Indirect effects and spatial scaling affect the persistence of multispecies metapopulations

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Quantifying the role of space and spatial scale on the population dynamics of ecological assemblages is a contemporary challenge in ecology. Here, we evaluate the role of metapopulation dynamics on the persistence and dynamics of a multispecies predator–prey assemblage where two prey species shared a common natural enemy (apparent competition). By partitioning the effects of increased resource availability from the effects of metapopulation structure on regional population persistence we show that space has a marked impact on the dynamics of apparent competition in multispecies predator–prey assemblages. Further, the role of habitat size and stochasticity are also shown to influence the dynamics and persistence of this multispecies interaction. The broader consequences of these processes are discussed.

Keywords: apparent competition; demographic stochasticity; extinction; population persistence; time series

1. INTRODUCTION

Ecological assemblages are defined by the way in which non-linear spatial and temporal processes interact in the regulation of populations (Hanski 1998; Grenfell *et al.* 2002; Crawley & Brown 2004). As species do not exist in isolation but interact with resources, competitors, mutualists and natural enemies (MacArthur 1972), developing theoretical and empirical tests of spatially explicit multi-species interactions is a contemporary challenge in ecology. While the theory of spatiotemporal multispecies interactions is relatively well-developed (Hassell *et al.* 1991, 1994; Holt 1997), there are few experimental tests of this theory using highly resolved spatial and temporal data of multiple species involved in indirect interactions (interactions between two species mediated by a third species). Our broad aim here is to resolve the impact of space on the dynamics of these sorts of indirect interactions.

One multispecies interaction where indirect interactions prevail is when two species shared a common natural enemy (Bonsall & Hassell 1997, 1998, 2000; Muller & Godfray 1997; Bonsall & Holt 2003). This indirect interaction is colloquially known as apparent competition (Holt 1977). Simple theory predicts that in the presence of alternative prey, a shared common natural enemy should effectively reduce the persistence time of the multispecies interaction (Holt 1977, 1984). This comes about as the availability of additional prey species in the diet of a natural enemy increases the population size of the natural enemy. A larger natural enemy population leads to increased attacks on the prey populations with the potential exclusion of the weaker species. While the phenomenon of apparent competition is now well documented (Holt & Lawton 1994; Bonsall & Hassell

1997, 1998; Chaneton & Bonsall 2000), testing how different dynamical factors prevent species exclusion and allow coexistence still remains relatively unexplored.

For instance, the spatial processes of limited dispersal (Levins 1969), rescue effects (Brown & Kodrick-Brown 1977) and the increased number of patches (Hanski 1999) can mitigate the effects of apparent competition by affecting the spatial covariances and effectively reducing the impact of predation at the per patch scale. Predictions from spatially explicit models of apparent competitive interactions suggest that the scale of interactions can affect the possibility of coexistence (Bonsall & Hassell 2000) with species responding differently to different scales of heterogeneity or to the effects of variability.

Here, using a well-replicated experimental system, we aim to understand how metapopulation processes and local dynamics interact to affect the dynamics and persistence of an extinction-prone multispecies predator–prey system. After presenting the details of the experimental design, we show that not only is spatial scale a major determinant of the persistence of this interaction but also that noise and stochasticity have a role on the dynamics of the indirect interaction. The results are discussed in the light of recent developments in the theory of multispecies metapopulation dynamics.

2. MATERIAL AND METHODS

(a) *Experimental design methods*

Laboratory microcosms were used to test the role of metapopulation structure on the persistence and dynamics of an apparent competition interaction between the bruchid beetles *Callosobruchus chinensis* and *Callosobruchus maculatus* mediated by their shared parasitoid, *Anisopteromalus calandrae*.

Clear plastic boxes (73 × 73 × 30 mm) were used as the baseline patch. Patches had a 4.4 mm hole in each of their four sides which could be either blocked or have 50 mm lengths of plastic tube inserted to connect horizontally into

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lattice arrangements of various sizes. For the apparent competition treatments (which included both bruchid species), patches were stacked into a double-layered system. A central mesh covered hole prevented vertical movement by the bruchids (and resource competition) but allowed the parasitoid free access to both host species. Two lattice sizes (4×4 and 2×2 patch systems) together with single patch controls were used to explore the effects of spatial structure on the interaction between *C. maculatus* and *C. chinensis* mediated by *A. calandreae*. To control the effects of resource increases on population size in the different sized lattices (Bonsall *et al.* 2002), unlimited dispersal controls for each metapopulation were used. All treatments were replicated four times.

Experiments were seeded over a three-week period by introducing three black-eyed beans (*Vigna unguiculata*) and four pairs of bruchids into the appropriate patch. Only beans were introduced in week four. Subsequently, resources were renewed chronologically on a four-week cycle. All old beans were stored and any emerging animals released back into the appropriate patch. Populations of prey in individual patches were allowed to establish over 21 weeks.

