

A general framework for the aggregation model of coexistence

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Summary

1. The aggregation model of coexistence has been used widely to explain the coexistence of competing species that utilize patchy and ephemeral resources. Over the years, it has been reformulated in many different ways, using different assumptions, indices and analyses, leading sometimes to contradictory conclusions. We present a general framework, from which many of the alternative approaches are derived as special cases.
2. A generalized distribution, composed of the distribution of visits across patches and the distribution of eggs per visit, is used to model changes in the mean individual-level experience of density that occur at different population-level densities.
3. New and more general criteria for coexistence are derived, based upon standard invasability analysis of Lotka–Volterra competition equations applied to a patchy system.
4. An important parameter in the new coexistence criteria is the mean per capita density of individuals in a single clutch (\bar{c}). Until now this measure has been relatively ignored, experimentally and theoretically.
5. We confirm earlier findings that the random distribution of clutches may be a sufficient cause of aggregated egg distributions to allow coexistence between species of unequal competitive ability, but only if the product of competition coefficients is less than one.

Key-words: clutch-laying, competition, mean crowding, patchy resources, spatial model.

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Introduction

The question of how so many competing species can coexist in the same place, at the same time, on the same resource, is one of the perennial challenges facing community ecology (Hutchinson 1959; Cornell & Lawton 1992). Solutions to this problem are generally found by contradicting the original premises. That is to say, species coexist either because they are not competing strongly (niches are not full and resources are not the limiting factor), because they are not using exactly the same resource (resource partitioning) or because they are not all in the same place at the same time experiencing the same conditions (explanations based upon spatial and temporal heterogeneity).

In this paper we shall consider one of the spatial explanations, namely, the ‘aggregation model of coexistence’ (Shorrocks, Atkinson & Charlesworth 1979; de Jong 1979; Atkinson & Shorrocks 1981, 1984; Hanski

1981; for early versions). The key feature of the model is that when the individuals of a species are clumped together they may limit their own population growth to such an extent that some resources are left over in low density patches, which are sufficient to support other (competitively inferior) species. It is especially appropriate for examining coexistence in invertebrate communities, where the larvae utilize patchy and ephemeral resources such as fruit, seeds, carrion, dung, fungi or small water bodies. Such systems are often characterized by a remarkably high species diversity (Beaver 1977).

The aggregation model has attracted considerable attention and has been modelled and simulated in many ways (Shorrocks *et al.* 1984; Ives & May 1985; Ives 1988a, 1988b; Jaenike & James 1991; Shorrocks & Sevenster 1995; Sevenster & van Alphen 1996). In addition, a number of explicit criteria for coexistence have been developed, each based on slightly different assumptions, indices or analyses (Hanski 1981; Kuno 1988; Ives 1991; Sevenster 1996; Heard & Remer 1997). A particularly contentious issue is whether a random distribution of clutches is ever a sufficient cause of aggregated egg distributions to allow coexistence (Green 1986, 1988; Shorrocks & Rosewell 1988; Heard & Remer 1997).

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In the following pages we attempt to synthesize these various approaches into a coherent framework, and show how many of the alternative models can be derived as special cases. We achieve this by an explicit consideration of the two processes that lead to the observed distribution of eggs across patches: the distribution of clutches across patches and the distribution of eggs across clutches. Having accounted for the resulting distribution of eggs (and how it will alter as adult densities approach either zero or their single-species equilibrium), we then develop the Lotka–Volterra competition model for a patchy system, as it is within patches that individuals experience competition from hetero- and conspecifics.

Methods

THE SYSTEM

As a premise, we assume that females visit patches (in order to lay a clutch of eggs) and that the distribution of visits over patches has a mean and variance (m_1 , v_1). Secondly, the number of eggs laid in a clutch also has its own distribution with mean and variance (m_2 , v_2). These two processes result in a generalized distribution of eggs across patches with overall mean, M , and variance, V , defined by equations 1 and 2 (Pielou 1977; Cliff & Ord 1981). Unless stated otherwise, we shall assume that m_2 and v_2 do not change as a function of m_1 , i.e. clutch size distributions are independent of population density. This is justified on the grounds that Ives (1991) observed no change in the proportion of female visits that resulted in oviposition, even as the total number of flies per patch increased.

$$M = m_1 m_2 \quad \text{eqn 1}$$

$$V = m_1 v_2 + m_2^2 v_1 \quad \text{eqn 2}$$

Lloyd's (1967) concepts of 'mean crowding' and 'mean demand' are used extensively (eqns 3 and 4, see also Iwao 1976). Mean crowding (\hat{M}) is the number of other (i.e. non-self) individuals in a patch, averaged across individuals. As the name implies, it represents the level of crowding (and hence competition) that the average individual will experience. For a random (Poisson) distribution of individuals $\hat{M} = M$, while in aggregated distributions $\hat{M} > M$. Mean demand ($\hat{M} + 1$) represents the density of individuals per patch that a typical individual can expect (i.e. including self). Mean crowding per clutch is symbolized by \hat{m}_2 , but for ease of expression, the symbol \hat{c} is used to represent ($\hat{m}_2 + 1$): the mean demand or mean per capita density of individuals in a single clutch (eqn 5 and Iwao 1976). As we shall see later, \hat{c} is often a more relevant measure than the straightforward mean clutch size, m_2 .

