

Species coexistence in a food web with intraguild predation

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Abstract– We studied species coexistence in a protist community consisting of a bacterial resource, five protist consumers, and an intraguild predator, *Blepharisma americanum*. Spatial heterogeneity was manipulated by constructing spatial arrays of interlinked bottles. In the heterogeneous treatment species were permitted to disperse naturally between bottles whereas in the homogenous treatment half the water was removed from the bottles every second day and redistributed throughout the array. Contrary to expectations, the final number of species able to coexist was lower in the spatially heterogeneous treatment. In the spatially heterogeneous treatment, global extinctions were observed for *Paramecium caudatum*, *P. multimicronucleatum*, and *P. bursaria*, and frequent local extinctions were observed for *Colpidium* sp. In the spatially homogeneous treatment, *Colpidium* and *P. bursaria* were the only species to become globally extinct. *Paramecium aurelia* and *B. americanum*, the intraguild predator, persisted under both treatment conditions. There were no differences between treatments in community density, community variability in density or population variability in density. The population dynamics of the intraguild predator, *B. americanum*, *P. bursaria*, *P. multimicronucleatum*, and *P. caudatum* did not differ between treatments. In contrast, the population dynamics of *P. aurelia* differed strongly between treatments. In the spatially heterogeneous treatment, *P. aurelia* was apparently able to escape predation through either direct escape behavior or by being unavailable as a prey. In the spatially heterogeneous treatment the high population growth rate of *P. aurelia* may have resulted in the competitive exclusion of the other consumer species, whereas in the spatially homogenous treatment, intraguild predation by *B. americanum* on *P. aurelia* appeared to reduce competition between *P. aurelia* and the other consumer species, facilitating coexistence.

Key words: intraguild predation, population dynamics, protist food webs, spatial heterogeneity, species coexistence.

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Habitat patchiness or between habitat spatial heterogeneity has been shown to facilitate species coexistence in simple tri-trophic linear food webs consisting of a resource, consumers, and a predator (Holyoak and Lawler 1996a, 1996b). Metapopulation models predict that spatial heterogeneity should facilitate population persistence and stabilize populations by decreasing

predator efficiency at capturing prey, creating refugia where prey can escape predation or enabling dispersal between patches (Stenseth 1980). Importantly, spatial heterogeneity may generate asynchrony in population dynamics that can allow populations to “rescue” locally extinct patches (Holyoak and Lawler 1996b). However, trophic relationships in natural systems are rarely linear

food chains. Instead, trophic relationships are arrayed in webs which often include omnivorous relationships with species feeding at more than one trophic level. Intraguild predation is a special case of omnivory where predation occurs among members of the same guild that exploit the same class of resources (Polis 1988, Polis et al. 1989, Polis and Holt 1992, Holt and Polis 1997). Theoretical studies show that intraguild predation can adversely affect species coexistence and destabilize population dynamics, but that the outcome is driven largely by resource levels and whether the intraguild prey is a better competitor for the basal resource than the intraguild predator (Holt and Polis 1997, McCann and Hastings 1997). Contrary to these theoretical observations, intraguild predation in some natural and laboratory food webs neither shortens species coexistence nor increases population fluctuations (Morin and Lawler 1995, 1996, Fagan 1997, Holyoak and Sachdev 1998, Morin 1999).

We investigated coexistence in a six species protist food web composed of a bacterial resource, five protist consumers, and an intraguild predator. The predator, *Blepharisma americanum*, has the ability to switch between two morphs, a “giant cannibalistic” or predatory morph and a bacterivore morph, depending on the abundance of protist prey (Giese 1973). The predatory morph can feed on protists and other individuals of *B. americanum*, while the competitive morph competes with other protists for the bacterial resource. We tested four predictions: (1) aggregate community, i.e. total abundance of all species, and population abundance would be greater in the spatially heterogeneous array than the homogeneous array, (2) species would persist longer and be less numerically variable in the spatially heterogeneous array than in a homogeneous array, (3) more species would coexist by the end of the experiment in the spatially heterogeneous array, (4) the predator-prey dynamics in the spatially heterogeneous array would be less coupled than in the homogeneous array.

Methods

Experimental design– Each spatial array consisted of 16 interlinked bottles (Fig. 1). The bottles were interlinked on the diagonal with Tygon

tubing to create a 4 x 4 array. The arrays were exposed to ambient light and temperature in a laboratory and all experiments were conducted concurrently. Spatially homogeneous (HO) and heterogeneous (HE) conditions were created on a local level (i.e. the bottle or patch). To create spatially homogeneous conditions the contents of the array were mixed together every second day by removing half the volume of each bottle, mixing this water together, and redistributing the water over the entire array. The spatially heterogeneous conditions were created by leaving the array unmixed for the duration of the experiment. Each bottle contained 50 ml of protozoan media for a total of 800 ml over the array.



