Aggregation, intraguild interactions and the coexistence of competitors on small ephemeral patches

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It is well established that intraspecific aggregation has the potential to promote coexistence in communities of species competing for patchy ephemeral resources. We developed a simulation model to explore the influence of aggregation on coexistence in such communities when an important assumption of previous studies – that interspecific interactions have only negative effects on the species involved – is relaxed. The model describes a community of competing insect larvae in which an interaction that is equivalent to intraguild predation (IGP) can occur, and is unusual in that it considers species exploiting very small resource patches (carrying capacity =1). Model simulations show that, in the absence of any intraspecific aggregation, variation between species in the way that resource heterogeneity affects survival increases the likelihood of species coexistence. Simulations also show that intraspecific aggregation of the dominant competitor's eggs across resource patches can promote coexistence by reducing the importance of interspecific competition relative to that of intraspecific competition. Crucially, however, this effect is altered if one competitor indulges in IGP. In general, coexistence is only possible when the species that is capable of IGP is less effective at exploiting the shared resource than its competitor. Because it reduces the relative importance of interspecific interactions, intraspecific aggregation of the eggs of a species that is the victim of IGP actually reduces the likelihood of coexistence in parts of parameter space in which the persistence of the other species is dependent on its ability to exploit its competitor. Since resource heterogeneity, intraspecific aggregation and IGP are all common phenomena, these findings shed light on mechanisms that are likely to influence diversity in communities exploiting patchy resources.

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Intraspecific aggregation of individuals across resource patches can influence interactions between species in a number of ecological contexts. Aggregation of natural enemies affects both the stability of host–parasitoid and predator–prey dynamics (Murdoch and Stewart-Oaten 1989, Godfray and Pacala 1992, Rohani et al. 1994), and the likelihood that species competing for shared hosts or prey will coexist (May and Hassell 1981, Klopfer and Ives 1997). Aggregation also affects the coexistence of species competing for other kinds of patchily dis-tributed resources. In particular, it appears to play an important role in the maintenance of diversity in invertebrate communities exploiting patchy ephe-meral resources such as fallen fruit, carrion, dung and fungal fruiting bodies (Sevenster and Van Alphen 1996, Mitsui and Kimura 2000, Krijger and Sevenster 2001, Woodcock et al. 2002, Inouye 2005, Takahashi et al. 2005). The "aggregation model" (Atkinson and Shorrocks 1981, Hanski 1981) predicts that intraspecific aggregation of individuals across patches in such

communities reduces the importance of interspecific competition relative to that of intraspecific competition, and thus reduces the probability of competitive exclusion.

Studies of the effects of aggregation on population and community processes have usually focussed exclusively on either competitive, predator–prey or host–parasitoid interactions. However, recent research has emphasised the prevalence, particularly in invertebrate communities, of interactions between species that include elements of both competition and predation or parasitism. For example, many species that compete also consume one another – an interaction known as "intraguild predation" (IGP) (Polis et al. 1989). Elaborations of simple models of interspecific competition show that the presence of IGP changes the conditions under which species can coexist (Holt and Polis 1997). Recent modelling work has shown that both resource partitioning and IGP can promote coexistence of invertebrate competitors, but that the effects of the two processes are not independent (Snyder et al. 2005). It is therefore likely that the impact that aggregation has on diversity in communities of competing species will be modified if competitors are able to consume or parasitise one another. In this paper, we use a simulation model to explore how aggregation affects the likelihood of competitive exclusion in the presence of an interaction that is equivalent to IGP.

The aggregation model of coexistence has mainly been applied to communities of flies exploiting fallen fruit and fungi (Jaenike and James 1991, Sevenster and Van Alphen 1996, Mitsui and Kimura 2000). Competition in such communities appears to be well described by the discrete-time Hassell–Comins equations (Inouye 1999), and most published forms of the aggregation model rely upon these equations, or continuous-time equivalents (i.e. the Lotka-Volterra competition equations, Hartley and Shorrocks 2002). When considering the effects of aggregation on diversity in other kinds of system, however, such an approach may not always be appropriate. It has been suggested that aggregation mitigates the effects of interspecific competition in a broad range of communities, including for example those exploiting seed-heads (Johannesen and Loeschcke 1996), rust galls (McGeoch and Chown 1997), and fish gills (Simková et al. 2000), but it is not clear if the standard approach to modelling competition is appropriate in all such cases.

In some systems with patchy resources, there are obvious reasons why a different description of competition is required. For example, some insects compete for patches that can each support only a single mature individual (Mitchell 1975, Stiling and Strong 1983, Craig et al. 1990). The "carrying capacity" of each patch in systems of this kind is strictly limited to one – a patch either produces an individual or it does not. In contrast, the carrying capacity in conventional models of competition is a continuous variable that describes a theoretical threshold to population size whose practical biological meaning is limited. Indeed, when modelled with the Hassell–Comins equations, patch population size can actually exceed carrying capacity (Heard and Remer 1997). To provide a more realistic description of competition for "very small" patches, the simulation model we present here describes competition between species for ephemeral resource patches with a strictly defined carrying capacity of one individual.

This work was inspired by a particular system in which gall-forming herbivores compete for plant stems. Exploiting the inherent flexibility of simulation models, we designed a model that describes the biology of our system in as realistic a fashion as possible. We then explored the behaviour of this model with various parameter values reflecting a range of conditions that might be encountered in real ecosystems. As is always the case with simulation models, the extent to which we can generalise from our results is constrained by our choice of parameter values, and this choice is in turn constrained by the logistics of computer simulation. However, we endeavoured to examine as broad a range of parameter space as possible, and have generated results that are generally informative about the roles that aggregation and IGP might play in coexistence.

Study system

We modelled interactions between two species of gall-forming fly that compete for stems of the common reed, *Phragmites australis* (Cav.) Trin. ex Steud. *Lipara lucens* Meigen and *Lipara rufitarsis* Loew (Diptera: Chloropidae) are univoltine, with eggs being laid on young reed stems in spring (Chvála et al. 1974). Hatchling larvae attack the reed meristem, and induce the formation of a single, species-specific gall at the top of the stem. *L. lucens* galls are much larger and thicker-walled than those of *L. rufitarsis*. The signal that induces the host plant to form the larger gall is dominant, and whenever larvae of both species are present on a stem, they compete for the occupancy of a *L. lucens* gall. Competition can be intense because, no matter how many eggs are laid on a stem, only one gall can form, and only one larva can reach maturity in that gall. When *L. rufitarsis* defeats *L. lucens* in competition for a gall, it actually benefits from the interaction because the occupancy of the larger *L. lucens* gall substantially enhances its survival, body mass and fecundity (Reader 2003). In such situations, *L. rufitarsis* larvae are effectively indulging in a form of "intraguild kleptoparasitism" that is identical to conventional IGP in its effects on fitness.

Field surveys and experiments indicate that interactions between *L. lucens* and *L. rufitarsis* on reed stems are common and have significant effects on survival and

fecundity, and that *L. rufitarsis* is competitively dominant (Reader 2003). In the face of such competition, the persistent coexistence of the two species at many field sites is puzzling. There are two obvious ways in which the effects of competition might be mitigated sufficiently to allow coexistence. Firstly, a difference in the responses of the two species to resource heterogeneity may provide *L. lucens* with a refuge from competition. The eggs of *L. lucens* and *L. rufitarsis* are distributed at random with respect to each other, suggesting that resource partitioning by adults does not occur (Reader 2001), but larvae of the two species do respond differently to variation in host plant defences (De Bruyn 1994, Reader 2001). Although both species are more likely to die before gall-formation on thick, vigorous reed stems, *L. lucens* is less strongly affected than *L. rufitarsis*. Secondly, the eggs of both species are intraspecifically aggregated (Reader 2001), and this is expected to decrease the relative importance of interspecific competition and promote coexistence (Atkinson and Shorrocks 1981, Hanski 1981). Our model describes the processes of competition and kleptoparasitism in this system, and allows us to explore how aggregation and resource heterogeneity might affect coexistence. In our model, kleptoparasitism is indistinguishable from IGP (as defined in Polis et al. 1989) in its effects on fitness; for this reason, and to emphasise the general relevance of our work to the study of systems other than that which originally inspired the model, we henceforth refer to the interaction in our model as IGP.

