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Big questions, small worlds: microbial model systems in ecology

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Although many biologists have embraced microbial model systems as tools to address genetic and physiological questions, the explicit use of microbial communities as model systems in ecology has traditionally been more restricted. Here, we highlight recent studies that use laboratory-based microbial model systems to address ecological questions. Such studies have significantly advanced our understanding of processes that have proven difficult to study in field systems, including the genetic and biochemical underpinnings of traits involved in ecological interactions, and the ecological differences driving evolutionary change. It is the simplicity of microbial model systems that makes them such powerful tools for the study of ecology. Such simplicity enables the high degrees of experimental control and replication that are necessary to address many questions that are inaccessible through field observation or experimentation.

Ecologists are faced with the challenge of understanding the structure and function of systems, the component parts of which interact with each other in complex and diffuse ways at different scales of space and time. The approaches used by ecologists to make sense of such complexity vary in their degree of abstraction from nature and include field observations, experimentation in the field or laboratory and mathematical modeling. Studies of model systems (simplified representations of more complex systems) have played a particularly important role in ecology (Box 1). In spite of the significance of model systems in ecology, the explicit use of microbial model systems has been relatively rare.

This limited use of microbial model systems stems, at least in part, from the historical division between ecologists and microbiologists. Throughout much of the 20th century, communication between the two disciplines was rare, and the study of general ecology developed separately from the ecological study of MICROORGANISMS (see Glossary) [1]. Even the field of microbial ecology, in spite of its crossdisciplinary name, developed as a distinct subdiscipline of microbiology, isolated from general ecology.

Recently, both general ecologists and microbial ecologists have become increasingly interested in bridging the gap between these disciplines [1,2]. Research programs that integrate theory and microbial model systems with observational studies or experiments in the field are becoming more common (e.g. [3]). The growing popularity of microbial model systems is due, in part, to the degree of experimental control they offer. In addition, the abundance of genetic and physiological information available for commonly used microorganisms, combined with their small size and short generation times, enables the design of replicated experiments across a wide range of spatial and temporal scales. Microorganisms are also amenable to genetic manipulation and to prolonged storage in a state of suspended animation. These advantages enable the ecologist to deconstruct the complexity of nature into its component parts and to explore the role of each part in creating patterns in nature, first in isolation, then in combination.

In spite of these advantages and the historic importance of microbial model systems in the development of ecology (Box 2), some ecologists remain skeptical about what microbial laboratory systems can tell us about the natural world. They are concerned, for example, that such laboratory model systems are overly simplified, contrived and too small in spatial and temporal scale to be useful (Box 3) [4–8]. However, these criticisms reflect confusion about the purpose of microbial model systems. Laboratory model systems are not intended to be miniature versions of

Glossary

Autotroph: an organism that uses an inorganic carbon source.
Bacteriophage (phage): viruses that infect bacteria.
Chemostat: a continuous culture device in which resources are supplied and waste is removed at a constant rate.
Continuous culture: cultures maintained in systems where resources are supplied at a constant rate (e.g. a chemostat). In such systems, population growth rate is determined by the resource renewal rate (dilution rate).
Heterotroph: an organism that uses an organic carbon source.
Microorganisms: operationally defined as organisms <0.1 mm in diameter, including eukaryotic microorganisms, bacteria and viruses.

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Box 1. Model systems in ecology

Model systems, both macrobial and microbial, have made important contributions to ecology, as shown by the following examples:

- The interaction between bacteriophage T4 (Figure Ia1) and *Escherichia coli* (Figure Ia2) (shown here during the attachment of T4 to *E. coli* K-12) offers a system with which to study predator–prey dynamics and other multitrophic interactions (e.g. [26,67]). Electron micrograph reproduced with permission from John Wertz.
- Experimental grassland plots in Cedar Creek, Minnesota (Figure Ib). Experiments manipulating the number of species in plots have explored the relationship between species diversity and ecosystem function (e.g. [31]). Reproduced with permission from David Tilman.
- Phenotypic diversity and niche specificity among *Pseudomonas fluorescens* colonies evolved from a single ancestral 'smooth' cell type (SM morph) in a spatially heterogeneous (unmixed) environment (Figure Ic) [54]. Evolved populations show diverse colony morphologies (Figures Ici–iii). Most phenotypic variants can be assigned to one of three main morph classes: (SM), wrinkly spreader (WS) and fuzzy spreader (FS). Evolved morphs exhibit clear niche preferences (Figures Iciv–vi). Reproduced, with permission, from [54].
- A typical rocky intertidal community comprising (Figure Id1) algae *Endocladia muricata*; (Figure Id2) acorn barnacles *Balanus glandula*; (Figure Id3) mussels *Mytilus californianus*; and (Figure Id4) seastar *Pisaster ochraceous*. Research in rocky intertidal communities has contributed to our general understanding of the ecological processes that are important in structuring communities, such as competition, predation and disturbance (e.g. [9,68]).
- The spatial pattern of three *E. coli* strains exhibiting nontransitive relationships in a spatially structured environment offered by a solid agar matrix (Figure Ie). 'Balanced chasing' enables the three types to coexist over time: the toxin-producing patches (1) chase the toxin-sensitive patches (2), which chase the toxin-resistant patches (3), which, in turn, chase the toxin-producing patches [11].