Fig. 1. The spatial arrays used in the experiment consisted of 16 interlinked bottles.

It is important to note that we did not replicate arrays, thus comparisons between HO and HE were made at the bottle level rather than for the entire array. This level of comparison has been used before by Holyoak and Lawler (1996) and Holyoak (2000) when they analyzed the data from spatial

arrays at both the level of the entire array (i.e. regional level) and for each bottle within the array as an independent observation. However, in their experiment they replicated each array three times, whereas the results that we present are for one array of both HO and HE. This problem with the final experimental design leads to two major issues with the conclusions that can be drawn. First, the lack of replication at the array level means that we cannot ascribe a cause and effect relationship between spatial heterogeneity on a regional level (i.e. the array level) and species patterns. Thus, at the array level our results are only a comparison of the dynamics of these communities in a heterogeneous spatial array versus a homogenous spatial array. Second, consideration of each bottle in the array as a sample unit could be viewed as pseudoreplication. However, previous studies using spatial arrays to study metapopulation dynamics have also analyzed patterns both at regional (entire array) and local levels (each bottle) (Holyoak and Lawler 1996, Holyoak 2000). Thus, we argue that while the lack of replication at the array level confounds the results of the experiment and renders it descriptive at a regional level, consideration of each sample bottle in the array is not pseudoreplication if the results are viewed from a local perspective.

Community assembly– Each array contained 800 ml of nutrient medium (one protozoan pellet per litre of deionized water). Bacteria were isolated from the stock protist cultures and grown in autoclaved media. One drop of bacterial solution (<1 ml) was added to each bottle in each array daily to maintain high levels of the basal resource. We assumed that bacterial dynamics were fast enough to be independent of the ciliates (Holyoak 2000). Six ciliate protozoan species were used in the experiment. *Paramecium aurelia*, *Paramecium caudatum*, *Paramecium multimicronucleatum*, *Paramecium bursaria*, and *Colpidium* sp., hereafter called *Colpidium*, are bacterivores and form the second trophic level. An omnivorous ciliate, *Blepharisma americanum*, formed the third trophic level as the intraguild predator. All species were obtained from Wards Biological Supply.

The initial densities of the consumer species were standardized to ensure that the biomass of

each species was equivalent. Biomass was standardized by first calculating the biovolume for each species and then calculating the volume of each stock culture to use in the inoculation. Biovolume was calculated according to procedures outlined in Wetzel (1983) by measuring the length and width of five randomly chosen individuals of each species on the 10 power objective where $\text{biovolume} = (\pi lw^2)/6$. The average density of each species in a 0.5 ml sample was then determined and multiplied by the biovolume of the species. The resulting average volume was then arbitrarily scaled to 50 for all species to determine the volume of stock culture to be added to the media.

Measures of time are presented as sampling times relative to the day (zero) when the consumer species were added to the arrays. All species except *B. americanum* were added to the array at d=0. Ten individuals of the intraguild predator *B. americanum* were added to each bottle of the array on d=2. The experiments ran on average for 25 days. Two of the arrays (A and B) had HO conditions while one array (C) had HE conditions. A leak that drastically reduced the volume of the experiment forced us to shut down array B after 16 days and thus we only use results from array A and C in the analysis. This resulted in an uneven number of samples from HO (n=4) and HE (n=8) treatments. There were some minor species invasions of rotifers and their associated algae during the experiment. No remedial measures were taken regarding the species invasions.

Community monitoring– Population density was estimated by removing a 0.5 ml sample and identifying and counting the protists. Before removing a sample, the water in the bottle was gently mixed. The sample was then fixed with Lugol's solution. Bottles were sampled every 2 days starting on d=1 and ending on d=25. To sample the arrays, either 4 (HO) or 8 (HE) fixed locations were chosen along the diagonal of the array. Clips were placed on the Tygon connections to prevent the forced movement of protozoans into adjacent bottles before sampling the HE arrays. The 0.5 ml removed was replaced with 0.5 ml of autoclaved media.

Data analysis– Persistence time, mean population density (time average of $\log + 1$), and coefficient of variation (cv) of untransformed density ($cv = \text{standard deviation}/\text{mean}$) were used to assess population dynamics (McGrady-Steed and Morin 2000). Persistence time was determined for each array as the last date on which at least one individual of each species was counted in the array. Global extinction was determined as the absence of a species across all bottles sampled in each array, whereas local extinction was determined as the absence of a species in each bottle. Differences in persistence time, mean population density and variability (CV) between HO and HE treatments were assessed by t-tests.