Methods

Fly populations were modelled in an environment with a fixed number (R = 1000) of ephemeral host plant patches (reed stems) with varying levels of defence against herbivory (W). In the first part of the fly life cycle, the model predicts the probability that a stem with a particular level of defence, which has received a particular number of eggs of the two species, will produce an adult of a particular species. When more than one larva survives on a patch, a contest ensues, the winner of which is the first larva to reach maturity. At maturity, a larva is assumed to be able to eliminate all other larvae, either by attacking them, or by denying them access to food. The competitive ability of the two species is thus determined by their maturation rates. The assumption that competition takes the form of a contest between larvae is based on the observation that the outcome of competition for a stem is decided well before the food available in a gall is exhausted (Reader, pers. obs.).

Before competition can occur, larvae must successfully induce a gall to form. Each stem is assumed to receive a number of *L. lucens* and *L. rufitarsis* eggs (E_L and E_R respectively). These eggs are assumed to suffer mortality,

some of which is related to the defences of the host plant. The probabilities that eggs of *L. lucens* and *L. rufitarsis* survive this mortality are given by:

Pr(*L. lucens* egg → survivor|W)

$$= \rho_L = \frac{1}{1 + e^{-\gamma_L + \delta_L W}} \quad \text{and} \tag{1}$$

Pr(*L. rufitarsis* egg → survivor|W)

$$= \rho_R = \frac{1}{1 + e^{-\gamma_R + \delta_R W}} \tag{2}$$

where γ_L and γ_R determine the levels of background mortality and δ_L and δ_R determine the levels of mortality related to host plant defence.

The number of individuals of each species surviving is assumed to be determined by a binomial process, where ρ_L and ρ_R give the probabilities of success, and E_L and E_R represent the numbers of trials, such that:

Number of survivors of *L. lucens* = $S_L \sim B(\rho_L, E_L)$ (3)

Number of survivors of *L. rufitarsis*

$$= S_R \sim B(\rho_R, E_R). \tag{4}$$

Maturation in the absence of interspecific competitiors

Larvae surviving background and plant defence related mortality initiate gall formation. Whenever a *L. lucens* individual survives, a *L. lucens* gall is induced. A *L. rufitarsis* gall only forms when a *L. rufitarsis* larva survives in the absence of any *L. lucens* larvae. The probability that a gall will then produce an adult *L. lucens* or *L. rufitarsis* is assumed to be a function of the number of survivors of the two species present in the gall. Galls can never produce more than one adult. In the absence of competitors, *L. lucens* survivors are assumed to suffer no further mortality in the gall (levels of predation and parasitism of *L. lucens* are typically very low – Mook 1967, Reader 2001). Given this assumption, and since competition is assumed to be a simple contest, the probability of a *L. lucens* gall producing a *L. lucens* adult in the absence of the other species is given by:

Pr(Gall → Adult *L. lucens*|$S_L \neq 0, S_R = 0$) = 1 (5)

Thus, in the absence of *L. rufitarsis* eggs, the probability that a stem will produce a *L. lucens* adult is simply one minus the probability that a young larva will die (Eq. 1) raised to the power of the number of trials:

Pr(Stem → Adult *L. lucens*|$E_L \neq 0, E_R = 0$)

$$= 1 - (1 - \rho_L)^{E_L} \tag{6}$$

L. rufitarsis galls offer larvae relatively poor protection from predation and parasitism (Reader 2001). Therefore, an additional parameter (β_a) is required to describe the effects of mortality on *L. rufitarsis* during maturation in

the gall. If *L. rufitarsis*, in the absence of the other species, is assumed to mature at a rate κ_R, and die at a rate μ_a, β_a is given by:

$$\beta_a = \frac{\kappa_R}{\mu + \kappa_R} \tag{7}$$

The parameter β_a can be thought of as the probability than an individual will successfully reach maturity and it approaches unity as the relative importance of mortality declines ($\mu_a \to 0$). It should be noted that the size of the maturation rate (κ_R) in this equation relative to the equivalent parameter for *L. lucens* (κ_L) effectively determines (and is thus synonymous with) the inter-specific competitive ability of *L. rufitarsis*. In the absence of *L. lucens*, the probability that a gall will produce a *L. rufitarsis* adult is equal to one minus the probability of a larva failing to mature raised to the power of the number of trials:

$$\Pr(\text{Gall} \to \text{Adult } L.\ rufitarsis | S_R \neq 0, S_L = 0)$$
$$= 1 - (1 - \beta_a)^{S_R} \tag{8}$$

In this equation, S_R is a simple function of the number of eggs laid and the probability that a young larva will survive background and plant defence related mortality (Eq. 4). Therefore, the probability that a stem will produce a *L. rufitarsis* adult can be written as one minus the probability of failure of an egg raised to the power of the number of trials:

$$\Pr(\text{Stem} \to \text{Adult } L.\ rufitarsis | E_R \neq 0, E_L = 0)$$
$$= 1 - [1 - \rho_R \beta_a]^{E_R} \tag{9}$$

Maturation in the presence of interspecific competitors

Because *L. lucens* larvae that have successfully induced a gall are assumed to suffer no further mortality other than that associated with competition, and since competition between larvae is assumed to be a contest, any gall in which *L. lucens* is present will produce an adult of some sort. *L. rufitarsis* galls, which are assumed to form only in the absence of *L. lucens*, will only produce an adult if *L. rufitarsis* survives the maturation process (Eq. 9). Thus, in all cases, the probability that a stem will produce an adult of either species is one minus the probability that no young *L. lucens* larvae survive and successfully induce a gall to form, multiplied by the probability that any surviving *L. rufitarsis* larvae fail to mature successfully:

$$\Pr(\text{Stem} \to \text{Adult} | E_L, E_R) = 1 - (1 - \rho_L)^{E_L} [1 - \rho_R \beta_a]^{E_R} \tag{10}$$

When both *L. lucens* and *L. rufitarsis* larvae are present in a newly developed gall, a contest between larvae is assumed to occur, the outcome of which is dependent on the maturation rates of the two species, and the mortality rate of *L. rufitarsis*. Since the gall that forms in such a situation is a *L. lucens* gall, the mortality rate of *L. rufitarsis* will be different from that seen in the case when *L. rufitarsis* matures in a *L. rufitarsis* gall. Therefore, a new parameter (equivalent to β_a) is required that includes the rate at which larvae die in a *L. lucens* gall (μ_b):

$$\beta_b = \frac{\kappa_R}{\mu_b + \kappa_R} \tag{11}$$

This parameter is one of two in the model that control the strength of the effects of IGP on *L. rufitarsis*. When *L. rufitarsis* mortality in a *L. lucens* gall is lower than it is in its own gall ($\beta_b > \beta_a$), gall "theft" is more profitable than simple herbivory.