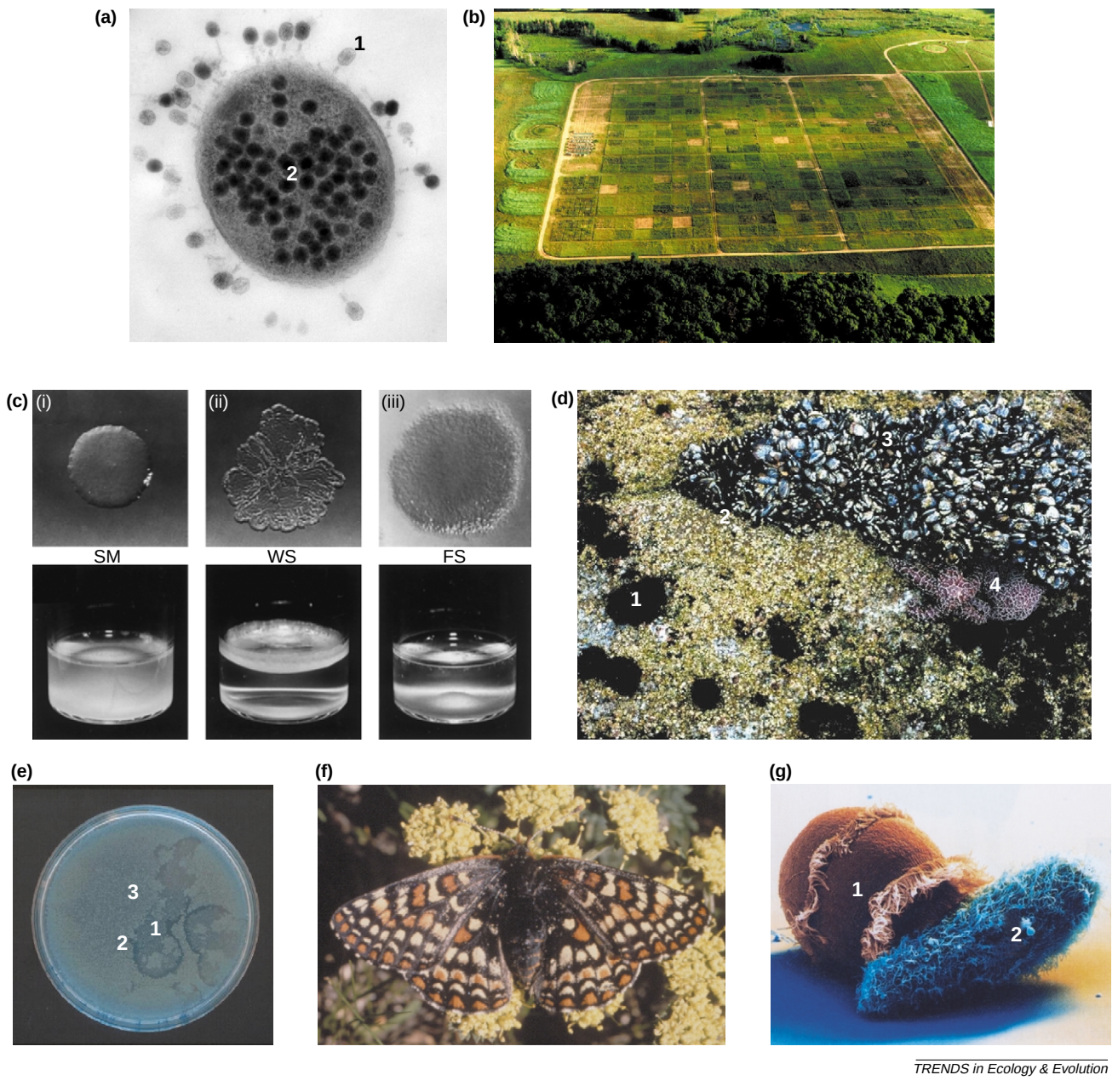

Figure I.

• The bay checkerspot butterfly *Euphydryas editha bayensis* has been the focus of some of the most extensive studies of metapopulation dynamics and coevolution (Figure If). (Reproduced with permission from Paul Ehrlich.) With the breadth and depth of behavioral, evolutionary, genetic and ecological information, butterflies in general constitute an important model system in ecology [69].

• *Didinium* (1) is a predatory protozoan that is used in some microbial model communities and is shown here feeding on a *Paramecium* (2) (Figure Ig) [70]. Reproduced with permission from Pearson Education, Inc., Upper Saddle River, NJ. Interactions between *C. striatum* and other protists and bacteria in laboratory communities have advanced our understanding of food webs (e.g. [41]).

field systems, and laboratory ecologists do not intend to reproduce nature in a laboratory model system. Rather, the purpose of laboratory model systems is to simplify nature so that it can be more easily understood. The ultimate test of our ecological understanding is if we can predict the behavior of an ecological system, whether in the laboratory or the field. If we cannot accurately predict the behavior of a simplified laboratory system, it is unlikely we understand enough to make predictions of field systems.

