Ecology Letters, (2001) **4**: 304–312

REPORT

Foraging trade-offs and resource patchiness: theory and experiments with a freshwater snail community

Jonathan M. Chase,[1]
Will G. Wilson[2]
and Shane A. Richards[3]
[1]*Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260, U.S.A.*
E-mail: jchase@pitt.edu
[2]*Department of Biology, Duke University, Durham, NC 27708, U.S.A.*
E-mail: wgw@duke.edu
[3]*Population Biology Section, University of Amsterdam, Kruislaan 320, 1098 SM Amsterdam, The Netherlands*
E-mail: richards@bio.uva.nl

Abstract

Empirical results concerning a freshwater snail community are interpreted using a two-species consumer model that incorporates resource structure. Behavioural-scale measurements on a guild of five species of freshwater pond snails (Mollusca: Pulmonata) indicate a trade-off between the ability to utilize a patch's resource and the ability to quickly find new resource patches. Community-level experiments demonstrate that both species richness and composition are affected by the patchiness of the environment. In particular, treatments with low patchiness are dominated by species best at exploiting local resources (diggers) whereas treatments with high patchiness are dominated by species best at finding new patches (grazers). Results from a controlled mesocosm experiment with two of the most common of these species, *Helisoma trivolvis* (a relative digger) and *Physella gyrina* (Physidae) (a relative grazer) show that the patchiness of the environment strongly influences the outcomes of interspecific competition among these two species: the digger performed much better in less patchy habitats, whereas the grazer performed better in more patchy habitats. A two-species model of diggers and grazers modified to incorporate behavioural aspects of patchiness produces this same pattern of competitive outcomes.

Keywords

Exploitation competition, herbivore coexistence, pond snails, resource structure.

Ecology Letters (2001) 4: 304–312

INTRODUCTION

Despite the enormous amount of research both theoretically and empirically on factors that determine the diversity of species, there remains much discussion and debate regarding the mechanisms that determine species coexistence (Ricklefs & Schluter 1993; Huston 1994; Rosenzweig 1995; Gaston 2000). Mechanisms promoting coexistence among species that share resources, and thus are likely to compete, include resource partitioning (Haigh & Maynard Smith 1972; Schoener 1974), predator-mediated effects (Holt *et al.* 1994; Leibold 1996; Chase *et al.* unpublished manuscript), and intraspecific interference competition (Abrams 1983; Vance 1985). In essence, all of these mechanisms promote coexistence by increasing the number of limiting factors which may be differentially exploited by each species.

Much work has focused on how environmental variability affects community structure. Temporal variability may arise through extrinsic factors (Stewart & Levin 1973; Chesson & Warner 1981; Chesson & Huntly 1997) or processes intrinsic to the resource–consumer interactions (Levins 1979; Armstrong & McGehee 1980; Huisman & Weissing 1999). An important theoretical finding in this line of work is that coexistence can occur through internally driven resource-consumer cycles and these cycles can be caused by differences in foraging traits exhibited by competing species (Armstrong & McGehee 1980).

Spatial variability also affects community structure. Perhaps the simplest form of extrinsically generated spatial structure is a patchily distributed resource, which can yield coexistence through the fugitive species mechanism (Armstrong 1976; Hastings 1980). Intrinsically generated spatial structure is also important. On top of a uniform, continuously distributed substrate, foraging activities can produce a spatially varying resource density (Possingham 1988, 1989) that promotes coexistence. For example, Wilson *et al.* (1999) demonstrated a consistent mechanism for the observed coexistence of two marine snails was through the resource structure produced by their differential foraging strategies, termed area-intensive (digging) and area-extensive (grazing) (Schmitt 1996). Snails exhibit a tradeoff between resource use and encounter: diggers greatly exploit resource in a local region and slowly move to new regions, whereas grazers discover new regions more quickly but leave more resource behind. Related pairs of strategies have been dubbed "milker–killer" strategies in reference to predation of mites (van Baalen & Sabelis 1995), "gleaner–exploiter or opportunist" strategies in reference to bacterial populations (Fredrickson & Stephanopoulos 1981; Grover 1997), "rover–sitter" strategies in reference to *Drosophila* larvae (Sokolowski 1980), and "cream skimmer–crumb picker" strategies in reference to desert rodents (Kotler & Brown 1988).

Predictions of coexistence between diggers and grazers are robust to many features of resource renewal (Mittler 1997; Richards *et al.* 2000), and further elaborations demonstrated the potential evolutionary stability of the two foraging strategies through spatial mechanisms (Wilson & Richards 2000). This digger–grazer trade-off might be a mechanism promoting coexistence among species in a variety of diverse natural communities, including benthic feeding marine gastropods (Underwood 1984; Schmitt 1985, 1996), freshwater invertebrates (Steinman *et al.* 1987; Kohler 1992), and desert rodents (Brown 1989; Brown *et al.* 1994).