The individual that matures first is the winner of the contest for the gall. Therefore, the likelihood that a *L. lucens* larva matures before any *L. rufitarsis* larvae must be established. Since *L. lucens* suffers no mortality in the gall, its maturation is a Markov process of rate $\kappa_L S_L$. This is because κ_L is the rate at which a single *L. lucens* larva matures, and there are S_L larvae, which mature independently of each other. The maturation process for *L. rufitarsis* is similar, but some individuals die (Eq. 11) before they mature. Using this information, the probability that the first individual to mature in the gall is a *L. lucens* larva can be written thus:

$$\Pr(\text{Gall} \to \text{Adult } L.\ lucens | S_L, S_R)$$
$$= \int_{t=0}^{t=\infty} \kappa_L S_L e^{-\kappa_L S_L t} \times \{1 - (1 - \beta_b)[1 - e^{-(\mu_b + \kappa_R)t}]\}^{S_R}\ dt \tag{12}$$

This equation can be simplified by creating a new parameter (α) and setting $x = \kappa_L t$. The probability that a *L. lucens* gall will produce a *L. lucens* adult then becomes:

$$\Pr(\text{Gall} \to \text{Adult } L.\ lucens | S_L, S_R)$$
$$= \int_{x=0}^{x=\infty} S_L e^{-S_L x} [1 - \beta_b(1 - e^{-\alpha x})]^{S_R}\ dx \tag{13}$$

where

$$\alpha = \frac{\mu_b + \kappa_R}{\kappa_L} \tag{14}$$

The parameter α provides information about the relative competitive abilities of *L. lucens* and *L. rufitarsis* in terms of their maturation rates and *L. rufitarsis* mortality. When κ_R is large, indicating that the relative competitive ability of *L. rufitarsis* is great, α is large, and the presence of *L. rufitarsis* larvae will have a strong negative effect on the probability that a *L. lucens* larva will reach maturity. Although α can also be large because

μ_b is large, in this case β_b will be small (Eq. 11), and the effect of the presence of *L. rufitarsis* larvae on the probability that a *L. lucens* larva will mature successfully will also be small.

Equation 13 can be written in terms of the numbers of eggs originally laid on stems. Setting $y = e^{-x}$, a more intuitive form of the equation for the probability that a stem will produce a *L. lucens* adult can be written:

$$\text{Pr}(\text{Stem} \rightarrow \text{Adult } L.\ lucens | E_L, E_R)$$

$$= \int_{y=0}^{y=1} \rho_L E_L [1 - \rho_L(1-y)]^{E_L-1}$$

$$\times [1 - \rho_R \beta_b (1 - y^\alpha)]^{E_R} \ dy. \tag{15}$$

The probability that a stem will produce a *L. rufitarsis* adult is then simply the probability that a stem will produce an adult of any type (Eq. 10), minus the probability that *L. lucens* reaches maturity first:

$$\text{Pr}(\text{Stem} \rightarrow \text{Adult } L.\ lucens | E_R, E_L)$$

$$= 1 - (1 - \rho_L)^{E_L} [1 - \rho_R \beta_a]^{E_R}$$

$$- \int_{y=0}^{y=1} \rho_L E_L [1 - \rho_L(1-y)]^{E_L-1}$$

$$\times [1 - \rho_R \beta_b (1 - y^\alpha)]^{E_R} \ dy. \tag{16}$$

Egg production by emergent adults

Larvae that have successfully matured in one year are assumed to pupate and emerge the following year as adults. The number of eggs in the next *L. lucens* generation (ΣE_L) is assumed to be a linear function of the number of emergent adults (A_L):

$$\sum E_L = \lambda_L A_L \tag{17}$$

where λ_L is the number of eggs produced per adult. The number of eggs contributed by each *L. rufitarsis* adult to the next generation is dependent on gall type. If the proportion of *L. rufitarsis* adults emerging from *L. rufitarsis* galls is φ, the total number of *L. rufitarsis* eggs in the next generation (ΣE_R) is given by:

$$\sum E_R = \varphi \lambda_R A_R + (1 - \varphi) m \lambda_R A_R \tag{18}$$

where m is the proportional change in the number of eggs produced per adult *L. rufitarsis* (λ_R) resulting from the theft of a *L. lucens* gall. The effect of gall type on egg production provides a second opportunity for IGP to affect *L. rufitarsis* fitness: when $m > 1$, gall theft is more profitable for *L. rufitarsis* than simple herbivory.

Simulations

The above equations were used to produce computer simulations of the dynamics of *L. lucens* and *L. rufitarsis* over many generations. At the beginning of each generation, the patches in a simulation were renewed. As in other versions of the aggregation model, we assume that the system is "donor controlled", such that the rate of supply of new patches is independent of consumer density. While herbivory is likely to affect plant fitness, we do not expect a strong link between the dynamics of *P. australis*, a long-lived clonal plant, and its consumers. The levels of host plant defence associated with each patch were assigned by randomly drawing a number from a normal distribution with a particular mean (W_A) and standard deviation (W_{SD}). Eggs were distributed across patches according to a negative binomial distribution, with the degree of aggregation being controlled by a clumping parameter (k_L for *L. lucens* and k_R for *L. rufitarsis*). Mortality of young larvae attempting to initiate galls was determined by randomly drawing numbers from a binomial distribution, with probabilities being defined by Eq. 1 and 2. Each patch was then assigned a gall type (according to the species present), and the outcome of competition determined by drawing numbers from a binomial distribution, with probabilities defined by Eq. 15 and 16. The total number of eggs produced by larvae that successfully reached maturity was determined using Eq. 17 and 18, and these eggs were made available at the beginning of the next generation.

All simulations were run for 1000 generations with identical starting conditions (each species having an average density of one egg per patch). Default parameter values are given in Table 1. We present the outcome of each simulation as the number of generations of coexistence that were observed. Thus, we focus on the persistence of the interaction in a stochastic environment rather than its strict mathematical stability. Simulations were programmed in Microsoft Visual C++ version 6.0.

For logistical reasons, it was not possible to vary all parameters of interest simultaneously. Therefore, the areas of parameter space of greatest interest (especially those where simulation outcomes were likely to flip between coexistence and exclusion) were explored. Particular attention was paid to parameters controlling competitive ability (α, δ_L and δ_R), aggregation (k_L and k_R), and the importance of IGP (β_b and m). In order to match the general conditions present in our system, we explored situations in which the species (*L. rufitarsis*) that is the dominant competitor in the contest for a gall ($\alpha > 1$) is capable of IGP, but is more seriously affected by host plant defences than its competitor ($\delta_R > \delta_L$).

Table 1. The parameter values employed in simulations. The "default value" is that used in all simulations discussed in the results unless otherwise stated in the figure legends. *The default value for k was arbitrarily chosen to be 20 – at large values of k such as this, the negative binomial distribution is indistinguishable from a Poisson distribution (i.e. eggs will be distributed at random with no aggregation).

