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# MULTITROPHIC INTERACTIONS IN TERRESTRIAL SYSTEMS

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# 17. COMMUNITY MODULES

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## INTRODUCTION

Ecological communities are among the most complex entities studied by scientists, not least because they harbour thousands (at least) of species interacting in all sorts of idiosyncratic ways. There is no single, best approach to understanding communities. In this chapter, I argue that a useful approach between the baroque complexity of entire communities, and the bare bones of single and pair-wise population dynamics, is provided by close analyses of models of 'community modules' – small numbers of species (e.g. three to six) linked in a specified structure of interactions.

In the food-web literature, the word 'module' at times refers to discrete blocks and interactions within more complex webs. Here, the term 'community module' simply denotes multispecies extensions of pair-wise interactions, such as basic predator–prey, host–pathogen, and resource–consumer interactions. Familiar modules include (Fig. 17.1): (i) shared resources (potentially leading to exploitative competition, Tilman 1982); (ii) food chains (Oksanen *et al.* 1981); (iii) shared predation (potentially leading to apparent competition, Holt 1977); (iv) predation upon competing prey (e.g. keystone predation, Holt *et al.* 1994; Leibold 1996); and, (v) intraguild predation (Polis *et al.* 1989). After a few remarks on rationales for studying modules, I examine the implications of models of community modules for three issues in community ecology: the determinants of food–chain length; the potential for community saturation to result from shared predation; and the puzzle of species coexistence with strong intra-guild predation.

In some instances, a system may closely resemble a particular module. This can be ensured in model laboratory systems (Lawton 1995), and can also apply to some subwebs of natural communities, if a few species strongly interact (Paine 1992), or multiple species cluster into well-defined functional groups (e.g. Morin 1995). Host–pathogen and host–parasitoid systems often nicely match particular module structures (for useful reviews see Jones *et al.* 1994; Begon & Bowers 1995; Begon *et al.* this volume).

Modules also provide bite-size conceptual units that build up towards fuller communities. The hope is that analyses of modules may, at the very least, illuminate general processes and qualitative features of complex communities. For the purpose at hand, two examples suffice. First, theoretical analyses of community modules

COMMUNITY MODULES



(a) Food chain

(b) Apparent competitio

(c) Exploitative competition

(d) Predation on competing prey
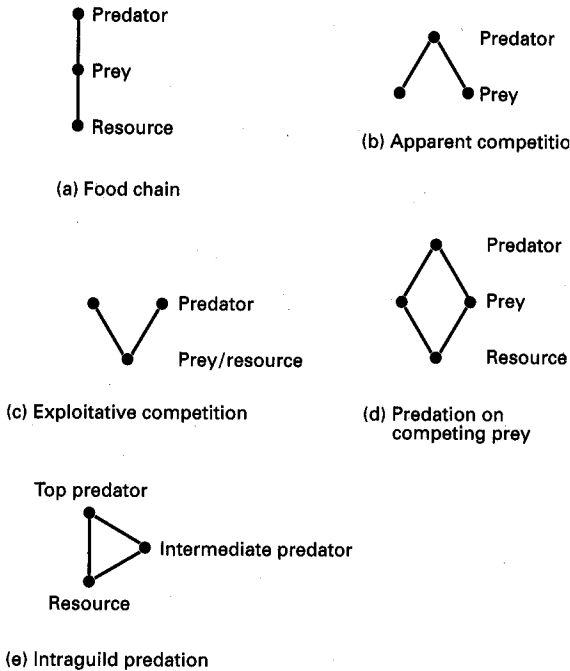
(e) Intraguild predation

FIG. 17.1. Examples of community modules.

clearly raised our consciousness about the potential importance of indirect inter-actions, a major theme in community ecology over the past two decades (Schoener 1993; Wootton 1994; Menge 1995). Second, models of systems with as few as three species can exhibit cyclical or chaotic dynamics (e.g. Gilpin 1979), even if all constituent pair-wise interactions are stable. As a novel example, I show that unstable dynamics arise in simple models of intra-guild predation. Because most species live in species-rich communities, these theoretical studies have helped motivate the search for chaotic dynamics in natural populations (Hastings *et al.* 1993).

