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Prey, predators, parasites: intraguild predation or simpler community modules in disguise?

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Summary

1. Competition and predation are at the heart of community ecology. The theoretical concept of intraguild predation (IGP) combines these key interactions in a single community module. Because IGP is believed to be ubiquitous in nature, it has been subject to extensive research, and there exists a well-developed theoretical framework.

2. We show that a general class of IGP models can be transformed to simpler, but equivalent community structures. This rather unexpected simplification depends critically on the property of 'indiscriminate predation', which we define broadly as the top-predator not distinguishing between its two different prey species.

3. In a broader context, the great importance of IGP and of the simplifying transformation we report here is enhanced by the recent insight that the basic IGP structure extends naturally to host–parasitoid and host–pathogen communities. We show that parasites infecting prey (predators) tend to render IGP effectively into exploitative competition (tritrophic food chain, respectively).

4. The equivalence between the original and simplified community module makes it possible to take advantage from already existing insights. We illustrate this by means of an eco-epidemiological IGP model that is strikingly similar to a classical exploitative competition model.

5. The change of perspective on certain community modules may contribute to a better understanding of food web dynamics. In particular, it may help explain the interactions in food webs that include parasites. Given the ubiquity of parasitism, food webs may appear in a different light when they are transformed to their simplified analogue.

Key-words: eco-epidemiology, exploitative competition, food chains, food webs, parasite–host ecology

Introduction

One approach to investigate the manifold forms of ecological communities with often thousands of interacting species is to identify, in the unmanageable structure of the larger system, a few general patterns of species interaction. Then, by looking at the dynamics that arise from those community modules (Holt 1997), the structure and population dynamics of the whole community may be addressed. Three species modules that have gained much attention among ecologists include tritrophic food chains, apparent competition and exploitative competition (EC). All of these modules assume that two of the three species involved do not directly interact with each other. By contrast, the community module of intraguild predation (IGP) includes direct interaction of all three species.

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In its simplest form, an intraguild predator (IG predator) grazes on an intraguild prey (IG prey), while both share a common prey or basal resource. IGP contains the aforementioned simpler modules as special cases, when either one of the three interactions can be neglected. The theoretical framework of IGP has been laid out in the work of Polis, Myers & Holt (1989) and Holt & Polis (1997). IGP has attracted much attention from ecologists and is believed to be a very common scenario in natural populations (Arim & Marquet 2004). Theoretical studies show that the occurrence of IGP may have important implications for the persistence of food webs and biodiversity; for a comprehensive review, see the special feature on IGP in *Ecology*, vol. 88 (11).

While the original concept of IGP focuses on interactions between predators and their prey, more recently, it has been recognized that the basic structure of IGP arises naturally in several subdisciplines of ecology. In particular, similarities between host–parasitoid and host–pathogen interactions

with classical IGP have been highlighted (Borer, Briggs & Holt 2007). Parasites are recognized as major players in the functioning of ecosystems (Lefèvre *et al*. 2009) and they have subsequently been incorporated into food webs on the trophic level above their hosts (Hochberg, Hassell & May 1990; Raffel, Martin & Rohr 2008). In a similar way, the field of eco-epidemiology has integrated host–pathogen epidemiology with community ecology (Anderson & May 1986; Holt & Dobson 2006; Holt & Roy 2007). As such, on the community level, parasites and pathogens have been found to play a role analogous to classical predators.

Thus, even though predators, parasites and pathogens differ substantially in terms of body size, generation times, durability and intimacy of the interaction with their resource, a unification of host–parasite and prey–predator interactions within the IGP framework may provide useful insights across the borders of ecological subdisciplines. This paper shows that parasitism does not only fit into the IGP framework, but that it may suggest a different and rather unexpected perspective on the underlying community structure. Technically, this change of perspective corresponds to a transformation of variables, a powerful tool routinely used across all scientific disciplines. Physics, for example, is abound in problems that may appear intractable in one coordinate system, but which get dramatically simplified by an appropriate coordinate transformation. Similar changes in the frame of reference have also lead to fresh insights into problems in ecology and evolution, such as replacing absolute values by time-averaged values to explain the coexistence of species in variable environments (Levins 1979) or looking at gene numbers rather than gene frequencies (Holt & Gomulkiewicz 1997).

Using this approach, we will first show that after an appropriate transformation of variables, particular cases of IGP are structurally similar to 'simpler' community modules. We will then demonstrate that this structural similarity also translates into remarkably similar community dynamics. These similarities can be effectively exploited to bridge gaps in our current understanding of food webs, as suggested already by Holt & Polis (1997).

Transformation of IGP

In this section, we show how an IGP module can be transformed into simpler module structures. The only condition concerns indiscriminate predation (see below for a definition). The model considered here is deliberately very general. This highlights that the transformation of IGP into other food web modules is not restricted to certain functional responses and growth functions. The next sections will introduce a more specific example illustrating the benefits of the module transformation.

A GENERAL MODEL OF IGP

We begin with an IGP module consisting of a basal prey A, an IG prey B and an IG predator P (Fig. 1). A, B and P are assumed to represent the total biomass of each species. Interactions between the species lead to the conversion of biomass, which is illustrated by the arrows in Fig. 1. In general, there is no one-to-one correspondence between the outflow of resource biomass and the subsequent increase of consumer biomass. To account for the conversion efficiency, the flow of biomass is often split into a functional response of the resource and the corresponding numerical response of the consumer. In Fig. 1, an upper (lower) case letter at the tail of an arrow corresponds to the biomass flow associated with the functional (numerical) response, respectively.

