

Resource specialization determines whether history influences community structure

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History, specifically the sequence of species arrival, can affect community composition. Tests for a locally operating mechanism that can produce this result remain rare. Here we show how interspecific competition for resources combined with history can produce different communities. Specifically, history should influence community structure much less when all competitors use the same resource base than when some resources are unavailable to some competitors. We manipulated the resources available to competing ciliates in aquatic microcosms to test this hypothesis. We created communities that had only bacteria, or both bacteria and algae as consumable resources. When only bacteria were available, the best competitor, *Colpidium striatum*, always dominated regardless of differences in colonization history. History did affect the densities of competitively equivalent subordinate species, *Paramecium tetraurelia* and *P. caudatum*. The least effective competitor, *Tetrahymena thermophila*, went extinct in almost every community. *P. tetraurelia* and *P. caudatum* can also consume algae in addition to bacteria. History had a much larger effect in communities where both bacteria and algae were available as resources. In these communities, the initially dominant species always maintained dominance throughout the experiment, with the exception of *T. thermophila* which still went extinct. The experiment lasted for over 30 generations of the dominant species, so all effects of history persisted over ecologically important time scales.

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The sequence of species arrivals can influence community composition (e.g., Diamond 1975, Shulman et al. 1983, Robinson and Dickerson 1987, Drake 1991, Drake et al. 1993, Lawler and Morin 1993, Shorrocks and Bingley 1994, Blaustein and Margalit 1996, Weatherby et al. 1998). This has led some to declare that community ecology is largely a historical science (Cornell and Lawton 1992, Cornell 1993, Drake et al. 1994). Other studies, however, demonstrate that local mechanisms cause communities to converge to a similar composition regardless of assembly sequences (MacArthur 1972, Tilman 1977, 1982, Tilman and Sterner 1984, Grover 1988, 1991, Sommer 1991). We resolve this apparent paradox by using interspecific resource competition to predict when different histories will lead to either convergent or divergent community compositions.

We follow MacArthur (1972) and define species that consume only one type of resource as “specialists”, and species capable of consuming multiple resources as “generalists”. When the community consists of both specialists and generalists competition can generate different equilibrium communities. The sequence of species arrivals determines where resources equilibrate, and some sequences will reduce resources to levels which preclude the invasion of additional species (MacArthur 1972). In contrast, when all species compete for the same resource(s), i.e. when the community consists of only specialists, the best competitor should always dominate. When competition occurs among specialists, the best competitor reduces resources below the level that allows the persistence of other competitors (MacArthur 1972, Tilman 1982).

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History can influence community structure when some resources are unavailable to some competitors, but history should not influence community structure when all resources are available to all competitors. We used aquatic microcosms to test this hypothesis; microcosms have a history of effectively addressing questions regarding community assembly (e.g., Robinson and Dickerson 1987, Drake 1991, Drake et al. 1993, Weatherby et al. 1998, Fox 2000, Law et al. 2000). We built simple communities containing up to four ciliate species with either bacteria alone or both bacteria and algae available as resources. When only bacteria are present, the four ciliate species used in this experiment consume and compete for this resource, and the ciliates function only as specialists. When both bacteria and algae are present, some ciliates still consume only bacteria, while some consume both algae and bacteria and function as generalists. These feeding relations allowed us to hold the identity of the species in both community types constant while manipulating whether species functioned as specialists or generalists in the presence of an additional resource. To manipulate history, we allowed each species to reach carrying capacity in monoculture then subjected the monocultures to invasion by the remaining competitors. This allowed us to test whether initial history influenced mean equilibrium population densities and community composition in communities consisting of only specialists or a mixture of specialists and generalists (henceforth “mixed” communities). This system also allowed us to observe the effects of initial history over multiple (approximately 30) generations and thereby determine if the effects are persistent, rather than transient.

Methods

We conducted our experiments with four ciliate species: *Paramecium caudatum*, *P. tetraurelia*, *Tetrahymena thermophila*, and *Colpidium striatum*. These four species can persist with bacteria as the only resource (Elliot 1973, Wichterman 1986, Foissner and Berger 1996). Both *Paramecium* species can also consume small unicellular algae (Foissner and Berger 1996). The feeding capabilities of these ciliates allowed us to construct communities that consisted of specialists and generalists and communities that consisted of only specialists. Including algae as a potential resource allowed both *Paramecium* species to function as generalists; the presence of algae created mixed communities of specialists and generalists (Fig. 1A). Not including algae as a resource forces all species to compete for bacteria, and all species functioned as specialists (Fig. 1B). Thus, we created two different types of communities with identical species composition, where the presence or absence of algae as a resource determined whether communities

were mixes of specialists and generalists or specialists only.