## FOOD CHAINS

The food-chain module has received more attention than any other module, excepting exploitative competition. Simple food chain models (e.g. May 1973; Rosenzweig 1973; Oksanen *et al.* 1981; Hallam 1986; DeAngelis 1992) have helped clarify issues in the long-standing debate in ecology about the relative importance of natural enemies and resources in population regulation, and stimulated interest

in the interplay of primary production and trophic interactions in determining community structure and ecosystem function (Carpenter & Kitchell 1993). In an influential paper, Oksanen *et al.* (1981) analysed a three-level model in which either herbivores or carnivores can potentially regulate their respective resources, and consumers only indirectly interact via such exploitation. This model led to some striking predictions: the number of trophic levels that could be sustained tended to increase with primary production, and the relation between plant standing crop and production varied qualitatively, in a step-like fashion, with changes in the number of trophic levels (Oksanen 1990).

The simplest qualitative prediction of food-chain models is that the addition or removal of a top enemy species indirectly produces dramatic changes in species abundances at lower trophic levels. In some cases, this 'trophic cascade' structures entire communities (Power 1992). Familiar examples include: (i) effects of pis-civorous fishes on the composition and productivity of lake phytoplankton, via shifts in the abundance of intermediate planktivorous consumers (Carpenter & Kitchell 1993); (ii) the influence of sea otters on space-occupying macroalgae in the North Pacific, by altered abundances of invertebrate herbivores (Estes & Duggins 1995); (iii) the impact of West Indies lizards on leaf damage by herbivorous insects (Spiller & Schoener 1994; Dial & Roughgarden 1995). Specialist parasitism upon potentially abundant herbivores can also lead to spectacular trophic cascades (Dobson & Crawley 1994).

These qualitative predictions are consistent with a wide range of food-chain models. More specific predictions of simple food-chain models often seem to fail. In particular, simple chain models predict a relationship between food-chain length and primary productivity. Except possibly at very low productivities, this does not appear to be the case (Pimm 1991). Moreover, along gradients in productivity, all levels typically increase in abundance, once again seeming to contradict the predictions of the simplest models (Ginzburg & Akcakaya 1992). For instance, Balciunas and Lawler (1995) in a laboratory study of a three-link food chain (bacteria–bacterivore–top predator) showed that manipulating either nutrient or predator levels led to an increase in the abundance of the intermediate level, unlike predictions of simple Lotka–Volterra food-chain models.

Two broad categories of explanations have been proposed for these discrepancies between simple food-chain theory and data. First, adding realistic features to the trophic interaction and direct density-dependence alters the impact of primary production on higher trophic levels; for instance, incorporating direct interference implies all levels should increase along gradients in productivity (Ginzburg & Akcakaya 1992; Schmitz 1992). Saturating (type 2) functional responses dilutes the response of consumer populations to basal enrichment (Oksanen 1990) and can induce cyclic or chaotic dynamics (Hastings & Powell 1991), particularly at high K for the basal resource (Abrams and Roth 1994). Given unstable dynamics,

the mean abundance of higher trophic levels may decline with increasing K (Abrams & Roth 1994; Lundberg & Fryxell 1995). Similar dynamic complexities occur in plant–herbivore–pathogen systems (Grenfell 1992).

Second, the 'stacked specialist' food-chain model may be a misleading carica-ture of whole communities (Strong 1992; Polis & Strong 1996). Even if distinct trophic levels are present, multiple species within each level can confound theoretical expectations: consumption by one level shifts the composition of lower levels toward more resistant prey (Leibold 1989; Abrams 1993; Grover 1995), therefore reducing the shunt of production to higher levels. Moreover, in many systems omnivory or intra-guild predation blurs the distinctness of trophic levels (Polis & Strong 1996). Elser *et al.* (1995) describe an example of manipulation of rainbow trout in a lake leading to unexpected increases in primary production, because of omnivory.

In spite of present disagreement about how to interpret discrepancies between simple food-chain theory and observed patterns, it seems to me that analyses of the simple food-chain module were crucial. Such work helped focus attention on a number of important issues, such as the importance of temporal heterogeneity, predator interference, and non-linear functional responses in community dynamics. As shown below, these same factors are important in governing the strength of apparent competition among prey.

It is useful to stand back for a moment from these details, and note that the simplest attribute of a food chain is that it describes sequential trophic dependencies among species. This fact alone has consequences, given that all local communities are assembled by colonization (MacArthur & Wilson 1967; Holt 1993).