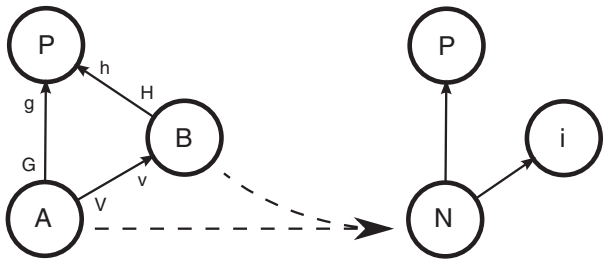

Fig. 1. Transfer diagram for IGP (left) and exploitative competition (right). An IGP module is equivalent to exploitative competition when the two prey species A and B are similar from the IG predator's (P) point of view; see the main text.

The IGP community is then described by the following set of differential equations

$$\frac{dA}{dt} = \underbrace{r(A,B)}_{\text{production}} \quad \underbrace{-V(A,B)}_{\text{consumption by } B} \quad \underbrace{-G(A,B,P)}_{\text{consumption by } P}, \qquad \text{eqn 1}$$

$$\frac{dB}{dt} = \underbrace{v(A,B)}_{\text{conversion of } A} \quad \underbrace{-H(A,B,P)}_{\text{consumption by } P} \quad \underbrace{-n(B)}_{\text{natural mortality}}, \qquad \text{eqn 2}$$

$$\frac{dP}{dt} = \underbrace{g(A,B,P)}_{\text{conversion of } A} \quad \underbrace{+h(A,B,P)}_{\text{conversion of } B} \quad \underbrace{-m(P)}_{\text{natural mortality}}, \qquad \text{eqn 3}$$

where $V(A,B)$ and $v(A,B)$ denote the biomass flow from species A to B; $G(A,B,P)$ and $g(A,B,P)$ the biomass flow from A to P; and $H(A,B,P)$ and $h(A,B,P)$ the biomass flow from B to P. There are three more demographic processes. First, there is an inflow r of biomass into the community, corresponding to intrinsic growth of the basal prey A. We assume that this growth may, in general, also depend on the IG prey. For example, the IG prey might be lowering the reproductive success of the basal prey through competition for essential resources, a scenario that arises naturally in eco-epidemiology. A model where this is the case will be discussed in the next section. The two other processes not describing direct interaction of two species are natural mortality of the IG prey, $n(B)$, and IG predator, $m(P)$.

INDISCRIMINATE PREDATION

Having thus formalized the description of an IGP community in very general terms, we now consider some scenarios where there is little or no distinction between the IG prey and

basal prey from the IG predator's point of view. Such scenarios, for example, arise naturally in eco-epidemiology, when a predator P grazes upon a prey population that is affected by an infectious disease. The disease splits the otherwise homogeneous prey population into a susceptible portion A and an infected portion B. Because both groups are subject to predation by P, the susceptibles A may be considered as a basal resource for the infecteds B and the IG predator P. Another example concerns host–parasitoid systems, where two different parasitoids depend on the same host species A and a parasitoid is able to outcompete the other one within the host (Holt & Hochberg 1998; Raffel *et al*. 2008). The underlying assumption is that the hyperparasitoid does not or is not able to distinguish between healthy hosts A and already parasitized hosts B. A similar scenario is related to hyperinfections, where one pathogen is able to infect healthy and already diseased hosts and becomes the solely transmitted pathogen. In the latter two examples, P denotes the portion of hosts that are infested by the hyperparasitoid or infected by the hyperinfectious agent, respectively.

Last but not least, 'classical' IGP communities with little or no distinction between basal prey and IG prey may also arise in predator–prey ecology. For example, the wolf spider species *Pardosa milvina* and *Hogna helluo* both ordinarily prey on crickets and they also readily consume smaller individuals of the other species. While the relative strength of these predatory interactions in natural situations is not fully known, at least under laboratory conditions *Pardosa* appeared to make no difference between its basal cricket prey and small juvenile *Hogna* intraguild prey (Rypstra & Samu 2005).

Let us now put into more rigorous terms the assumption that the IG predator does not or cannot distinguish between IG prey and basal prey. This means, first, that the IG predator's attack rate is the same for both prey species. That is, the ratio of the consumption rates of B and A equals the ratio of abundances B and A:

$$\frac{H(A,B,P)}{G(A,B,P)} = \frac{B}{A}. \qquad \text{eqn 4}$$

Second, the total flow of biomass to the IG predator and its conversion from the two prey species depend only on the sum of the two prey species:

$$\begin{aligned} g(A,B,P) + h(A,B,P) &= f(A+B,P), \\ G(A,B,P) + H(A,B,P) &= F(A+B,P). \end{aligned} \qquad \text{eqn 5}$$

In other words, the numerical and functional responses can be subsumed when we lump together the two prey species A and B. Equations (4–5) express that the IG predator does not distinguish between IG and basal prey, and that the latter two are energetically equivalent. We will refer to these properties as *indiscriminate predation*. Obviously, they do not hold in general. In particular, they are not fulfilled for predators with a preference for certain prey, or for manipulative parasites that make their host easier to catch.