The purpose of this paper is to investigate how intrinsic and extrinsic spatial variation in resource combine to affect community structure. We first examine a group of competing freshwater pond snails (Mollusca: Pulmonata) for covariation between digging and grazing foraging traits. We then show that manipulating extrinsic patchiness leads to divergent species composition. Next, we present a model of a simplified community (two competitors) that explicitly incorporates resource patchiness. This model predicts that with increasing habitat patchiness, the system can change from being dominated by diggers to having digger–grazer coexistence to being dominated by grazers. Finally, we present results from a controlled two-species experiment where diggers and grazers competed under varying degrees of resource patchiness, and show that the results are consistent with those predicted by the model.

FORAGING TRADEOFFS

Five co-occurring species of snails were collected from a pond on the Lux Arbor reserve of the Kellogg Biological Station (Barry County, Michigan, USA): *Physella gyrina* (Physidae), *Pseudosuccinea collumnella*, *Lymnea elodes* (Lymneidae), *Helisoma trivolvis* and *Gyralus deflectus* (Planorbidae). We measured two foraging traits of each species: resource utilization in a given patch [i.e. its Giving Up Density (Brown 1988)] and the ability to find new patches (i.e. its colonization ability).

Resource utilization was determined for each species using 20 g of individuals (biomass was used to control for species-specific individual sizes) placed into circular tubs (0.1 m diameter × 0.06 m depth) in which algae had been allowed to colonize for 2 weeks. Each tub contained one clay flower pot (2 cm diameter × 4 cm tall) filled with Osmocote (14 : 14 : 14) time-release fertilizer supporting a high-density resource; resources were sparse elsewhere on the surface of the tub. Trials were replicated in three tubs and ran for 1 month (a time long enough for snails to reduce resources to a steady-state). Algae was scraped off the flower pots and analysed for ash free dry matter (AFDM), providing an estimation of the ability of each species to utilize local resources (see also Schmitt 1996).

Patch-finding ability was measured by tracking individuals in large circular pools (1 m diameter × 0.1 m depth) recently filled with nutrient-poor water (< 2 days prior to commencement of the experiment). The pool bottoms were covered with sand to eliminate unwanted periphyton growth and four high-density patches of algae (a square ceramic 4 × 4 cm tile incubated for 2 weeks in a nutrient-rich pool) were placed at the edge of the pool at equidistant points from the centre. In each trial, five individuals of a given species were placed in the centre of the pool. When each snail found a patch, it was removed; the time to find a food patch averaged over the five individuals from each trial provided one estimate of patch-finding ability. Trials were repeated three times for each snail species.

Results demonstrated the digger–grazer trade-off by showing a strong inverse relationship between a species' local resource utilization and its ability to find new resource patches (Fig. 1a). We classify, in a relative manner, *Gyralus parvus* and *Helisoma trivolvis* as diggers in that they are slow to find patches, but good at exploiting resources within patches. In contrast, *Physella gyrina* and *Pseudosuccinea collumnella* are grazers in that they are good at finding patches, but poor at reducing resources within those patches. *Lymnea elodes* is intermediate in both traits.

COMMUNITY-LEVEL RESPONSES TO PATCHINESS

Influences of resource patchiness on the interactions, composition, and coexistence among these species were analysed with an experiment performed in a natural pond where all five species occurred. The 1.13-ha pond at the Lux Arbor Reserve consisted of large areas of submerged and emergent macrophytes with considerable snail abundance, and a large area of essentially open sandy shore with very little plant or periphytic growth and very little snail activity. In this latter area, we manipulated the patchiness of periphytic algae using arrays of six 15 × 15 cm (1.35 m^2) ceramic tiles distributed within a 2 × 2 m area. An array belonged to one of four treatments of spatial arrangement and each treatment had three replicates. Arrays were separated by at least 10 m. Four spatial arrangements were used: (1) all tiles were placed adjacent to one another to form a single patch; (2) tiles were placed in two smaller