Assume the food chain occurs in a landscape with numerous habitat patches, and that a consumer species is absent from any patch that is missing that consumer's required resource. The simplest descriptor of a patch is chain length, which can change by colonization (lengthening the chain) or extinction (shortening it). Describe the landscape by the fraction of patches, $P_i$, with chains of length $i$. May (1994) describes a two-level metapopulation model for a specialist predator attacking a prey species. The prey can use only a fraction $k$ of habitat patches in the landscape. We can generalize this model to a three-link food chain as follows (see Holt 1993, 1995, 1996, for more details and alternative models):

$$\frac{dP_1}{dt} = (c_{01}P_1 + c_{01}P_3)\,(k - P_1 - P_2 - P_3)P_1 - c_{12}P_1P_2 - e_{10}P_1$$

$$\frac{dP_2}{dt} = c_{12}P_1P_2 - c_{23}P_2P_3 - e_{20}P_2$$

$$\frac{dP_3}{dt} = c_{23}P_2P_3 - e_{30}P_3$$

The $c_{ij}$ and $e_{ij}$ characterize rates of colonization and extinction taking patches from

state $i$ to $j$. Colonization is sequential; the basal prey always precedes the intermediate predator, followed by the top predator; the intermediate predator when alone suppresses prey colonization. All extinctions are assumed to involve the basal species; if it goes extinct, so do species directly or indirectly dependent upon it.

The basal species invades when rare, provided $k > e_{10}/c_{01}$. The intermediate predator in turn invades, given that the basal species is at equilibrium, when $k > e_{10}/c_{01} + e_{20}/c_{12}$. Finally, given that the intermediate species has equilibrated, for the top predator to invade, $k > e_{10}/c_{01} + e_{20}/c_{12} + e_{30}/c_{23}[(c_{12} + c_{01})/c_{01}]$. May (1994) notes that the requirement for a specialist predator to persist in a metapopulation is more stringent than the requirement faced by its prey. Comparing the above inequalities shows that as trophic levels are added, the condition for persistence of the top level becomes increasingly stringent.

The parameter $k$ measures the sparseness (or ubiquity) of the habitat utilized by the basal species, and is in a way akin to $K$ for the basal species in a standard Lotka–Volterra food-chain model. If there are constraints on species' colonization abilities, and local extinctions occur, specialist food chains are likely to be shorter in sparser habitats (Holt 1996). Because maximal $k$ is unity, spatial dynamics may limit food-chain length even in widespread habitats. Moreover, high rates of extinction for the basal species (e.g. in successional habitats) are likely to restrict food-chain length.

As with the simple Lotka–Volterra model for local chain dynamics, however, the strength of this conclusion may, in the end, be tempered by a consideration of more realistic dispersal scenarios (e.g. lattice models; Hassell *et al.* 1994), or the effects of multiple species and complex trophic interactions in each trophic level. None the less, this model for a food-chain module clearly highlights the potential for spatial dynamics and habitable area to constrain food-chain length, in a fashion reminiscent of the role of productivity in more standard food-chain models.

## APPARENT COMPETITION

The second module I consider is shared predation. Just as consumer species can reciprocally reduce each other's abundance via depleting a shared resource, prey species can indirectly depress each other by increasing the abundance of a shared natural enemy (Holt 1977; Holt & Lawton 1993). Apparent competition can, in principle, generate all the community patterns produced by standard competition for resources (e.g. habitat partitioning, Holt 1984) and act as a force limiting local species richness. If shared predation typically generates (–, –) interactions between alternative prey, shared natural enemies could provide one mechanism by which local communities become saturated in their species composition, via the exclusion of species drawn from some larger species pool (Cornell & Lawton 1992).

Though I believe such patterns are important and still largely underappreciated, in broad comparisons among communities or along environmental gradients, predation may in the end prove to have inconsistent effects on community saturation. To set the stage for this argument, it is useful to reprise the basic logic of apparent competition. In Holt (1977), I showed that apparent competition was a generic phenomenon in spatially homogeneous, multiprey systems where: (i) the predator was strictly food limited; (ii) the predator had a positive numerical response to each prey; and (iii) the system settled into a point equilibrium. Prey with high values for $r/a$ [= (intrinsic growth rate)/(attack rate)] can withstand high predator numbers and potentially exclude prey with lower values. The likelihood of exclusion depends upon the predator's capacity for limiting dominant prey numbers to well below $K$; increases in $K$ indirectly increase predator numbers, magnifying the potential for exclusion by apparent competition. Similar effects emerge in multihost–parasitoid (Holt & Lawton 1993) and multihost–pathogen models (Holt & Pickering 1985; Begon & Bowers 1995), and models with mixed exploitative and apparent competition (Holt et al. 1994; Grover 1995).