When bacteria was the only resource present, equilibrium bacterial abundance determined the relative competitive abilities of these species (i.e. R^* , Tilman 1982). Previous work (Fox 2000) showed that *C. striatum* is the best competitor (lowest R^*), followed by *P. tetraurelia*, followed by *P. caudatum*, and *T. thermophila* was the worst competitor (highest R^*) (Fig. 1B). In order to determine relative competitive abilities of the four species in mixed communities, we measured equilibrium bacterial densities when both bacteria and algae were present by counting bacterial abundances in monocultures of each ciliate species.

Community assembly and experimental design

We established monocultures of the four ciliate species with bacteria (a standardized inoculum of *Serratia marcescens*, *Bacillus subtilis*, *B. cereus*, and *Proteus vulgaris*) and a small amount of algae (*Chlamydomonas* spp.) available as resources in January 2000, in 2-l flasks containing 1.37 l of nutrient medium (0.75 g of Carolina Biological protozoan pellets and two sterile wheat seeds per 1.37 l of filtered and sterilized well water). The presence of *Chlamydomonas* allowed the *Paramecium* species to function as generalist consumers, while *C. striatum* and *T. thermophila* remained as specialists because they consume only bacteria. Each ciliate species grew in monoculture in one large batch for two weeks, then 100-ml samples from each monoculture were separated into 240-ml jars to form replicate microcosms. We initially grew our monocultures in one large batch, rather than in the multiple 240-ml jars to increase homogeneity among microcosms. Each microcosm also contained two sterile wheat seeds for additional nutrients. We invaded four replicates of each microcosm with about 0.12 ml of each of the three ciliate species not present in the monoculture. This volume led to invading densities of approximately 0.06 *P. caudatum* individuals per ml, 0.39 *P. tetraurelia* individuals per ml, 2.66 *C. striatum* individuals per ml, and 1.34 *T. thermophila* individuals per ml. This created four treatments with different initial histories, with four replicates per treatment. We maintained the microcosms in constant environmental conditions (22°C, L:D 14:10 cycle).

We sampled each microcosm at 4- to 5-d intervals. After thoroughly swirling to mix the protists, we withdrew a small volume (< 0.5 ml) of the medium with a sterile pipette. We then counted each species in 8 to 10 drops (each ~ 0.04 ml) of medium on a tared Petri dish to estimate density per ml. Serial dilutions were used when the number of individuals in a drop was too high to accurately count. We sampled without replacement to reduce the risk of contamination. Population dynam-

ics were followed for 31 d after the addition of the invaders.

We repeated the above experiment with just bacteria (no algae present) in June 2000. With only bacteria, all four ciliates consume and compete for this resource, and the system contains only specialists. We used three replicates of each initial history and this experiment lasted for 32 d after the addition of the potential invaders. We realize that, ideally, both types of communities would have been established and monitored at the same time. Unfortunately, due to an oversight, this did not occur.

Statistical analyses

Populations in the microcosms reached relatively stable densities after approximately 10 d (Fig. 2). Thus, for all analyses we used log transformed mean species density in each microcosm averaged over time after day 10. Densities were transformed as $\log_{10}(\text{density per ml} + 1)$ before analyses to minimize heteroscedasticity (McArdle et al. 1990).

We tested if community composition, measured as densities of all species simultaneously, depended on the number of potential resources present (only bacteria vs both bacteria and algae), which species was initially dominant, and/or an interaction between these factors with a multivariate analysis of variance (MANOVA: Proc GLM in SAS/STAT version 6.12; SAS 1990). We tested if the number of potential resources present (only bacteria vs both bacteria and algae), which species was

initially dominant, and/or an interaction between these factors influenced populations of each species, measured as the average density of each species, with two-way analyses of variance (Proc GLM in SAS/STAT version 6.12; SAS 1990). This produced four ANOVAs, one for each of the four different ciliates. When any population was significantly affected by initial history, we compared means of that species within community type with Bonferroni adjusted multiple comparisons.

Results

We found that *C. striatum*, *P. tetraurelia*, and *P. caudatum* all reduce bacteria to statistically indistinguishable levels in mixed communities when both bacteria and algae are present, and all reduce bacteria to lower levels than *T. thermophila* ($F_{3,44} = 20.5$, $P < 0.0001$).