Here, we discuss recent studies that illustrate the utility of microbial model systems for studying ecology, focusing on their successes in addressing ecological issues, such as the effect of spatial interactions on community dynamics, the interplay between ecology and evolution, and the generation and maintenance of biological diversity. We take a broad approach, discussing select studies that illustrate the strengths of microbial model systems, as well as their limitations. Overall, we argue that the simplicity of microbial model systems provides a stark contrast to the complexity of the natural world, enabling researchers to test competing hypotheses about ecological processes and to establish the plausibility of mechanisms presumed to be operating in field systems.

Local interactions lead to patterns at large spatial scales

One of the central questions in ecology is how the sum of repeated local interactions gives rise to ecological patterns at larger spatial scales. For example, distributions of organisms in the rocky intertidal form large-scale regional patterns that are the result of ecological processes acting at multiple spatial scales, ranging from localized competition to regional recruitment [9,10]. The small size of microorganisms provides a unique opportunity to explore questions of scale in controlled, replicated experiments. Although small in absolute terms, microbial microcosms are orders of magnitude larger than the organisms they contain, making it possible to explore ecological patterns occurring at several spatial scales.

The importance of local interactions in governing patterns of diversity at larger spatial scales is emphasized in a recent study by Kerr *et al.* on the coexistence of toxin-producing, toxin-sensitive and toxin-resistant bacteria (Box 1, Figure Ie) [11]. These three populations of *Escherichia coli* exhibit nontransitive competitive relationships, similar to the game rock–paper–scissors. Kerr *et al.* showed that coexistence of all three types is favored when competition and dispersal occur locally (e.g. when the community is grown on the surface of an agar plate and propagated in a way that preserves spatial structure). Diversity is rapidly lost when these processes occur globally (e.g. in a well mixed flask where spatial structure does not develop) [11]. Many biological communities exhibit nontransitive interactions (e.g. [12,13]). Studying such interactions in microbial systems can provide valuable insight regarding their ecological and evolutionary roles in structuring communities.

Another goal of ecologists is to understand the processes governing the spatial and temporal distribution of diversity. The amount of energy available in an ecological system is thought to be a key determinant of diversity. Several studies have demonstrated a hump-shaped relationship between diversity and productivity in macroorganisms and some microorganisms [14–16], but the mechanisms underlying such trends are poorly understood. Recent work on the relationship between diversity and productivity in a microbial model system [17] provides another example of how local interactions, in this case competition among niche specialists in a heterogeneous environment, can explain patterns of diversity occurring at larger spatial scales. The familiar hump-shaped relationship between diversity and productivity (Figure 1) was observed when populations of the bacterium *Pseudomonas fluorescens* were allowed to compete in the spatially

Box 2. History of the use of microbial model systems in ecology

Microbial microcosms have played a central, if sometimes underappreciated, role in the history of ecology. The earliest published record of a microbial microcosm experiment is that by W.D. Dallinger who, in his address as the president of the Royal Microscopy Society in 1887, described his attempt to discover 'whether it was possible by change of environment, in minute life-forms, whose life-cycle was relatively soon completed, to superinduce changes of an adaptive character, if the observations extended over a sufficiently long period' [71]. Dallinger demonstrated that the evolution of ecological specialization is underlain by a cost of adaptation and that evolution was amenable to study in the laboratory.

Almost 20 years later, L.L. Woodruff [72] conducted experiments with hay infusions and concluded that interactions among organisms were an important driving force in the successional sequence of protozoans that he observed. Later, G.F. Gause conducted several more ecological experiments on competition and predation using microcosms comprising bacteria, yeast and protozoa [73]. Several key principles in ecology are attributed to these studies. For example, through estimating growth parameters for each species grown alone, Gause was able to predict which species would be competitively dominant. The interpretation of this work by G. Hardin ultimately led to the niche exclusion principle [74]. Furthermore, Gause's work on predator–prey dynamics using *Didinium nasutum* and *Paramecium caudatum* demonstrated the importance of spatial refugia and immigration for the maintenance of predator and prey.

Since Gause's pioneering experiments, microbial microcosms have been used to study various topics in ecology, such as succession [75], the diversity–stability relationship [76], predator–prey dynamics (e.g. [77]), the coexistence of competitors (e.g. [78]) and the coexistence of generalists and specialists [79].

Box 3. Addressing the criticisms of microbial model systems

Many ecologists remain skeptical that microbial model systems can tell us something useful about ecological processes in 'natural' communities. This is due, in large part, to the strong tradition of field research in ecology. Recent criticisms include assertions that microcosms, in general, and microbial model systems, in particular, are too contrived, too simple, too small in spatial and temporal scale, and fundamentally different from macrobial systems (e.g. [5,6,8,27]).

Microbial model systems are too simple and lack generality

Microbial model systems are simple. Indeed, they must be if these experiments are to be informative tests of ecological theory. This simplicity is a strength of laboratory model systems and its purpose is to simplify nature so that aspects of it can be better understood [27,36]. That laboratory systems lack generality is a misconception. Laboratory experiments with microorganisms usually address fundamental ecological questions using simple systems and, because of this, they potentially have more generality than do studies of more complex and often more idiosyncratic field systems [36].

