

HABITAT STRUCTURE AFFECTS INTRAGUILD PREDATION

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Abstract. Intraguild predation is thought to be ubiquitous in natural food webs. Yet, theory on intraguild predation predicts the intraguild prey to persist only under limited conditions. This gap between theory and empirical observations needs scrutiny. One reason might be that theory has focused on equilibrium dynamics and a limited set of species (usually three) that interact in well-mixed populations in unstructured habitats, and these assumptions will often not hold in natural systems. In this review, we focus on the effects of habitat structure on intraguild predation. Habitat structure could reduce encounter rates between predators and prey and could create refuges for prey. In both cases, habitat structure could reduce the strength of intraguild interactions, thereby facilitating species coexistence. A meta-analysis of studies on manipulation of habitat structure shows that intraguild prey indeed suffer less from intraguild predation in structured habitats. This was further confirmed by a meta-analysis in which studies on intraguild predation were classified according to habitat structure. Intraguild predation reduced densities of the intraguild prey significantly more in habitats with little structure than in habitats rich in structure. The effect of intraguild predation on the shared prey was negative, and not significantly affected by habitat structure. We conclude that habitat structure may increase persistence of the intraguild prey by decreasing the strength of the interaction between intraguild predator and intraguild prey.

Key words: behavior; cascade; food web; indirect interactions; interaction strength; meta-analysis; predator–prey interactions.

INTRODUCTION

Theory on intraguild predation is based on models of the simplest food web in which intraguild predation can occur: well-mixed populations of intraguild predators (IG predators), intraguild prey (IG prey), and shared prey (or shared resource). The shared prey is consumed by intraguild predators as well as intraguild prey, whereas the latter is consumed by the intraguild predator only. Theory predicts that stable coexistence of all three species is often impossible (Polis and Holt 1992, Holt and Polis 1997, Diehl and Feissel 2000, 2001, Mylius et al. 2001). In particular, IG prey are excluded when they are the inferior competitor for the shared prey or when productivity levels are high. Yet, intraguild predation is a ubiquitous phenomenon in natural food webs (Polis et al. 1989, Polis and Holt 1992, Rosenheim et al. 1995, Polis and Winemiller 1996), and it is still not clear why theory and reality differ.

Besides being of interest for understanding the persistence of species assemblages, intraguild predation is also important from an applied point of view. Since

the publication of two seminal papers by Rosenheim and colleagues (1993, 1995), there is concern about the effects of intraguild predation among natural enemies on biological control. Indeed, theory predicts that intraguild predation among natural enemies would never promote pest control under the following circumstances: (1) When the IG predator is the superior competitor for the pest it would decrease the pest to lower levels than would the IG prey and the IG prey would be excluded by the IG predator. Hence, it is better to use only the IG predator for pest control. (2) When the IG prey is the superior competitor, the use of IG predators or of a combination of IG predators and IG prey would result in higher levels of the pest than when the IG prey is used alone. Hence, theory predicts that it is not a good idea to use pairs of intraguild prey and intraguild predators for biological control (Janssen et al. 2006). Recently, however, it has been shown that there is not much evidence in the literature for such negative effects of intraguild predation on biological control (Janssen et al. 2006, Rosenheim and Harmon 2006). This is further proof for theory and empirical evidence being at odds.

Several reasons for the discrepancy between theory and empirical research have been suggested (Briggs and Borer 2005, Janssen et al. 2006, Rosenheim and Harmon 2006). First, most theory considers equilibrium dynamics, whereas experiments are often too short for the

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system to reach a stable equilibrium, if there is any (Briggs and Borer 2005). It is difficult to extrapolate short-term experiments to long-term effects of intraguild predation, especially when the populations exhibit fluctuations (Janssen et al. 2006). Second, theory takes three species into consideration, whereas many natural and experimental systems consist of more species. Third, most theory does not consider size-structured populations (but see Mylius et al. 2001). Such size structure can result in invulnerable size classes (van Rijn et al. 2002) or even in role reversals between predator and prey (Janssen et al. 2002, Magalhães et al. 2005). Fourth, theory is about well-mixed populations in an unstructured environment, whereas real populations are often patchy and may actually consist of many subpopulations connected by dispersal. Such dispersal may result in coexistence of predators and prey even when local populations cannot coexist (Huffaker 1958, Holyoak and Lawler 1996, Janssen et al. 1997, Ellner et al. 2001). Moreover, evidence is accumulating that the strength of predator-prey interactions can be modified by habitat structure (Persson and Eklov 1995, Langellotto and Denno 2004), and this also holds for species involved in intraguild predation (Warfe and Barmuta 2004, Harvey and Eubanks 2005, Finke and Denno 2006, Griffen and Byers 2006).