The number of potential resources present, initial history, and the interaction between both factors influenced overall community composition (Table 1). *T. thermophila* was essentially excluded, regardless of the number of resources present and initial history. The best competitor for bacteria, *C. striatum*, dominated in specialist communities despite history. However, initial history led to different overall community compositions because of changes in the hierarchy of the subordinate competitors (Fig. 2). *P. caudatum* maintained dominance over *P. tetraurelia* when it was initially dominant in the specialist communities (Fig. 2). This dominance

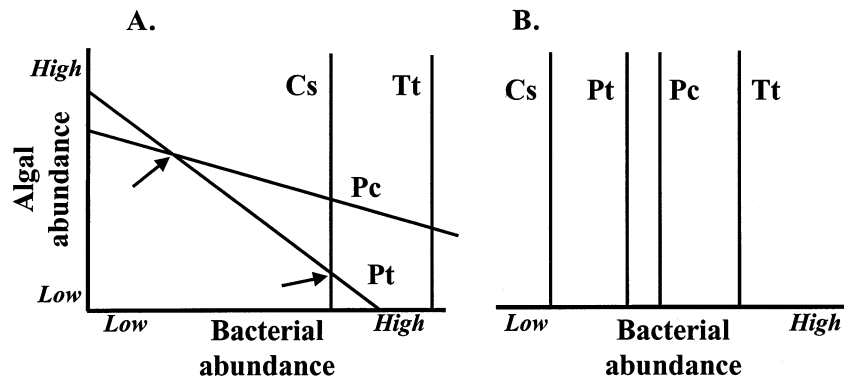


Fig. 1. Schematics of potential zero net growth isoclines of the mixed and specialist communities with all competitors present. Each line represents the zero net growth isocline of a different species. The letters next to each isocline represent which species the isocline describes: Cs denotes *C. striatum*, Pt denotes *P. tetraurelia*, Pc denotes *P. caudatum*, and Tt denotes *T. thermophila*. The isocline represents the resource(s) level(s) at which the species population growth rate is zero. In areas where resource levels are less than the isocline, population growth rate is negative, in areas where resource levels are greater than the isocline, population growth rate is positive. When a species isocline is perpendicular to a resource, that species only consumes that resource and therefore is a "specialist" on that resource. When a species isocline crosses both axes, that species can consume both resources and is therefore a "generalist". A. MacArthur's (1972) model of communities composed of both specialists and generalists predicts two equilibrium community compositions, indicated by arrows. History can potentially influence which community is realized. B. In contrast, when communities are composed of only specialists, history should have little influence on equilibrium community composition. The best competitor should always dominate (Tilman 1982).