Microbial model systems are highly artificial

G.E. Hutchinson criticized laboratory studies as being highly artificial and essentially 'a rather inaccurate analogue computer…using organisms as its moving parts' [80]. However, the experimental organisms and their interactions are not creations of the experimenter, neither are they under the direct control of the experimenter [81]. Although a researcher can control the initial composition of a community, the subsequent dynamics result from ecological interactions and natural selection. Thus, outcomes not predicted by simulation models are often observed (e.g. [56]). Furthermore, most studies use species that co-occur in a particular habitat and, in that sense, they are no more artificial than exclosure experiments in the field [4].

Microorganisms are fundamentally different

Among ecologists, there is some hesitation to accept microbial model systems because microbes are thought to have a unique biology. However, both prokaryotic and eukaryotic microorganisms share the fundamental properties of macroorganisms [2]. Thus, microorganisms are valid model organisms for questions that are concerned with these fundamental properties, such as trade-offs in life-history traits and resource competition. A related criticism is that it is inappropriate to use asexual genotypes as analogs for species in a community. However, most theory only assumes that 'species' do not exchange genes; thus, for many questions, asexual genotypes and species are equivalent.

Experiments with microbial model systems are too small in scale

Laboratory studies have been criticized for being too small in spatial scale and too short in temporal scale [4,27]. However, based on a literature search, Ives *et al.* [82] concluded that microbial microcosm studies might be of longer average duration, in terms of generations of the organisms involved, than most field studies. Similarly, the size of a 30-mL chemostat relative to the size of *E. coli* cells contained therein is orders of magnitude larger than the ratio for growth chambers in greenhouses and enclosure studies in the field. One of the advantages of using microorganisms is that such relatively large temporal and spatial scales are possible. Furthermore, scale is an issue that confounds ecological inference in many experimental systems and is not unique to microbial model systems (e.g. [6,7,83]).

heterogeneous environment of an unshaken microcosm. In this microcosm, microenvironments developed as a result of gradients in oxygen and the production of metabolic byproducts [18]. In homogeneous (shaken) environments, such gradients did not develop and the hump-shaped diversity–productivity pattern was not observed. This study enabled the identification of key processes underlying diversity patterns, a difficult task in many field systems where such patterns can occur on regional scales (*c*. 10^6 km^2) [14].

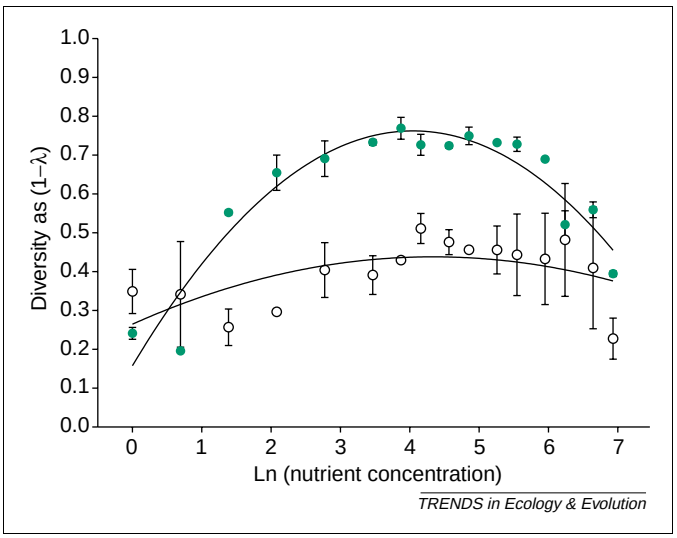

Figure 1. Response of *Pseudomonas fluorescens* diversity (expressed as 1–λ) to nutrient concentration in homogeneous (open circles) and heterogeneous (solid circles) environments, with bars marking ±1 S.E. of two replicates. Reproduced, with permission, from [17].

The role of habitat patchiness in facilitating the persistence of extinction-prone populations across large spatial scales has played a central role in the development of metapopulation theory. Metapopulation models predict a lower probability of extinction for many small patchily distributed populations connected by dispersal than for a single large population of the same size, because dispersal enables locally extinct populations to be recolonized (e.g. [19,20]). However, for many populations, determining interpatch dispersal and identifying the extinction and recolonization patterns predicted by classic metapopulation models remains challenging [21,22]. Holyoak and Lawler compared predator–prey communities of protists in small patches linked by dispersal (i.e. arrays of connected microcosms) with communities in isolated large patches (i.e. single undivided microcosms of the same total volume as the array of small microcosms) to demonstrate that populations persist longer in spatially subdivided habitats [23]. Furthermore, by quantifying densities of predators and prey in individual patches, the authors identified many of the features predicted by metapopulation theory [19,24], including extinction-prone patches and asynchronous population dynamics among patches.