After week 21, resource-control lattices (unlimited dispersal) were linked and dispersal (2 h per week) was initiated for the limited dispersal lattices. Parasitoids were introduced after week 28. Four pairs of wasps were introduced on two consecutive weeks into the four corner patches of 4×4 and one corner of the 2×2 lattices, as well as the appropriate single patch controls.

Time series were obtained for all species by counting both dead and alive insects for every patch. All experiments were undertaken in controlled environmental conditions (30°C , 70% relative humidity and 16 : 8 light : dark cycle).

(b) Statistical analysis

Identifying the conditions for persistence of an apparent competitive interaction in different metapopulations was evaluated in terms of the potential for patches to support locally breeding populations, the risk of extinction (survival analysis), the probability of recolonization (from transition state probabilities) and the degree of asynchrony between patches (Hanski 1999; Bonsall *et al.* 2002). Recolonization potential was determined from the conditional probability of reinvasion (by one of the host species) into the interaction from where it was absent. For instance, *C. maculatus* could invade empty patches, patches occupied by *C. chinensis*, patches occupied only by the wasp or patches occupied by both the wasp and *C. chinensis*.

To explore the dynamics and the effects of demographic structure on metapopulation persistence we used a non-linear mixed model (Pinheiro & Bates 2000; Bonsall *et al.* 2002)

$$n_{ij} = \mathbf{p}_{1i} \cdot \exp(\mathbf{p}_{2i} \cdot t_{ij}) + \epsilon_{ij}, \quad (2.1)$$

where n_{ij} is the population size of *C. chinensis* (the species always driven to extinction in the apparent competition) in the i th lattice ($i=1,2,\dots,12$) at the j th time point ($j=1,2,\dots,54$). $\mathbf{p}_q$ is a vector of parameters

$$\mathbf{p}_q = \begin{bmatrix} p_1 \\ p_2 \end{bmatrix} = \begin{bmatrix} \beta_1 \\ \beta_2 \end{bmatrix} + \begin{bmatrix} \nu_{1i} \\ \nu_{2i} \end{bmatrix}, \quad (2.2)$$

where the fixed effects (β) represent the average value of the individual parameters (p_q) from all the different treatment replicates and the random effects (ν_i) represent deviations of

the parameter (p_q) from the population average. Random effects are assumed to be independent for different lattices and the within-group (patch) errors (ϵ_{ij}) are, initially, also assumed to be independent for each different lattice and time point, and independent of the random effects. We relax the assumption that errors are time-independent to explore how demographic structure affects persistence. As mentioned, *C. chinensis* abundance is the determinant of persistence as this species was always excluded in the apparent competition by the action of the shared wasp.

3. RESULTS

Single patch, single-species systems are regulated around an equilibrium (figure 1a,b) and the system is clearly capable of supporting local breeding populations. In these single-patch systems, the presence of a natural enemy leads to the rapid exclusion of the prey species through apparent competition (figure 1c) (median time to extinction is 1.5 weeks). *C. chinensis* was the inferior apparent competitor species that was driven extinct in all cases by the action of the shared natural enemy (figure 1d–g).

Mean persistence times (with s.e.) of the interaction between *C. chinensis* and *A. calandreae* were 2.25 (0.25) weeks for the single-patch systems, 18.5 (4.48) weeks for the 4-patch limited dispersal metapopulation, 3 (0) weeks for the 4-patch unlimited dispersal metapopulation, 17.5 (3.77) weeks for the 16-patch limited dispersal systems and 5 (0.92) weeks for the 16-patch unlimited dispersal system. In the apparent competition systems, mean persistence times (with s.e.) were 2.50 (1.06) weeks for the single patch systems, 6.25 (0.67) weeks for the 4-patch limited dispersal treatment, 5.00 (1.32) weeks for the 4-patch unlimited dispersal treatment, 25.25 (8.16) weeks for the 16-patch limited dispersal treatment and 3.75 (0.22) weeks for the 16-patch unlimited dispersal metapopulation. The distribution, skew and kurtosis in persistence times between these two systems are illustrated in the box-whisker plot (figure 2).