To determine whether population growth rates were spatially cross-correlated, raw densities were transformed by $\ln(x+1)$. Population growth rate was then calculated per bottle as the difference from t_1 to t_2 divided by 2. To calculate cross-correlations, population growth in each bottle was then regressed against population growth in adjacent bottles (one link apart) and bottles two links apart. We were unable to calculate cross-correlations from only adjacent bottles in the HO treatment as only 4 bottles were sampled resulting in only two slopes. The slope of the regression indicated the degree of correlation between the population growth rates. A positive slope indicated a positive correlation between the two population growth rates. A slope of 1 indicated that the relative growth rates were perfectly synchronous while a slope of -1 indicated perfect asynchrony. Positive slopes below and above 1 indicated that both populations were increasing with one population increasing faster than the other. This analysis was performed for each species separately to assess spatial synchrony or asynchrony in growth rates as well as for *B. americanum* and each of its prey species to determine whether *B. americanum* affected the growth rates of the prey species. A t-test was used to detect differences between the HO and HE treatments in the slope of the correlation between each pair of species. Pearson correlation coefficients were used to determine correlations between predator and prey growth rates.

A Mann-Whitney U test was used to determine whether rank-abundance structure differed between

HO and HE treatments for the three most dominant prey species (*P. aurelia*, *P. caudatum*, and *P. multimicronucleatum*). The Mann-Whitney U test tested the hypothesis that species abundances differ significantly between HO and HE according to relative rank-abundance of species. *P. bursaria* and *Colpidium* were not included in the analysis because of their high rates of extinction. Four bottles were chosen randomly from the HE treatment (of the eight possible) bottles for the test. All analyses were performed using Statistica 6.0 (StatSoft, 2001).

Results

At a local level, there was no difference in aggregate community abundance (HO=798.25 \pm 107.05 SD, HE=1017.85 \pm 202.18; $F_{1,10}=4.04$, $p=0.07$) or variability over time (CV) in community abundance ($F_{1,10}=0.23$, $p=0.642$) between the HO and HE treatments. The abundance of *P. aurelia* and *B. americanum* was higher in HE than in HO (Table 1). There were no differences in the abundance or in the variability of any of the species between HO and HE (Table 1).

The only species to become globally extinct in HO were *P. bursaria* and *Colpidium* (Fig. 2). *P. bursaria* became globally extinct at $d=8$ and *Colpidium* at $d=11$. In HE, *P. bursaria*, *P. multimicronucleatum*, and *P. caudatum*, went globally extinct. *P. bursaria* became globally extinct at $d=8$ and *P. multimicronucleatum* and *P. caudatum* went extinct at $d=12$. *Colpidium* also showed high local extinction in HE, with only one individual observed by $d=12$ in a single patch. *P. aurelia* was present in all samples at the end of the experiment in both HO and HE (Fig. 2b). *B. americanum* was present in all samples at the end of the experiment in HO and was locally extinct in 2 of the 8 samples bottles in HE by the end of the experiment. Despite these differences in population persistence between HO and HE, persistence times differed significantly only for *P. multimicronucleatum* ($F_{1,10}=25.60$, $p=0.0005$) and *P. caudatum* ($F_{1,10}=12.51$, $p=0.006$).

The slopes of the cross-correlations for community growth rates were significantly higher in HO (t-test, $t=6.28$, d.f. 9, $p=0.0001$; Table 2). The slopes of the cross-correlation for prey growth rates

were also significantly higher in HO for *P. aurelia* ($t=2.12$, $p=0.042$) and marginally significant for *P. multimicronucleatum* ($t=2.32$, $p=0.053$). In contrast, there were no differences in the cross-correlation slopes of the prey growth rate for *P. caudatum*, *Colpidium*, or *P. bursaria* ($p>0.05$) between HO and HE. Likewise, there was no difference in the slopes of the growth rate cross-correlations between HO and HE for *B. americanum*. Cross-correlation analysis showed that *P. caudatum* was the only species to show both asynchrony (negative slopes) and synchrony (positive values) in population growth rates in HO. In HE, *P. bursaria*, *P. aurelia*, and *Colpidium* displayed both synchronous and asynchronous growth rates while the growth rates for *P. caudatum* and *B. americanum* were always positively correlated.