To facilitate comparisons across the literature we also refer to the index of aggregation, J , which measures the level of within-patch density, averaged across

individuals, relative to a random distribution of the same regional mean (eqn 6, and Ives 1988a). The use of J does not imply any particular frequency distribution, as it is simply a function of variance and mean; but if the distribution is negative binomial then $J = 1/k$, where k is the aggregation parameter of the negative binomial distribution (low values of k correspond to a high degree of aggregation).

$$\text{mean crowding: } \hat{M} = M + (V/M) - 1 \quad \text{eqn 3}$$

$$\text{mean demand or per capita density:} \\ \hat{M} + 1 = M + (V/M) \quad \text{eqn 4}$$

$$\text{per capita density within a single clutch:} \\ \hat{c} = \hat{m}_2 + 1 = m_2 + (v_2/m_2) \quad \text{eqn 5}$$

$$\text{index of aggregation or 'patchiness':} \\ J = (V - M)/M^2 = (\hat{M}/M) - 1 \quad \text{eqn 6}$$

For simplicity, we assume that all patches are equal in size and quality, and hence have equal carrying capacities of e . (Carrying capacities can be made patch-specific following the methods of Watanabe (1988) and Sevenster (1996)). The symbol K is used to indicate the system-wide, single-species carrying capacity that would be attained in a well-mixed population inhabiting a single homogeneous 'super-patch'. If the number of patches is P , then $K = eP$. E is the system-wide, single-species, equilibrium population size that is attained in a patchy-system. In general, $E < K$, except where individuals are distributed uniformly across all available patches, in which case the two are equal. In most situations the coefficient of variation (CV) of individuals across patches increases with mean density, and a growing population will meet the ceiling of E when $K/E = 1 + CV^2$ (Sevenster 1996). Let $\hat{M} = E/P$, the mean density of individuals per patch at this system-level equilibrium. At this equilibrium density, the ratio of mean demand to mean also equals K/E because $(\hat{M} + 1)/M = 1 + CV^2$ (Iwao 1976).

When introducing competition between species x and y , the standard Lotka–Volterra model is applied. It is the continuous version of the commonly used Hassell & Comins's (1976) competition equation, with the simplifying assumption of pure contest intraspecific competition. The relative strengths of inter- vs. intraspecific competition are given by the coefficients α_{xy} and α_{yx} , while species-specific values of e and E are similarly denoted by subscripts x and y . Most models assume that patch-carrying capacities are the same for both species, $e_x = e_y$ (e.g. Jaenike & James 1991; Heard & Remer 1997) and often that the effect of the inferior competitor on the superior competitor is negligible, $\alpha_{xy} = 0$ (e.g. Atkinson & Shorrocks 1981; Green 1986). Sevenster (1996) assumes a relationship between the relative patch-carrying capacities and competitive effects such that $\alpha_{xy} = e_x/e_y$ and $\alpha_{yx} = e_y/e_x$. This relationship amounts to an assumption of ideal exploitation

(i.e. resource-mediated) competition. This assumption appears to be justified for at least some of the systems that have been studied (e.g. Bakker 1961).

SINGLE-SPECIES POPULATION GROWTH

The standard logistic growth model for a non-patchy system is:

$$dN/dt = rN[1 - (N/K)] \quad \text{eqn 7}$$

where, N is the total number of individuals. Dividing by P , the number of patches, one can begin to model the system on a per patch basis:

$$dM/dt = rM[1 - (M/e)] \quad \text{eqn 8}$$

However, for a patchy system, the average per capita inhibition is a function of per capita density ($\hat{M} + 1$), instead of density averaged across all patches (M) (Kuno 1988), thus:

$$dM/dt = rM[1 - (\hat{M} + 1)/e] \quad \text{eqn 9}$$

and $dM/dt = 0$ when $(\hat{M} + 1) = e$. Substituting from eqn 4 we find that the overall mean density per patch at the single-species, system-level equilibrium (denoted by the hat \wedge) is:

$$\hat{M} = e - (\hat{V}/\hat{M}) \quad \text{eqn 10}$$

This accords with our earlier observation that an uneven distribution ($V > 0$) lowers the equilibrium number of individuals supported per patch.

POPULATION GROWTH WITH COMPETITION

By analogy with eqn 9, the Lotka–Volterra equation for competition in a patchy system (assuming random association between species) becomes:

$$\frac{dM_x}{dt} = r_x M_x \left[1 - \frac{(\hat{M}_x + 1 + \alpha_{xy} M_y)}{e_x} \right] \quad \text{eqn 11}$$

If the two species exhibit a non-random association, then the number of species y competing with a typical individual of species x is the mean, M_y , weighted by an index of relative interspecies crowding, \hat{M}_{xy}/M_y (Lloyd 1967; Iwao 1977), which we denote as Θ_{xy} (eqn 12). This index represents how many times more (or fewer) individuals of species y an individual of species x can expect to share a patch with, relative to the situation of random association. The index is symmetrical, $\Theta_{xy} = \Theta_{yx}$, and will be equal to 1 when the two species are distributed independently. It has a minimum of zero (complete avoidance) and a theoretical maximum of infinity (complete overlap of infinite populations) and it is equivalent to $(C_{xy} + 1)$, where C_{xy} is the measure of association introduced by Ives (1988a). In this

paper we assume that Θ_{xy} is constant, irrespective of the densities of the two species

$$\frac{\hat{M}_{xy}}{M_y} = \frac{Cov_{xy}}{M_x M_y} + 1 = \Theta_{xy} \quad \text{eqn 12}$$

Incorporating Θ_{xy} , the effect of non-random species association, eqn 11 can be rewritten as below.

$$\frac{dM_x}{dt} = r_x M_x \left[1 - \frac{(\hat{M}_x + 1 + \alpha_{xy} \Theta_{xy} M_y)}{e_x} \right] \quad \text{eqn 13}$$

Following standard invasability analysis, coexistence of two species should be possible if both have a positive growth rate at very low densities, when invading a monospecific equilibrium population of the other (Chesson 2000). Thus, for species x to be able to invade an equilibrium population of species y , implies that $dM_x/dt > 0$ when $M_y = \hat{M}_y$, $M_x \rightarrow 0$, and $\hat{M}_x + 1 \rightarrow \hat{m}_{2x} + 1 (= c_x^*)$. Substituting these values into eqn 13 produces a general condition (G_{xy}) for the successful invasion of species x into an equilibrium population of y :

$$G_{xy} = \frac{c_x^* + \alpha_{xy} \Theta_{xy} \hat{M}_y}{e_x} < 1 \quad \text{eqn 14}$$

Applying the same logic for the invasion of species y , the general conditions for mutual coexistence in a patchy system are:

$$G_{xy} < 1 < (1/G_{yx}) \quad \text{eqn 15}$$

Note that the crucial difference between this derivation and most others is that even though patch density, M , tends towards zero at very low population densities, the laying of clutches means that mean demand ($\hat{M} + 1$) tends to the per capita density of a single clutch, \hat{c} , not zero. Strictly speaking, \hat{c} in the above constraints is \hat{c} when rare and invading, although we have assumed that clutch-size distributions are constant, irrespective of population density.