To test that this extinction-prone multispecies assemblage can persist as a result of metapopulation processes, the extinction times from different sized systems (1-patch, 4-patch and 16-patch) were compared. Metapopulation size is a significant determinant ($\chi^2_4=14.57$, $p=0.0057$) affecting the persistence of multispecies assemblages (the statistical model explains just over 72% of the variation in the data): apparent competition interactions persist longer in larger systems (figures 1 and 2). In order to validate that these differences are due to the effects of the metapopulation processes of dispersal and the rescue effect, and are not a consequence of the increased availability of resources, persistence times between limited and unlimited dispersal systems were compared. Significant differences were observed in the predator–prey metapopulation assemblages ($\chi^2_1=6.16$, $p=0.013$) with limited dispersal systems persisting at least 2.5 times longer than the unlimited dispersal systems. Model simplification indicates that there is no differences in persistence between single patch, four patch (free and restricted) and 16-patch (free) dispersal systems and that the statistical model can be simplified to two levels (16-patch limited dispersal systems versus all other treatments) ($\chi^2_3=3.622$, $p=0.305$). Under this

Figure 1. Population dynamics of the interactions in single-patches and metapopulations. (a,b) Dynamics show that single patches are able to support sustained breeding populations of the prey populations (*Callosobruchus chinensis* and *Callosobruchus maculatus*). Prey populations are regulated about equilibrium values in single patches. (c) The introduction of a natural enemy leads to apparent competition with the exclusion of the inferior host (*C. chinensis*) first in single patches. (d–g) Metapopulation processes can mitigate the effects of apparent competition through limited dispersal (d, 4-patch limited dispersal metapopulation, f, 16-patch limited dispersal metapopulation) rather than the increased availability of resources (e, 4-patch unlimited dispersal metapopulation, g, 16-patch unlimited dispersal metapopulation). Time series are shown as the square-root of population abundances (solid black line: *C. chinensis*, solid grey line: *C. maculatus*, dashed black line: *Anisopteromalus calandrae*).

simplified model, mean persistence time of 16-patch limited dispersal systems is 20.99 weeks while mean persistence time of all the other systems is 5.67 weeks. The simpler model explains 54.67% of the variation in the data. Recolonization and rescue of extinct patches is possible: conditional probabilities of recolonization show that each host reinvades patches from which it is absent with probability 0.04 (*C. chinensis*) and 0.331 (*C. maculatus*) in the 16-patch metapopulations. In the three species, 4-patch metapopulations, recolonization events were rarely observed. Spatiotemporal analysis of patch-specific population abundances shows that correlations decline with distance and are highly variable through time (figure 3). Typically, the variogram for

each of the metapopulations is an increasing function of distance and variable through time as the correlation in species' abundances decreases with increasing separation in time and space. Asynchronous dynamics (figure 3a,c,e) allow the persistence of the metapopulations be to enhanced (through the rescue of extinct patches by dispersing hosts).

Given that the recolonization events and asynchrony differ amongst the different sized metapopulations, we postulate that the mechanisms responsible for differences in persistence are influenced by local demographic and stochastic processes operating at the patch level. Metapopulation-average and individual lattice-specific (dashed line) predicted rates of decline

Figure 2. Persistence times for a two (host–wasp) and a three (host–host–wasp) species interaction. (a) The single host–single wasp interaction between *Callosobruchus chinensis* and *Anisopteromalus calandreae*. (b) The apparent competition interaction between *C. chinensis*, *Callosobruchus maculatus* and *A. calandreae*. Comparisons of the limited dispersal systems illustrate differences in the distribution of persistence times between the pairwise and apparent competitive interactions. Note the box–whisker plots show the distribution, dispersion and skew in extinction times. The box represents the interquartile range and the bars show the distance to 1.5 times the interquartile range. The solid line in each box is the median time to extinction.

in *C. chinensis* for the non-linear mixed model with autocorrelated patch (within-group) errors and metapopulation size included as a covariate are shown in figure 4. Although this non-linear statistical model (equations (2.1) and (2.2)) is appropriate for describing the decline in bruchid beetle abundance (through apparent competition), the explanatory power of the model is increased by incorporating the effects of metapopulation size (as a covariate: likelihood ratio test=26.046, $p<0.001$) and population demographic structure (as correlated autoregressive-moving average errors) (likelihood ratio test=146.970, $p<0.001$). Further model simplification of the non-linear mixed model reveals that this demographic structure does not differ between the single patch and smaller (4-patch) metapopulation systems but is different for the larger (16-patch) metapopulation.

4. DISCUSSION

Here, we have explored the dynamics and persistence of an apparent competitive metapopulation. Our important result is that metapopulation structure affects the persistence and dynamics of apparent competitive predator–prey interactions. In comparison to theoretical models (Bonsall & Hassell 2000) we show that space and limited dispersal can extend the persistence time of this otherwise non-persistent ecological interaction. In contrast to theory, finite metapopulation size can still restrict the long-term coexistence of species that shared natural enemies. Notwithstanding, the effects of limited dispersal and habitat structure have a significant effect on species interactions as spatial scale alters (McLaughlin &

Roughgarden 1992; Bonsall & Hassell 2000). Differences in species couplings and habitat heterogeneities influence both the patterns of species coexistence and the abundance of species through time and across space.