Table 1. Results of ANOVA for differences in mean abundance and variability (CV) for each species in HO (homogeneous) and HE (heterogeneous) treatments.

| | | df | MS | F | p |
|--------------------------------------|-----------|----|-------|-------|--------|
| <u>Paramecium bursaria</u> | | | | | |
| Mean | Treatment | 1 | 0.029 | 0.691 | 0.425 |
| | Error | 10 | 0.041 | | |
| CV | Treatment | 1 | 0.002 | 0.029 | 0.868 |
| | Error | 10 | 0.052 | | |
| <u>Paramecium aurelia</u> | | | | | |
| Mean | Treatment | 1 | 0.627 | 105.4 | <0.001 |
| | Error | 10 | 0.006 | | |
| CV | Treatment | 1 | 0.142 | 3.999 | 0.073 |
| | Error | 10 | 0.036 | | |
| <u>P. multimicronucleatum</u> | | | | | |
| Mean | Treatment | 1 | 0.004 | 0.279 | 0.609 |
| | Error | 10 | 0.014 | | |
| CV | Treatment | 1 | 0.009 | 0.550 | 0.475 |
| | Error | 10 | 0.015 | | |
| <u>Colpidium sp.</u> | | | | | |
| Mean | Treatment | 1 | 0.064 | 0.992 | 0.343 |
| | Error | 10 | 0.065 | | |
| CV | Treatment | 1 | 0.160 | 3.253 | 0.101 |
| | Error | 10 | 0.049 | | |
| <u>Paramecium caudatum</u> | | | | | |
| Mean | Treatment | 1 | 0.000 | 0.005 | 0.946 |
| | Error | 10 | 0.014 | | |
| CV | Treatment | 1 | 0.002 | 0.175 | 0.684 |
| | Error | 10 | 0.014 | | |
| <u>Blepharisma americanum</u> | | | | | |
| Mean | Treatment | 1 | 0.038 | 5.978 | 0.035 |
| | Error | 10 | 0.006 | | |
| CV | Treatment | 1 | 0.000 | 0.006 | 0.939 |
| | Error | 10 | 0.067 | | |

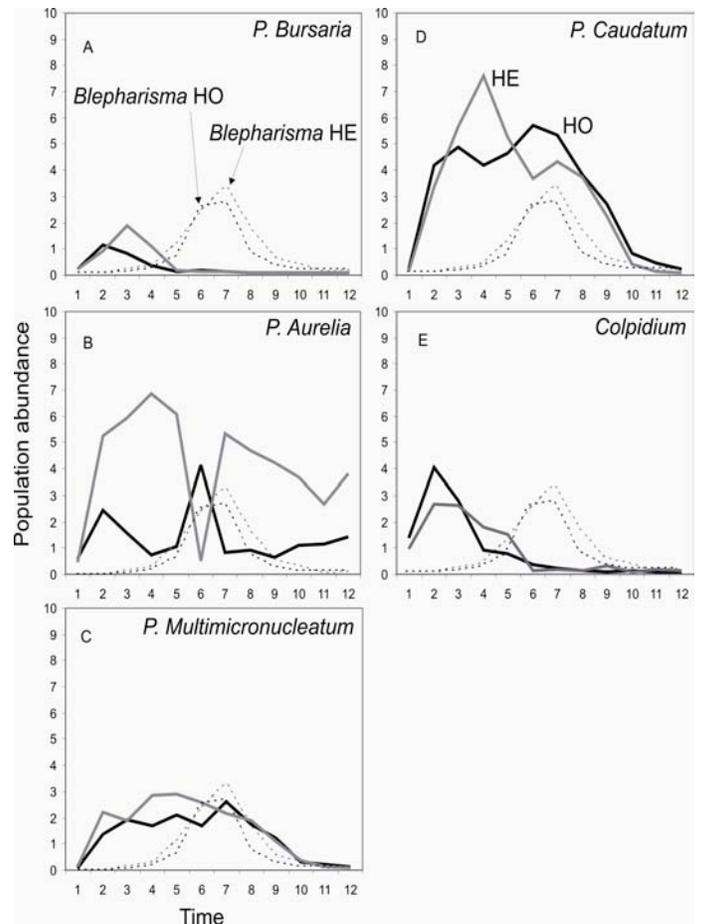


Fig. 2. Population dynamics of a) *P. bursaria*, b) *P. aurelia*, c) *P. multimicronucleatum*, d) *P. caudatum* and e) *Colpidium*. Population dynamics in the homogeneous (HO) treatment are shown in black and the heterogeneous (HE) treatment in grey. The hatched lines show the population dynamics of *B. americanum* in the HO (black hatched line) and HE (grey hatched line).