From eqn 14 we can see that successful invasion by species x will be made more likely if its patch-carrying capacity (e_x) is high, if its per capita crowding within clutches (\hat{c}_x^*) is low, if the relative competitive effect of the other species (α_{xy}) is low, if its association with the other species (Θ_{xy}) is low, or if the equilibrium population density of the resident species (\hat{M}_y) is low. Referring back to eqn 10 we see that a low equilibrium population density of the resident occurs when the resident's patch-carrying capacity (e_y) is low and/or its equilibrium distribution of eggs across patches is aggregated, i.e. (\hat{V}_y/\hat{M}_y) is high. In order to assess whether the conditions for mutual invasability are met it is therefore necessary to obtain estimates for a total of nine different parameters. As we shall see in the following sections, this number can be reduced if one is willing to make some simplifying assumptions.

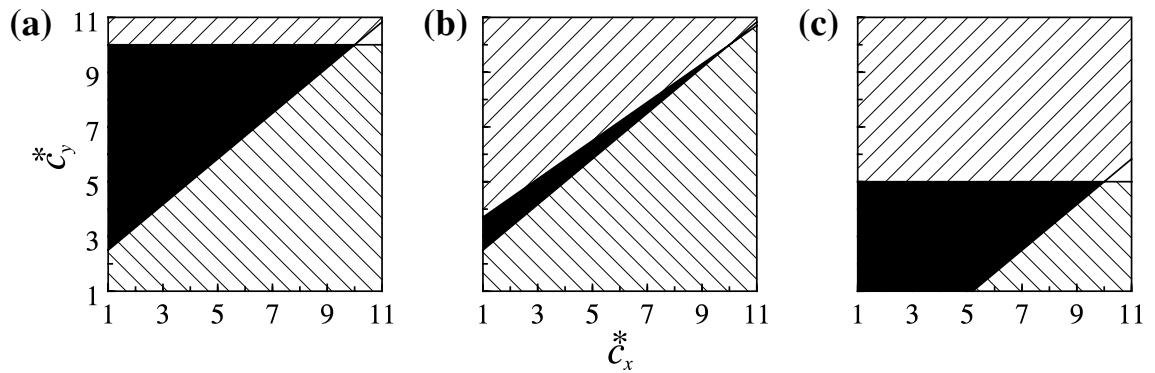


Fig. 1. Invasibility phase-space diagrams plotted as a function of each species' intraclutch per capita density (\hat{c}_x) assuming a random and independent distribution of clutches (i.e. $v_{1x} = m_{1x}$, $v_{1y} = m_{1y}$, $\Theta_{xy} = 1$). Hatching from lower-left to upper-right indicates invasion of species x ($G_{xy} < 1$) and from lower-right to upper-left invasion of species y ($G_{yx} < 1$). Shading indicates mutual invasibility and hence coexistence. (a) $e_x = 10$, $e_y = 10$, $\alpha_{xy} = 1.2$, $\alpha_{yx} = 0$ (b) $e_x = 10$, $e_y = 10$, $\alpha_{xy} = 1.2$, $\alpha_{yx} = 0.7$ (c) $e_x = 10$, $e_y = 5$, $\alpha_{xy} = 1.2$, $\alpha_{yx} = 0$.

Results

COMPARISON WITH EARLIER MODELS:
 1. MODELS THAT EXPLICITLY INCLUDE
 A GENERALIZED DISTRIBUTION

Various analytical and simulation scenarios have been constructed to test the idea that aggregation can permit coexistence. We show below how several of these approaches can be understood as special cases of the general model presented above in eqn 14. In discussing generalized distributions we use the shorthand notation: distribution1 \setminus distribution2, where distribution1 describes the distribution of visits across patches and distribution2 describes the distribution of eggs across clutches. In this paper we use the term 'generalized distribution' in line with the definitions of Pielou (1977) and Cliff & Ord (1981); however, in much of the previous literature on the aggregation model (e.g. Atkinson & Shorrocks 1984; subsequent citations) they are called compound distributions. An example of a compound distribution (*sensu* Pielou 1977; Cliff & Ord 1981) is the heterogeneous Poisson sampling mechanism discussed by Atkinson & Shorrocks (1984), in which the defining parameter of the distribution of eggs per clutch (in their case the mean of a Poisson) varies from patch to patch according to some other distribution (in their case a gamma distribution). The implications of this mechanism for generating aggregated distributions are considered further by Inouye (1999) in his analysis at nested spatial scales.

Random (Poisson) distribution of visits

The question of whether a random distribution of female visits can generate the aggregated egg distributions necessary for coexistence has been the subject of considerable debate. Green (1986, 1988) suggested that an aggregated distribution of female visits was necessary for coexistence, while Shorrocks & Rosewell (1988) and Heard & Remer (1997) maintained that the

random distribution of clutches could be sufficient. Before exploring the particular details of different models, let us consider the general consequences of assuming a random (Poisson) distribution of visits in the context of the framework developed above. A random distribution of visits implies $v_1 = m_1$, substituting this result into equations 1, 2 and 10 we find the single-species equilibrium population density can now be expressed simply in terms of e and \hat{c} (eqn 16):

$$\hat{M} = e - \hat{c} \tag{eqn 16}$$

and the condition for successful invasion reduces to:

$$G_{xy} = \frac{\hat{c}_x + \alpha_{xy}\Theta_{xy}(e_y - \hat{c}_y)}{e_x} < 1 \tag{eqn 17}$$

If we assume further that there is random association between species ($\Theta_{xy} = 1$), the criterion for coexistence (eqn 17) can be evaluated with just three parameters for each species. It can be shown that mutual invasibility is possible with this model for a variety of parameter values. Figure 1 illustrates three such examples, plotting invasibility as a function of each species' per capita intraclutch density. Even with a degree of positive association between species it is still possible to achieve mutual invasibility, although the conditions become more restrictive (see also Ives 1988b).