THE TRANSFORMED MODEL

For many communities such as those described earlier, we may safely assume indiscriminate predation. In this case, we can sum up both groups A and B and deal with the total prey biomass $N = A + B$. Because we still want to keep track of the distinct groups that make up the total prey population N, we introduce the prey ratio $i = B/A$ of IG prey B to basal prey A, assuming $A > 0$. The IG predator variable is not modified and the original prey quantities can be obtained as $A = N/(1+i)$ and $B = Ni/(1+i)$.

Now, how does the general model look like from this perspective? As the new variables N and i essentially correspond to a change of coordinates, eqns (1–3) can be transformed accordingly. This leads to the following model (see Appendix S1 for more details):

$$\frac{\mathrm{d}N}{\mathrm{d}t} = \underbrace{r(N,i) - n(i)}_{\text{total prey growth}} \quad \underbrace{-[V(N,i) - v(N,i)]}_{\text{transition to } i} \quad \underbrace{-F(N,P)}_{\text{consumption by } P}, \qquad \text{eqn 6}$$

$$\frac{\mathrm{d}i}{\mathrm{d}t} = \left[\underbrace{v(N,i) + i\,V(N,i)}_{\text{increase of portion } i} \quad \underbrace{-i\,r(N,i)}_{\text{emergent loss}} \quad \underbrace{-n(i)}_{\text{natural mortality}} \right] \frac{1+i}{N}, \qquad \text{eqn 7}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = \underbrace{f(N,P)}_{\text{consumption of totalprey}} \quad \underbrace{-m(P)}_{\text{natural mortality}}, \qquad \text{eqn 8}$$

In this different but equivalent description of the general IGP scenario (1–3), the IG predator P appears as a consumer on the total prey population N. Note that eqn (8) does not depend on i. The most important difference to model (1–3) is that the prey ratio i interacts only with the total prey N, i.e. Equation (7) is independent of P. The emergent loss term in eqn (7) for the prey ratio is because of the differential growth of basal prey and IG prey, and it reflects the lag with which basal prey growth is propagated through the trophic link to the IG prey. It will become clear in the next section that for biologically meaningful growth functions r, the prey ratio i can in fact be regarded as a consumer on N. This places the total prey biomass N at the bottom of the resulting community diagram, and we end up with two consumers P and i on a single resource N. This is the well-known structure of EC. A corresponding transfer diagram is shown in Fig. 1.

AN EXAMPLE FROM ECO-EPIDEMIOLOGY

We now apply the transformation described in the previous section for the general system to an example from eco-epidemiology (Hilker & Malchow 2006). This model is of IGP type and describes a predator–prey community with an infection of the prey. The infectious disease splits the prey population into a susceptible portion A and an infected portion B. The predator is denoted by P and is assumed not to distinguish

Table 1. Model equations of the intraguild predation (IGP) and exploitative competition (EC) modules; see main text for the meaning of variables

Model	Equations	
IGP Hilker & Malchow (2006)	$\frac{dA}{dt} = \underbrace{r\,(1-(A+B))\,A}_{\text{susceptible growth}} \quad \underbrace{-\frac{\lambda\,A\,B}{A+B}}_{\text{infection}} \quad \underbrace{-\frac{a\,A\,P}{h+A+B}}_{\text{predation}}$	(T1)
	$\frac{dB}{dt} = \underbrace{\frac{\lambda\,A\,B}{A+B}}_{\text{infection}} \quad \underbrace{-\frac{a\,B\,P}{h+A+B}}_{\text{predation}} \quad \underbrace{-\mu\,B}_{\text{virulence}}$	(T2)
	$\frac{dP}{dt} = \underbrace{\varepsilon\,\frac{a\,(A+B)\,P}{h+A+B}}_{\text{predation of all prey}} \quad \underbrace{-m_P\,P}_{\text{natural mortality}}$	(T3)
Transformed IGP	$\frac{dN}{dt} = \underbrace{\frac{r}{1+i}(1-N)\,N}_{\text{total prey growth}} \quad \underbrace{-\frac{\mu\,i\,N}{1+i}}_{\text{infection within prey}} \quad \underbrace{-\frac{a\,N\,P}{h+N}}_{\text{predation}}$	(T4)
	$\frac{di}{dt} = \underbrace{r\,i\,N}_{\text{linear infection increase}} \quad \underbrace{-(\mu+r-\lambda)\,i}_{\text{constant loss}}$	(T5)
	$\frac{dP}{dt} = \underbrace{\varepsilon\,\frac{a\,N\,P}{h+N}}_{\text{predation of all prey}} \quad \underbrace{-m_P\,P}_{\text{natural mortality}}$	(T6)
EC Armstrong & McGehee (1980)	$\frac{dA}{dt} = \underbrace{r\,(1-A)\,A}_{\text{prey growth}} \quad \underbrace{-a_1\,A\,B}_{\text{linear predator}} \quad \underbrace{-\frac{a_2\,A\,P}{h+A}}_{\text{nonlinear predator}}$	(T7)
	$\frac{dB}{dt} = \underbrace{\varepsilon_1\,a_1\,A\,B}_{\text{prey consumption}} \quad \underbrace{-m_1\,B}_{\text{natural mortality}}$	(T8)
	$\frac{dP}{dt} = \underbrace{\varepsilon_2\,\frac{a_2\,A\,P}{h+A}}_{\text{prey consumption}} \quad \underbrace{-m_2\,P}_{\text{natural mortality}}$	(T9)

between sound and diseased prey, thereby fitting the above-mentioned scenario of indiscriminate predation. The model equations are given in Table 1 ('IGP model').