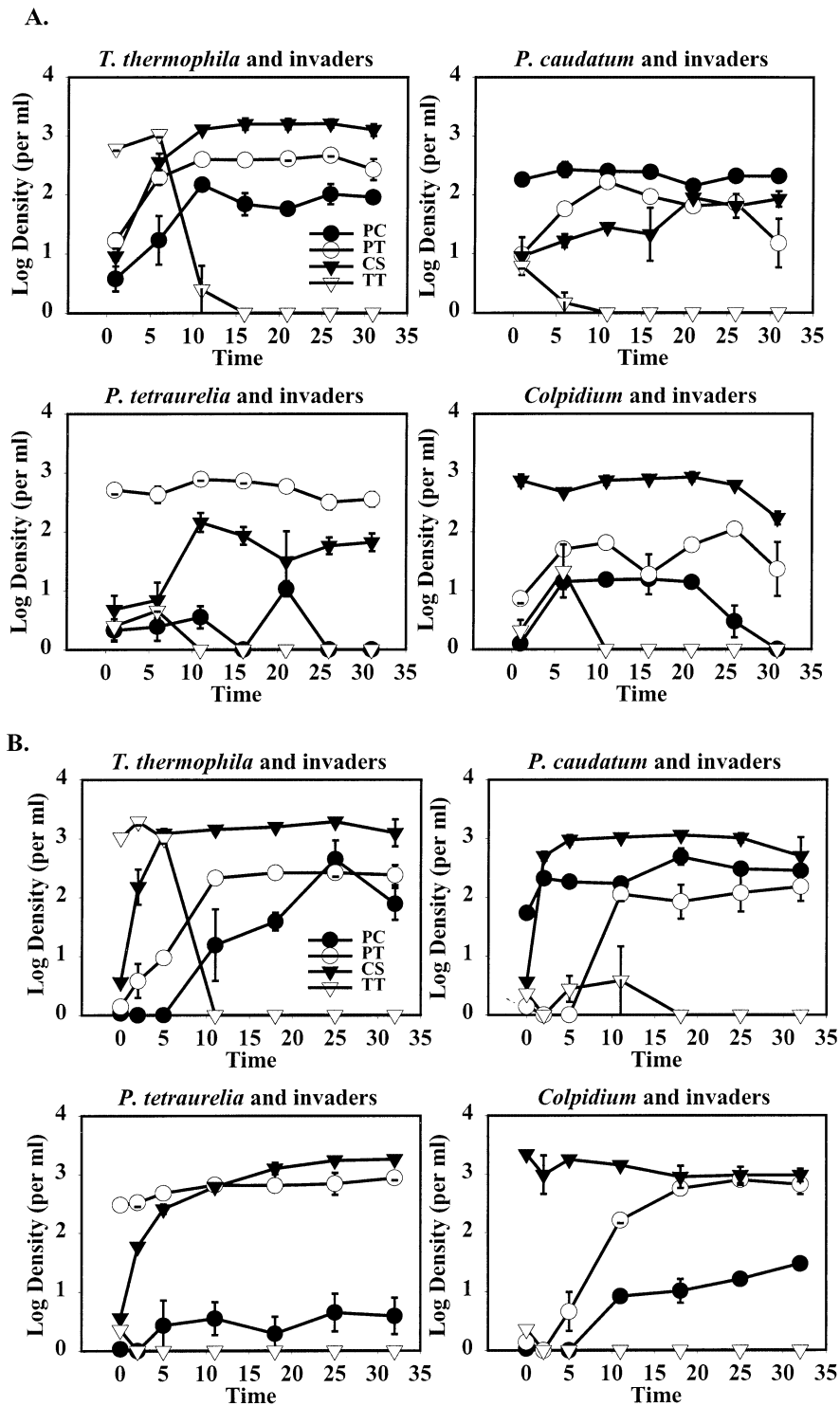


Fig. 2. Population dynamics of each species within each historical treatment in communities of (A) both specialists and generalists and (B) just specialists. The title of each graph indicates which species was initially abundant. Time 0 indicates when competitors were added to monocultures of the initial species. Error bars indicate one standard error. CS denotes *C. striatum*, PT denotes *P. tetraurelia*, PC denotes *P. caudatum*, and TT denotes *T. thermophila*.

Table 1. Effects of the number of resources present (only bacteria vs both bacteria and algae), which species was initially dominant, and/or an interaction between these factors on mean population densities. A) Results of the MANOVA which tested for differences in density of all species among treatments simultaneously. B) Results of the univariate ANOVAs which tested for differences in density of each species among treatments. The species column denotes on which species each univariate analysis was conducted.

A. MANOVA				
	Treatment	d.f.	<i>F</i>	<i>P</i>
	Resources present	4	17.21	<0.001
	Initial dominant	12	42.21	<0.001
	Resources × initial dominant	12	6.51	<0.001
B. Univariate ANOVAs				
Species	Treatment	d.f.	<i>F</i>	<i>P</i>
<i>C. striatum</i>	Resources present	1	57.16	<0.001
<i>C. striatum</i>	Initial dominant	3	22.36	<0.001
<i>C. striatum</i>	Resources × initial dominant	3	12.30	<0.001
<i>P. caudatum</i>	Resources present	1	9.75	0.005
<i>P. caudatum</i>	Initial dominant	3	360.51	<0.001
<i>P. caudatum</i>	Resources × initial dominant	3	4.31	0.017
<i>P. tetraurelia</i>	Resources present	1	16.87	<0.001
<i>P. tetraurelia</i>	Initial dominant	3	28.34	<0.001
<i>P. tetraurelia</i>	Resources × initial dominant	3	11.92	<0.001
<i>T. thermophila</i>	Resources present	1	0.18	0.680
<i>T. thermophila</i>	Initial dominant	3	0.70	0.563
<i>T. thermophila</i>	Resources × initial dominant	3	1.48	0.249

pattern follows the order of competitive abilities when bacteria are the only resource (Fox 2000). In mixed communities, however, history did not influence just the densities of subordinate competitors, but influenced densities of all species. All species (except *T. thermophila*) maintained dominance when they were initially dominant, and all species did not reach as high an abundance when they were not the initial dominant as when they were the initial dominant (Figs 2, 3).