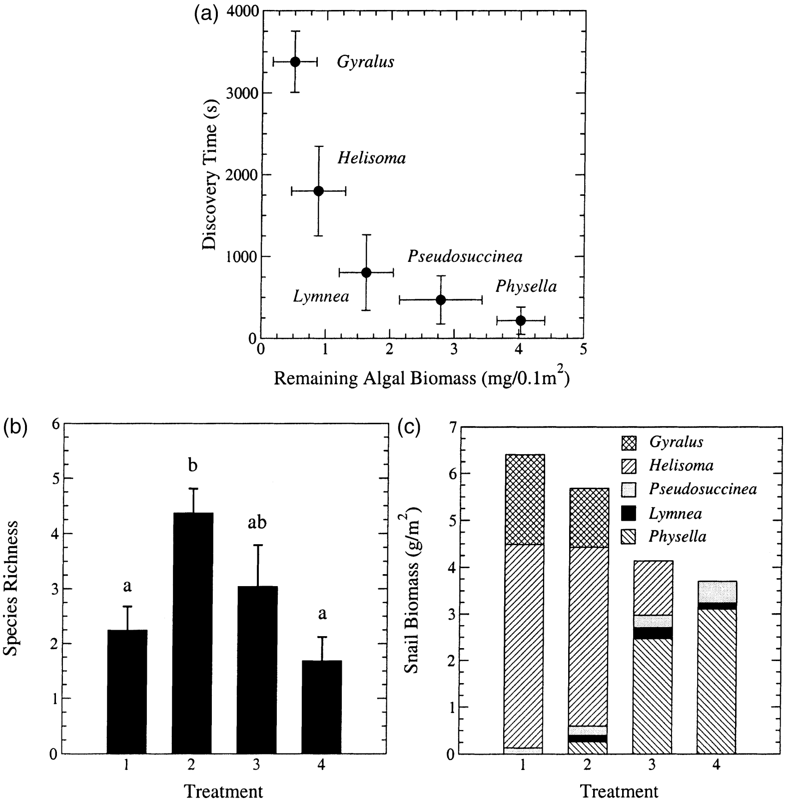

Figure 1 (a) The relationship between the time to discover a resource patch and the ability of a species to reduce algal biomass on a patch for five species of common pond snails. Time and resource reduction were measured in laboratory trials as described in the text. Circles represent the mean, while bars represent ± 1 Standard Deviation (SD). (b) The richness of snail species (number of species observed) ± 1 SD on tiles placed with different levels of patchiness (1 = least patchy, 4 = most patchy; see text). Letters above bars refer to significant differences among treatments as determined from ANOVA followed by Tukey's HSD ($P < 0.05$) (e.g., bars with different letters are significantly different from one another). (c) The composition of the five most common species of snails from the same treatments in (b).

patches consisting of three tiles each; (3) tiles were placed in three patches of two tiles each and (4) each tile was placed alone within the array.

The experiment was placed out in early June 1996, and censused monthly until September 1996. We counted all snails and recorded their size and species. Results showed a significant shift in snail species richness and composition with the patchiness of the treatment (Fig. 1b,c). In the least patchy treatments, species richness was relatively low, and were dominated by the two relative diggers, *Helisoma* and *Gyralus*. With increasing patchiness, species richness first increased at intermediate levels, then declined with the highest patchiness treatments. The relative composition of species also shifted to increasing dominance of the relative grazers, *Physella* and *Pseudosuccinea*. Thus, this experiment showed that resource patchiness seems to play an important role in determining both species richness and composition.

DIGGER–GRAZER MODEL

Our goal in this section is to interpret the change in community structure with patchiness in terms of a parsimonious conceptual framework. An important question surrounds the level of detail needed to understand the observed community shift: Does this shift arise from a complex cascade of ecosystem level processes, or can it be understood within a simpler two-species competition model? To this end, we extend a model addressing competitors exploiting a single renewable resource, developed with reference to the marine snails, *Tegula eiseni* and *T. aureotincta*, which exhibit complementary digging and grazing foraging patterns (Schmitt 1985, 1996; Wilson *et al.* 1999).

When diggers and grazers co-occur, their foraging behaviours structure the resource into one of three levels (see Fig. 2a). The lowest level is unusable by either the digger or the grazer, and represents a resource refuge. Resource at the lowest level enters the middle level with transition rate α_0, and mid-level resource enters the highest resource level with transition rate α_1. Diggers benefit from middle and high resource levels, whereas the grazer benefits only from the high resource level. In the absence of consumers, all patches exist in the high level, but consumer attacks deplete resource to lower levels depending on the consumer's foraging type.