Ecological patterns and processes at multiple temporal scales

The results of many field-based studies in ecology are limited by the temporal resolution of the experiments. However, many processes that might be important in structuring plant and animal communities, such as succession, coevolution, invasion and climate change, occur over much longer timescales than those of the

average research grant or doctoral dissertation project, and short-term trends often yield different conclusions than long-term analyses [25]. Because of their rapid generation times, microbial model systems can be used to address ecological questions over multiple temporal scales, and to explore community-level responses to environmental change [26,27].

The problem of temporal scale hinges on whether the observed responses to a perturbation reflect equilibrium properties of the community or transient dynamics. This issue has particularly limited our understanding of the relationship between community diversity and ecosystem function. Since Odum, Elton and Macarthur [28–30] first reasoned that more complex communities are more stable, researchers (e.g. [31]) have sought empirical tests for these predictions and a more mechanistic understanding of the diversity-stability relationship (reviewed in [32]). Although large-scale field experiments are undoubtedly key to understanding the relationship between diversity and many important ecosystem properties, their experimental design and execution presents logistical challenges. Recently, researchers used microbial model systems to test these predictions. McGrady-Steed *et al.* assembled laboratory communities of algae, bacteria, protists and small metazoans that differed in their initial diversity, both within and across different trophic levels [33]. The different communities rapidly stabilized within 40–80 generations of the dominant organisms, at diversities that were lower than initial levels. Measuring the functional attributes of the stable communities after six weeks revealed that the more diverse communities showed both less variation in CO_2 flux and more resistance to invasion by an exotic species than did the less diverse communities.

These results provide support for the biological insurance hypothesis, which posits that the redundancy within functional groups is important to overall ecosystem performance [32]. Similarly, Naeem and Li used replicated microcosms comprising algae, bacteria and protists with differing degrees of diversity within functional groups to test the hypothesis that more diverse communities should exhibit more predictable ecosystem properties [34]. Measures of biomass and density were more predictable as the number of species per functional group increased (i.e. the standard deviation of density measures decreased as the number of species per functional group increased, irrespective of environmental conditions). Both studies demonstrate a positive relationship between diversity and measures of stability and show that patterns observed among macroorganisms are also relevant for microorganisms.

Microbial microcosms can also be used to investigate the effects of simulated climate change on communities. Petchey *et al.*, for example, explored the effects of ecosystem warming on community structure and function using communities of eukaryotic microorganisms [35]. Communities differing in trophic structure and diversity were gradually warmed by 2°C per week (or 0.1 to 0.2°C per generation, roughly scaling to temperature changes that long-lived organisms might experience based on global warming predictions). In warmed communities, herbivores and predators tended to go extinct more frequently than in unwarmed communities, suggesting that global warming could result in significant extinctions of organisms in higher trophic levels.

Direct manipulation of ecological complexity

One of the more significant benefits of microbial model systems is that the degree of complexity is determined by the experimenter and is not imposed upon the experiment by nature [5,27,36]. This benefit is particularly apparent in studies that have used microbial model systems to explore food-web theory.

Consider the large body of theory about the causes and implications of food-chain length (e.g. [37,38]). Food-chain models suggest that productivity is an important determinant of food-chain length, and that food-chain length influences the population-level responses of trophic levels to changes in productivity [38]. Experimental tests of this theory are especially challenging, in part, because it is difficult to simplify natural food-web relationships into the clearly defined trophic categories required of food-chain theory [39,40]. Microbial model systems sidestep this problem by defining, *a priori*, all components of a food chain. The properties of these food chains can then be studied in detail, and compared with the patterns observed in natural food webs.

For example, Kaunzinger and Morin [41] explored the effect of productivity on the length and stability of microbial food chains of different lengths (one-, two-, and three-level food chains) by manipulating the resource concentration available to the primary producer. Food-chain length increased with productivity, with the longest food chains persisting only at the highest resource concentrations. The abundance of individuals within any given trophic level changed with productivity in a manner consistent with the theory of trophic cascades: the increased production associated with increasing the resource concentration available to primary producers percolates up through the food chain to increase the population density of the top consumer and those trophic levels an even number of levels below it (Figure 2). These results provide some of the most compelling experimental evidence for the interplay among primary productivity, food-chain length and population regulation.

An intriguing problem in the study of trophic interactions has been that of omnivory. Although omnivory is commonly observed in nature (e.g. [42]), many models predict that it should be rare overall [38] and that coexistence of omnivores and their prey and/or competitors should depend on productivity (e.g. [43]). Furthermore, whereas many population models predict destabilization of predator–prey dynamics with resource enrichment, some theoretical models predict that the presence of omnivory can actually stabilize these dynamics [44,45]. The difficulties of testing these predictions in most systems (e.g. accurate descriptions of current food web structure are rarely paired with data on population dynamics [46]) can be avoided by using microbial model systems in the laboratory. For example, Morin explored the effect of omnivory on population dynamics using communities of protists and bacteria [47]. His model communities comprised bacteria, the bacteriovorous ciliate *Colpidium striatum* and the omnivorous ciliate *Blepharisma americanum*,