Initial history influenced the equilibrium densities of all species except *T. thermophila* within specialist and mixed communities. *P. tetraurelia* and *P. caudatum* benefited from initial dominance in both specialist and mixed communities, while *C. striatum* benefited from initial dominance only in mixed communities. *P. caudatum* had highest density when it was the initial dominant, followed by when it invaded *T. thermophila* monocultures, and had lowest density when invading *C. striatum* or *P. tetraurelia* monocultures. This pattern occurred in both specialist and mixed communities (Fig. 3).

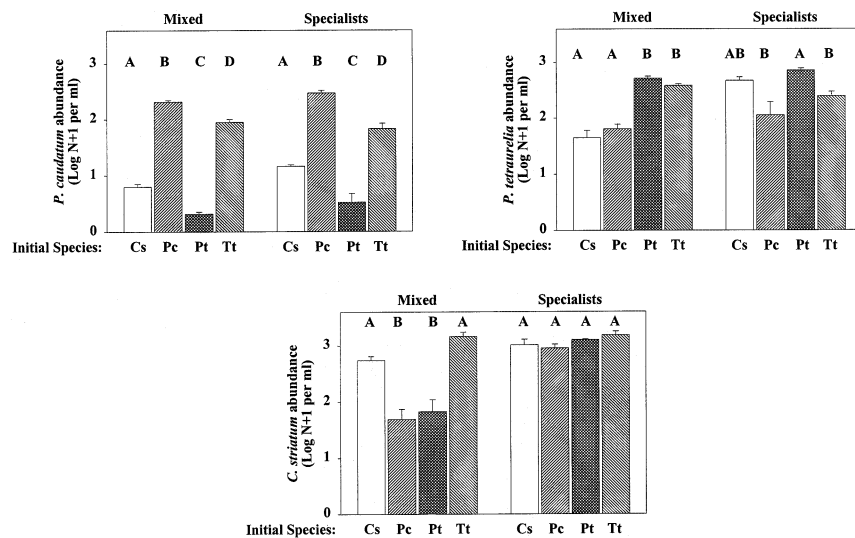
In mixed communities, *P. tetraurelia* had higher densities when it was the initial dominant and when it invaded *T. thermophila* monocultures than when it invaded *P. caudatum* and *C. striatum* monocultures (Fig. 3). In specialist communities, *P. tetraurelia* reached its highest density when it was the initial dominant, and reached its lowest density when *P. caudatum* was the initial dominant. The density of *P. tetraurelia* when *C. striatum* or *T. thermophila* were the initial dominant did not differ from density of *P. tetraurelia* when either of the *Paramecium* species were initially dominant in specialist communities (Fig. 3).

In the specialist communities, history did not affect the abundance of the best competitor, *C. striatum* (Fig. 3). In mixed communities, *C. striatum* reached higher densities when it was initially dominant and when it invaded *T. thermophila* monocultures than when it invaded either *P. caudatum* or *P. tetraurelia* monocultures (Fig. 3).

Discussion

Our experiment demonstrates that the sequence of species arrivals can influence species densities and therefore have significant effects on community composition. The effects of history persisted for the duration of the experiment, representing at least 30 generations of the dominant organism, and thus do not represent transient effects. The effect of history was stronger in mixed communities because the initially dominant species remained dominant, with the exception of the weakest specialist competitor which was consistently excluded. In contrast, in specialist communities the best competitor always became dominant and history only influenced densities of subordinate species. These results are consistent with simple resource competition theory that predicts when and how history will affect populations and communities. We realize that measures of bacteria and algal abundances would strengthen our inferences by allowing us to directly tie our results to consumptive competition and mechanistic theories. Unfortunately, we do not have these measures and must stop at saying that our results are consistent with the predictions made by resource competition theories.

Fig. 3. Average density ($\log N + 1$) of *P. caudatum*, *P. tetraurelia*, and *C. striatum* after day 10 in each history treatment in both community types. We did not include *T. thermophila* in this figure because it was essentially excluded from all communities. Titles above each graph indicate the resources present. "Mixed" communities have both algae and bacteria present as resources, while "specialist" communities have only bacteria present. Initials under each bar indicate initial history by identifying which species was initially present in monoculture. Univariate analyses were conducted within community type on each species density to determine differences among means. Different letters above each bar indicate significant differences between means based on Bonferroni-adjusted multiple comparisons.