Habitat structure could affect predator-prey interactions, including those between IG predators, IG prey, and shared prey, in several ways. For example, it could simply reduce encounter rates between predators and prey by enlarging the area in which interactions occur or through impeding the perception of prey by predators. Prey could also actively use habitat structure as refuge (Persson and Eklov 1995). In both cases, the interaction strength between predators and prey will be reduced, which may contribute to increased persistence (May 1973, McCann et al. 1998).

In this review, we focus on habitat structure as one of the potential explanations for the discrepancy between theory and empirical observations. We review the literature to compare the effects of IG predators on populations of IG prey and shared prey in the presence and absence of habitat structure, hypothesizing that habitat structure may weaken the effects of intraguild predation, thus facilitating persistence of systems with intraguild predation.

LITERATURE REVIEW

Theory predicts that persistence of the IG prey is reduced by intraguild predation, hence, an obvious choice for analysis of the literature would be to evaluate the effect of habitat structure on persistence of IG prey. However, most published experiments lasted too short to show coexistence or exclusion (with the exception of Lawler and Morin 1993, Morin 1999). Nevertheless, if habitat structure reduces the negative effect of intraguild predation on densities of the IG prey in the short term, this could be taken as evidence that the long-term effect

will also be weaker, resulting in increased persistence. A second effect predicted by theory is that the density of the shared prey will increase with intraguild predation, provided the IG prey is a better competitor for the shared prey than the IG predator is (Polis and Holt 1992, Holt and Polis 1997, Mylius et al. 2001). If habitat structure would reduce effects of predation in systems with intraguild predation, this would result in weaker positive effects on the shared prey with increasing spatial structure. We tested both these predictions with a meta-analysis of the literature.

Methods

We used meta-analyses to quantify the effects of intraguild predation (Arnqvist and Wooster 1995). The literature was searched for publications that reported either (1) experiments in which habitat structure was manipulated and the effect of intraguild predation was measured in simple vs. structurally complex habitats or (2) experiments on the effects of intraguild predation, which we classified according to habitat structure as follows: (a) low (no or little structure; experiments on single small plants, in aquaria without vegetation, or in small field enclosures with low spatial structure) or (b) high (cages in greenhouses or in the field with several plants, ponds and aquaria with vegetation, field plots with monoculture, large enclosures or open plots or ponds with natural vegetation; see Appendix). In order to be included in our meta-analysis, the studies had to contain information on densities, standard errors or standard deviations, and sample sizes of shared prey and IG prey in the presence and absence of the IG predator. Because we were interested in the effect of intraguild predation, we considered studies that used an additive design, i.e., studies in which IG predators were added without reducing the densities of IG prey. This avoids confounding effects of reduction of IG prey with the addition of IG predators (Finke and Denno 2005, Rosenheim and Harmon 2006).

Theory predicts that the IG prey will not persist if it is a weaker competitor for the shared prey than the IG predator (Polis and Holt 1992, Holt and Polis 1997, Mylius et al. 2001). Moreover, the prediction that the density of the shared prey will increase because of intraguild predation does not hold when the IG predator is the better competitor. We therefore also assessed which of the two predators was the best competitor, this being the predator that reduced the shared prey to the lowest densities in the absence of the other predator (Polis and Holt 1992, Holt and Polis 1997).

We found 10 studies that manipulated habitat structure (see Appendix), and analyzed the effect of intraguild predation on IG prey and shared prey in structurally simple and complex habitats. For the second approach, the classification of habitats according to spatial structure, we found 38 studies. Several studies contained separate experiments on various species of IG

predators or IG prey; these were considered independent cases.