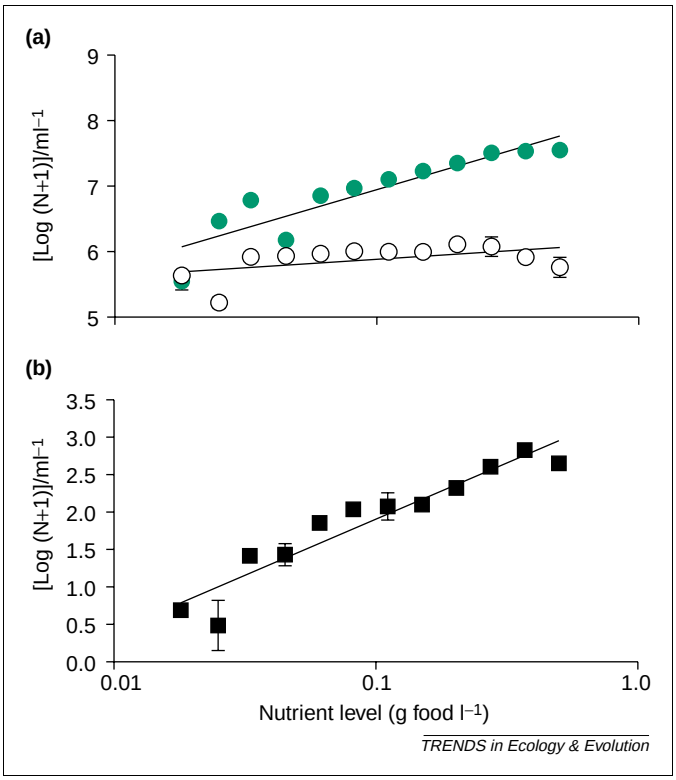

Figure 2. Effects of productivity on population abundances in trophic levels one and two of a microbial food chain. **(a)** Response of the bacterium *Serratia marcescens* abundance to a productivity gradient when cultured alone (solid circles) and with the bacterivorous ciliate predator *Colpidium striatum* (open circles). **(b)** Response of the abundance of *C. striatum* (in the presence of *S. marcescens*) to the same productivity gradient. Lines fitted by regression; error bars indicate S.E.M. Productivity scales with grams of food l^{-1}, which indicates the concentration of the protozoan pellet in the nutrient medium. Reproduced, with permission, from [41].

which could consume bacteria and *C. striatum*. Both ciliates coexisted at high productivity levels, but at low productivity levels, the omnivore was excluded through resource competition with its prey and/or competitor, as predicted by theory. In addition, the interaction between *B. americanum* and *C. striatum* showed increased stability with resource enrichment, suggesting that the response of food webs to enrichment can depend on the amount of omnivory. Studying these interactions in simplified microbial model systems enables identification of key determinants of food web structure and characterization of the consequences of particular food web configurations.

Evolution of ecological characters

In microbial model systems, the traditional distinction between ecology and evolution is blurred [48], enabling researchers to study the evolution of important ecological characters. For example, Bell and colleagues addressed the evolution of the ecological niche in a series of experiments with the unicellular alga *Chlamydomonas reinhardtii* (e.g. [49,50]), which grows as an AUTOTROPH in the light, but can also grow as a HETEROTROPH in the dark when an exogenous source of carbon is provided. Theory predicts that the breadth of adaptation will evolve to match the amount of environmental variation [51]. Indeed, this is exactly what happens: light- or dark-specialists evolve when selection occurs solely in the light or the dark, respectively, whereas broadly adapted generalists evolve in environments that vary in time.

Recent laboratory experiments with the alga *Chlorella vulgaris* as prey and the rotifer *Brachionus calyciflorus* as predator demonstrated that ecological dynamics are ultimately inseparable from evolution [52,53]. Classic predator–prey models predict inherent oscillations in predator and prey dynamics and a one-quarter-cycle phase shift between predators and prey. When the rotifer–algal system was cultured in laboratory CHEMOSTATS, the authors observed cycle periods that were longer than predicted and were almost exactly out of phase. Subsequent experiments manipulating the degree of clonal diversity in the alga population demonstrated that these dynamics were a consequence of rapid prey evolution. The results of these experiments highlight the importance of considering real-time evolution in understanding ecological processes such as population dynamics.

Post-hoc analysis of ecological mechanisms

Many microbial populations can be stored indefinitely in ultra-low temperature freezers and revived as required. The results of completed experiments can thus be dissected *a posteriori* to gain a more detailed understanding of the mechanisms underlying the ecological and evolutionary processes at work. Rainey and Travisano [54], for example, documented a striking example of adaptive radiation in the soil bacterium *Pseudomonas fluorescens* occupying a spatially structured (static) microcosm. They showed, through competition experiments using strains that were archived during diversification, that diversity in these cultures is maintained by negative frequency-dependent selection, exactly as predicted by theory [55].