Per capita intraclutch density, \hat{c}

The value of per capita intraclutch density (\hat{c}) is determined by the mean and variance of the distribution of eggs per clutch (eqn 5). Unfortunately, there are very few direct data available from which natural values of \hat{c} can be evaluated. Hoffmeister & Rohlf (2001) provide details of the frequency distribution of clutch sizes laid by female *Drosophila subobscura* Collin flies visiting fruits of *Sorbus aucuparia* L. in an experimental arena. Their results provide values of 3.6, 7.3 and 5.6 for m_2 , v_2 and \hat{c} , respectively. An alternative approach is to

Table 1. The relationship between the distribution of eggs across clutches and the mean per capita intraclutch density. ¹The logarithmic series distribution is defined by a single parameter (a) from which the mean (m_2) and variance (v_2) can be calculated. See Getis & Boots (1978) or Appendix II

Distribution of eggs across clutches	Per capita intraclutch density (\bar{c}^*)
Constant clutch size, $v_2 = 0$	m_2
Poisson, $v_2 = m_2$	$m_2 + 1$
Negative binomial, $v_2 = (m_2/k) + m_2$	$m_2 + (m_2/k) + 1$
Logarithmic series ¹	$1/(1 - a)$

assume a particular statistical distribution of clutch sizes, then \bar{c}^* can be expressed in terms of the parameters defining the distribution (see Table 1). Note that per capita intraclutch density is always greater than the mean clutch size (m_2), except when clutch sizes are constant, in which case the two are equal.

The results from the previous two sections can now be combined to create some of the scenarios considered by other authors.

Green's model with a Poisson distribution of clutches

Green (1986) argued that mutual coexistence was not possible (in the models of Atkinson & Shorrocks 1981, 1984) if females visited patches at random (i.e. $v_1 = m_1$) and that the only cause of aggregated distribution of eggs was the fact that eggs were laid in clutches (i.e. $m_2 > 1$), although his proof included the additional proviso that the two species 'differ only in their interspecific competitive ability', i.e. $\bar{c}_x^* = \bar{c}_y^*$, $e_x = e_y$ and $\alpha_{xy} \neq \alpha_{yx}$. Atkinson & Shorrocks (1981) assumed $\Theta_{xy} = 1$, $\alpha_{xy} = 2$, $\alpha_{yx} = 0$ and $e_x = e_y$. Substituting all of these conditions into the coexistence criteria for random clutches (eqn 17), we find that it is impossible to generate a situation in which mutual invasibility could occur. However, if we relax either the assumption of equal per capita intraclutch densities, or that of equal carrying capacities, then coexistence is possible (see the results of Heard & Remer (1997), discussed below). Thus, although Green (1986) did find conditions in which the model of Atkinson & Shorrocks (1981, 1984) would not allow coexistence, his conditions were rather strict and do not support the general argument that a random distribution of clutches cannot create the necessary conditions for coexistence between a superior and inferior competitor.

To create a slightly more realistic situation, let us now assume a random distribution of clutches, random association between species ($\Theta_{xy} = 1$), but that both α_{xy} and α_{yx} must be positive. Under these conditions, coexistence is only possible if $\alpha_{xy}\alpha_{yx} < 1$. Fulfilling this constraint implies that competition is not of the ideal exploitation type (where $\alpha_{xy} = e_x/e_y = 1/\alpha_{yx}$), and is suggestive of either some form of resource partitioning, consistent priority effects or differences in

developmental time, such that the 'late' or 'slow' species has little influence on the survival of the 'early' or 'fast' species. (Sevenster & van Alphen 1993; Shorrocks & Bingley 1994). Thus, in some sense, Green (1986) was right after all: the random distribution of clutches does not generate the aggregation needed for coexistence unless one includes an additional mechanism for ensuring that $\alpha_{xy}\alpha_{yx} < 1$.

The Poisson-logarithmic model (RVRC)

In many natural systems, the negative binomial distribution (NBD) is often found to provide a good description of the overall distribution of eggs across patches (Atkinson & Shorrocks 1984; Rosewell, Shorrocks & Edwards 1990), although it is less common that a single value of the clumping parameter, k , will fit across all population densities (Taylor, Woivod & Perry 1979). Atkinson & Shorrocks (1984) suggested several possible mechanisms that would generate such a distribution, their favoured explanation being that females visit patches at random (therefore $m_1 = v_1$), and have a constant probability of leaving while laying eggs. Modelling this process by a generalized Poisson-logarithmic series distribution leads precisely to a NBD (Atkinson & Shorrocks 1984). This model has been dubbed the random visit random clutch (RVRC) model by Sevenster (1996), although caution is required as this name could be interpreted as a description of a Poisson-Poisson process.

The logarithmic distribution is defined by a single parameter, a , from which the per capita intraclutch density is calculated as $\bar{c}^* = [1/(1 - a)]$ (Table 1, Appendix II). Substituting this result into eqn 17 produces the conditions for mutual invasibility under a Poisson-logarithmic model.