Each small area of resource habitat is classified into the fractions of the area at each level: A_0, A_1, and A_2, for the lowest, middle and highest levels, respectively, with $A_0 + A_1 + A_2 = 1$. These are converted to resource biomass using resource density parameters ϕ_0, ϕ_1 and ϕ_2 (resource biomass/area). Resource consumption rates at

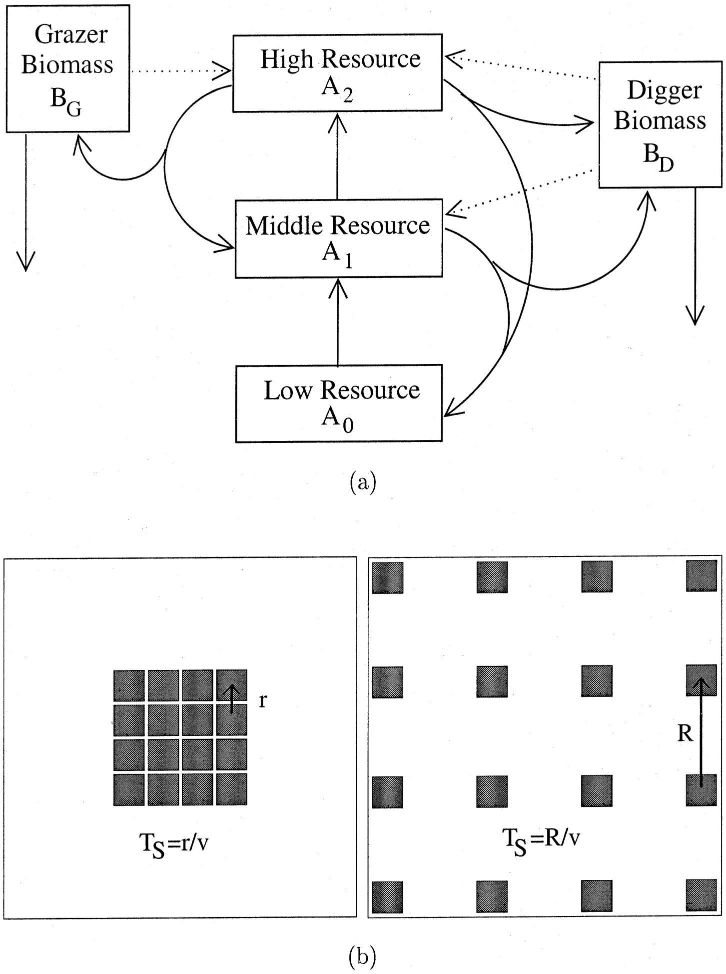

Figure 2 (a) Digger–grazer model (from Wilson *et al.* 1999). Dotted lines indicate consumption and solid lines indicate the flow of biomass between compartments. (b) Caricature of habitat patchiness. Total time spent finding a patch and consuming its resource is $T_S + T_0$, with the search time being the separation distance, r or R, divided by the consumer's speed v. This relationship leads to a decreased patch attack rate as the patch separation increases (equation 3).

each level depend linearly on consumer populations' biomass density, giving a Type I functional response. These assumptions lead to the model equations,

$$\frac{dA_0}{dt} = -\alpha_0 A_0 + \mu_D B_D (A_1 + A_2) \tag{1a}$$

$$\frac{dA_1}{dt} = \alpha_0 A_0 - \alpha_1 A_1 - \mu_D B_D A_1 + \mu_G B_G A_2 \tag{1b}$$

$$\frac{dA_2}{dt} = \alpha_1 A_1 - \mu_D B_D A_2 - \mu_G B_G A_2 \tag{1c}$$

where B_D and B_G are the digger and grazer populations' biomass densities (biomass/area). Parameters μ_D and μ_G (area cleared/consumer biomass/time) denote the digger and grazer resource clearance rates.

The model for consumer dynamics depends on two processes, consumption and respiration, with consumed resource biomass converted into consumer biomass through both growth and reproduction combined with efficiencies γ_D and γ_G (consumer biomass/resource biomass). We assume that the loss of consumer biomass through mortality and respiration combined is directly proportional to consumer biomass with species-specific rates δ_D and δ_G (time^{-1}). These two processes yield

$$\frac{dB_D}{dt} = \gamma_D \mu_D B_D (\phi_{10} A_1 + \phi_{20} A_2) - \delta_D B_D \tag{2a}$$

$$\frac{dB_G}{dt} = \gamma_G \mu_G B_G \phi_{21} A_2 - \delta_G B_G. \tag{2d}$$

Parameters $\phi_{ij} = \phi_i - \phi_j$ represent the reduction in algal biomass density caused by consumers; for example, in the above example grazers reduce resources in high-level patches by $\phi_{21} = \phi_2 - \phi_1$.