A second example comes from a study of the stability properties of predator–prey communities. Schrag and Mittler documented the stable coexistence, over ~50 generations, of BACTERIOPHAGE and bacteria under CONTINUOUS CULTURE conditions, a situation where theory predicted that coexistence was not possible [56]. They found that a small fraction (~5% or less) of the bacterial population was phage-sensitive and so enabled the phage to persist. Furthermore, the phage-sensitive population was sustained because the culture environment was much less homogeneous than was first thought – populations of bacteria grew on the walls of the culture vessel, as well as in the bulk fluid. Thus, stability was conferred on the community through the spatial structure of the culture vessel itself. This was confirmed by manipulations of the degree of spatial structure. Increasing the surface area of the culture vessel by the addition of glass beads increased the duration of coexistence of phage and bacteria. Removing the effect of the wall-associated populations by transferring cultures into clean vessels daily led to the rapid extinction of phage. Thus, although most basic models of predator–prey interactions fail to predict the stable coexistence of predator and prey that is observed in many environments, these studies identified the importance of spatial refuges in maintaining coexistence.

Conclusions

The experiments discussed here underscore the utility of microbial model systems for answering ecological questions that can be difficult to address using field systems. Moreover, the rapidly increasing pool of genetic information concerning many microorganisms provides the opportunity to understand ecological processes at all scales of biological organization. For example, the work on adaptive radiation in *P. fluorescens*, discussed above, has been extended to identify the loci responsible for niche specialization [57], with the ultimate aim of providing a comprehensive explanation for adaptive radiation in this system.

The studies reviewed represent a subset of those that have used microbial model systems to address ecological questions. Microbial microcosm studies have also been successfully used to explore ecosystem-level selection [58], the effect of resource supply ratios on the outcome of competition [59], the ecology and evolution of mutualisms [60], predator–prey coevolution [61,62], and the ecology and evolution of sociality (e.g. [63,64]).

However, microbial model systems are not appropriate for all ecological questions. For example, the small scale of microorganisms makes it difficult to manipulate explicitly environmental heterogeneity at relative scales similar to those in experiments with plants and animals. Heterogeneity in resources or conditions on such scales does develop in microbial model systems (e.g. gradients in oxygen availability or metabolic byproducts), and such heterogeneity is important for subsequent ecological and evolutionary dynamics. However, researchers are usually forced to describe this heterogeneity after the fact. Another limitation of microbial systems is that evolution of organisms in some microbial microcosms can occur over the order of days, often changing interaction dynamics before characterization has been completed by the researcher. Furthermore, some questions in ecology, such as those related to extinction and genetic drift, may require small populations, which are difficult to work with in microbial systems. Some of the unique aspects of microorganisms, such as clonal reproduction, unicellularity and lack of morphological diversity, also make microbial model systems inappropriate for addressing questions concerning age-based phenomena or behavioral ecology [2]. That said, several questions that were once thought to be outside the realm of microorganisms have since been addressed using particular microbial model systems (e.g. senescence [65]). Finally, there are limits to our ability to extrapolate from microbial experimental systems to larger and often more complex systems. Such limitations are not unique to microbial systems, but are shared by ecological studies in general. Identifying the appropriate experimental scale and the limits of extrapolation from this scale are critical aspects of conducting research in all areas of biology, not just microbial systems.

Microbial model systems offer a complementary approach to field and laboratory studies of macroorganisms. While there are practical limitations to microbial model systems, their simplicity makes microbial microcosm experiments especially powerful for determining the biological plausibility of theoretical predictions. Topics that are particularly ripe for exploration include studies of the genetic basis of ecological traits, and the evolution of self-supporting ecosystems. Microorganisms also offer a unique opportunity to explore more practical problems in fields such as toxicology and agriculture (e.g. [66]). Finally, microbial model systems can reveal much about the natural history of microbes themselves, which is essential given that microorganisms are important in nutrient cycling, industry and medicine.

The complexity of natural communities has both inspired and frustrated progress in community ecology and making sense of this complexity requires the use of multiple approaches, including rigorous experimentation. With their advantages in control, replication, *post-hoc* analysis and range of experimental scale, microbial model systems are particularly powerful experimental tools in the ecologist's toolbox.