Parameter	Description	Default value	Range explored
R	Number of patches (host plant stems)	1000	
W_A	Average level of host plant defence	1.5	0 to 2.5
W_{SD}	Standard deviation of host plant defence levels	0.2	0 to 2
γ_L	Determines level of background mortality of *L. lucens*	1	
γ_R	Determines level of background mortality of *L. rufitarsis*	1	
δ_L	Determines strength of the effect of host plant defence on *L. lucens*	1	
δ_R	Determines strength of the effect of host plant defence on *L. rufitarsis*	2	0.5 to 2
α	Determines relative competitive ability of *L. lucens* and *L. rufitarsis*	4	1 to 20
β_a	Determines probability that a *L. rufitarsis* larva survives maturation in its own gall	0.5	0.05 to 0.5
β_b	Determines probability that a *L. rufitarsis* larva survives maturation in a *L. lucens* gall	0.5	0.5 to 0.95
λ_L	Number of eggs produced per adult *L. lucens*	25	
λ_R	Number of eggs produced per adult *L. rufitarsis* emerging from its own gall	25	2.5 to 25
m	Proportional change in *L. rufitarsis* fecundity owing to theft of *L. lucens* gall	1	1 to 9
k_L	Clumping parameter of the negative binomial distribution for *L. lucens*	20*	10^{-1} to $10^{1.5}$
k_R	Clumping parameter of the negative binomial distribution for *L. rufitarsis*	20*	10^{-1} to $10^{1.5}$

Results

Resource heterogeneity promotes coexistence

The simplest scenario that we investigated with the model was one in which there was no intraspecific aggregation and no IGP, but in which the two species differed in their susceptibility to host plant defences, and in their competitive ability. Under these circumstances, the model predicts that in some areas of parameter space competitive exclusion will occur, while in others resource heterogeneity alone is sufficient to allow the two species to coexist (Fig. 1, 2). If *L. lucens* is less susceptible to host plant defences, it can persist in habitats with well defended host plants while *L. rufitarsis* goes extinct. If *L. rufitarsis* is a better competitor in the contest for a gall, and its chances of overcoming host plant defences are sufficiently high, it drives *L. lucens* to extinction. In habitats of intermediate quality, each species has a competitive advantage on a proportion of the available host plant patches, and coexistence occurs as a result. Unsurprisingly, coexistence is more likely when variation in host plant defences is greater (Fig. 1), and when the ecological differentiation between the two species is greater (Fig. 2).
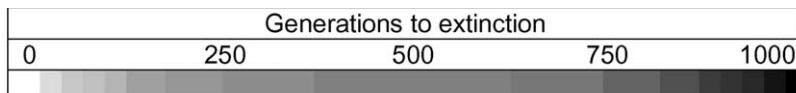
Key to Figures. In all figures, each pixel represents the outcome of one simulation, and the colo[ur] the pixel indicates the number of generations in the simulation for which the two species coex[isted] before one became extinct (simulations were terminated after 1000 generations).
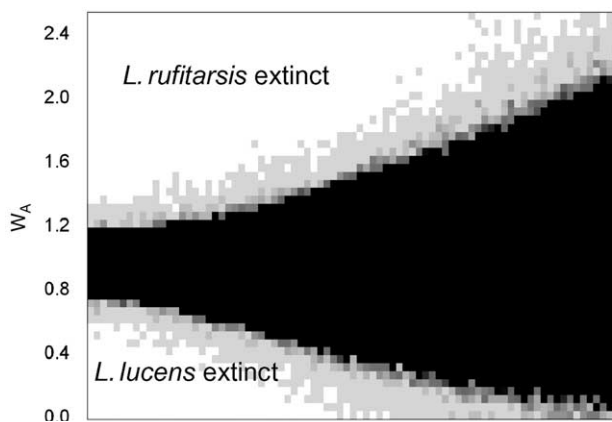

Fig. 1. Outcomes of simulations when the mean (W_A) and standard deviation (W_{SD}) of host plant defence levels were varied in the absence of aggregation or IGP. In these simulations, *L. rufitarsis* was dominant in competition ($\alpha = 20$) but its survival declined rapidly as host plant defences increased ($\delta_R = 2$). For an explanation of pixel shading, see key to figures.
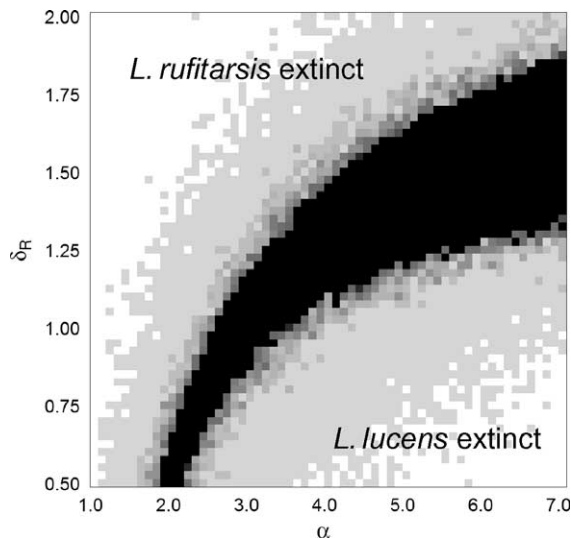
Fig. 2. Outcomes of simulations when the dominance of *L. rufitarsis* in contest competition (α) and the strength of the effect of host plant defences on *L. rufitarsis* (δ_R) were varied in the absence of aggregation or IGP. For an explanation of pixel shading, see key to figures.

Aggregation promotes coexistence in the absence of IGP

We next explored the effect of intraspecific aggregation of the eggs of the two species on coexistence in the absence of IGP. As expected, when the eggs of the species that is superior in competition for a gall (*L. rufitarsis*) are moderately aggregated, the relative importance of the effect of interspecific competition on the inferior competitor (*L. lucens*) is reduced, allowing it to persist where previously it would have

been driven to extinction (Fig. 3). Similarly, if strong effects of host plant defences on *L. rufitarsis* give *L. lucens* the com petitive edge, moderate aggregation of *L. lucens* eggs can reduce interspecific competitive effects sufficiently to promote coexistence where *L. rufitarsis* would otherwise be driven to extinction (Fig. 4). Thus, in the absence of IGP, the model's behaviour is consistent with the hypothesis that aggregation of a superior competitor can promote coexistence between two species competing for shared limiting resources (Hartley and Shorrocks 2002).

IGP alters the conditions that favour coexistence

We next looked to see if the conditions necessary for coexistence of the two species in the absence of intraspecific aggregation were altered by the presence of IGP. When success in a competitive contest leads to improved fecundity or survival for *L. rufitarsis*, co-existence is still determined by a trade-off between competitive ability and susceptibility to host plant defences, but the region of parameter space in which coexistence occurs is altered (Fig. 5, 6). Because inter-specific encounters enhance *L. rufitarsis* fitness, the balance is shifted in its favour throughout parameter space. Firstly, it is more likely to persist alongside its competitor in situations in which it was previously vulnerable to extinction as a result of its susceptibility to host plant defences. Secondly, it is more likely to drive *L. lucens* to extinction in regions of parameter space where it has the competitive advantage.

Interestingly, the introduction of IGP tends to lead to an expansion in the zone of parameter space in which coexistence occurs (Fig. 6). When *L. rufitarsis*
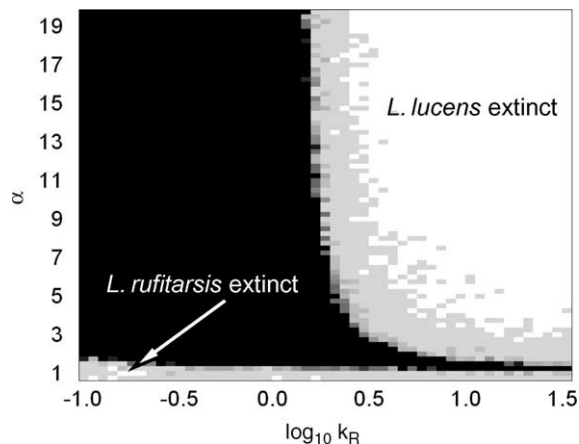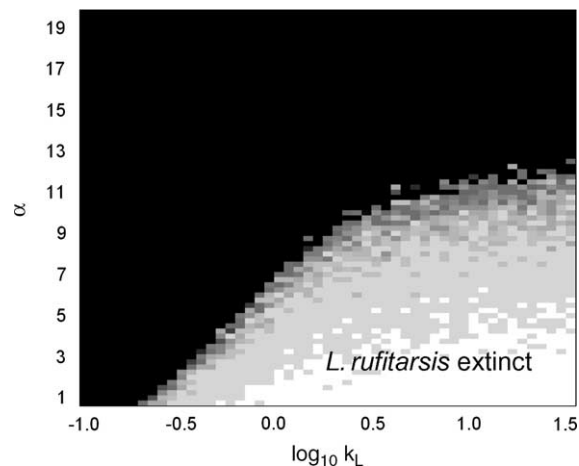

Fig. 3. Outcomes of simulations when the dominance of *L. rufitarsis* in contest competition (α) and the strength of *L. rufitarsis* egg aggregation (k_R) were varied. In these simulations, there was no aggregation of *L. lucens* eggs, and no IGP. For an explanation of pixel shading, see key to figures.