The clumping parameter, k , of the resultant NBD of eggs across patches is a function of m_1 of the Poisson distribution and a of the logarithmic series distribution as shown in eqn 18 (Getis & Boots 1978). From this relationship we can see that if a is fixed and population density (assumed to be monotonically related to m_1) is increased, then k of the resultant NBD will increase with overall mean (but the overall variance to mean ratio ($V:M$) will remain constant at a value of $[1/(1 - a)]$). This is at odds with the simulation of Atkinson & Shorrocks (1984) and the analysis of Ives & May (1985) which assume a constant k at all densities. In order to maintain a constant k , any increase in the value of m_1 must require a related increase in a of the logarithmic series. Thus, in proposing a Poisson-logarithmic model one must choose between the assumption of a constant overall k , or that of a constant distribution of clutch sizes (i.e. a constant a in the logarithmic series distribution). As Green (1986) pointed out, models which suggest that both are maintained are not internally consistent.

$$k = m_1 / \ln[1/(1 - a)]$$

eqn 18

A Poisson v constant model (after Heard & Remer 1997)

Heard & Remer (1997) used simulations and an analytical model to demonstrate that aggregation due to clutch-laying behaviour alone is sufficient to allow coexistence. They modelled the situation in which females of both species visit patches independently and at random to lay clutches of a constant size, although the species may differ in their clutch-size. In the context of the current paper their assumptions can be expressed as: $\Theta_{xy} = 1$, $m_1 = v_1$, and $v_2 = 0$ (i.e. $\tilde{c}^* = m_2$). With reference to equations 1, 2 and 10, these assumptions imply that $\hat{M} = e - m_2$. Substituting into eqn 14 we obtain the criterion for coexistence assuming a Poisson v constant distribution of eggs and clutches and random species association:

$$G_{xy}^{PvC} = \frac{m_{2x} + \alpha_{xy}(e_y - m_{2y})}{e_x} \quad \text{eqn 19}$$

Heard & Remer (1997) also assumed equal patch-carrying capacities for the two species ($e_x = e_y = e$). Making this change to eqn 19, the conditions $G_{xy} < 1$ and $G_{yx} < 1$ can be re-written as equations 20 and 21; exactly the criteria for successful invasion developed in the Appendix of Heard & Remer (1997).

For successful invasion of x :

$$m_{2y} - m_{2x} > (\alpha_{xy} - 1)\hat{M}_y \quad \text{eqn 20}$$

and for successful invasion of y :

$$m_{2y} - m_{2x} < (1 - \alpha_{yx})\hat{M}_x \quad \text{eqn 21}$$

It is possible to find parameter values such that both conditions are satisfied and mutual coexistence is predicted, but once again we require that $\alpha_{xy}\alpha_{yx} < 1$. Interestingly, the persistence criteria developed above predict long-term coexistence for a much wider range of parameter values than Heard & Remer actually found in their simulation (Table 3 in Heard & Remer 1997). This is because their simulation was based upon difference equations and stochastic sampling within a finite system of patches as opposed to differential equations and an infinite system; an important point to bear in mind when applying invasability criteria to real world situations. None the less, both simulations and analysis support the conclusions of Heard & Remer (1997): the aggregation that results purely from clutch-laying is sufficient to allow coexistence under certain conditions, it can also result in the exclusion of the superior competitor if the clutch size of the superior competitor is sufficiently large.

A Poisson v Poisson model

Another simple null-model that can be used to generate an aggregated distribution of individuals across patches is independent, random (i.e. Poisson) distributions of visits and random (i.e. Poisson) distributions of

eggs per clutch (the result being a Neyman type A distribution of individuals). Although it has not been used in the literature, this model would also allow coexistence under certain conditions as long as $\alpha_{xy}\alpha_{yx} < 1$ if $\Theta_{xy} = 1$ (substitute $\tilde{c}^* = (m_2 + 1)$ into eqn 17, for proof).

Models with ideal exploitation competition

If competition between species is almost entirely exploitative (i.e. a consequence of resource consumption) and species have similar feeding periods, then it seems reasonable to suppose that the value of the competition coefficient, α_{xy} , will be approximately equal to the ratio of patch-carrying capacities, ϵ_{xy} ($= e_x/e_y$), and $\alpha_{xy}\alpha_{yx}$ will equal one (Sevenster 1996). Adopting this assumption, the criterion for persistence (eqn 14) can be rewritten as below (using the identity $e_x = \epsilon_{xy}e_y$ and substituting from eqn 10).

$$G_{xy}^{ec} = \frac{\tilde{c}_x^* + \epsilon_{xy}\Theta_{xy}\hat{M}_y}{e_x} = \frac{\epsilon_{xy}\Theta_{xy}}{1 + \frac{\hat{V}_y}{\hat{M}_y^2} - \frac{\tilde{c}_x^*}{\epsilon_{xy}\hat{M}_y}} < 1 \quad \text{eqn 22}$$

Sevenster (1996) developed two versions of a persistence criterion, T_{xy} , which utilize the simplification of $\alpha_{xy} = \epsilon_{xy}$. In the first (eqn 28 in Sevenster 1996; eqn 23 below), he also assumed that eggs are laid singly.

$$T_{xy}^{28} = \frac{1 + C_{xy}}{1 + J_y} = \frac{\Theta_{xy}}{1 + \frac{\hat{V}_y}{\hat{M}_y^2} - \frac{1}{\hat{M}_y}} < 1 \quad \text{eqn 23}$$

Applying the assumption of single-egg clutches to eqn 22 ($\tilde{c}^* = 1$), it should become obvious that the two criteria are not equivalent. This is because Sevenster derived his persistence criterion based upon a 'relative effect' argument rather than an invasability analysis. The crucial difference is that the relative effect approach does not account for the inhibitory effect that a focal individual has upon its own growth in a finite resource patch (relative to growth in an infinite super-patch). In other words, it compares the mean crowding experience of a rare x -individual with that of a typical y -individual rather than comparing the mean demands on resource use which each will experience, which includes ones own equilibrium requirements for a $1/e_x$ or $1/e_y$ share of the resource patch. As Sevenster (1996) noted, the two approaches agree only if the patch-carrying capacities, and hence the self-inhibition, of the two species are equal ($e_x = e_y$; $\epsilon_{xy} = 1$).

In the second version of T_{xy} , eggs may be laid in clutches (implicitly assumed to be of a constant size, thus $\tilde{c}^* = m_2$), but more restrictively, the patch-carrying capacities of each species are assumed to be equal, $e_x = e_y$ (after Jaenike & James 1991). Consequently, ϵ_{xy} does equal 1 and eqn 22 reduces to an equivalent expression of the alternative T_{xy} (eqn 31 in Sevenster 1996).