Table 2. Mean value of the slopes (r) of cross-correlation in growth rates for the total community abundance and for each protist species between adjacent bottles in the homogenous (HO) and heterogeneous (HE) arrays. P-value indicates the probability that the observed difference between HO and HE would occur by chance (calculated by t-test).

| | HO | HE | P |
|-------------------------------|-------|-------|--------|
| Total community | 1.169 | 0.752 | <0.001 |
| <i>P. bursaria</i> | 0.923 | 0.529 | 0.102 |
| <i>P. aurelia</i> | 1.008 | 0.370 | 0.042 |
| <i>P. multimicronucleatum</i> | 0.817 | 0.506 | 0.054 |
| <i>Colpidium</i> | 0.277 | 0.247 | 0.909 |
| <i>P. caudatum</i> | 0.504 | 0.638 | 0.719 |
| <i>B. americanum</i> | 0.648 | 0.696 | 0.738 |

Correlation analysis for synchrony in growth rates between *B. americanum* and the five prey species showed that the only prey species in HO whose growth rate was significantly correlated with *B. americanum* was *P. caudatum* ($r=0.445$, $p=0.015$; Fig. 3a). In HE, the growth rate of *Colpidium* was negatively correlated with the growth rate of *B. americanum* ($r=-0.289$, $p=0.05$; Fig. 3b) and the growth rates of *P. multimicronucleatum* ($r=0.481$, $p=0.0001$; Fig. 3b) and *P. caudatum* ($r=0.526$, $p=0.00002$; Fig. 3b) were positively correlated with the growth rate of *B. americanum*. Rank-abundance structure over time differed significantly between HO and HE for *P. aurelia* and *P. caudatum* in 2 of the 4 bottles and in 3 of the 4 bottles for *P. multimicronucleatum* (Table 3, Fig. 4). For *P. aurelia* sum of ranks was higher in HE, whereas for *P. multimicronucleatum* and *P. caudatum* sum of ranks was higher in HO.

Table 3. Results of Mann-Whitney U tests for differences between the homogeneous (HO) and heterogeneous (HE) arrays for rank-abundance over time for *P. aurelia* (*P.a.*), *P. multimicronucleatum* (*P. m.*), and *P. caudatum* (*P.c.*) in four bottles (B1, B6, B11, B16) of the arrays.

| Bottle/Species | Rank Sum HO | Rank Sum HE | U | Z | p |
|------------------|-------------|-------------|------|--------|-------|
| B1 <i>P. a.</i> | 122 | 178 | 44 | -1.617 | 0.106 |
| B1 <i>P. m.</i> | 190 | 110 | 32 | 2.309 | 0.021 |
| B1 <i>P. c.</i> | 169.5 | 130.5 | 52.5 | 1.126 | 0.260 |
| B6 <i>P. a.</i> | 108 | 192 | 30 | -2.425 | 0.015 |
| B6 <i>P. m.</i> | 185 | 115 | 37 | 2.021 | 0.043 |
| B6 <i>P. c.</i> | 194 | 106 | 28 | 2.540 | 0.011 |
| B11 <i>P. a.</i> | 109 | 191 | 31 | -2.367 | 0.018 |
| B11 <i>P. m.</i> | 187 | 113 | 35 | 2.136 | 0.033 |
| B11 <i>P. c.</i> | 192 | 108 | 30 | 2.425 | 0.015 |
| B16 <i>P. a.</i> | 124.5 | 175.5 | 46.5 | -1.472 | 0.141 |
| B16 <i>P. m.</i> | 179.5 | 120.5 | 42.5 | 1.703 | 0.089 |
| B16 <i>P. c.</i> | 175.5 | 124.5 | 46.5 | 1.472 | 0.141 |