Fig. 4. Outcomes of simulations when the dominance of *L. rufitarsis* in contest competition (α) and the strength of *L. lucens* egg aggregation (k_L) were varied. In these simulations, there was no aggregation of *L. rufitarsis* eggs, and no IGP. For an explanation of pixel shading, see key to figures.
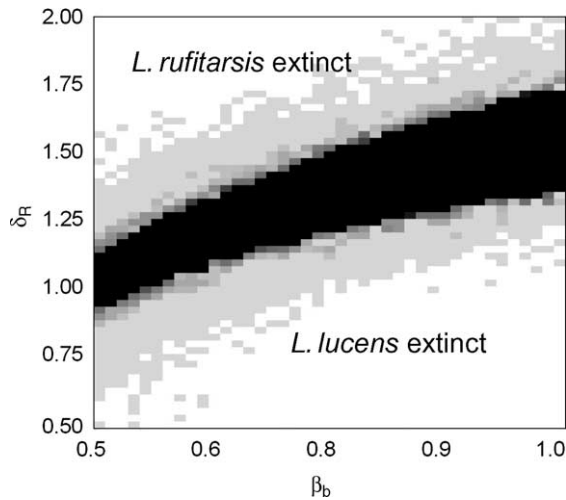
Fig. 5. Outcomes of simulations when the strengths of the effects of IGP and host plant defences (δ_R) on *L. rufitarsis* were varied in the absence of aggregation. In this case, the effect of IGP was varied by altering the probability of *L. rufitarsis* survival in a *L. lucens* gall (β_b). For an explanation of pixel shading, see key to figures.

Fig. 7. Outcomes of simulations when the strengths of the effects of IGP and host plant defences (δ_R) on *L. rufitarsis* were varied in the absence of aggregation. In this case, the effect of IGP was varied by altering the probability of *L. rufitarsis* survival in *L. rufitarsis* (β_a) and *L. lucens* (β_b) galls. A tradeoff was envisaged in which increased benefits to *L. rufitarsis* of IGP are associated with reduced survival in the absence of *L. lucens*, such that in all simulations $\beta_b + \beta_b = 1$. For an explanation of pixel shading, see key to figures.

benefits substantially from interactions with *L. lucens*, its persistence is affected less significantly by changes in susceptibility to host plant defences because it is able to "specialise" in IGP while *L. lucens* "specialises" in herbivory. The introduction of IGP has effectively introduced a new axis to the niche-space which the two species are exploiting. The effect is seen more clearly if it is assumed that there is an evolutionary trade-
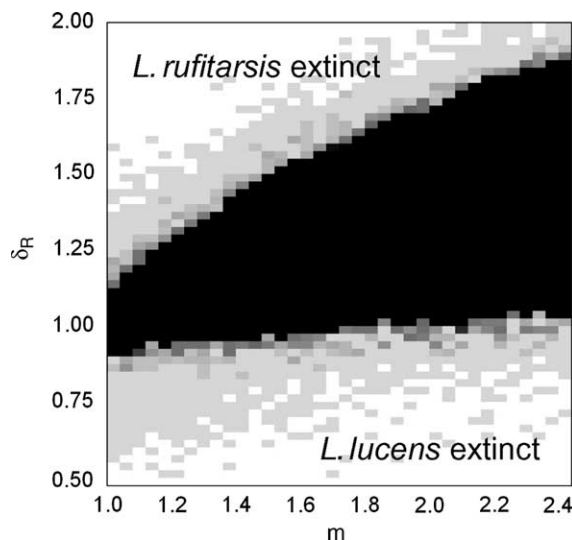
off between the ability of *L. rufitarsis* to indulge in IGP and its ability to consume the shared resource (Fig. 7, 8). As the exploitation of *L. lucens* becomes an increasingly important contributor to *L. rufitarsis* fitness, the region of parameter space in which coexistence can occur expands. With IGP incorporated into the model, coexistence is possible wherever the combined advantages of superior competitive ability and IGP are

Fig. 6. Outcomes of simulations when the strengths of effects of IGP and host plant defences (δ_R) on *L. rufitarsis* were varied in the absence of aggregation. In this case, the effect of IGP was varied by altering the strength of the effect of maturation in a *L. lucens* gall on *L. rufitarsis* fecundity (m). For an explanation of pixel shading, see key to figures.
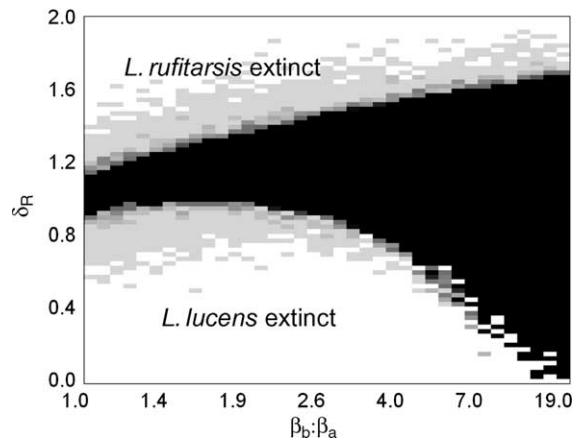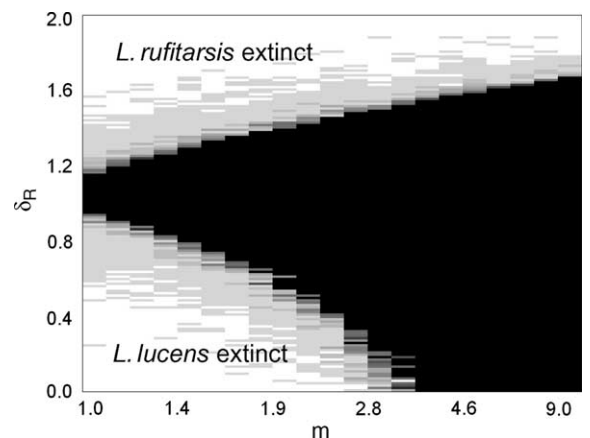

Fig. 8. Outcomes of simulations when the strengths of the effects of IGP and host plant defences (δ_R) on *L. rufitarsis* were varied in the absence of aggregation. In this case, the effect of IGP was varied by altering the strength of the effect of maturation in a *L. lucens* gall on *L. rufitarsis* fecundity (m). A tradeoff was envisaged in which increased benefits to *L. rufitarsis* of IGP are associated with reduced fecundity in the absence of *L. lucens*, such that in all simulations $m\lambda_R = 25$. For an explanation of pixel shading, see key to figures.

balanced in *L. rufitarsis* by greater susceptibility to host plant defences and reduced effectiveness in herbivory.

