveniles that hatch from the eggs. Such behaviour would promote spatial segregation of IG-predator and IG-prey populations. In the experiments here, we found that the oviposition rate of the IG-prey was two times higher when only pollen was present than when it could feed on pollen plus IG-predator protonymphs (Fig. 2c, compare first and fourth bar). Such a reduction in oviposition suggest that *I. degenerans* protonymphs also induce egg retention in *N. cucumeris*. This is not surprising, given that protonymphs of *I. degenerans* and other species of phytoseiids are very active and voracious predators. Furthermore, this behavioural change was not induced by the presence of larvae (Fig. 2c, compare first and second bars), which are the least voracious stage.

Overall, our experiments provide experimental support for the mechanism leading to mutual exclusion in systems with (even weak) reciprocal intraguild predation. We suggest that the size/stage structure of populations and the transient dynamics following first arrival of the potential invader should be the subject of further development of RIGP theory as well as of experimental studies. Furthermore, theoretical and experimental works should explore if habitat structure promotes coexistence of IG-predator and IG-prey, especially because both direct (predation, reciprocal predation) and indirect (i.e. anti-predator behaviour) behavioural interactions can facilitate spatial segregation, with patches occupied only by IG-predators and patches occupied only by IG-prey. Based on our results, we predict that persistence of metapopulations of IG-prey and IG-predators will be possible, even when mutual exclusion occurs at a local scale.

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