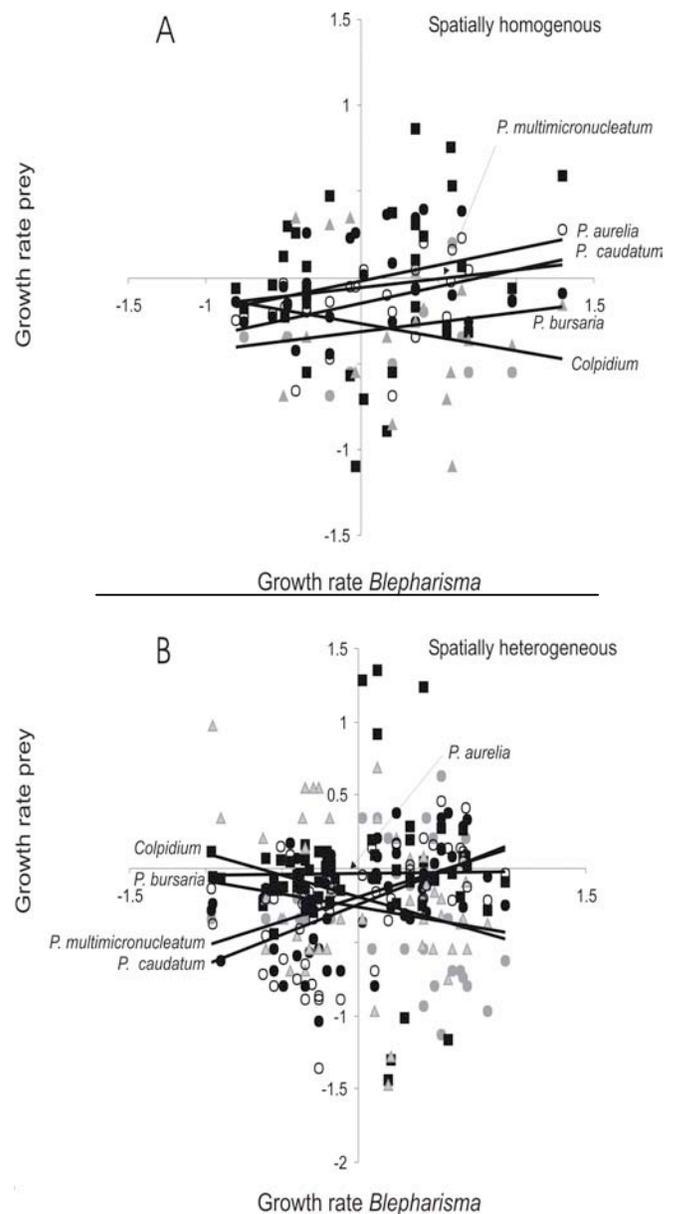


Fig. 3. Cross-correlations between the growth rates of *B. americanum* and each prey species in the a) homogeneous (HO) treatment, and b) heterogeneous (HE) treatment indicating that in HO the cross-correlations between the growth rates of *B. americanum* and each of the prey species are positively correlated except for *Colpidium*, whereas in HE the cross-correlations between the growth rates of *B. americanum* are positive for *P. multimicronucleatum* and *P. caudatum*, negative for *Colpidium* and *P. bursaria*, and independent for *P. aurelia*.

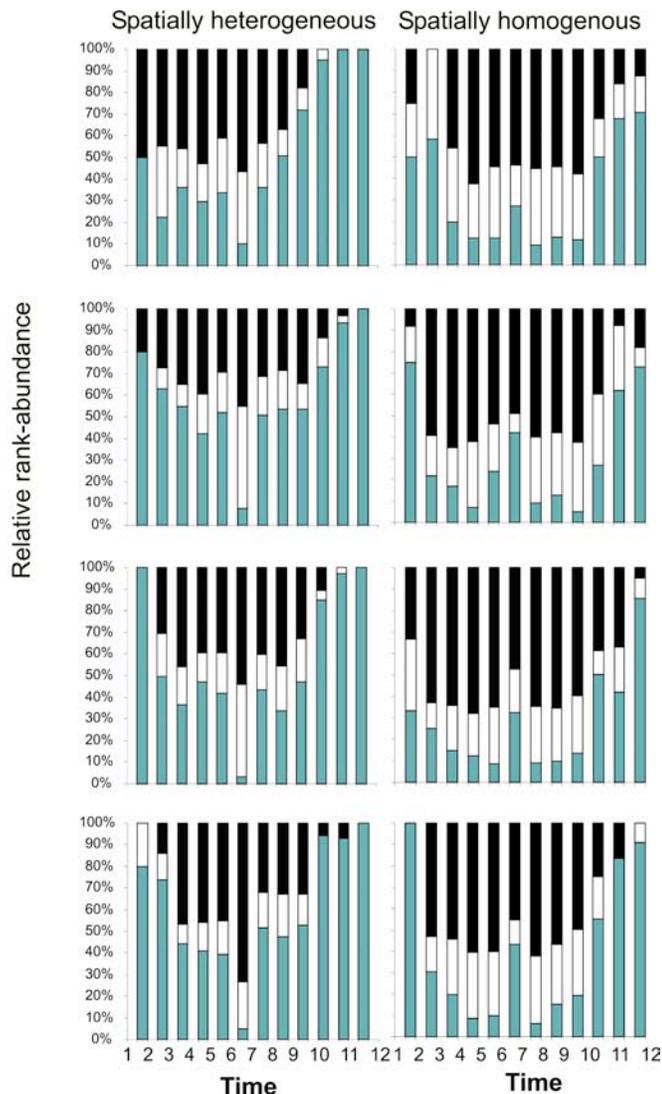


Fig. 4. Relative abundance of *P. aurelia* (blue bars), *P. multimicronucleatum* (white bars), and *P. caudatum* (black bars) in the spatially homogenous (HO) treatment and the spatially heterogeneous (HE) treatment.

Discussion

Intraguild predation is a special case of omnivory where predation occurs among members of the same guild that exploit the same class of resources (Polis 1998). *Blepharisma americanum* is an intraguild predator that switches between two morphs. When feeding on its own guild it is called a “giant” or predatory morph and when it competes directly with members of its guild for resources it is called a competitive morph. The morph switching behavior occurs in response to the abundance of available protist prey such as *Paramecium*. When protist prey is rare, *B. americanum* divides back to a

competitive morph (Giese 1973). Thus, *B. americanum* is able to switch rapidly between morphs in response to changes in the food supply.