We calculated effect size on the IG prey per case i as

$$L_i = \ln(R) = \ln\left(\frac{X_i^E}{X_i^C}\right)$$

with X^E being the average density or number of the IG prey in the presence of the IG predator and the shared prey and X^C the average density of the IG prey in the absence of the IG predator but in the presence of the shared prey (Hedges et al. 1999, Rosenberg et al. 2000). Theory predicts lower densities of the IG prey in the presence of the IG predator, hence negative L 's. For the shared prey, X^E was the average density of the shared prey in the presence of the IG predator and the IG prey and X^C was the average density in the absence of the IG predator but in the presence of the IG prey. Theory predicts higher densities of the shared prey in the presence of the IG predator (positive L 's), provided the IG prey is the best competitor, and lower densities when the IG predator is the best competitor (negative L 's). The absolute value of the effect size can be taken as indicative for the strength of the interactions under test. Effect sizes were combined into an overall effect size as

$$L^* = \frac{\sum_{i=1}^n w_i L_i}{\sum_{i=1}^n w_i}$$

with L_i the effect size and w_i the reciprocal of the sampling variance of the i th study. We analyzed effect sizes with random-effects models using MetaWin (Rosenberg et al. 2000). For studies in which habitat structure was manipulated, we tested the effects in unstructured habitats against those in structured habitats with a random model with categorical data (Rosenberg et al. 2000). Analogous to an ANOVA, such an analysis partitions the variance in effect sizes into that explained by a model including categorical factors (Q_M , the factor in this case being habitat structure) and residual variance (Q_E). Both variances can be tested against a χ^2 distribution (Rosenberg et al. 2000). This analysis was also done for studies for which we classified habitat structure. Effect sizes were considered significantly different from zero if the bootstrapped 95% confidence intervals (constructed by resampling the data set 999 times) did not include zero (Rosenberg et al. 2000). For significant effects, we also calculated the fail-safe number, which is the number of studies with nonsignificant effect that need to be added to the analysis to render the result nonsignificant. If this number is large relative to the number of observed studies, the observed results are a reliable estimate of the true effect (Rosenberg et al. 2000). This number thus serves as a proxy for the power of our analysis. Because of the a priori hypothesis of habitat structure decreasing the effects of intraguild predation, we used one-tailed tests.

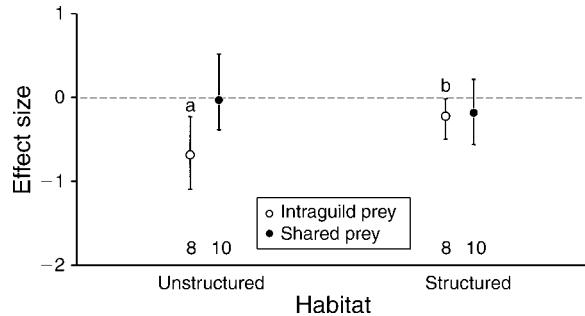


FIG. 1. The effects of manipulation of habitat structure on intraguild predation. Shown are the combined effect sizes (L^*) and their 95% confidence intervals on IG prey (open circles) and shared prey (solid circles). Effect sizes with different lowercase letters are significantly different (see *Results: Effects of manipulation of habitat structure*). Numbers above the x -axis are the number of cases.

RESULTS

Effects of manipulation of habitat structure

The effect of intraguild predation on populations of the IG prey was significantly negative in unstructured habitats and just different from zero in structured habitats, and the difference between structured and unstructured habitats was significant (Fig. 1, $Q_M = 3.41$, $df = 1$, $P = 0.033$). Because the number of studies is low (Fig. 1) and the number of fail-safe studies is high (27.4), we tentatively conclude that IG prey may indeed use habitat structure to escape from predation.

The significant negative effect on the IG prey in unstructured habitats did not result in a positive effect on the shared prey in unstructured habitats compared to habitats with structure (Fig. 1), and habitat structure had no notable effect on the densities of the shared prey (Fig. 1, $Q_M = 0.26$, $df = 1$, $P = 0.30$). When focusing on studies in which the IG prey was the best competitor ($N = 5$), the same pattern emerged as for all studies together (data not shown).