Wilson *et al.* (1999) formulated the above consumer equations on a behavioural time-scale model due to the measurements on the empirical system considered (Schmitt 1996). Equilibration arose as a constant number of individuals adjusted their size to the point where respiration balanced consumption. In the present scenario, the individual turnover rate is much greater and equilibration of consumer biomass occurs through changes in both the size of individuals and the total population number. There are three assumptions needed such that the form of the dynamic model is unchanged with this change in timescale: (1) either mortality and metabolism are both linear with an individual's mass, or the biomass lost at an individual's death is negligible compared with the biomass lost during its lifetime due to metabolism; (2) reproduction and growth are both proportional to the amount of resource consumed and (3) the resource attack rates on the various resource levels are constant with an individual's mass. We have not examined the sensitivity of our model's qualitative predictions to violations of these assumptions.

INCORPORATING PATCHINESS

Our interest in this paper is how resource patchiness of the type caricatured in Fig. 2b affects the competitive outcome in systems demonstrating the digger–grazer foraging trade-off. In this work we assume that resource patchiness has no influence on within-patch resource dynamics, and only affects the encounter rate of resource patches by consumers. Considering a general consumer, define T_0 as the clearance time required to ingest the resource on a single patch once encountered. We assume that habitat patchiness does not affect this clearance time, but does affect the search time per patch, $T_S = R/v$, where R is the average distance between successively encountered patches and v is the consumer's speed. With this linear dependence between R and T_S we have assumed that consumers have directed motion over the length scale of R.

The total time devoted by a consumer to a patch is then the sum of the search time and clearance time, leading to the patch encounter rate,

$$\mu(R) = \frac{1}{T_0 + T_S} = \frac{\mu_0}{1 + R/\rho} \qquad (3)$$

where $\mu_0 = 1/T_0$ represents the patch encounter rate for a homogeneous resource ($R = 0$), and $\rho = vT_0$ is the distance an individual would travel during the time spent clearing a patch. These parameters are given digger and grazer subscripts leading to consumer-specific patch encounter rates.

COEXISTENCE

Wilson *et al.* (1999) assumed that resource growth occurred on a much faster time scale than consumer growth, yielding quasiequilibrium algal fractions dependent on consumer biomasses. They then produced a coexistence plot (shown in Fig. 3) using the two invasion criteria; one specifying when grazers can invade an equilibrium system of diggers, and the other specifying when diggers can invade an equilibrium grazer system. Three possible competitive outcomes are shown in Fig. 3: (1) grazers win; (2) diggers win and (3) digger–grazer coexistence. A fourth outcome, not shown on the plotted scales, is extinction of both species. Coexistence occurs in the narrow region indicated by the overlap of the two invasibility conditions, and the region's size depends, in part, on the ratio of the patch transition rates α_1/α_0, reflecting a dependence on the detailed form of the resource growth function. Richards *et al.* (2000) demonstrated that the qualitative form of this coexistence picture is robust against broad changes in the form of resource replenishment.

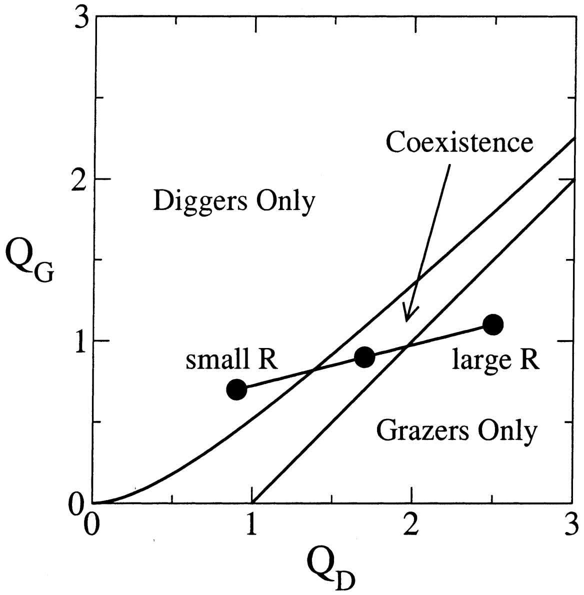

Figure 3 Effects of habitat patchiness on coexistence. The coexistence diagram of the digger–grazer model is plotted using the parameter values listed in table 2 of Wilson *et al.* (1999). The solid line with filled circles demonstrates the possible effect of increasing subpatch separation: patchiness moves a digger–grazer pair from the digger-only region through the coexistence region and to the grazer-only region. This line is only a caricature of the process, and not a fit to data.