These models depict reasonably well the outcome of shared predation in some systems. Qualitatively, there are now numerous well-documented examples of apparent competition arising from shared predation in laboratory microcosms, field experiments, and 'natural' experiments, in a wide variety of taxa and habitats (Holt & Lawton 1994); for instance, Nakajima and Kurihara (1994) studied a laboratory microcosm consisting of mixed clones of E. coli attacked by the protozoan Tetrahymena thermophila. Clones with either higher growth rates or lower predation rates (namely, higher $r/a$) dominated, because these prey traits increased predator equilibrium density, thereby leading indirectly to exclusion of the alternative prey clone (with lower $r/a$). The laboratory experiments of Lawler (1993) and Balciunas and Lawler (1995) similarly show that in two-prey cultures, the prey with lower $r/a$ tends to be excluded. Shared predation can lead to local exclusion even in quite complex systems (e.g. Hochberg et al. 1994). Mobile predators can generate apparent competition even between prey living in distinct habitats, because of predator 'spillover' (Holt 1984), or coupled colonization–extinction dynamics (Holt 1996).

As with exploitative competition, these theoretical and empirical findings suggest that one sensible research programme is to search for mechanisms of coexistence between prey (Holt & Lawton 1993); for instance, in a patchy environment, if one prey has a greater $r/a$, but the inferior prey is a superior disperser, coexistence may occur at a landscape scale (Hassell et al. 1994).

However, the module of shared predation is intrinsically more complex than that of shared resources. In exploitative competition, species indirectly interact *only* through effects on resource levels. By contrast, predators have functional responses – as well as numerical responses – to prey, leading to the possibility of

indirect mutualisms; for instance, time spent handling one prey species necessarily reduces the time available to capture a second species.

With sufficient constraints on the numerical response, alternative prey might either not interact (if the functional response is linear), or experience a *net* effect of indirect mutualism (Holt & Lawton 1994). This possibility was noted in Holt (1977), some circumstances leading to apparent mutualism have been addressed (e.g. Holt & Kotler 1987; Holt 1987), and empirical examples of indirect mutualism with shared predation are known (Holt & Lawton 1994). Abrams and Matsuda (1996) have recently examined in some detail the conditions leading to apparent competition vs. apparent mutualism in specific models including both non-linear functional responses (producing an indirect (+, +) interaction between prey), and direct density dependence in the predator (reducing the potential for (−, −) apparent competition interactions). They argue that one should expect a mixture of negative and positive net indirect interactions between prey in communities.

Here, I take a different but complementary approach to that of Abrams and Matsuda (in press), using a graphical model that encapsulates important qualitative features of many specific models. I argue that shared predation should have a variable effect on community saturation, and in particular that it may not lead to saturation at all in some circumstances.

Consider a focal prey species (species 2) invading a local community with resident predators, supported by prey species 1. Prey species 2 has a net growth rate when rare of $r_2 - a_2P$, where $P$ is predator density, $a_2$ is the per predator attack rate imposed upon prey 2 (when rare), and $r_2$ is the intrinsic growth rate of this prey. The invader is excluded if $r_2 < a_2P$.

The attack rate on prey 2 can vary directly with resident prey density; for instance, assume predator feeding follows a two-species disc equation, $a_i(R_1,R_2) = a_i'/(1 + a_1'h_1R_1 + a_2'h_2R_2)$, where $a_i'$ is the maximal attack rate on prey species $i$, and $h_i$ the handling time (Murdoch & Oaten 1975). With this model, the per predator attack rate on the invading prey declines with resident prey density.

But predator density also varies with the density and productivity of the resident prey. Assume the predator has a growth equation ($dP/dt = PF(R_1,R_2,P)$), such that $F$ increases with each $R_i$, and declines with $P$, and where prey densities are fixed (say experimentally). Let $R_2 \approx 0$. Equilibrial predator abundance can be determined by setting the predator equation to zero and solving for predator density. Below some prey abundance, the predator cannot persist. Greater prey numbers sustain more predators, but other limiting factors should become progressively more important at higher prey levels, leading to a concave-down relation between realized predator numbers and ambient prey levels. Combining the functional and numerical responses determines the total rate of predation (i.e. $aP$) upon an invader as a function of resident prey abundance. In general, this relation will be an asymmetrical

hump, with the greatest resistance to invasion by a novel prey species at intermediate values of resident prey number (see Fig. 17.2).

Total removal of resident prey eliminates the predator, and so always facilitates invasion by additional prey species. In this broad sense, an invading prey always experiences apparent competition with the entirety of the resident predator's food supply. However, substantial reductions in resident prey abundance (without total removal) may sometimes not markedly alter the intensity of predation experienced by invading prey, and sometimes even lead to more intense predation on the invader. To illustrate this point, consider the following simple model for predator dynamics (the model assumes a type II functional response, a linear relation between prey consumption and predator reproduction, and linear predator density dependence):

$$\frac{dP}{dt} = P\left[\frac{a_1'b_1R_1 + a_2'b_2R_2}{1 + a_1'h_1R_1 + a_2'h_2R_2} - iP - m\right]$$

At low $R_2$, given that the predator is at equilibrium, the relation between resident prey abundance and predator abundance is $P(R_1) = ([b_1a_1'R_1/(1+a_1'h_1R_1)] - m)/i$. The saturating functional response weakens the predator's numerical response as prey numbers rise. The per prey attack rate on the invading prey is $a_2(R_1,0)P(R_1)$.