An attractive feature of the T_{xy} criteria is that they eliminate the need to assess patch-carrying capacities

and competition coefficients, which makes them convenient for analysis of field data. However, to achieve this one must accept the relative effect approach or else use an invasibility analysis with the assumption of equal patch-carrying capacities.

If neither of these approaches seem satisfactory the assumption of ideal exploitation competition may still prove useful if one could find a way to estimate the ratio of patch-carrying capacities as required by eqn 22. One practical solution might be to use the inverse ratio of body masses (ideally measured as pupae or the emerging adult plus puparium) assuming, of course, that resource use is directly proportional to final body weight. A prediction that stems from this assumption is that, all other things being equal, large-bodied species will be limited to relatively smaller and less variable clutches if they are to satisfy the general persistence criteria of eqn 22. Further work is needed to test the validity of this prediction.

2. MODELS THAT DO NOT EXPLICITLY INCLUDE A GENERALIZED DISTRIBUTION

The second class of models and simulations we wish to consider are those which ignore the two underlying distributions (m_1, v_1 and m_2, v_2) and which set constraints on the overall distribution (M, V). For example, M and V must follow the Iwao & Kuno quadratic (IKQ) equation (Kuno 1988), Taylor's Power Law (TPL) (Hanski 1981), or a particular NBD (Shorrocks *et al.* 1979; Atkinson & Shorrocks 1981; Ives & May 1985). A general problem with this class of models is that the relationship which describes the data well at moderate to high densities (and whose parameters are usually fitted across this range of densities) does not often hold at the extremely low densities of a rare invader, when the distribution of eggs per clutch is the dominant process.

The Iwao and Kuno quadratic equation

The Bartlett or Iwao & Kuno quadratic equation (IKQ) for the relationship between overall variance and mean is given in eqn 25. It was suggested originally as an empirical description of variance-mean relationships (Bartlett 1936), although it was later given a theoretical grounding based upon the premise of a generalized distribution with constant aggregation of visits (J_1) and constant mean crowding within clutches (\hat{m}_2) (Iwao & Kuno 1968, 1971; Iwao 1968). If these conditions apply, then the parameters A and B will equal \hat{c}^* and J_1 , respectively. In practice these parameters can be found by regression of \hat{M} against M , eqn 24 (Iwao & Kuno 1968, 1971; Iwao 1968), or preferably by non-linear regression of eqn 25 (Taylor, Woiwod & Perry 1978; Kuno 1991). Where the non-linear regression method has been used in the context of the aggregation model (Jaenike & James 1991; Shorrocks & Sevenster 1995), parameter A was equated to mean clutch size (m_2) not \hat{c}^* . As we have shown already

(Table 1), this is only correct if we assume a constant clutch size.

If \hat{m}_2 and J_1 are independent of M , then:

$$\hat{M} = \alpha + \beta M \quad \text{eqn 24}$$

$$\Rightarrow V = AM + BM^2 \quad \text{eqn 25}$$

where $A = (\alpha + 1) = \hat{c}^*$, and $B = (\beta - 1) = J_1$.

It should be borne in mind that it is also possible for populations to follow eqns 24 and 25 exactly even when J_1 is not density-independent. In these cases, one cannot interpret A and B in terms of \hat{c}^* and J_1 . As an example, consider the situation where single-egg clutches are laid with a constant variance to mean ratio of 4. In plotting \hat{M} against M a perfect straight line results with $\alpha = 3$ and $\beta = 1$, implying that clutches are laid at random, with intraclutch mean-crowding of 3. A situation quite different from the generating process, with potentially very different consequences for species coexistence.

Notwithstanding the problems above, if we assume that eqn 25 applies for the moderate-to-high population densities of the resident species y (irrespective of whether J_{1y} is density-independent), and that the invader (x) has a per capita clutch density of \hat{c}_x^* , the criterion for invasion is given by eqn 26 (since by substituting eqn 25 into eqn 10 we find: $\hat{M}_y = (e - A)/(1 + B)$).

$$G_{xy}^{IKQ} = \frac{\hat{c}_x^* + \alpha_{xy} \Theta_{xy} (e_y - A_y) / (1 + B_y)}{e_x} < 1 \quad \text{eqn 26}$$

Under a similar set of assumptions, Kuno (1988) derived almost exactly the same criterion, except that he did not allow for the fact that when rare (i.e. $M \rightarrow 0$) the mean per capita density of an invader cannot fall below \hat{c}^* . Therefore, his criterion is found by setting $\hat{c}_x^* = 0$ (even though there is a logical lower limit of $\hat{c}^* = 1$, which is achieved when all clutches consist of only a single egg). He also assumed neutral association between species ($\Theta_{xy} = 1$).

Distributions which follow Taylor's Power Law

Hanski (1981) considered the situation in which the overall distribution of individuals followed Taylor's (1961) power law relationship: $V = aM^b$, with the simplification of $b = 2$ and neutral association between species. Hanski's derivation also ignores the mean per capita density term, and his criterion for invasion is a special case of G_{xy}^{IKQ} with $\Theta_{xy} = 1$, $\hat{c}_x^* = 0$, $A_y = 0$, and B_y equal to parameter a in the TPL relationship. Note, that when empirical examples of TPL are extrapolated to very low densities (as experienced during an invasion event) they often predict a regular distribution of individuals ($M > V$), when in practice, there is very little evidence to suggest that this would be the case. Indeed, Kuno (1991) suggests that as mean densities become low, parameter b tends to 1 and most distributions become indistinguishable from spatial randomness

(see also Yamamura 1990). So, although the TPL often provides an excellent description of empirical data, its use in invasibility analyses may not be as appropriate.