The susceptibles are assumed to grow logistically with intrinsic growth rate r, while the infecteds do not reproduce anymore. However, they still do contribute to the common carrying capacity. The spread of the infection is assumed to follow a frequency-dependent incidence rate with transmissibility λ. Note, however, that the alternative assumption of density-dependent disease transmission yields qualitatively similar results. Predation is modelled by a Holling type II functional response for both susceptibles and infecteds, with equal predator attack rate a and half-saturation constant h. The conversion efficiency is given by ε lying between 0 and 1. The parameter m_P is the predator mortality rate and the infecteds suffer a disease-induced mortality μ.

We now apply the coordinate transformation with $N = A + B$ denoting the total prey population and $i = B/A$ the ratio of infecteds to susceptibles, to obtain the 'transformed IGP model' shown in Table 1. While the equation of the IG predator remains essentially unchanged, the most interesting part is the interaction between prey ratio i and total prey N. Focusing on eqn (T5), the prey ratio i can be viewed as a linear predator of Lotka–Volterra type on N. The associated functional response of the total prey N however is nonlinear, saturating for large prey ratios i. Nevertheless, it can be shown that this yields the same nullcline structure as for a linear predator (Turchin 2003).

As a consequence, the prey ratio i and the IG predator P are consumers of the shared resource N. Besides this structural change, the growth rate of the total prey N has an additional factor $1/(1 + i)$ reflecting that only susceptibles reproduce. In summary, the per-capita growth rates of P and i are functions only of the total prey population. The transformed IGP model thus describes two coupled consumer-resource systems. As suggested in the previous section, it thus corresponds to the community module of EC.

In fact, the transformed IGP model is very similar to a well-known model of EC proposed by Armstrong & McGehee (1980). It describes a linear predator B and a nonlinear predator P sharing a common prey species A. The equations are given in Table 1 ('EC model'), where a_1 and a_2 are attack rates, ε_1 and ε_2 conversion efficiences and m_1 and m_2 per-capita mortalities. The remainder parameters are similar in their meaning to the eco-epidemiological model. There are only two structural differences between the two models, namely the reduced growth rate of the prey N in eqn (T4) and the saturating functional response associated with the prey ratio i. The next section will show that, despite these differences, the overall structural similarity is reflected in a similar dynamical

behaviour, revealing a deep connection between the original eco-epidemiological IGP model and the ecological EC model.

IGP AND EC MODELS: SIMILARITY IN STRUCTURE AND BEHAVIOUR

The eco-epidemiological IGP model predicts a switch in dominance from one consumer to another along an environmental gradient. For example, if the basal prey productivity (r) varies, the disease excludes the predators at low values of r, whereas the predators exclude the disease at high values of r. Coexistence of all three species is possible at intermediate productivities. In a general IGP model, the IG prey should be the better competitor for the shared basal prey, whereas the IG predator should primarily exploit the IG prey (Holt & Polis 1997). These conditions for coexistence, however, are only necessary but not sufficient. Interestingly, coexistence in our transformed IGP model is only possible in form of non-equilibrium dynamics. This is also a very characteristic feature of EC models, cf. Koch (1974); Armstrong & McGehee (1980); Abrams, Brassil & Holt (2003), where cyclic oscillations allow two consumers to persist on a single resource; the heuristic principle of competitive exclusion (Hardin 1960) does not hold in general for nonlinear EC models.

This similarity between the IGP and the EC model already gives a hint of the usefulness of the simple coordinate transformation. In the following, we will investigate the cyclic coexistence in more detail. Throughout this investigation, we will use a fruitful cross-fertilization between the EC and the IGP model: Well-known results from the EC model also hold for the IGP model, and new insights discovered in the IGP model apply to the EC model as well. A summary is given in Table 2.

One similarity in dynamical behaviour that is already known for both models concerns extremely long transients before the cycling populations phase-lock to a regular oscillation. Abrams *et al.* (2003) illustrate this with an example of transient asynchronous cycles, while Hilker & Malchow (2006) refer to this phenomenon as 'strange' periodic cycles.

It is also Abrams *et al.* (2003) who present the first numerical evidence for even more complicated dynamics, namely chaos, in Armstrong and McGehee's EC model. This raises the question whether chaos may occur in the eco-epidemiological IGP model as well. And indeed, the population cycles undergo a cascade of period-doublings before eventually becoming chaotic. This is shown in the bifurcation diagrams for both the IGP and EC models in Fig. 2.

Moreover, numerical experiments show that there exist at least two stable attractors in the IGP model for certain parameter ranges. Abrams *et al.* (2003) also briefly report on alternative attractors, which are periodic in all cases they observed. Here, we show in Fig. 2 that one of the coexisting attractors can be chaotic.

In both models (Fig. 2), one of the two attractors exists over the whole parameter range investigated. By contrast, the other attractor seems to exist only for a certain parameter range. Both attractors undergo a period-doubling cascade to chaos. At some point in the parameter space, this leads to the coexistence of a periodic and a chaotic attractor.