Effects of intraguild predation in systems with different habitat structure

As expected, the overall effect of intraguild predation on the IG prey was negative ($L^* = -1.15$, confidence intervals = -1.49 to -0.85 , fail-safe number = 1495.2). In agreement with our hypothesis, habitat structure reduced the effect of intraguild predation on the IG prey (Fig. 2, all studies, $Q_M = 10.9$, $df = 1$, $P = 0.0005$, fail-safe number = 1455.2). This effect was most pronounced when the IG prey was the best competitor, which was true in 23 cases out of 58 (Fig. 2, IG prey best, $Q_M = 7.61$, $df = 1$, $P = 0.0029$, fail-safe number = 239.5), whereas there was no significant effect of habitat structure when the IG predator was the superior competitor (Fig. 2, IG predator best, $N = 17$, $Q_M = 0.23$, $df = 1$, $P = 0.32$).

The overall effect of intraguild predation on the shared prey was also negative ($L^* = -0.42$, confidence

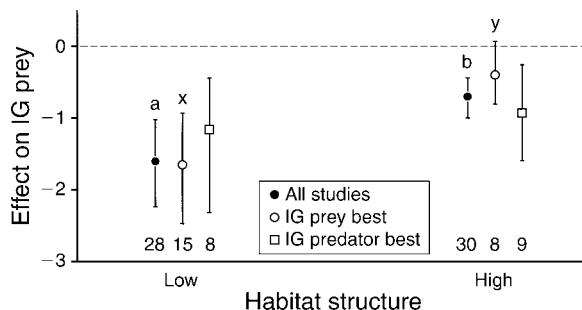


FIG. 2. The effects of habitat structure on the IG prey. Shown are the combined effect sizes (L^*) and their 95% confidence intervals for all studies (solid circles), for studies in which the IG prey was a better competitor for the shared prey (open circles), and for studies in which the IG predator was the better competitor (open squares). Not all studies gave information on which predator was the best competitor. Effect sizes with different lowercase letters are significantly different (see *Results: Effects of intraguild predation in systems with different habitat structure*). Numbers above the x-axis are the number of cases. See *Methods* for classification of habitat structure.

interval = -0.74 to -0.13 , fail-safe number = 344.5). There was no significant effect of habitat structure on the shared prey (Fig. 3, all studies, $Q_M = 2.23$, $df = 1$, $P = 0.068$), but a slight trend of a larger negative effect in structured habitats.

When the IG predator is the best competitor, theory predicts a negative effect of intraguild predation on the shared prey, whereas a positive effect is expected when the IG prey is the best competitor. There was indeed a significant effect of which predator was the best competitor ($Q_M = 26.1$, $df = 1$, $P = 0.0001$, fail-safe number = 160.2), and the effect size was significantly negative when the IG predator was the best competitor ($N = 22$, $L^* = -1.07$, confidence interval = -1.83 to -0.42). Contrary to expectation, the overall effect did not differ from zero when the IG prey was the best competitor ($N = 33$, $L^* = 0.11$, confidence interval = -0.11 to 0.39).

DISCUSSION

Effects on the IG prey

In agreement with theoretical predictions, the presence of IG predators had a negative effect on the IG prey, but as we hypothesized, this effect was reduced by habitat structure. This was seen in experiments in which habitat structure was manipulated (Fig. 1) as well as in a meta-analysis in which habitat structure was classified, rather coarsely, as low or high (Fig. 2). Judged by the high number of fail-safe studies relative to the number of studies analyzed, this effect is rather robust. Because weak interactions (i.e., smaller absolute values of L^*) may facilitate persistence (May 1973, McCann et al. 1998), we conclude that habitat structure may promote persistence of species involved in intraguild predation.

Long-term experiments are needed to further test this hypothesis.

According to theory, the IG prey would be excluded if the IG predator were the superior competitor. Although the length of most of the studies was not sufficient to test this, several experimental systems in which the IG predator was the best competitor were natural ecosystems, in which the IG prey and IG predator coexist (i.e., Menge et al. 1986, Crumrine and Crowley 2003, Denno et al. 2004, Finke and Denno 2004), suggesting that the IG prey is not excluded in these systems.

Curiously, habitat structure resulted in a smaller effect of intraguild predation on IG prey when the IG prey was the superior competitor for the shared prey, but not when the IG predator was the better competitor (Fig. 2). In the first case, habitat structure reduces predation on the IG prey, which does not suffer much from competition with the IG predator. However, when the IG predator is the superior competitor, predation on the IG prey may be lower in the presence of habitat structure, but the IG prey may still suffer from competition, and this may partially counter the effect of reduced predation. We think that this is not necessarily a general phenomenon but will depend on the relative strength of intraguild predation and competition between IG predators and IG prey.