Negative binomial distributions with a constant k

Finally, if one assumes that V and M follow independent NBDs with a constant k , and that clutches always consist of a single egg, then the criterion G_{xy}^{IKO} (eqn 26) can be applied with

$$\Theta_{xy} = 1, c_x^* = 1, A_y = 1 \text{ and } B_y = 1/k_y = J_y.$$

This is essentially the model used by Shorrocks *et al.* (1979), Atkinson & Shorrocks (1981, 1984) and Ives & May (1985).

As an example, consider the simulation of Atkinson & Shorrocks (1981), where $e_x = e_y = 10$, $\alpha_{xy} = 2$ and $\alpha_{yx} = 0$. Using equations 26 and 16 the criteria for mutual invasion become:

$$\frac{1 + [18/(1 + J_y)]}{10} < 1 < \frac{10}{1} \quad \text{eqn 27}$$

Immediately, we can see from the right-hand inequality that species y , the superior competitor, will always be able to invade; and from the left-hand inequality, species x will invade as long as $J_y > 1$, or equivalently $k_y < 1$. This result agrees reasonably well with the stochastic simulation results presented in Table 2 of that paper: at $k_y = 2$ the inferior competitor was driven extinct after 50 generations or less, whilst at $k_y = 1$ (when the two populations should be in neutral equilibrium) coexistence was maintained for at least 350 generations.

Discussion

THE LOTKA–VOLTERRA MODEL OF COMPETITION

Throughout this paper we have highlighted the different assumptions underlying various versions of the aggregation model of coexistence. However, it must be remembered that all the persistence criteria developed in this paper are based ultimately upon an invasibility analysis of single-species logistic growth and the related Lotka–Volterra model of competition. Consequently, the assumptions underlying the Lotka–Volterra model (i.e. growth rates that are linearly dependent upon density, frequency- and density-independent α s) must also apply throughout. Although there are good grounds for questioning these assumptions (e.g. Gilpin & Ayala 1973; DeBenedictis 1977), one of the most unrealistic assumptions that limits the applicability of the Lotka–Volterra model is the implicit spatial homogeneity required if population growth rates are to be determined from the total population count (or mean density) rather than the sum of individual experiences.

In adapting the Lotka–Volterra model of competition to a patchy system we replaced mean-field estimates of intra- and interspecific density with the mean *per capita* experience of density within a patch. An implicit assumption of this method is that individuals within the *same* resource patch are well-mixed and ‘fully interactive’, but that individuals in *separate* patches have no effect upon one another. This ‘all or nothing’ partitioning of interactions is likely to be true for the types of system we envisage where invertebrate larvae are contained within small, discrete patches of fruit, fungi, dung and carrion. For a more continuous approach, where low mobility individuals inhabit a homogeneous environment, the methods of Bolker & Pacala (1999) and Law & Dieckmann (2000) hold much promise. In their models, per capita competitive effects are calculated as distance-weighted functions to all other individuals within a local neighbourhood, and intraspecific aggregation occurs due to limited dispersal of progeny from parents. Despite these mechanistic differences, many of the general conclusions are the same: intraspecific aggregation can limit the population growth of a competitively superior species, such that unused resources are available for other species to invade.

WITHIN-PATCH DENSITY AND PATCH SIZE

Most non-spatial invasibility analyses assume that as the overall mean density tends towards zero an individual will not have to compete with other conspecifics. For clutch-laying species using patchy resources this is clearly wrong, and it is this fallacy that Ives (1988a), Jaenike & James (1991) and Sevenster (1996) have drawn attention to in the past. However, even when eggs are laid singly, an individual cannot expect to occupy a patch of zero density because it will always be present itself. This subtle point explains why Sevenster’s (1996) persistence criterion based upon a ‘relative effect’ approach does not agree with the corresponding invasibility analysis.

In this paper we ignored the fact that resource patches typically vary in size or quality (and hence patch-carrying capacity). This was largely for reasons of clarity in developing the links between the current framework and the many previous versions of the aggregation model. None the less, variation in patch size is an important issue that needs to be addressed in determining the mean individual-level experience of intra- and interspecific density (Sevenster 1996). The crucial point is whether, and in what manner, females respond to patch size when distributing their eggs. If they ignore patch size, then on average each patch will receive the same number of eggs, but large patches will harbour lower densities. Conversely, if females distribute eggs in proportion to patch size, then all patches will have similar densities, but large patches will receive the greatest number of eggs. Importantly, this latter situation will result in a lower per capita experience of

density than the former, and hence will lead to higher equilibrium population sizes. Empirical evidence suggests a variety of responses, with reports of positive, negative and no relationship between patch size and the density of emerging adults (Sevenster & van Alphen 1996; Mitsui & Kimura 2000). However, because these studies counted the number of emerging adults, rather than eggs, the results could be confounded by Allée effects and other sources of density-dependent mortality.

MEAN CLUTCH SIZE AND INTRA-CLUTCH DENSITY

All the generalized models derived in this paper assume that the per capita intraclutch density, \bar{c} , is density-independent. However, one can envisage that mean clutch sizes (and most probably also \bar{c}) might decrease with increasing adult density due to interference between ovipositing females and an increased likelihood of harassment by males (McLain & Pratt 1999). This would mean that \bar{c} would be higher during invasion than when present as a resident at equilibrium, making invasion that much harder and thereby decreasing the possibility of coexistence between competing species.

Heard (1998) presents evidence suggesting that clutch sizes increase as the distance between patches increases (the travel cost hypothesis). If this effect acts on both resident and invader, then \bar{c}_x would increase when resources patches are at low density (making invasion more difficult), but so also would the relative equilibrium population, \hat{M}_y , of the resident decrease (making invasion easier). Thus, depending upon the functional response of each species, the prospects for coexistence could be enhanced or worsened by a loss of resource patches.