The competitive outcome also depends on the resource parameters and the aggregate digger and grazer parameters, $\mathcal{Q}_D(R) = \delta_D/\phi_{10}\gamma_D\mu_D(R)$ and $\mathcal{Q}_G(R) = \delta_G/\phi_{10}\gamma_G\mu_G(R)$. Substituting the above form for the encounter rates, equation, leads to the following expressions for $\mathcal{Q}_D(R)$ and $\mathcal{Q}_G(R)$:

$$\mathcal{Q}_D(R) = \frac{\delta_D}{\phi_{10}\gamma_D\mu_{0D}}\left(1 + \frac{R}{\rho_D}\right) = q_D\left(1 + \frac{R}{\rho_D}\right) \qquad (4a)$$

$$\mathcal{Q}_G(R) = \frac{\delta_G}{\phi_{10}\gamma_G\mu_{0G}}\left(1 + \frac{R}{\rho_G}\right) = q_G\left(1 + \frac{R}{\rho_G}\right), \qquad (4b)$$

demonstrating a linear dependence of the $\mathcal{Q}_S$ on the mean patch separation R.

Consider now a digger–grazer pair defined by a specific point in the coexistence plot. Effects of patch separation on coexistence can be examined by following a curve $Q_G(Q_D)$ parameterized by the patch separation R; given Eq. (4). we find

$$\frac{dQ_G}{dQ_D} = \frac{dQ_G}{dR}\frac{dR}{dQ_D} = \frac{q_G \mu_{0G}}{q_D \mu_{0D}}\frac{v_D}{v_G} \qquad (5)$$

where (q_G, q_D) is the location in the coexistence plot of the homogeneous (nonpatchy) digger–grazer system (the $R = 0$ limit). Assuming the products $q\mu$ for the digger and grazer are roughly equal, then the slope of the line in the coexistence plot is proportional to the ratio of the digger's speed to the grazer's speed. We do not know these numbers for the system discussed here, but for the *Tegula* system the ratio $q_G\mu_{0G}/q_D\mu_{0D}$ is roughly 1.5, whereas the ratio of the speeds is roughly 1/7 (Schmitt 1996; Wilson *et al.* 1999). Indeed, as long as $q_G\mu_{0G}/v_G < q_D\mu_{0D}/v_D$, then as depicted schematically in Fig. 3, the system can progress from one dominated by diggers for closely spaced resource patches (small R) to one with digger–grazer coexistence for intermediately spaced patches (intermediate R) to one dominated by grazers for widely separated patches (large R).

CONTROLLED EXPERIMENTS

The above results were examined more closely in a controlled experiment using two of the snail species from the community-level experiment: *Physella gyrina* moves relatively fast but with poor utilization of local resources (grazer); and *Helisoma trivolvis* moves relatively slowly but has a better ability to reduce local resources (digger; see Fig. 1a). These species are typically the most abundant snails throughout small fishless ponds, marshes and swamps in southern Michigan, and are known to compete for periphytic algal resources (Chase 1998).

We devised an experiment in circular pools (2 m diameter × 0.2 m depth) to evaluate the role of habitat patchiness on the dynamics of competition and coexistence among these two species. The sides of each pool were covered with silicon and the bottom covered with sand to retard unwanted periphytic growth. Sixteen 15 × 15 cm (0.36 m^2) ceramic tiles were arranged on the bottom of each pool according to five treatments: (1) all tiles placed adjacently to form one large block; (2) two blocks of eight tiles placed on separate sides; (3) four blocks of four tiles placed at the sides; (4) eight blocks of two tiles with six along the outer edge and two near the centre and (5) individual tiles placed equidistantly throughout the pool. Each treatment was replicated with five pools.

Pools were established in late June 1996, and run through October 1996, allowing sufficient time for snail reproduction and mortality (roughly four generations of *Physella* and two generations of *Helisoma*). Snail populations were visually sampled monthly, and exhaustively sampled at the end of the experiment. Snails of each species were counted, measured and compared with size-specific dry-weight biomass conversions (Chase 1998). Periphyton from each tile was scraped and analysed for AFDM to determine algal abundance in the different patchiness treatments.

Monthly censuses showed that snail abundance increased for the first two months of the experiment, but there was no significant change in the abundance of either snail species over the last two months even though there were considerable births and deaths. In each treatment, the average change in abundance of each species between the last two census periods was not significantly different from zero (*t*-test; $P < 0.1$). Although not strong evidence for having reached equilibrium, below and in Fig. 4, we only present results from the final, exhaustive census of snail abundance and composition.

Results from this experiment showed that the patchiness of the environment strongly influenced the abundance of each species. With decreasing patch size and increasing patch distance (treatments 1–5), the abundance of *Helisoma* strongly declined (ANOVA; d.f. 4,15, $F = 48.02$, $P < 0.001$), while that of *Physella* increased (ANOVA; d.f. 4,15, $F = 70.49$, $P < 0.001$) (Fig. 4). Thus, the digger (*Helisoma*) dominated when food resources were in a few large patches, but the grazer (*Physella*) dominated when resources were in many small patches. The two species coexisted when the resources were divided into intermediate-sized patches. These results are in direct accordance with our model predictions.