Aggregation can be detrimental to coexistence in the presence of IGP

When we examined the combined effects of aggregation and IGP on coexistence, we discovered that intraspecific aggregation does not always have a positive effect on diversity. Unsurprisingly, IGP does not interfere qualitatively with the effects of aggregation of *L. rufitarsis* eggs on *L. lucens*. Clumping of the eggs of the superior competitor always reduces the likelihood that the inferior competitor is excluded (Fig. 9). However, aggregation of *L. lucens* eggs has a very different effect on its competitor in the presence of IGP. If *L. rufitarsis* benefits from interactions with
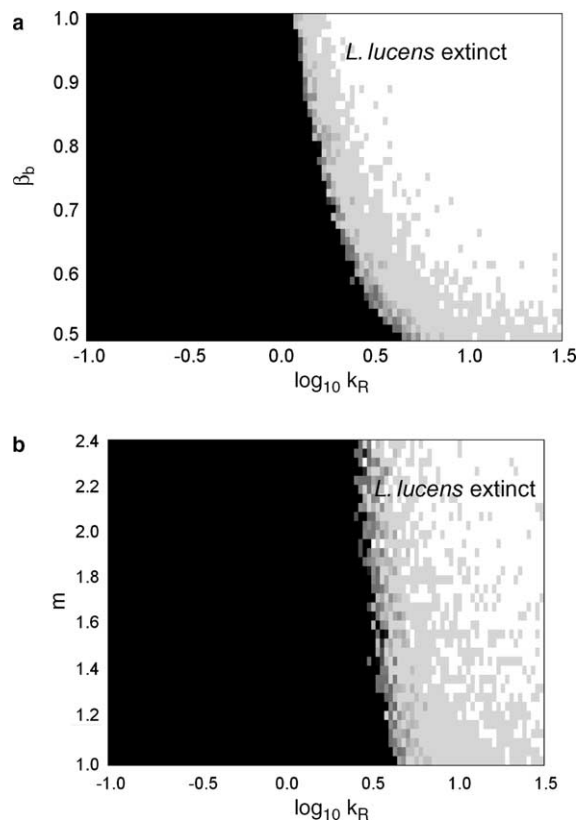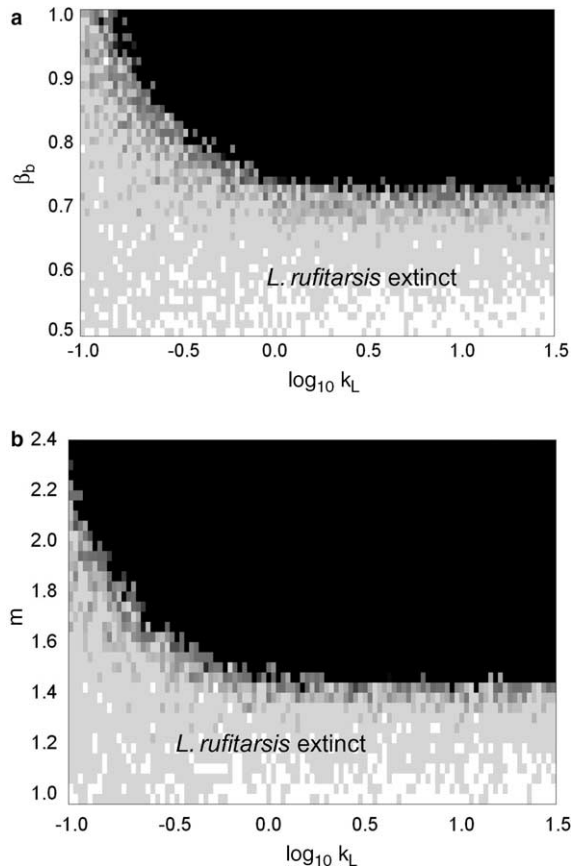
Fig. 10. Outcomes of simulations when the strengths of the effect of IGP on *L. rufitarsis* and of *L. lucens* egg aggregation (k_L) were varied. In (a) the effect of IGP was varied by altering the probability of *L. rufitarsis* survival in a *L. lucens* gall (β_b). In (b) the effect of IGP was varied by altering *L. rufitarsis* fecundity in a *L. lucens* gall (λ_{RL}). In all simulations, *L. rufitarsis* was dominant in competition ($\alpha = 20$) and there was no aggregation of *L. rufitarsis* eggs. For an explanation of pixel shading, see key to figures.

Fig. 9. Outcomes of simulations when the strengths of the effect of IGP on *L. rufitarsis* and of *L. rufitarsis* egg aggregation (k_R) were varied. In a) the effect of IGP was varied by altering the probability of *L. rufitarsis* survival in a *L. lucens* gall (β_b). In b) the effect of IGP was varied by altering the strength of the effect of maturation in a *L. lucens* gall on *L. rufitarsis* fecundity (m). In all simulations, *L. rufitarsis* was dominant in competition ($\alpha = 20$) and relatively resistant to host plant defences ($\delta_R = 1.0$), and there was no aggregation of *L. lucens* eggs. For an explanation of pixel shading, see key to figures.

L. lucens, extinction becomes more likely if its "host" is aggregated (Fig. 10). This is because, as well as reducing the relative strength of interspecific competition, aggregation reduces the strength of interspecific interactions that are beneficial to one party. When *L. lucens* is aggregated, *L. rufitarsis* has access to fewer hosts, more *L. rufitarsis* larvae mature in their own (inferior) galls, and survival and fecundity are reduced. Thus, the inclusion of IGP in the model produces a qualitative change in the predicted effect of aggregation on coexistence.

Discussion

The two fly species that inspired our model share and compete strongly for a single host plant resource that

is in limited supply, but they coexist stably (Reader 2003). Thus, like many competing species, *L. lucens* and *L. rufitarsis* appear to violate the principle of competitive exclusion (Hardin 1960). Our model simulations shed light on the mechanisms that might permit coexistence in this system, and in a broader context have interesting implications for the study of the maintenance of diversity in communities in which the division between competition and parasitism or predation is blurred.

Resource heterogeneity and coexistence on patchy ephemeral resources

Our results show that resource partitioning has an important role to play in coexistence in our study system. When examining the potential of resource heterogeneity to play a role in promoting coexistence, previous studies of communities exploiting patchy ephemeral resources have focussed in particular on the distribution of individuals across patches: if different species show different patterns of patch occupancy such that interspecific competitive interactions are less common than if those species were distributed at random, coexistence will be favoured (Ives 1988, Sevenster 1996). Although results vary from system to system, there is often little evidence for repulsion between the distributions of competing species, and this has led to the conclusion that classical resource partitioning is unlikely to make an important contribution to coexistence on patchy ephemeral resources (Shorrocks and Sevenster 1995, Sevenster and Van Alphen 1996, Wertheim et al. 2000, Mitsui and Kimura 2000, Krijger and Sevenster 2001). In many of the systems studied, however, the effects of patch quality on survival, fecundity and competitive ability are not as well understood as are the distributions of species across patches. In theory, any difference between species in the way that fitness responds to resource variability could allow niche differentiation between species (Ives 1995). Thus, although classical resource partitioning is often not sufficient to explain coexistence in these systems, resource heterogeneity may still have an important role to play.

In our case, although observations of egg laying behaviour indicate that there is no repulsion between the distributions of *L. lucens* and *L. rufitarsis* eggs across patches (Reader 2001), subtle effects of patch quality on larval survival in the two species are well documented (De Bruyn 1994, Reader 2001). Model simulations show how this differential can promote coexistence in some areas of parameter space. While similar effects on coexistence of variation among species in the relationship between resource heterogeneity and *survival* are only likely in systems where larval mortality

is strongly related to resource quality, it does seem probable that subtle or cryptic variation in the effects of patch quality on other factors affecting fitness (e.g. body size, development rate) almost certainly exists in most communities exploiting patchy ephemeral resources. Thus, we should be careful not to underestimate the role that resource heterogeneity plays in explaining observed patterns of diversity. While observations of the distribution of individuals across patches can tell us much about species interactions, the only way to understand fully coexistence in these species-rich insect communities is to conduct appropriate competition experiments across a range of patch qualities (Ives 1995).