Consequently, fundamentally different dynamics can be observed depending on the initial conditions, or the 'history' of the ecological community. The alternative basins of attraction of the two attractors are arranged in an intricate way (Appendix S2), which implies that the community dynamics are extremely fragile to perturbations.

Returning to the bifurcation scenario itself, a closer look reveals that there are some discontinuities in the attractors. Such sudden qualitative changes in the shape of a chaotic attractor as a parameter is varied are called attractor crises. Figure 2 suggests that there are two types of crises, namely a

Table 2. Types of dynamical behaviour in the exploitative competition (EC) and intraguild predation (IGP) modules

Behaviour	Biological meaning	EC model		IGP model
Cyclic coexistence	Community persistence, regular oscillations	Armstrong & McGehee (1980)		Hilker & Malchow (2006)
Asynchronous transients	Asynchronous oscillations which may prevail depending on initial conditions	Abrams *et al.* (2003)		Hilker & Malchow (2006)
Chaos	Irregular fluctuations, long-term unpredictability	Abrams *et al.* (2003)	$\longrightarrow$	This paper
Coexistence of periodic attractors	Cycle amplitudes and frequency depend on initial conditions	Abrams *et al.* (2003)	$\longrightarrow$	This paper
Coexistence with a chaotic attractor	Oscillations may be regular or irregular depending on initial conditions	This paper	$\longleftarrow$	This paper
Boundary crisis	Sudden population crashes, transient chaos	This paper	$\longleftarrow$	This paper
Interior crisis	Irregular spikes corresponding to population outbreaks	This paper	$\longleftarrow$	This paper

The arrows indicate the direction of cross-fertilization; i.e. the knowledge existing for one community module can be transferred to another community module.

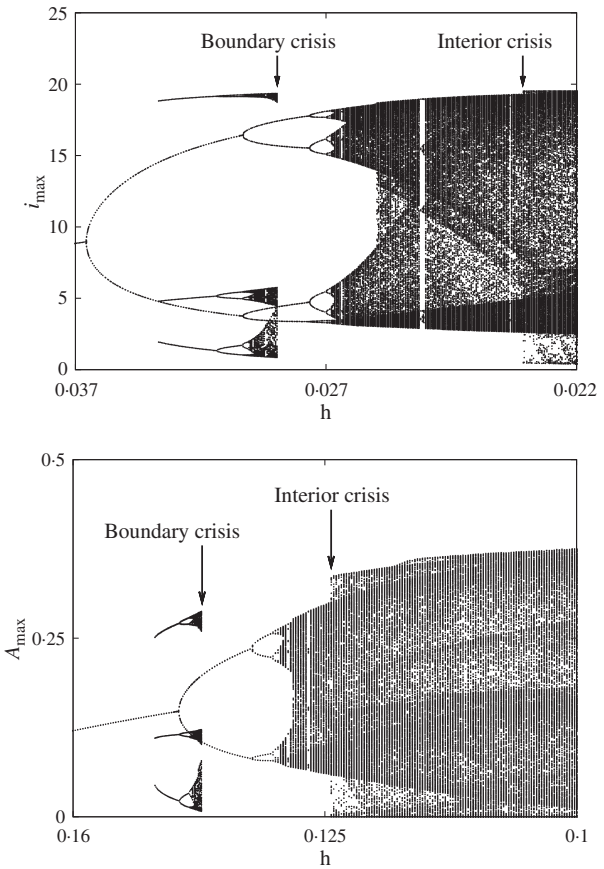

Fig. 2. Dynamical behaviour of the eco-epidemiological (transformed IGP) model (top) and the Armstrong–McGehee (EC) model (bottom). The bifurcation diagrams are qualitatively similar, suggesting an equivalence between the two community modules. Parameter values (top) $r = 1$, $\mu = 0{\cdot}15$, $m_P = 0{\cdot}8$, $\lambda = 0{\cdot}8$, $a = 1$, $\varepsilon = 1$; (bottom) $r = 0{\cdot}5$, $a_1 = 2{\cdot}5$, 1 and $0{\cdot}85$, $m_2 = 0{\cdot}3$, $\varepsilon_1 = \varepsilon_2 = 1$. The half-saturation constant h is the control parameter, note the reversed axis.