Differences in abundance and variability in abundance between homogeneous and heterogeneous arrays— In theory, intraguild predation should destabilize population dynamics because the intraguild prey have difficulty persisting in a food web where they compete for food with and are eaten by the intraguild predator (Holt and Polis 1997, McCann and Hastings 1997). However, in many experimental studies the introduction of an intraguild predator neither affected species coexistence nor increased population variability (Morin and Lawler 1995, 1996; Fagan 1997, Holyoak and Sachdev 1998, Morin 1999). In our experiment, there was no difference in aggregate community abundance or variability in community abundance and no difference in population variability for any species between the homogeneous (HO) and heterogeneous (HE) arrays. This finding, while preliminary, contrasts with the majority of studies that have shown that spatial heterogeneity stabilizes populations by decreasing predator efficiency at capturing prey, allowing refugia for prey, or allowing for dispersal between patches (Holyoak 2000, Holyoak and Lawler 1996a, 1996b). The lack of difference between HO and HE for community abundance may have been due to strong effects of interspecific density-dependence. The spatial arrays were effective in facilitating escape behavior for the prey species as can be seen in the higher population abundances of *P. aurelia* and *P. caudatum* in HE. However the patterns of population growth were very similar for all species between HO and HE except for *P. aurelia*. Furthermore, the differences in synchrony between HO and HE treatments suggest that spatial heterogeneity affected the synchrony of population growth rates for *P. caudatum*, *P. bursaria*, *P. aurelia*, and *Colpidium*. For *P. caudatum*, spatial heterogeneity may have mediated the spatial dynamics by forcing synchrony, whereas for *P. bursaria*, *P. aurelia*, and *Colpidium* spatial heterogeneity may have mediated spatial dynamics by permitting both synchronous and asynchronous growth rates.

Population persistence in the homogeneous and heterogeneous arrays– More species coexisted in HO than in HE by the end of the experiment. Of the six species used in the experiment two became globally extinct in HO and four were either globally extinct or locally extinct in all but one patch in HE (see Figures 2 and 4). The degree of population persistence with habitat subdivision depends to a large extent on the characteristics of the species involved; however, previous studies using similar protist communities and spatial arrays (Holyoak and Lawler 1996b) have shown that the spatial heterogeneity generated from dispersal in the arrays promotes persistence and coexistence. Holt (1984) proposed that high prey coexistence can be achieved if one of three conditions are met: (1) prey have similar sensitivities to predation, (2) prey with low sensitivity to predation have low carrying capacities, or (3) the intensity of predation is low. It seems likely that prey coexistence was facilitated in HO due to the first condition. Mixing the water every second day would have redistributed species throughout the array, interrupting the escape behavior of the prey and making the sensitivities of the different prey species to predation more even. The second condition was not met as the largest prey species, *P. multimicronucleatum* and *P. caudatum* had higher abundances than *Colpidium* and *P. bursaria* which are smaller and thus more sensitive to predation. The third condition was reversed in our experiment with lower predation intensity in HE. While we did not quantitatively assess the relative frequencies of *B. americanum* competitive and predator morphs, we did observe a higher proportion of competitive morphs in HE (E. Tan, personal observations). Thus, predation intensity would have been lower in HE than HO. Similarly, the abundance of *P. aurelia* was higher in HE than in HO. In turn, this may have led to *P. aurelia* outcompeting the other prey species resulting in shorter persistence times and lower numbers of species coexisting in HE.

Population dynamics of Blepharisma americanum– The population dynamics of the intraguild predator, *B. americanum*, were qualitatively similar in both HO and HE (Fig. 2), rising to peak abundance at $d=7$ and then dropping to on average one individual

in each patch by the end of the experiment. In both HO and HE, the introduction of *B. americanum* resulted in a very rapid reduction in population abundance of both *P. bursaria* (Fig. 2a) and *Colpidium* (Fig. 2e) likely as a result of both direct predation as well as competition for resources with the larger species of *Paramecium* that were able to escape predation more effectively. *B. americanum* then began to prey on *P. caudatum* and on smaller individuals of *P. multimicronucleatum* reducing their numbers as well as reducing their negative effects on *P. aurelia* as competitors for the bacterial resource. Despite their very low abundance, *B. americanum* persisted until the end of the experiment in both HO and HE. This raises two questions. First, given the assumption that mixing did facilitate greater species coexistence, what mechanism facilitated greater species coexistence in HO? Second, how was the similarity in the dynamics of *B. americanum* achieved in both the HO and HE?