IGP and coexistence

The "intraguild kleptoparasitism" that we have modelled clearly has important consequences for the maintenance of diversity in our study system. IGP is a widespread phenomenon in terrestrial food webs (Polis et al. 1989, Polis and Strong 1996, Coll and Guershon 2002, Müller and Brodeur 2002). Facultative kleptoparasitism like that observed in our study system is also well documented in insect communities (Crespi and Abbot 1999, Sivinski et al. 1999), and species that kleptoparasitise their competitors are functionally indistinguishable from intraguild predators. Theory suggests that IGP can alter the competitive balance between species, and change the conditions under which coexistence is likely to occur (Holt and Polis 1997, McCann and Hastings 1997). An important general finding is that when two consumers share a single resource, and one consumer can indulge in IGP, the intermediate species (the consumer that is incapable of IGP) will be driven to extinction unless it is the superior competitor for the shared resource (Holt and Polis 1997). The behaviour of our model supports this prediction: the more effective *L. rufitarsis* is as an intraguild "predator", the bigger the advantage that *L. lucens* must have over its competitor when it comes to exploiting the shared resource if it is to persist.

While it is true that IGP may destabilise interactions between competitors by driving intermediate species to extinction, it is equally true that IGP can facilitate the persistence of species that would otherwise be excluded through competition (Holt and Polis 1997). Our results show this effect clearly: there are areas of parameter space in which *L. rufitarsis* is unlikely to persist unless it can exploit *L. lucens*. In such regions, coexistence is effectively facilitated by the predator–prey nature of the relationship between the two species. If susceptibility to host plant defences puts *L. rufitarsis* at a competitive disadvantage, it can still persist because the more abundant its competitor becomes, the greater the

likelihood that it will benefit from an interspecific encounter.

The positive impact that the evolution of IGP may have on diversity is demonstrated more clearly if we envisage that there is a trade-off between the ability of a species to indulge in IGP and its ability to exploit a shared resource (Fig. 7, 8). These results are supported by the findings of deterministic analyses of "exploitation–interference" trade-offs. In the absence of other coexistence mechanisms, a species that is superior in interference competition can coexist with a species that is superior in exploitation competition as long as interference competition actually benefits the former (e.g. via IGP) (Amarasekare 2002). Interestingly, there is evidence from our study system that is consistent with the idea that such a trade-off occurred in the evolutionary history of the genus *Lipara*. Although the fecundity of *L. rufitarsis* females that have developed in galls stolen from their competitors is very similar to that of *L. lucens*, females that develop in their own galls produce significantly fewer eggs (Reader 2003). Given the evidence that *L. rufitarsis* is more susceptible to host plant defences than the two other common members of the genus in Europe (De Bruyn 1994), it seems possible that this is a species that has become increasingly adept at exploiting a previously vacant kleptoparasitic niche at the expense of the ability to attack the host plant. Such a scenario would certainly be consistent with the idea that the evolution of kleptoparasitism and inquilinism has played an important role in the diversification of phytophagous lineages (Ronquist 1994, Miller 2005).

While it is a poorly studied phenomenon, there is good evidence that facultative kleptoparasitism influences diversity in systems other than our own. Whenever herbivores or natural enemies that are susceptible to the defences of their food plants or prey can enhance their fitness by stealing resources, their persistence is likely to be affected. For example, the facultatively kleptoparasitic aphid *Eriostoma yangi* can only persist on host plants of a particular type when a competitor species whose galls it is able to usurp is present (Akimoto 1988). Similarly, the parasitoid *Asobara tabida* only coexists with *Leptopilina boulardi* on *Drosophila simulans* because it can act as a kleptoparasite (Kraaijeveld 1999).

Aggregation, IGP and coexistence

Our model predicts that the ability of intraspecific aggregation to promote the coexistence of species that share a patchy, ephemeral resource is strongly dependent on the relative strengths of competition and IGP. The prediction that intraspecific aggregation of a superior competitor can reduce the relative importance of inter-specific competition for an inferior competitor, and therefore promote coexistence, has been around for more than twenty years (Atkinson and Shorrocks 1981, Hanski 1981), and aggregation is now widely believed to be an important factor determining diversity in communities exploiting patchy ephemeral resources. Our results add weight to the idea that the prediction is robust (Hartley and Shorrocks 2002), and is not dependent on the specific details of any particular competition model. However, in contrast to other theoretical studies of this kind (Atkinson and Shorrocks 1981, Sevenster 1996, Heard and Remer 1997, Hartley and Shorrocks 2002), we have found that the clumping of conspecifics does not always promote diversity in communities of competing insects. As one of a pair of competing species becomes more dependent on IGP, the three-species system that we modelled becomes more linear (less triangular), and intraspecific aggregation actually reduces the likelihood of coexistence. This is because intraspecific aggregation reduces the relative frequency of interspecific encounters, and can thus weaken the trophic link between an intraguild predator/parasite and its prey/host.

Conclusions

In this paper, we have explored how three factors can affect the persistence of competitors in a community exploiting a patchy ephemeral resource. Intraspecific aggregation, resource heterogeneity and the strength of IGP combine to determine the probability that competitive exclusion will occur. These factors are likely to be of widespread importance in communities of insects in which competition is intense. Strong intraspecific aggregation has frequently been documented, not just in communities exploiting fallen fruit, animal dung, carrion and fungi (Ives 1991, Jaenike and James 1991, Giller and Doube 1994, Sevenster and Van Alphen 1996, Wertheim et al. 2000), but also in many other systems, including those in which phytophagous insects forage on patchy plant resources (Taylor et al. 1978, Faeth 1990, Morris et al. 1992). Resource heterogeneity that impacts upon fitness is likely to be ubiquitous, even if its effects are difficult to measure. Finally, complex and indirect interactions that do not fit neatly into categories like "competition" or "predation" appear to be very common in terrestrial systems (Polis et al. 1989, Coll and Guershon 2002), and clearly have important implications for community stability (Polis and Strong 1996, Holt and Polis 1997, McCann and Hastings 1997). Our results emphasise that it is crucial to understand the interactions between these factors, and others that influence coexistence, if we are to explain fully the patterns of diversity that we observe in nature.

References

Akimoto, S. 1988. Competition and niche differentiation among *Eriosoma* aphids occurring on the Japanese elm. – Oecologia 75: 44–53.

Amarasekare, P. 2002. Interference competition and species coexistence. – Proc. R. Soc. Lond. 269: 2541–2550.

Atkinson, W. D. and Shorrocks, B. 1981. Competition on a divided and ephemeral resource: a simulation model. – J. Anim. Ecol. 50: 461–471.

Chvála, M., Doskocil, J., Mook, J. H. et al. 1974. The genus *Lipara* Meigen (Diptera: Chloropidae), systematic morphology, behaviour and ecology. – Tijdschrift Entomol. 117: 1–25.

Coll, M. and Guershon, M. 2002. Omnivory in terrestrial arthropods: mixing plant and prey diets. – Annu. Rev. Entomol. 47: 267–297.

Craig, T. P., Itami, J. K. and Price, P. W. 1990. Intraspecific competition and facilitation by a shoot-galling sawfly. – J. Anim. Ecol. 59: 147–159.

Crespi, B. and Abbot, P. 1999. The behavioral ecology and evolution of kleptoparasitism in Australian gall thrips. – Florida Entomol. 82: 147–164.

De Bruyn, L. 1994. Life cycle strategies in a guild of dipteran gall formers on the common reed. – In: Williams, M. A. J. (ed.), Plant galls. Clarendon Press, pp. 259–281.