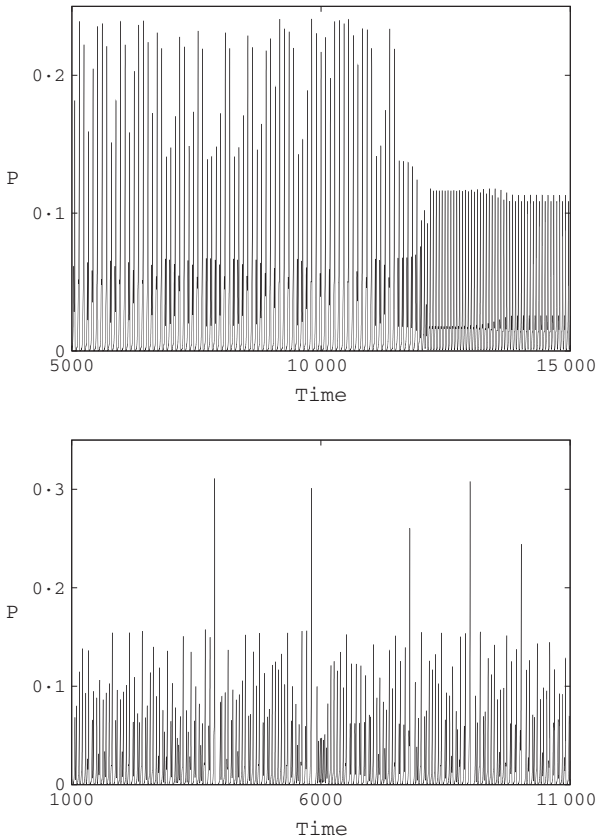

Fig. 3. Sample time plots in the vicinity of the attractor crises of the eco-epidemiological IGP model. Top: Transient chaos close to the boundary crisis ($h = 0{\cdot}0284$). The solution starts close to the formerly existing chaotic attractor but eventually settles on a periodic cycle. Bottom: Irregular spikes of unusually high population densities occur after the interior crisis of the chaotic attractor ($h = 0{\cdot}0222$). These correspond to a blow-up of the attractor in phase space. Other parameter values as in Fig. 2.

boundary crisis and an interior crisis. The former is associated with the destruction, or creation, of a chaotic attractor. The latter causes changes in the size of the attractor, for example the blow-up of an attractor, so that it suddenly occupies a larger region in phase space (Grebogi, Ott & Yorke 1983).

The consequences of attractor crises are illustrated in Fig. 3. First, the sudden loss of a chaotic attractor because of a boundary crises is associated with transient chaotic dynamics. That is, time series starting from initial values formerly in the basin of attraction of the chaotic attractor show a chaotic transient before eventually approaching the remaining periodic attractor (Fig. 3). Second, interior crises lead to irregular spikes of significantly higher population sizes. This can also be seen in the time series of population sizes (Fig. 3). These spikes correspond to infrequent visits of the chaotic trajectory to regions of the phase space, which did not belong to the attractor before the crisis. These regions are sometimes called the halo of the attractor, and for decreasing half-saturation constant h, the trajectory spends more and more time in the halo.

From intraguild predation to food chains

In the previous sections, we transformed a module of IGP into EC. This rested on the assumption that both the basal prey and IG prey are similar from the IG predator's point of view. In the case that the IG predator and the IG prey are similar from the basal prey's point of view, the IGP module may be transformed into a food chain. An example is given in Appendix S3, where we consider a special case of a model of IGP suggested by Tanabe & Namba (2005). By transforming variables to total predator population and the ratio of IG predator to IG prey, we arrive at a module structure corresponding to a food chain.

While this example originally stems from classical predator–prey ecology, it may also be interpreted as an eco-epidemiological model describing the spread of a vertically as well as horizontally transmitted disease in the predator population. In this interpretation, the IG prey represents the susceptible predator subpopulation and the IG predator the infected subpopulation, with the attack rate of the IG predator corresponding to the transmissibility of the disease and

assuming a perfect conversion efficiency. Underlying this interpretation is the assumption that the disease does not significantly alter the predation or consumption behaviour of infected individuals, thus only manipulating the mortality rate of the infected subpopulation.

Discussion

Food webs and their basic modules are fundamental in our understanding of ecosystems and their stability (McCann 2000). The results presented here suggest a new perspective on the structure and topology of food webs. Modules that were previously thought of as IGP may be equivalent to apparently simpler units. IGP could effectively be EC or a tritrophic food chain 'in disguise'.

The equivalence of these modules depends critically on two assumptions that can be described shortly as indiscriminate predation. First, the consumer does not discriminate between its two resources. Second, the two resources are energetically equivalent for the consumer. In other words, even though one resource species predates the other one, they are quite similar – at least from the consumer's point of view. Note that this is not to be confused with a general similarity that would suggest to lump the species together. We actually need to keep track of their ratio because the two species function differently. Instead of the ratio, however, one can alternatively use the notion of prevalence, which is particularly apt in epizootic contexts.

Eco-epidemiological systems constitute prominent examples, because infection with a disease does not always alter predation preferences. For instance, this is believed to hold for the grazing of virally infected phytoplankton by zooplankton (Suttle 2005; Hilker & Malchow 2006). However, if parasites manipulate their host to induce discriminate predation (e.g. Lefèvre *et al.* 2009), then the transformation of food web modules presented here is not possible. Nevertheless, it should be noted that the results of this paper are not limited to nonmanipulating parasites; the critical conditions are rather general and likely to apply to other IGP structures as well, which involve top-predators, parasitoids, hyperinfections and size-structured cannibalism when large adult predators do not discriminate between small conspecifics and the shared basal prey.

When does an IGP module transform into EC and when into a food chain? In simple words, infection of the prey leads to EC, whereas infection of the predator leads to a tritrophic food chain. In the former case, we subsume the basal and IG prey. In the latter case, we subsume the IG prey and predator. There is one combination left, namely combining the IG predator and the basal prey. Doing so leaves the position of the IG prey in the food web essentially unchanged; it still retains its distinct feature of being both a resource (to the IG predator) and a consumer (of the basal prey). In particular, such a coordinate transformation does not lead to the module of apparent competition, the only trophic module that does not appear within these transformations. This is noteworthy as many studies addressing parasites shared by multiple host species concern apparent competition phenomena (Hatcher, Dick & Dunn 2006; Lefèvre *et al.* 2009).