COEXISTENCE WITH A RANDOM DISTRIBUTION OF CLUTCHES

By an explicit consideration of the two steps which lead to the distribution of individuals across patches, both at single-species equilibrium and during invasion, we have derived a general condition for coexistence between species competing across a system of patchy and ephemeral resources (eqn 16). One variation of this condition (eqn 19) demonstrates that the random distribution of *clutches* may be a sufficient cause of overall aggregation in the resident species, to allow an inferior species to invade, as suggested by Atkinson & Shorrocks (1984), Shorrocks & Rosewell (1988) and later confirmed by Heard & Remer (1997). The reason that Green (1986) found that coexistence was not facilitated by a random distribution of clutches was because he implicitly insisted that the species have equal patch-carrying capacities and equal per capita intraclutch densities. However, in relaxing this constraint we also note that coexistence is possible only with random visits when the product of competition coefficients is

less than unity. This condition cannot be achieved under the assumption of ideal exploitation (resource-mediated) competition; instead it requires some form of resource partitioning, consistent priority effects or differences in the rate of development.

In practice, the product of competition coefficients may often be greater than one, implying interference competition (e.g. Ayala, Gilpin & Ehrenfeld 1973). In such cases, the aggregation model cannot explain coexistence without invoking at least some degree of aggregation of clutches by the resident species. Nevertheless, a small degree of aggregation in the distribution of clutches can result in a highly aggregated distribution of eggs across patches if clutch sizes are large (Ives & May 1985).

FUTURE DIRECTIONS

The general framework developed in this paper places a renewed emphasis on the two underlying distributions which generate the observed aggregation. This highlights two areas where more data are greatly needed: (i) empirical measurements of clutch size distributions, in order to determine \bar{c} , and (ii) information on the pattern of female visits across patches. In combination, these two distributions determine how the overall variance : mean ratio changes with population density. This is important information if we are to predict the value of this ratio at its single-species equilibrium (as required by eqn 10), as most empirical studies can only measure the degree of aggregation a species achieves while embedded within a multispecies assemblage (e.g. Sevenster & van Alphen 1996; Wertheim *et al.* 2000).

On a modelling front, future effort could be directed towards determining the internal stability of multispecies assemblages. Then, it should be possible to ask not just 'Why so many species coexist?' on patchy, ephemeral resources, but also more challenging questions such as 'Why are certain species rare and others common?', and 'Which will increase and which will decrease in response to changes in resource abundance?'

Conclusion

The aggregation model, in its many guises, represents just one class of explanation for species coexistence, based upon heterogeneity in the spatial distribution of individuals. In reality, it will act in concert with other explanations that rely upon niche partitioning and temporal heterogeneity. None the less, in situations where organisms utilize patchy and ephemeral resources it is likely to be a powerful explanation. In this paper we have demonstrated how the specific mechanism(s) by which individuals achieve a particular distribution across resource patches may subtly alter the conditions required for mutual invasibility. More importantly, however, we have underscored the importance of assessing the individual-level experience

of density as the basic building block from which population dynamics are derived.

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Appendix I

SYMBOLS AND ACRONYMS

α_{xy}	Lotka–Volterra competition coefficient, the per capita effect of species y on x .
α	y -intercept of the regression of \hat{M} against M . (Often assumed equal to \hat{m}_2)
β	slope of the regression of \hat{M} against M .
ϵ_{xy}	ratio of patch-carrying capacities (e_x/e_y) (Sevenster 1996)
Θ_{xy}	measure of association between species x and y ($= C_{xy} + 1$).
A	parameter in the Iwao & Kuno quadratic variance–mean relationship ($= \alpha + 1$)
a	coefficient in Taylor's (1961) variance–mean Power Law relationship
a	shape parameter in the logarithmic series distribution
B	parameter in the Iwao & Kuno quadratic variance–mean relationship ($= \beta - 1$)
b	exponent in Taylor's (1961) variance–mean Power Law relationship
\hat{c}_x	mean per capita density in a single clutch of species x ($= \hat{m}_{2x} + 1$) (Iwao 1976)
C_{xy}	measure of association between species x and y (Ives 1988a).
CV^2	coefficient of variation squared ($= V/M^2$)
E_x	regional equilibrium population size in a patchy system for species x
e_x	carrying capacity of a single patch for species x .
G_{xy}	general criterion for the successful invasion of species x into an equilibrium population of species y
J	index of crowding relative to a random distribution of the same mean (Ives 1988a)
K_x	regional carrying capacity of species x , in a homogeneous environment ($= e_x P$)
k	aggregation parameter of the negative binomial distribution
\hat{M}	mean crowding (Lloyd 1967)
M_x	overall mean number of eggs per patch, laid by species x
\hat{M}_x	overall mean number of eggs per patch, laid by species x , at its single-species equilibrium.
\hat{M}_{xy}	mean interspecies crowding (Lloyd 1967)
m_{1x}	mean number of clutches laid per patch species x
m_{2x}	mean number of eggs per clutch laid by species x
N_x	total number of individuals of species x , across all patches
NBD	negative binomial distribution
P	number of patches in the system
RVRC	random visit, random clutch (i.e. a Poisson–logarithmic model)
r_x	intrinsic rate of increase for species x
T_{xy}	invasibility criterion (Sevenster 1996)
TPL	Taylor's power law
V_x	overall variance of the number of eggs laid per patch by species x
v_{1x}	variance of the number of clutches laid per patch by species x
v_{2x}	variance of the number of eggs per clutch laid by species x

Appendix II

THE LOGARITHMIC SERIES DISTRIBUTION

The logarithmic series distribution is defined by a single parameter, a , from which the mean and variance can be calculated (eqns A1 & A2, after Getis & Boot 1978).

$$m_2 = a / [\ln\{1/(1-a)\}(1-a)] \quad \text{eqn A1}$$

$$v_2 = [m_2/(1-a)] - m_2^2 \quad \text{eqn A2}$$

When the number of eggs per clutch follows a logarithmic series distribution, the per capita intraclutch density (\bar{c}^* , eqn 5) simplifies to $[1/(1-a)]$. As $a \rightarrow 0$, all clutches consist of a single egg; as $a \rightarrow 1$, clutches become infinitely large with $v_2 \gg m_2$; and when $a = 0.632$, $m_2 = v_2 = 1.72$.