Faeth, S. H. 1990. Aggregation of a leafminer, *Cameraria* Sp. Nov. (Davis): consequences and causes. – J. Anim. Ecol. 59: 569–586.

Giller, P. S. and Doube, B. M. 1994. Spatial and temporal co-occurrence of competitors in Southern African dung beetle communities. – J. Anim. Ecol. 63: 629–643.

Godfray, H. C. J. and Pacala, S. W. 1992. Aggregation and the population dynamics of parasitoids and predators. – Am. Nat. 140: 30–40.

Hanski, I. 1981. Coexistence of competitors in patchy environments with and without predation. – Oikos 37: 306–312.

Hardin, G. 1960. The competitive exclusion principle. – Science 131: 1292–1297.

Hartley, S. and Shorrocks, B. 2002. A general framework for the aggregation model of coexistence. – J. Anim. Ecol. 71: 651–662.

Heard, S. B. and Remer, L. C. 1997. Clutch-size behavior and coexistence in ephemeral patch competition models. – Am. Nat. 150: 744–770.

Holt, R. D. and Polis, G. A. 1997. A theoretical framework for intraguild predation. – Am. Nat. 149: 745–764.

Inouye, B. D. 1999. Estimating competition coefficients: strong evidence for competition between three species of frugivorous flies. – Oecologia 120: 588–594.

Inouye, B. D. 2005. Scaling up from local competition to regional coexistence across two scales of spatial heterogeneity: insect larvae in the fruits of *Apeila membranacea*. – Oecologia 145: 188–196.

Ives, A. R. 1988. Covariance, coexistence and the population dynamics of two competitors using a patchy resource. – J. Theor. Biol. 133: 345–361.

Ives, A. R. 1991. Aggregation and coexistence in a carrion fly community. – Ecol. Monogr. 61: 75–94.

Ives, A. R. 1995. Measuring competition in a spatially heterogeneous environment. – Am. Nat. 146: 911–936.

Jaenike, J. and James, A. C. 1991. Aggregation and the coexistence of mycophagous *Drosophila*. – J. Anim. Ecol. 60: 913–928.

Johannesen, J. and Loeschcke, V. 1996. Distribution, abundance and oviposition patterns of four coexisting *Chiastocheta* species (Diptera: Anthomyiidae). – J. Anim. Ecol. 65: 567–576.

Klopfer, E. D. and Ives, A. R. 1997. Aggregation and the coexistence of competing parasitoid species. – Theor. Popul. Biol. 52: 167–178.

Kraaijeveld, A. R 1999. Kleptoparasitism as an explanation for paradoxical oviposition decisions of the parasitoid *Asobara tabida*. – J. Evol. Biol. 12: 129–133.

Krijger, C. L. and Sevenster, J. G. 2001. Higher species diversity explained by stronger spatial aggregation across six neotropical *Dosophila* communities. – Ecol. Lett. 4: 106–115.

May, R. M. and Hassell, M. P. 1981. The dynamics of multiparasitoid-host interactions. – Am. Nat. 117: 234–261.

McCann, K. S. and Hastings, A. 1997. Re-evaluating the omnivory-stability relationship in food webs. – Proc. R. Soc. Lond. 264: 1249–1254.

McGeoch, M. A. and Chown, S. L. 1997. Evidence of competition in a herbivorous, gall-inhabiting moth (Lepidoptera) community. – Oikos 78: 107–115.

Miller, D. G. 2005. Ecology and radiation of galling aphids (*Tamalia*; Hemiptera: Aphidae) on their host plants (Ericaceae). – Basic Appl. Ecol. 6: 463–469.

Mitchell, R. 1975. The evolution of oviposition tactics in the bean weevil, *Callosobruchus maculatus* (F.). – Ecology 56: 696–702.

Mitsui, H. and Kimura, M. T. 2000. Coexistence of drosophilid flies: Aggregation, patch size diversity and parasitism. – Ecol. Res. 15: 93–100.

Mook, J. H. 1967. Habitat selection by *Lipara lucens* Mg. (Diptera, Chloropidae) and its survival value. – Arch. Neerl. Zool. 17: 469–549.

Morris, W. F., Wiser, S. D. and Klepetka, B. 1992. Causes and consequences of spatial aggregation in the phytophagous beetle *Altica tombacina*. – J. Anim. Ecol. 61: 49–58.

Müller, C. B. and Brodeur, J. 2002. Intraguild predation in biological control and conservation biology. – Biol. Control 25: 216–223.

Murdoch, W. W. and Stewart-Oaten, A. 1989. Aggregation by parasitoids and predators: effects on equilibrium and stability. – Am. Nat. 134: 288–310.

Polis, G. A., Myers, C. A. and Holt, R. D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. – Annu. Rev. Ecol. Syst. 20: 297–330.

Polis, G. A. and Strong, D. R. 1996. Food web complexity and community dynamics. – Am. Nat. 147: 813–846.

Reader, T. 2001. Competition, kleptoparasitism and intraguild predation in a reedbed community. – PhD thesis, Dept of Zoology, Univ. of Cambridge, p. 292.

Reader, T. 2003. Strong interactions between species of phytophagous fly: a case of intraguild kleptoparasitism. – Oikos 103: 101–112.

Rohani, P., Godfray, H. C. J. and Hassell, M. P. 1994. Aggregation and the dynamics of host-parasitoid systems: a discrete-generation model with within-generation redistribution. – Am. Nat. 144: 491–509.

Ronquist, F. 1994. Evolution of parasitism among closely related species: phylogenetic relationships and the origin of inquilinism in gall wasps (Hymenoptera, Cynipidae). – Evolution 48: 241–266.

Sevenster, J. G. 1996. Aggregation and coexistence: I. Theory and analysis. – J. Anim. Ecol. 65: 297–307.

Sevenster, J. G. and Van Alphen, J. J. M. 1996. Aggregation and coexistence. II. A neotropical *Drosophila* community. – J. Anim. Ecol. 65: 308–324.

Shorrocks, B. and Sevenster, J. G. 1995. Explaining local species diversity. – Proc. R. Soc. Lond. 260: 305–309.

Simková, A., Desdevises, Y., Gelnar, M. et al. 2000. Coexistence of nine gill ectoparasites (*Dactylogyrus*: Monogenea) parasitising the roach (*Rutilus rutilus* L.): history and present ecology. – Int. J. Parasitol. 30: 1077–1088.

Sivinski, J., Marshall, S. and Petersson, E. 1999. Kleptoparasitism and phoresy in the Diptera. – Florida Entomol. 82: 179–197.

Snyder, R. E., Borer, E. T.and and Chesson, P. 2005. Examining the relative importance of spatial and nonspatial coexistence mechanisms. – Am. Nat. 166: E75–E94.

Stiling, P. D. and Strong, D. R. 1983. Weak competition among *Spartina* stem borers by means of murder. – Ecology 64: 770–778.

Takahashi, K. H., Tuno, N. and Kagaya, T. 2005. The relative importance of spatial aggregation and resource partitioning on the coexistence of mycophagous insects. – Oikos 109: 125–134.

Taylor, L. R., Woiwod, I. P. and Perry, J. N. 1978. The density-dependence of spatial behaviour and the rarity of randomness. – J. Anim.Ecol. 47: 383–406.

Wertheim, B., Sevenster, J. G., Eijs, I. E. M. et al. 2000. Species diversity in a mycophagous insect community: the case of spatial aggregation vs. resource partitioning. – J. Anim. Ecol. 69: 335–351.

Woodcock, B. A., Watt, A. D. and Leather, S. R. 2002. Aggregation, habitat quality and coexistence: a case study on carrion fly communities in slug cadavers. – J. Anim. Ecol. 71: 131–140.