Manipulating the expression for $a_2P$ reveals that, overall, exclusion of an invading prey species at any given $R_1$ is more likely if: (i) the resident prey is high quality (high $b_1$); (ii) the predator does not easily satiate (low $h_1$); (iii) direct density dependence in the predator is weak (small $i$); and (iv) the predator has a low inherent death rate (low $m$). These parameter combinations enhance the numerical response of the predator to the resident prey and reduce the magnitude of indirect mutualism via the functional response, and thereby ensure that predation upon an invading prey increases with $R_1$ over a wide range of resident prey densities. Converse parameter choices (e.g. high $h_1$) vitiate the numerical response, enhance apparent mutualism resulting from the saturating functional response, and at higher prey levels lead to inverse relations between resident prey abundance and predation pressure on invading prey. There is always some range of prey densities over which increasing $R_1$ heightens predation upon an invading prey, but for some parameter choices this may be observed only for a narrow range of resident prey densities.

There are two ways to interpret the $R$-axis in Fig. 17.2. Increasing the productivity of a single-prey species tends to increase both prey and predator densities, given predator interference. So the figure could describe how predator impact on an invading prey species varies along an environmental gradient in productivity. Alternatively, one could imagine that several roughly equivalent prey species are present, each with their own exclusive resource. Given direct density dependence in the predator, increasing the number of similar prey species should be reflected

in increased total prey numbers (Holt, unpublished data). In this case, the $R$-axis is a reasonable proxy for total prey species richness in the resident community.

For the parameter values leading to Fig. 17.2a, the prey 'guild' (those prey sharing a given predator) could readily exhibit saturation; as prey abundance/species richness rises, additional species should find it increasingly difficult to invade. In Fig. 17.2b, there is little effect of prey abundance/richness, except at low densities; overall there could be considerable variation in the resident prey community, with little effect upon the chance of invasion by additional species. And finally, in Fig. 17.2c, increases in prey abundance/richness may actually facilitate invasion by other prey; a given prey species may be able to invade at very low, or quite high, R, but be excluded at intermediate values.
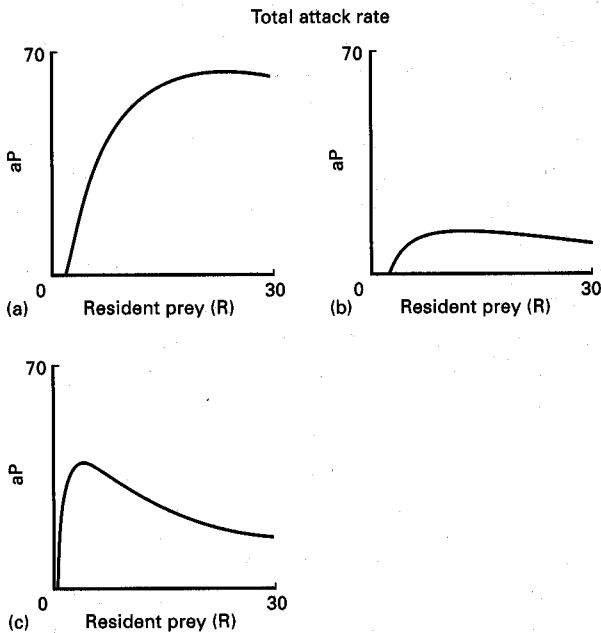


FIG. 17.2. Examples of net effects by resident prey on invasion by an alternative prey (aP), expressed as variation in total mortality along a gradient in resident prey abundance, R (implicitly, gradients in prey productivity or species richness). (a) The predator has a small handling time for the resident prey, and over most of the observed range in resident prey abundance, predation pressure on the invader increases with R ($i = 0.1$, $b_1 = 0.6$, $a_1 = 5$, $h_1 = 0.01$, $m = 5$, $a_2 = 1$). (b) The handling time is larger; this reduces both the attack rate on the invader, and the number of predators sustained by any given prey density (parameters as in Fig. 17.3a, but $h_1 = 0.03$). (c) The predator has weaker density dependence, but a larger handling time, than in (a) or (b); the greatest net effect of the resident prey on the invader is at rather low resident prey densities (parameters as above, but $i = 0.05$, $h_1 = 0.06$).