Habitat heterogeneity has recently been shown to affect patterns of diversity in a wide range of organisms from bacteria (Horner-Davine *et al.* 2004) through to plants (Hill & Hamer 2004) and animals (Bonesi & MacDonald 2004). Theoretical studies have also shown how disturbance or habitat heterogeneities can affect the persistence of spatially extended ecological assemblages (Hastings 2003; Childs *et al.* 2004). Habitat heterogeneity and the availability of suitable habitat can disrupt persistence and drive metapopulations extinct. Here, we have illustrated that the dynamics differ as the spatial scale of the system changes. Different-sized metapopulations are driven by differences in the ecological processes that promote or destroy heterogeneities. At the smaller spatial scales, it is likely that the impact of the shared natural enemy predominates while in the larger metapopulations density-dependent processes and parasitism act concomitantly to affect persistence. Understanding how the local within-patch dynamics interact with changes in the patch quality or heterogeneities are clearly of importance in determining the persistence of ecological assemblages.

Stochasticity is known to affect the persistence and dynamics in simple predator–prey metapopulations (Bonsall *et al.* 2002; Bonsall & Hastings 2004). Here, in this study, the most appropriate correlated error structure (an autoregressive—moving average process) for the non-linear mixed model suggests that the combined effects of both population densities and stochasticity at the local

Figure 3. Levels of asynchrony for limited and unlimited dispersal metapopulation systems. (a) Semi-variogram for *Callosobruchus maculatus* in the 16-patch limited dispersal metapopulations. (b) Semi-variogram for *C. maculatus* in the 16-patch unlimited dispersal metapopulations. (c) Semi-variogram for *Callosobruchus chinensis* in the 16-patch limited dispersal metapopulations. (d) Semi-variogram for *C. chinensis* in the 16-patch unlimited dispersal metapopulations. (e) Semi-variogram for *Anisopteromalus calandrae* in the 16-patch limited dispersal metapopulations. (f) Semi-variogram for *A. calandrae* in the 16-patch unlimited dispersal metapopulations. Under limited dispersal (a,c,e) the high degree of asynchrony is punctuated with periods when the systems appear to be in phase; in unlimited dispersal metapopulations (b,d,f), the systems rapidly loses asynchrony and the dynamics are completely coupled by the action of the rapidly dispersing natural enemy. Spatiotemporal semi-variograms for each metapopulation series (of length n) were calculated using $\gamma(d, \tau) = (1/2W) \sum_{i=1}^n \sum_{j=1}^n w_{ij}(x_{i,\tau} - x_{j,\tau})^2$ where x is the individual patch-specific abundance for a species for equally weighted ($w_{ij} = 1$) time point τ and spatial reference point d ($W = 1$) (Legendre & Legendre 1998).

scale have an impact on determining persistence time of the apparent competitive interaction. As mentioned previously, at the smaller spatial scales, the impact of parasitism is overwhelming and apparent competition predominates in the system. At the larger scale other ecological processes such as the effects of self-regulation and dispersal are likely to influence the persistence of the trophic interaction. Stochasticity is likely to impact on

these processes through an individual's ability to reproduce, survive and disperse (demographic stochasticity). While it is appreciated that the importance of this demographic stochasticity scales with population size (Hanski 1998; Grenfell *et al.* 2002), it has been shown here that these stochastic processes are also affected by assemblage diversity and differences in habitat structure and/or size.

Figure 4. Persistence of the apparent competition interaction (using *C. chinensis* as the determinant of persistence) for (a) the four single patch apparent competition populations, (b) the four 4-patch limited dispersal metapopulations and (c) the four 16-patch limited dispersal metapopulations. Each panel shows the abundance of *C. chinensis* (open circles), and the overall (solid line) and the individual lattice fits (dashed line) of the non-linear model. Models incorporating correlated errors provide a better description of the dynamical changes in *C. chinensis* abundance.

Appreciating the broader consequences of these processes on spatial interactions requires appropriately replicated and designed experiments. Interpreting such results requires evaluating simultaneously the role of stochasticity and determinism on the dynamics of species interactions (Leirs *et al.* 1997; Bonsall *et al.* 2003; Laakso *et al.* 2003), and as argued here, our understanding of metapopulation dynamics must be shaped by understanding both these processes. The significance of this, requires moving from simple hypothesis testing to a broader, more complete appreciation of the dynamics of ecological systems by challenging data with appropriate conceptual and mathematical models (Bonsall & Hassell 2005). Only this has the potential for advancing understanding of the role of space on the persistence and dynamics of ecological assemblages.

M.B.B. is a Royal Society University Research Fellow. The work was supported by the NERC and the Royal Society.

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