The equivalence of food web modules can be fruitfully utilized to find analogies in community dynamics and stability. We have transferred the knowledge stemming from a well-known and long-investigated EC model (Armstrong & McGehee 1980; Abrams *et al.* 2003) to a recent eco-epidemiological model exhibiting IGP structure. Furthermore, we found a whole suite of dynamical behaviour in the eco-epidemiological model that has, to our knowledge, not been reported before in any IGP structure (Table 2). We have also shown that all these types of behaviour may arise in the classical EC model as well. The dynamics in both the IGP and EC are remarkably similar (cf. Fig. 2).

For instance, both the IGP and EC model can be bistable and have coexisting attractors, one of them possibly being chaotic. The noise inherent in the environment and typical for nature can repeatedly trigger a population to jump from a low-abundance to a high-abundance state. Dwyer, Dushoff & Yee (2004) find this mechanism to be instrumental in explaining episodic outbreaks of forest-defoliating insects such as the gypsy moth (*Lymantria dispar*) which occur at long, but irregular intervals. Interestingly, both pathogens and predators seem to be key in understanding these outbreaks.

Coexisting attractors and associated boundary crises have also been found in a stage-structured model of flour beetle (*Triboleum castaneum*) population dynamics (Cushing *et al.* 2003). McCann & Yodzis (1994) point out how boundary crises can be responsible for unexpected population crashes. The equivalence of food web structure implies that IGP models are prone to such sudden extinctions of species as well – even though this may not be readily anticipated from the model formulation.

Parasitism is the most common consumer strategy (Price 1980; de Meeûs & Renaud 2002) and increasingly recognized to dominate food webs (Lafferty, Dobson & Kuris 2006; Lafferty *et al.* 2008). The presence of parasites typically renders predator–prey interactions into IGP modules (Borer *et al.* 2007). In this paper, we have shown that these seemingly more complicated modules can be equivalent to EC or food chains. That is, the omnivory link typical for IGP appears to be redundant when a pair of interacting species is relatively similar to their consumer or their shared resource.

This redundant link may well alter topological statistics of food webs. Parasites remain difficult to be incorporated into food web models, even though their importance is acknowledged in recent findings. Food webs can contain more host–parasite than predator–prey links (Lafferty *et al.* 2006) and parasite biomass can exceed that of top-predators (Kuris *et al.* 2008). This ubiquity of parasites underlines the need of a holistic food web theory. The results presented in this paper highlight the potential impact of parasites (and other consumers) and open avenues to a better understanding of their dynamical behaviour.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details of the coordinate transformation.

Appendix S2. Basins of attraction in the case of multistability.

Appendix S3. An example of an IGP module transformed into a food chain.

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Supporting Information

Michael Sieber and Frank M. Hilker. Prey, predators, parasites: intraguild predation or simpler community modules in disguise?

Appendix S1. Details of the coordinate transformation

Here we show how to change the state variables of a differential equation model. The idea is to subsume two populations (e.g. total prey) and to keep track of the distribution of the two prey populations in another new variable (e.g., ratio of prey B to prey A, $A > 0$). That is, we transform the model according to the map

$$\begin{pmatrix} A \\ B \\ P \end{pmatrix} \mapsto \begin{pmatrix} A+B \\ B/A \\ P \end{pmatrix} = \begin{pmatrix} N \\ i \\ P \end{pmatrix}.$$

With the assumption of indiscriminate predation (see main text), the transformed system (6-8) is then obtained as follows.

1. The differential equation for the predators P is easiest to determine, as we keep this state variable. We simply have to subsume $A+B=N$ in the original Eq. (3) to give Eq. (8) in the main text.
2. The differential equation for the total prey population $N=A+B$ is obtained by

$$\frac{\mathrm{d}N}{\mathrm{dt}} = \frac{\mathrm{d}A}{\mathrm{dt}} + \frac{\mathrm{d}B}{\mathrm{dt}}.$$

   The predation terms can be subsumed by using the identity $N=A+B$. The growth term applies only to the susceptible prey $A= N/(1+i)$, and the virulence only to the infected prey $B=N\,i/(1+i)$. This gives Eq. (6).
3. Finally, the differential equation for the ratio i of prey species (e.g. infecteds to susceptibles) requires a bit more care. The reason is that we have to use the quotient rule in order to get the time derivative. That is

$$i' = \left(\frac{B}{A}\right)' = \frac{B'A - BA'}{A^2},$$

where the prime denotes differentiation with respect to time. We can replace B' and A' by the right-hand sides of Eqs. (2) and (1), respectively. Then we are left with substituting A and B as before. Simplifying terms eventually gives Eq. (7).

Appendix S2. Basins of attraction in the case of multistability

In the case of alternative attractors, the initial conditions determine which one of the attractors will be eventually approached. This raises the question how the basins of attraction of the two attractors are arranged in phase space. Here, the basin of attraction of an attractor denotes the set of all initial values for which the corresponding solution asymptotically approaches this attractor. Since we consider a three-dimensional model, a high resolution scan of the phase space would require an immense amount of computation time. Thus, we restrict the scan to a plane with $B = 0.5$ fixed in order to give an impression of the basins of attraction.