The above heuristic argument highlights the importance of jointly considering limiting factors other than prey availability, and of non-linear functional responses, in determining the potential for apparent competition, vs. apparent mutualism, in prey guilds. Predator density dependence alone weakens apparent competition, but on its own does not lead to apparent mutualism; without such direct density dependence in the predator, the short-term non-linear functional response, which tends towards indirect mutualism between prey, is overshadowed by the longer-term numerical response, leading to a net effect of apparent competition. However, putting these factors together weakens apparent competition and increases the importance of apparent mutualism via the functional response, particularly at higher resident prey densities.

It should be noted that this graphical argument is incomplete, because the realized abundance of the resident prey is a dependent variable of the system. However, fuller analyses that account for prey dynamics preserve the essential features of the above conclusions (Abrams & Matsuda 1996; Holt, unpublished data). Moreover, the graphical argument assumes that the system is at a stable equilibrium. Recently, Peter Abrams, James Roth and I (unpublished data) have investigated the influence of non-equilibrial dynamics on the net interaction between alternative prey. Briefly, population fluctuations tend to reduce the magnitude of apparent competition, and can produce apparent mutualism even without direct density dependence in the predator.

The following argument reveals a key element in the effect of non-equilibrial dynamics on apparent competition to be direct density dependence in the prey themselves. Consider a system where a predator can persist with either of two alternative prey species. Prey $i$ is initially the resident species. The resident prey dynamics are described by:

$$\frac{1}{R_i}\frac{dR_i}{dt} = r_i(t)g_i(R_i) - a_iP, \quad \frac{dg_i}{dR_i} < 0$$

where $g_i$ describes intra-specific density dependence in prey species $i$. Populations may show temporal variability because of exogenous causes (e.g. variation in $r$), or endogenous causes (e.g. limit cycles due to a saturating functional response).

We assume the resident prey and predator persist indefinitely, despite such fluctuations. Levins (1979) argued that if a population of density $X_i$ varies between an upper bound and a lower bound $> 0$, the long-term time average of the per capita growth rate must be zero:

$$E\left[\frac{1}{X_i}\frac{dX_i}{dt}\right] = \lim_{t \to \infty}\int_0^t\left(\frac{1}{X_i}\frac{dX_i}{dt}\right)dt = 0$$

The expectation operator $E$ is linear, which simplifies consideration of the average consequences of temporal variability in the above model.

Using an overbar as shorthand for expected value, if the resident prey population (say species 1) persists, then

$$\overline{r_1 g_1} = \overline{a_1 P}$$

In other words, average prey productivity must equal average mortality due to predation.

Now consider the invader, prey species 2. Using time averaging again, the invader increases when rare if

$$\overline{r_2} > \overline{a_2 P}$$

Assume that the relative predation pressure imposed on the resident and the invader is constant, or $a_2 P / a_1 P = u$; for instance, with the two-species disc equation, $u = a_2' / a_1'$. After substitution, the condition for invasion now involves a comparison of the average intrinsic growth rate of the invader, and the average productivity of the resident prey, so that prey 2 invades only if

$$\overline{r_2} > u \overline{r_1 g_1}$$

Now assume that the predator is consistently effective at limiting prey numbers (for each species) well below the level where prey experience density dependence, so that $g_i$ is approximately unity. (For persistence of the predator–prey system, this usually requires density-dependence in the predator, such as direct interference, or the induced density dependence provided by a small trickle of immigrant predators, Holt 1993.) This implies that

$$\overline{r_1 g_1} \approx \overline{r_1}.$$

The condition for invasion is now simply

$$\overline{r_2} > u \overline{r_1}$$

Were prey 2 initially present alone, sustaining an efficient predator, one can repeat the above line of argument to show that prey species 1 can invade when rare, provided

$$\overline{r_1} > u^{-1} \overline{r_2}$$

For most combinations of relative attack rates and intrinsic growth rates, it is impossible for both these inequalities to hold; the prey with the higher average intrinsic growth rate, or lower relative attack rate (or both), will exclude the alternative

prey from the community, even if the predator experiences direct density dependence, the prey experience indirect mutualism via the predator's functional response and the environment fluctuates (without affecting relative attack rates). Holt and Lawton (1993) present a similar argument for a two-host, one-parasitoid model.

What this argument shows is that if environmental variability weakens apparent competition, it must be because variability enhances the effects of direct density dependence in the prey. The basic idea is that given a saturating functional response, predator population growth is more sharply and negatively affected by prey declines, than positively affected by prey increases. Thus, for a predator population to match its own density-independent mortality, higher average resource levels are needed in a fluctuating environment, than in a constant environment. With direct density dependence in the prey, higher numbers imply lower prey productivity, which (from above) directly translates into a lower average rate of predation upon the resident prey, and in turn upon the invading prey.