The density of algal resources also varied with the patchiness of the environment, as expected with a change in dominance from a digger to a grazer (ANOVA; d.f. 4,15; $F = 3.49$, $P < 0.03$). When *Helisoma* (the digger) represented a large proportion of the snail biomass (Treatments 1–3) the algal abundance was relatively low, whereas when *Physella* (the grazer) represented a large proportion of the snail biomass (Treatments 4 and 5) the algal abundance was significantly higher (Tukey's HSD; $P > 0.05$).

We suggest that these results support our theoretical arguments that the competitive interactions among species with different foraging strategies can vary as a result of different levels of extrinsically generated patchiness. However, the experiments presented here can not more specifically tell us whether the mechanism of the observed response actually occurred due to interspecific competition instead of some other unknown mechanism. Nevertheless, we believe that our results occurred due to interspecific competition because these species are known to compete for limiting algal resources (Chase 1998), and in the absence of interspecific competitors, isolated populations of both species can thrive under a variety of habitat patchiness conditions in experimental pools similar to the ones used here (J.M. Chase, unpublished data).

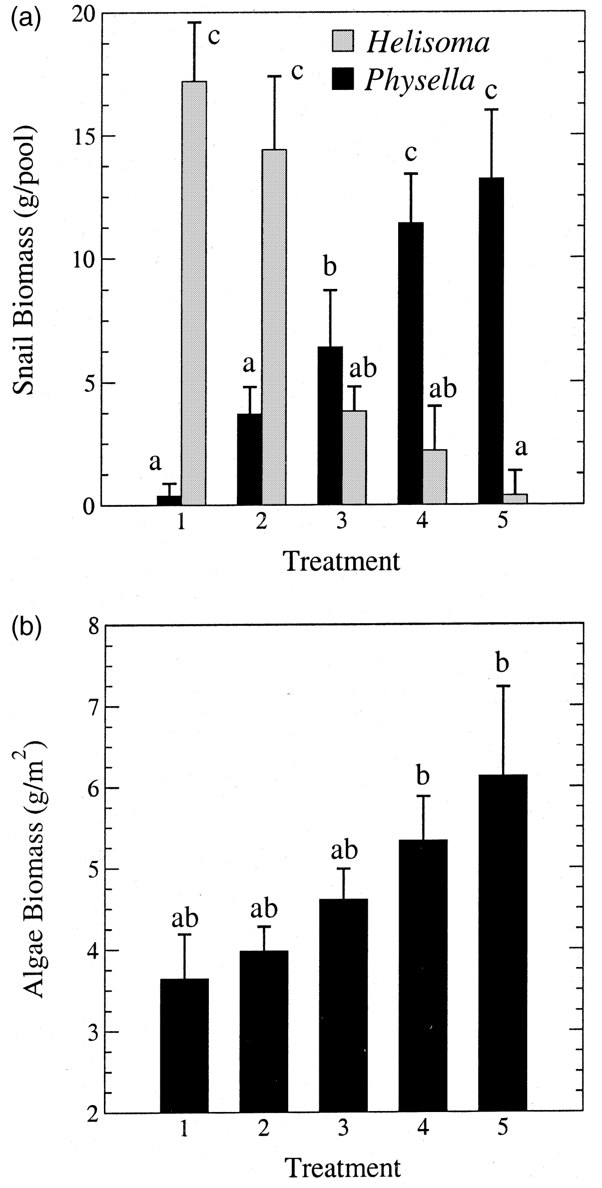

Figure 4 (a) The biomass of the two snails (± 1 SD), *Physella* and *Helisoma*, from the controlled mesocosm experiment that varied resource patchiness (1 = least patchy, 5 = most patchy, see text). Letters denote significant differences of each species of snail among treatments as determined from ANOVA followed by Tukey's HSD ($P < 0.05$). (b) The biomass of algae remaining on the patches from the different patchiness treatments. Error bars and letters are as in (a).

DISCUSSION

Increasing resource patchiness produces a shift from digger-like species to grazer-like species. The empirical results we presented above demonstrate a change in consumer dominance (from diggers to coexistence to grazers) produced by a change in habitat patchiness while keeping the total productive area constant. Previous analyses of the interactions among diggers and grazers consuming a common resource have considered only a single type of resource patchiness, usually homogeneous, when determining the competitive outcomes (e.g. Wilson *et al.* 1999). Our work here has shown that the degree of habitat patchiness can also influence the competitive outcome. Even though digger–grazer coexistence may occur through the foraging-induced resource heterogeneity within a uniformly patchy environment, alterations in the extrinsically produced resource heterogeneity still influence the competitive outcome (Kotler & Brown 1988).

