SPECIAL FEATURE

Intraguild Predation: New Theoretical and Empirical Perspectives[1]

Theory holds out the promise of helping us to dissect and understand the rich web of interactions found in speciose communities. But, to be useful, theory must achieve a delicate balance. Models that are too simple may not capture the essential elements of nature, and thus can produce misleading predictions. Models that are too complex may become as inscrutable as nature itself.

The study of intraguild predation has been typified by a struggle to reconcile theory with empirical observation, and with a growing suspicion that we should perhaps explore models of greater complexity. Intraguild predation occurs when two predators that compete for a shared prey population also engage in predator–prey interactions with each other. The top predator feeds from two trophic levels (i.e., it is an omnivore) by consuming the intermediate predator and the shared resource. Intraguild predation therefore refers to a three-species module in which both direct and indirect effects may be important.

Basic theory for intraguild predation laid out in the seminal work of Robert Holt and Gary Polis makes two prominent predictions that have been very robust to subsequent elaborations of the theory. First, it is difficult to achieve stable three-species equilibria; in large areas of the parameter space, one of the two predators is excluded. Second, to achieve a stable three-species equilibrium, the intermediate predator must be the superior competitor for the shared resource, because the intermediate predator must have an advantage as a competitor if it is to offset the disadvantage of being eaten by the top predator. The superior competitive status of the intermediate predator means that, if the top predator is removed from the system, the intermediate predator is freed to drive the equilibrium density of the shared resource to a lower equilibrium density.

Ecologists studying intraguild predation have not found it easy to reconcile these predictions with their observations of the natural world. Intraguild predation is now known to be extremely common. How can this be if the basic intraguild predation module is often unstable? Researchers who have experimentally removed intraguild predators from animal communities have, in some cases, observed the predicted decrease in the density of the shared prey, but in many cases have not. Why don't we more consistently see the outcome that is predicted by the models?

The articles in this Special Feature address these questions. First, in a synthetic introduction to intraguild predation, Borer et al. demonstrate that the fundamental features of this three-species module are shared by models that have previously been framed as representations of interactions of multiple predators (top and intermediate predators) with a shared prey, multiple parasitoids (facultative hyperparasitoids and primary parasitoids) with a shared host, or pathogens (one of which displaces the other from doubly infected hosts) and hosts. Despite the many differences in the biological characteristics of these interactions, Borer et al. demonstrate that in each case the central predictions from intraguild predation theory described above are obtained.

Vance-Chalcraft et al. present a meta-analysis that quantifies the support within the experimental literature for the predictions that the intermediate predator must be the superior competitor and that the density of the shared resource will decline in the absence of the top predator. Their analysis encounters a problem that permeates the study of intraguild predation: theory has been almost entirely focused on equilibrium conditions, whereas experimental work is rarely of sufficient duration to move beyond the earliest transient effects. With this important caveat, their analysis suggests that whereas there is some overall support for both predictions, the support is derived almost exclusively from studies of terrestrial invertebrates, and there is considerable variation in observed outcomes both within and across different types of ecosystems.

[1] Reprints of this 50-page Special Feature are available for $10.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, DC 20006 (esaHQ@esa.org).

The next two papers argue that while lessons can be learned by studying the three-species intraguild predation module in its simplest, isolated form, it is also important to recognize that intraguild predation interactions are generally embedded in complex communities. Top predators are, by definition, omnivores and are often generalized in their diets. This sets the stage for two important types of interactions. First, Rudolf notes that size structure within predator populations creates opportunities for cannibalism. He demonstrates that the predictions of the basic intraguild predation model can change significantly when either the top predator or the intermediate predator is cannibalistic. When the top predator is cannibalistic, the three-species intraguild predation module can be stable even when the top predator is the better competitor. When the intermediate predator is cannibalistic, a decrease in the density of the top predator can lead to an increase in the density of the shared resource, the opposite of what is expected under a model without cannibalism. Second, Holt and Huxel explore the consequences of adding additional resources, beyond the shared resource for which the top and intermediate predators compete. When the top predator has exclusive use of alternative resources, conditions for coexistence of the top and intermediate predators are made still more stringent. However, when the intermediate predator has exclusive use of an alternate resource, coexistence no longer requires the intermediate predator to be the superior competitor for the shared resource, and thus the presence of the top predator need not lead to elevated densities of the shared resource.

Finally, the last two papers conjure with the spatial and temporal heterogeneity of nature. Janssen et al. demonstrate that increasing the structural complexity of experimental arenas weakens the impact of top predators on intermediate predators, potentially stabilizing interactions that would otherwise not persist. They emphasize that behaviorally mediated effects may be crucial in modulating interaction strengths within intraguild predation modules. Amarasekare shows that temporal refuges may also be important. In one of the few experimental studies long enough to demonstrably reach equilibrium densities following a press perturbation, she shows that a parasitoid intraguild predation system is stable across a broad range of resource productivities, an outcome best explained by an early season temporal refuge for the primary parasitoid.

These papers suggest, then, that by increasing the complexity of intraguild predation models to include cannibalism, alternative prey resources, or spatial or temporal heterogeneity—features that we expect to be common, if not ubiquitous—the basic stability of the system can be enhanced and the range of expected behaviors can be fundamentally broadened. The intermediate predator may, or may not, be the superior exploiter of the shared resource, and the removal of the top predator may, or may not, lead to a decline in the equilibrium density of the shared resource. How then can we know what dynamics to expect from a given system? Several of the papers in this Special Feature begin to address this question. Future work will also be critical to bridge the gap between equilibrium theory and experiments, which rarely reach equilibrium conditions. Needed are theoretical treatments of the transient dynamics observed in short-term experiments and the long-term behavior of systems that rarely reach equilibria, and further theoretical examinations of the implications of population structure and labile behaviors. Also needed are experiments that implement longer-term manipulations to produce decisive tests of equilibrium theory. An enhanced marriage of theoretical and empirical studies of intraguild predation can contribute importantly to the broader challenge of deciphering the structure and function of speciose communities.

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