Hence, the magnitude of apparent competition is reduced by temporal fluctuations in prey abundance, which magnify the importance of limiting factors (e.g. resource competition) other than the shared predator.

As prey species are added to a community, their shared predator in effect experiences an enriched resource base. In single-prey species models, enrichment can lead to a decline in average predator abundance, given unstable dynamics (Abrams & Roth 1994). With multiple-prey species, the magnitude of population fluctuations increases with increasing prey species richness, diminishing the overall numerical response by the predator to its prey base and thus making the beneficial effect via the functional response potentially more important. However, if the unstable dynamics induced by high productivity include excursions to low densities by resident prey, the risk of prey extinction due to demographic stochasticity is also enhanced. If enrichment is destabilizing this facilitates initial colonization but can also increase local extinction rates.

Thus, interesting complications may arise if high productivity causes trophic dynamics to become destabilized. This weakens or reverses the expected relationship between productivity and predator abundance, and so tends to reduce the magnitude of apparent competition upon invading prey, but also may increase the extinction rate of resident prey species. The overall effect of these opposing forces on the likelihood of prey community saturation cannot be addressed outside the context of rather detailed models.

The above results permit us to identify major axes of variation among prey communities; different natural enemy–prey ensembles should be more (or less) likely, *inter alia*, to exhibit local saturation in defined prey 'guilds' (prey exploited by the same suite of predators) because of shared predation (namely competition for enemy-free space; Jeffries & Lawton 1984). For instance, prey communities in

variable environments should experience apparent competition less intensely than do prey communities in constant environments, and may be less likely to exhibit saturation because of shared predation.

Along a gradient in productivity, given stable dynamics, saturation in a prey community (defined by difficulty of invasion for non-resident prey) should be most likely at intermediate points on the gradient. At high productivity, the shared predator is likely to be increasingly limited by factors other than prey availability, including higher-order predators and specialist pathogens, reducing the importance of apparent competition relative to indirect mutualism in determining the impact of resident prey on invasion by additional prey species.

However, different prey guilds are likely to reach this maximal level of resistance to invasion at different points along any given environmental gradient, due to idiosyncratic differences in predator and prey traits, and in the suite of limiting factors (particularly other species) impinging on both the prey and their shared predator. The net effect is that saturation due to shared predation may be difficult to discern at the level of entire communities.

## INTRA-GUILD PREDATION

The final module I briefly discuss is 'intra-guild predation' (IGP), which arises whenever predators and their prey also compete for resources (Polis *et al.* 1989). This module combines the elements of exploitative and apparent competition, but in a different way than keystone predation: the intermediate predator competes with the top predator for the basal resource, and the basal resource, by sustaining the top predator, indirectly increases mortality on the intermediate predator. IGP has received much less theoretical attention than the other modules of Fig. 17.1.

Simple models of IGP highlight a substantial problem of species coexistence (Pimm & Lawton 1978; Pimm 1991; Polis & Holt 1992). A necessary condition for coexistence is that the intermediate species be a superior competitor for the basal resource (Pimm 1991; Polis & Holt 1992). Even if this holds, however, exclusion may occur if the top predator imposes too high a rate of mortality on the intermediate predator (Holt & Polis, in press).

Moreover, simple IGP models reveal that highly variable dynamical behaviour can arise, further hampering sustained coexistence. Consider the simplest IGP model, a Lotka–Volterra food chain with an added link between the top and bottom species:

$$\frac{dR}{dt} = R[r(1 - R/K) - aN - a'P]$$

$$\frac{dN}{dt} = N[abR - m - \alpha P]$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = P'[\alpha\beta N + a'b'R - m']$$

Numerical studies of conditions for joint invasibility, and stability of the resulting equilibrium, reveal that relatively small amounts of IGP can strongly destabilize the system (Holt & Polis, in press). Figure 17.3 shows an example. In the case shown, both the top and intermediate predator, when alone, persist stably with the resource, and each can invade the community containing the other. Such invasions, however, set up dramatically violent oscillations, which in practice would foster local extinctions.