Previous studies have shown that coexistence between an intraguild (IG) predator and an IG prey can only be achieved in either high productivity environments, or if the IG predator is a less efficient competitor for the bacterial resource. Using Tilman's R^* rule (Tilman 1990), Holt and Polis (1997) showed that IG predators and IG prey can coexist only if the IG predators are inferior to the prey at exploiting the common resource. If the IG predator is a superior competitor for the shared resource the IG prey will be outcompeted and excluded even without intraguild predation. If intraguild predators follow optimal foraging strategies, coexistence may be achieved by dropping the IG prey from the predator's diet when the basal resource is abundant. This would allow the intraguild prey population to recover, which again could be included in the intraguild predator's diet (Holt and Polis 1997).

Blepharisma americanum may be a less efficient competitor for the bacterial resource as suggested in a study by Morin (1999). Using *Colpidium striatum* (intraguild prey) and *B. americanum* (intraguild predator), at two different bacterial levels (common resource), Morin showed that while *B. americanum* density increased with increased bacterial density, *Colpidium* did not.

However, at the lower level of environmental productivity, *Colpidium* was able to exclude *B. americanum* in three of four replicates, suggesting that *B. americanum* was a less efficient competitor for the bacterial resource. Contrary to Morin (1999), Lawler and Morin (1993) observed that IG predators sometimes excluded their prey. In our experiment the bacterial resource was added daily thus maintaining a high level of productivity, which should have promoted coexistence by lessening competition between prey and the bacterivore morph of *B. americanum*. Thus, the patterns we found may have been mediated by a trade-off between predation and competition, with predation dominating in the HO treatment and competition dominating in the HE treatment. Such a trade-off is well documented for *B. americanum* (Giese 1973). Furthermore, Holt (1984) showed that the net intraguild prey (IGP) interaction pattern may resemble competitive or predator-prey interactions depending on the realized densities of the species, rates of resource renewal, and details of the predator-prey interaction. Hence, even subtle differences in initial conditions and resources can have dramatic consequences for IGP. In HE the possible change in *B. americanum* to a bacterivore morph would have facilitated the growth of the strongest competitor (*P. aurelia*) resulting in the extinction of the other prey species.

Population dynamics of Paramecium aurelia–*Paramecium aurelia* was the only prey species whose population dynamics differed strongly between HO and HE (Fig. 2b) suggesting that *P. aurelia* was responsible for mediating differences in species coexistence between the two treatments. *P. aurelia* is a very strong competitor for the bacterial resource and has been shown to outcompete other protozoans such as *P. bursaria* and *B. americanum* in two-species systems (Vandermeer 1969). In HO, population abundance of *P. aurelia* was more than three times lower than in HE. There are at least two possible explanations for this pattern. First, *B. americanum* may have been a more effective predator on *P. aurelia* in HO. In HO, half the volume of each bottle (total 400 ml) was removed every second day and redistributed throughout the array. This repeated mixing may have moved *P.*

aurelia back into bottles where *B. americanum* was present by disrupting their escape behavior. The second possibility is that the relative proportions of morphs (i.e. predators versus bacterivores) of *B. americanum* differed between the two treatments. In HO *B. americanum* may have remained as a giant predatory morph due to the constant interaction with its protist prey, whereas in the HE, *B. americanum* may have divided to become a bacteriomorph and thus a competitor for the basal resource. The lower abundance of *P. aurelia* in HO would have facilitated the survival of the other prey species as it was unable to monopolize the resources. In HE, *P. aurelia* was apparently able to escape from predation (either through finding bottles where *B. americanum* was absent or because *B. americanum* existed as a competitive morph). The high population growth of *P. aurelia* and possibly strong competitive effects on the other prey species were correlated with the extinction or near extinction of all of *P. aurelia*'s competitors. Thus, mixing in HO appeared to facilitate species coexistence by reducing the negative competitive effect of *P. aurelia* on the other prey species.

Conclusion– We predicted that between habitat spatial heterogeneity would stabilize community dynamics in a protist food web with an intraguild predator. However, contrary to our predictions, spatial heterogeneity decreased species coexistence. *P. aurelia* was the strongest competitor for the bacterial resource and the only species whose population dynamics differed strongly between the homogeneous and heterogeneous arrays. While the patterns of dynamics of *B. americanum* in HO and HE did not differ substantially, the mechanisms driving the dynamics of *B. americanum* in HO and HE were different and likely due to the different dynamics of *P. aurelia* in HO and HE. In HO the interaction between *B. americanum* and *P. aurelia* resembled predator-prey dynamics whereas in HE they resembled competitive dynamics. This switch in interaction type was achieved through the morph switching behaviour of *B. americanum*. Higher species coexistence in HO may have been achieved through the effects of predation on *P. aurelia* and the subsequent reduction in the competitiveness of *P. aurelia* over the other protist species.

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