Stochastic vs deterministic influences

The traditional explanation of coexistence requires that all species must show some niche differentiation in order to coexist (MacArthur 1972, Chesson 1991, Chesson and Huntly 1997). Alternatively, species may be competitively equivalent, and chance factors may play a large role in allowing coexistence (Strong et al. 1984, Hubbell and Foster 1986, Hubbell 1997). At the extreme, these views are dichotomous; either deterministic processes (e.g. Paine 1966, Tilman 1982) determine composition and coexistence, or composition reflects a random collection of species available from the regional species pool (e.g. Strong et al. 1984, Hubbell and Foster 1986). More realistically, these two views represent the endpoints of a gradient, and deterministic and stochastic events interact to determine community composition. In nature, abiotic conditions and assembly sequences certainly contain stochastic elements. In the absence of stochastic influences, within communities with identical resources and assembly sequences in this experiment, competition produced convergent compositions. But competition produced divergent compositions among communities with different abiotic conditions (i.e. resources available) and different assembly sequences.

Stochastic events, such as assembly sequences, will influence community composition more when interactions are among equivalent species than among asymmetrically interacting species. Deterministic processes can still occur, but may appear to have no net effect because the relative strengths of interactions are symmetric. For example, when competition is symmetric, initial conditions can influence the outcome of competi-

tion. Competition still occurs but the outcome depends on chance initial conditions, and the initial densities of each species determine the outcome of competition. This may occur because the sum of per-capita effects of a high density population on a low density population will be much greater than the sum of per-capita effects of a low density population on a high density population. Thus the high density population should severely limit or exclude the low density population, even though competition between individuals of different species may be symmetric. Mechanistic (R^*) and Lotka-Volterra models can both predict this result (Tilman 1982). Alternatively, initial conditions determine each species density, and densities of each species drift around initial densities in the absence of any other directional force. Densities will drift around initial means based on inherent variability of each population. Populations with high initial densities are less likely to drift to local extinction than populations with low initial density. In either case, deterministic processes interacted with stochastic events to produce community composition.

In this study, we found that initial conditions influenced densities of species with similar competitive abilities more than species with very different competitive abilities. The *Paramecium* species were more similar to each other in competitive ability when competing solely for bacteria at this level of productivity than either is to *C. striatum* or *T. thermophila* in specialist communities (Fox 2000), and the outcome of competition between *Paramecium* species depended on initial conditions. Further, *P. caudatum*, *P. tetraurelia*, and *C. striatum* were similar in competitive abilities and much more

effective than *T. thermophila* in mixed communities, and the outcome of competition between these three species depended on initial conditions.

When will history influence community composition?

When species compete for the same resource(s), history should not have a large effect. In this experiment when all species competed for bacteria only, history influenced the abundance of subordinate competitors, but the best competitor ultimately dominated regardless of history. Simple models of resource competition among specialists predict this result (MacArthur 1972, Tilman 1982) and there are numerous examples of the best competitor dominating when all resources are available to all competitors. Dominance by the best competitor in specialist communities occurs in a wide range of systems, including plant communities (Tilman and Wedin 1991), phytoplankton communities (Tilman and Sterner 1984, Grover 1988, 1991, Sommer 1991), and snails (Byers 2000).

In contrast, different potential equilibrium communities exist when some species consume resources unavailable to other species. We found that when both algae and bacteria were available as resources, and some species could not consume algae, the initially dominant species maintained dominance (except *T. thermophila*). Simple models of resource competition among specialists and generalists predict this result (MacArthur 1972). Given sufficient time in the absence of competition, the initially dominant species can draw resources to levels which may preclude invasion or dominance by other species (MacArthur 1972). A number of studies demonstrate the existence of alternative persistent states in constant environments and enough time allowed for species interactions to occur (Robinson and Dickerson 1987, Drake 1991, Drake et al. 1993, Weatherby et al. 1998, Law et al. 2000). These studies generally use species pools in which some species can utilize resources that are unavailable to other species, either through consuming different resources or from being on different trophic levels (Robinson and Dickerson 1987, Drake 1991, Drake et al. 1993, Weatherby et al. 1998, Law et al. 2000).

We have used competition theory to provide one answer to the question of when history will affect community composition. History will influence community composition communities when some resources are not available to all competitors. This can occur a number of different ways including feeding preferences and capabilities (e.g., this study), spatial segregation of resource use (e.g., Shorrocks and Bingley 1994), or even temporal segregation of resource use (e.g., Lawler and Morin 1993) In contrast, history will have much less of an effect when species compete for the same resource(s).

Plants, for example, compete for the same small number of limiting nutrients, and in algae (e.g., Sommer 1991), grasslands, (e.g., Tilman and Wedin 1991), and forests (e.g., Pacala et al. 1996) the best competitor dominates.

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