Lotka–Volterra models for food chains and multiprey, single-predator systems, always reach stable point equilibria. Complex dynamics in three-species Lotka–
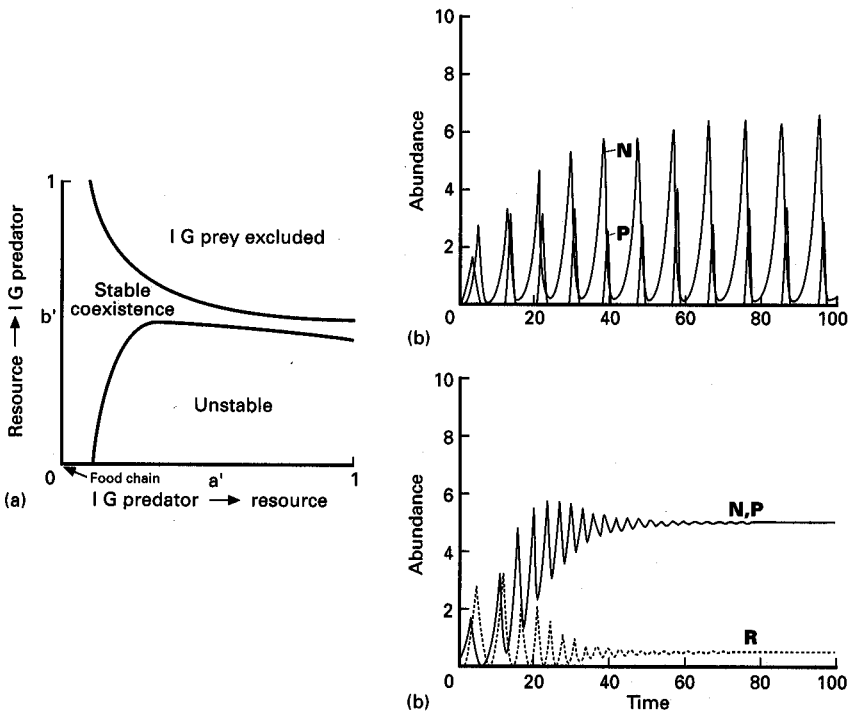


FIG. 17.3. (a) Example of stability domains for the Lotka–Volterra intra-guild model. In the case depicted, $r = 1$, $K = 10$, $a = 1$, $\alpha = 1$, $b = 1$, $m = 0.1$, $m' = 0.5$. (See Holt & Polis, in press for more details). For the stable and unstable parameter sets, each predator can increase when rare. The $a'$-axis is the rate of attack by the top predator on the basal resource ($a' = 0$ leads to a simple food chain); the $b'$-axis is the benefit the predator derives from such attacks. (b) Illustrative samples of dynamical behaviour. Parameter values are as in (a), with $b' = 0.3$ and $a' = 0.01$ (bottom), and $a' = 0.3$ (top).

Volterra systems have previously been reported for three directly competing species (May & Leonard 1975), and for a generalist predator feeding upon two directly competing prey (Gilpin 1979). To my knowledge, this is the first demonstration of unstable dynamics in a Lotka–Volterra model arising when all the inter-specific interactions are linear trophic interactions (though it should be noted that dynamical instability is known in comparable host–pathogen systems, see Hochberg and Holt (1990).

The dynamical instability produced by IGP illustrated in Fig. 17.3 makes it even less likely that simple IGP modules will persist. Yet, there are numerous empirical systems in which IGP is conspicuous (Diehl 1993, 1995; Polis *et al.* 1989). This raises the interesting possibility that something systematic may be missing from the simple models; for example, Diehl (1993) notes in his review that in many examples, the IGP prey has a refuge from predation, and Pimm (1991) notes other recurrent features of systems with IGP. If top predators consistently experience strong intra-specific density dependence, for instance, that would suffice for persistence of the intermediate predator (Holt & Polis, in press). Whether any of these suggestions provide a general, robust explanation for the paradox of systems persisting with strong IGP remains to be seen. What the simple model of the IGP module does is to alert one to an interesting question regarding species persistence in complex communities, and provide guidelines as to key parameters that should be measured, or additional processes that should be considered.

## CONCLUSIONS

Community modules provide community ecologists with a research path that with any luck skirts both the Scylla of unrealistic simplicity, and the Charybdis of unmanageable complexity. Analyses of modules help crystallize our understanding of core processes, which can then be discerned (albeit at times obscurely) as a driving force in many disparate systems. They provide fresh hypotheses for empirical studies. It may be even more interesting when the predictions of a particular module model fail; characterizing the possible reasons for failure helps provide a conceptual framework for organizing the complexity of natural communities, and may provoke the search for new approaches (e.g. constraints on food-chain length may need be sought at the level of regional processes, e.g. colonization–extinction dynamics, rather than local, production-driven dynamics). The examples of community modules explored above all provide examples of this healthy intellectual dynamic.

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