We suggest that the results of laboratory experiments and field work in small enclosures in nature (which is the norm in much of experimental ecology) could be skewed towards dominance by one species or another if the natural habitat's patchiness is not accurately reproduced. In particular, we would expect that laboratory results obtained from these studies performed on small spatial scales would consist of primarily homogeneous resource patchiness, and could potentially be dominated by diggers. Alternatively, in experiments of larger spatial scale, more heterogeneity is incorporated, and could allow the invasion and perhaps dominance of species with more grazer-like traits. Indeed, this mechanism may be one possible reason why there is often an observed incongruence or 'scale-dependence' in the outcomes of experimental manipulations of interspecific competition performed in different sized enclosures (Gurevitch *et al.* 1992; Raffaelli & Moller 2000).

A simple incorporation of patchiness – an alteration of the consumer's attack rate – in a resource–consumer model demonstrates a similar change in competitive outcomes. Grazers gain an advantage as patch separation is increased because they experience a smaller relative decrease in average intake rate than that experienced by the diggers. Thus, as demonstrated above, extrinsic resource patchiness coupled with the intrinsically generated resource distribution of a digger–grazer system can be dominated by diggers when resource patches are close, or by grazers when resource patches are widely separated. It is important to note, as a caveat, that our model equations were not parameterized for the *Physa–Helisoma* system, and thus the comparison is only qualitative. The connection between the model and the empirical system could be made stronger through an extensive series of short time scale measurements on consumer behaviour and physiology, as well as resource renewal.

Empirical results were shown for an open community of five consumer species, and a closed system consisting of two consumer species. The digger–grazer model strictly applied only to the two-consumer experiments, and the extension to the community-level experiments is purely speculative. An extension of the digger–grazer model to include more than two species, and concomitant greater resource structure, might also demonstrate similar changes in consumer community. A more explicit and detailed approach could extend the simulation work of Wilson & Richards (2000) examining the evolutionary stability of digger–grazer foraging strategies. That work demonstrated the coexistence of many foraging strategies that possessed a tradeoff in local resource utilization and patch finding ability, much like the species displayed in Fig. 1a. This evolutionarily stable coexistence depended strongly on an emergent consumer grouping response – we are unaware of any critical tests of consumer grouping for these snail species. However, incorporating extrinsic resource patchiness may indicate the change in consumer "community" demonstrated empirically, favouring specific foraging phenotypes dependent on resource patchiness. Finally, the model results presented for the two-species system depends on a simplistic alteration of the attack rate in the grazer–digger model. A more mechanistic incorporation of habitat patchiness should examine both patch separation and patch size. For example, when patch size is too small to support a persistent population, each species has a critical patch separation beyond which there is also no global persistence.

Finally, in both the theoretical and empirical sections of this paper, we have primarily focused on interspecific competitive interactions in the absence of other factors, such as predators, that would be likely to influence these results. These snails often co-occur in communities with few predators, or where predators are essentially inept at limiting snail populations (Chase 1998; unpublished ms). In these sorts of communities, foraging trade-offs combined with differences in the spatial arrangement of habitat patches are likely to play a strong role in the coexistence among snail species. However, in addition to the apparent foraging trade-off among this guild of freshwater snails (Fig. 1a), these snails also differ in their susceptibility to predators, which is known to sometimes mediate the competitive interactions among these snails (Chase 1998; unpublished ms). The addition of predators (or other limiting factors) may indeed mediate the outcome of competition regardless of the foraging trade-off and spatial patchiness (Chase 1998; unpublished ms). As such, the work presented here addresses but one component of the complexities underlying variation in species distribution in natural systems.

ACKNOWLEDGEMENTS

This work was conducted as part of the Competition Theory Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (DEB-94–21535), the University of California at Santa Barbara, the California Resources Agency and the California Environmental Protection Agency. Field work was greatly facilitated by the members of the Kellogg Biological Station community, and in particular, G. Mittelbach. The authors would like to thank Peter Abrams for helpful comments on the manuscript. WGW was funded in part by a grant from the National Science Foundation (DEB-98–73650).

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BIOSKETCH

Jon Chase's research focuses on the interplay between theory, pattern and experimentation in community ecology.

Editor, L. Blaustein
Manuscript received 22 September 2000
First decision made 2 November 2000
Second decision made 18 December 2000
Manuscript accepted 16 January 2001