Effects on the shared prey

The effect of intraguild predation on the shared prey was not different from zero in studies in which habitat structure was manipulated (Fig. 1), and it was negative in studies that were classified according to habitat structure (Fig. 3). Theoretical predictions of the effect of intraguild predation on shared prey populations differ depending on the competitive capacity of the IG prey and IG predators. When the IG prey is the best competitor, theory predicts a positive effect of intraguild predation on the shared prey, but we found no effect.

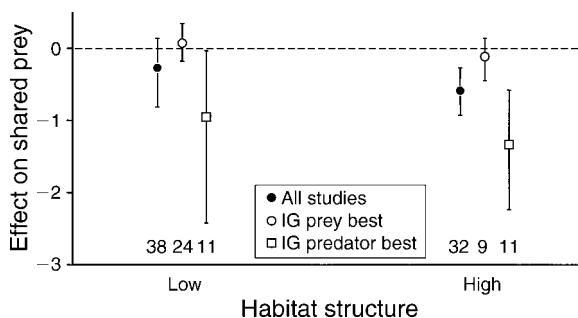


FIG. 3. The effects of habitat structure on the shared prey. Shown are the combined effect sizes (L^*) and their 95% confidence intervals for all studies (solid circles), for studies in which the IG prey was a better competitor for the shared prey (open circles), and for studies in which the IG predator was the better competitor (open squares). Not all studies gave information on which predator was the best competitor. Numbers above the x-axis are the number of cases. See *Methods* for classification of habitat structure.

by the shared prey, affecting the interaction between the shared prey and the IG prey. In conclusion, the combination of direct and indirect interactions in simple three-species systems with intraguild predation (Fig. 4) makes it hard to predict the effects of intraguild predation, especially because many of the interactions can have positive, neutral, or negative effects.

Predators could also induce other types of behavior in their prey, such as counterattack (Janssen et al. 2002), escape, or avoidance of areas with predators. These other types of antipredator behavior are not necessarily associated with habitat structure, but can result in the same indirect interactions among prey and predators (Fig. 4). Antipredator behavior has been studied extensively in systems consisting of predators and prey (Sih 1980, Lima and Dill 1990, Lima and Bednekoff 1999, Werner and Peacor 2003), but there are only few publications on the effects of antipredator behavior induced by the IG predator (Soluk and Collins 1988, Huang and Sih 1991, Wissinger and McGrady 1993, Okuyama 2002, Crumrine and Crowley 2003, Magalhães et al. 2004, Griffen and Byers 2006). In order to gain better insight into the effects of all behavioral interactions on the dynamics of systems with intraguild predation, experiments should not only include treatments for assessing induction of antipredator behavior by IG predators, but also by IG prey plus all possible combinations (Wissinger and McGrady 1993, Crumrine and Crowley 2003, Griffen and Byers 2006).

Conclusions

Theory on intraguild predation is based on models of three well-mixed populations. Given that the IG prey is the best competitor, it predicts that predation on the IG prey cascades down to a positive effect on the shared prey. If we consider the studies in unstructured habitats with the IG prey the best competitor as approaching the models best, we would thus expect a positive effect of intraguild predation on the shared prey in these studies. However, we did not find any evidence for this. Perhaps this is a consequence of other differences between model assumptions and real systems, such as the presence of more than three species, differences in time scale, or because of indirect interactions. The discrepancy between model predictions and experimental results shows that there is a clear need for long-term experiments with simple experimental systems that meet the assumptions of theoretical model systems in order to test theory further.

The existing literature shows a clear trend towards reduced negative effects of intraguild predation on the IG prey in structured habitats. If this trend of reduced interaction strength carries over to long-term dynamics, habitat structure increases the possibilities for persistence of systems with intraguild predation. Challenges for future research will be to assess the effect of habitat structure in carefully designed experiments (e.g., Finke and Denno 2002, Warfe and Barmuta 2004, Harvey and

Eubanks 2005, Griffen and Byers 2006), as well as identifying how habitat structure affects the direct and indirect interactions in systems with intraguild predation.

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APPENDIX

Effects of intraguild predation on the intraguild prey and shared prey in unstructured vs. structured habitats and in habitats categorized according to structure (*Ecological Archives* E088-167-A1).