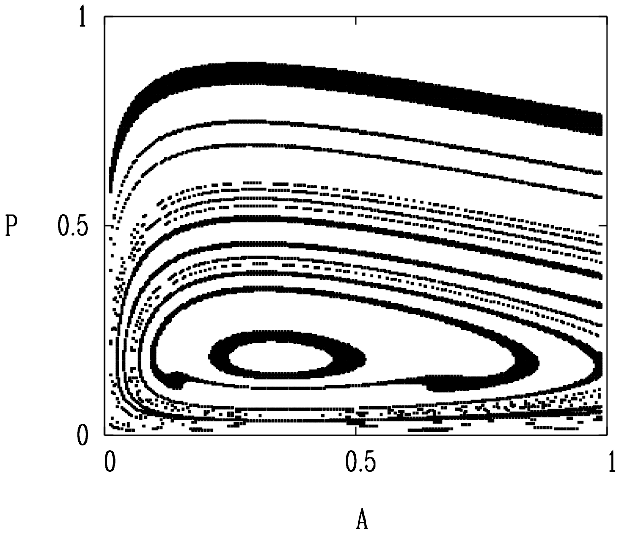

Figure S1: Basins of attraction for the exploitative competition (EC) model (Armstrong & McGehee, 1980). Black indicates initial values, for which the corresponding solution approaches the chaotic attractor. White indicates initial values, for which the periodic attractor is approached. For this diagram, solutions starting in 46,522 different points on the fixed plane *B = 0.5* have been investigated for their asymptotic behavior. Model equations are (T7)-(T9) in the main text; parameters: $r = 1, a_1 = 5, a_2 = 1, h = 1/7, m_1 = 1.7, m_2 = 0.6, \varepsilon_1 = \varepsilon_2 = 1$**.**

The result of the scan is shown in Fig. S1. The parameter set is chosen such that one attractor is periodic and the other one is chaotic. Even though only a two-dimensional transect has been explored and the resolution of the scan is not high enough to reproduce all details of the basin boundaries, the intricate structure of the basins of attraction is nevertheless visible.

The basins of attraction seem to be made up of interleaved circular regions on the plane. This gives a hint of the three-dimensional structure of the basins, which might look like nested tubes.

Appendix S3. Transformation of IGP into a food chain

Here we show that an IGP module can be transformed into a food chain when the IG predator and prey are similar from the basal prey's point of view. We start with the following IGP model studied by Tanabe & Namba (2005), where *A*, *B*, and *P* are the basal prey, IG prey and IG predator, respectively:

$$\frac{dA}{dt} = \underbrace{r(1-A)A}_{\text{logistic growth}} - \underbrace{qAP}_{\text{predation by } P} - \underbrace{qAB}_{\text{predation by } B}, \quad \text{(S1)}$$

$$\frac{dB}{dt} = \underbrace{\varepsilon qAB}_{\text{consumption of } A} - \underbrace{\lambda BP}_{\text{predation by } P} - \underbrace{m_B B}_{\text{natural mortality}}, \quad \text{(S2)}$$

$$\frac{dP}{dt} = \underbrace{\varepsilon qAP}_{\text{consumption of } A} + \underbrace{\delta\lambda BP}_{\text{consumption of } B} - \underbrace{m_P P}_{\text{natural mortality}}. \quad \text{(S3)}$$

Note that the two predators have equal preferences for and attack rates of the basal prey. This satisfies the condition of indiscriminate predation and yields a special case of the original Tanabe-Namba model ($a_{12} = a_{13}$ and $a_{21} = a_{31}$ in their formulation). Introducing the total predator population $C=P+B$ and the ratio $i=P/B$ of IG predator to IG prey leads to

$$\frac{dA}{dt} = \underbrace{r(1-A)A}_{\text{logistic growth}} - \underbrace{qCA}_{\text{predation by } C}, \quad \text{(S4)}$$

$$\frac{dC}{dt} = \underbrace{\varepsilon qAC}_{\text{consumption of } A} - \underbrace{\frac{(1-\delta)\lambda C + m_P}{1+i} Ci}_{\text{loss due to } i} - \underbrace{\frac{m_B}{1+i} C}_{\text{mortality}}, \quad \text{(S5)}$$

$$\frac{di}{dt} = \underbrace{\frac{\delta + i}{1+i} Ci}_{\text{gain from C}} - \underbrace{(m_P - m_B)i}_{\text{mortality}}. \quad \text{(S6)}$$

This is a food chain from *A* to *C* to *i*. While *C* is a linear predator on *A*, the biomass flow from *C* to *i* is a bit more complicated. For $\delta = 1$ (perfect conversion efficiency), the “top-predator” *i* is linear in Eq. (S6) and nonlinear in Eq. (S5), yielding again a linear nullcline structure. This assumption would apply to the case of *P* and *B* being diseased and healthy predators, respectively.

In this model, coexistence of all three species is possible on a stable equilibrium. For some parameter ranges, we found numerical evidence of bistability (stable coexistence vs. extinction of one species and oscillations in the remainder two populations). However, we could not find chaotic dynamics that has been reported in Tanabe & Namba (2005) and is also known to occur in tri-trophic food chains with nonlinear predators (Hastings & Powell, 1991). This may be due to the fact that we are considering the special case of non-discriminating predators.

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