Acknowledgements

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References

1 Atlas, R.M. and Bartha, R. (1998) *Microbial Ecology: Fundamentals and Applications*, 4th edn, Benjamin/Cummings
2 Andrews, J.H. (1991) *Comparative Ecology of Microorganisms and Macroorganisms*, Springer-Verlag
3 Zhou, J. *et al.* (2002) Spatial and resource factors influencing high microbial diversity in soil. *Appl. Environ. Microbiol.* 68, 326–334
4 Lawton, J.H. (1996) The Ecotron facility at Silwood Park: the value of 'big bottle' experiments. *Ecology* 77, 665–669
5 Diamond, J.M. (1986) Overview: laboratory experiments, field experiments and natural experiments. In *Community Ecology* (Diamond, J.M. and Case, T.J., eds), pp. 3–22, Harper and Row
6 Carpenter, S.R. (1996) Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77, 677–680
7 Peters, R.H. (1991) *A Critique for Ecology*, Cambridge University Press
8 Hairston, N.G. (1989) *Ecological Experiments: Purpose, Design and Execution*, Cambridge University Press
9 Paine, R. and Levin, S. (1981) Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.* 51, 145–178
10 Wootton, J.T. (2001) Local interactions predict large-scale pattern in empirically derived cellular automata. *Nature* 413, 841–844
11 Kerr, B. *et al.* (2002) Local dispersal promotes biodiversity in a real-life game of rock-paper-scissors. *Nature* 418, 171–174
12 Buss, L.W. and Jackson, J.B.C. (1979) Competitive networks: nontransitive competitive relationships in cryptic coral-reef environments. *Am. Nat.* 113, 223–234
13 Sinervo, B. and Lively, C.M. (1996) The rock–paper–scissors game and the evolution of alternative male strategies. *Nature* 380, 240–243
14 Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*, Cambridge University Press
15 Leibold, M. (1999) Biodiversity and nutrient enrichment in pond plankton communities. *Evol. Ecol. Res.* 1, 73–95
16 Horner-Devine, M.C. *et al.* (2003) Bacterial diversity patterns along a gradient of primary productivity. *Ecol. Lett.* 6, 613–622
17 Kassen, R. *et al.* (2000) Diversity peaks at intermediate productivity in a laboratory microcosm. *Nature* 406, 508–512
18 Travisano, M. and Rainey, P.B. (2000) Studies of adaptive radiation using model microbial systems. *Am. Nat.* 156, S35–S44
19 Hanski, I. (1991) Single-species metapopulation dynamics: concepts, models and observations. *Biol. J. Linn. Soc.* 42, 17–38
20 Levins, R. (1969) Some demographic and genetic consequences of

environmental heterogeneity for biological control. *Bull. Ecol. Soc. Am.* 15, 237–240
21 Harrison, S. and Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. In *Metapopulaion Biology: Ecology, Genetics and Evolution* (Hanski, I.A. and Gilpin, M.E., eds), pp. 27–42, Academic Press
22 Ims, R.A. and Yoccoz, N.G. (1997) Studying transfer processes in metapopulations. In *Metapopulaion Biology: Ecology, Genetics and Evolution* (Hanski, I.A. and Gilpin, M.E., eds), pp. 247–265, Academic Press
23 Holyoak, M. and Lawler, S.P. (1996) Persistence of an extinction-prone predator–prey interaction through metapopulation dynamics. *Ecology* 77, 1867–1879
24 Hanski, I.A. (1999) Metapopulation Ecology, Oxford University Press
25 Risser, P.G. ed. (1991) *Long-term Ecological Research: an International Perspective* John Wiley and Sons
26 Bohannan, B.J.M. and Lenski, R.E. (2000) The relative importance of competition and predation varies with productivity in a model community. *Am. Nat.* 156, 329–340
27 Lawton, J.H. (1995) Ecological experiments with model systems. *Science* 269, 328–331
28 Odum, E.P. (1953) *Fundamentals of Ecology*, W.B. Saunders
29 Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*, Methuen & Co
30 MacArthur, R. (1955) Fluctuations of animal populations, and a measure of community stability. *Ecology* 36, 533–536
31 Tilman, D. and Downing, J.A. (1994) Biodiversity and stability in grasslands. *Nature* 367, 363–365
32 McCann, K.S. (2000) The diversity-stability debate. *Nature* 405, 228–233
33 McGrady-Steed, J. *et al.* (1997) Biodiversity regulates ecosystem predictability. *Nature* 390, 162–165
34 Naeem, S. and Li, S. (1997) Biodiversity enhances ecosystem reliability. *Nature* 390, 507–509
35 Petchey, O.L. *et al.* (1999) Environmental warming alters food-web structure and ecosystem function. *Nature* 402, 69–72
36 Drake, J.A. *et al.* (1996) Microcosms as models for generating and testing community theory. *Ecology* 77, 670–677
37 Elton, C. (2001) *Animal Ecology* (reprint of 1927 edition), The University of Chicago Press
38 Pimm, S.L. and Lawton, J.H. (1977) Number of trophic levels in ecological communities. *Nature* 268, 329–331
39 Power, M.E. (1992) Top-down and bottom-up forces in food webs: do plants have primacy? *Ecology* 73, 733–746
40 Vander Zanden, M.J. *et al.* (1999) Patterns of food chain length in lakes: a stable isotope study. *Am. Nat.* 154, 406–416
41 Kaunzinger, C.M.K. and Morin, P.J. (1998) Productivity controls food-chain properties in microbial communities. *Nature* 395, 495–497
42 Coll, M. and Guershon, M. (2002) Omnivory in terrestrial arthropods: mixing plant and prey diets. *Annu. Rev. Entomol.* 47, 267–297
43 Holt, R.D. and Polis, G.A. (1997) A theoretical framework for intraguild predation. *Am. Nat.* 149, 745–764
44 McCann, K. and Hastings, A. (1997) Re-evaluating the omnivory–stability relationship in food webs. *Proc. R. Soc. Lond. Ser. B* 264, 1249–1254
45 Fagan, W.F. (1997) Omnivory as a stabilizing feature of natural communities. *Am. Nat.* 150, 554–567
46 Lawler, S.P. and Morin, P.J. (1993) Food web architecture and population dynamics in laboratory microcosms of protists. *Am. Nat.* 141, 675–686
47 Morin, P. (1999) Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* 80, 752–760
48 Lenski, R.E. (2001) Testing Antonovics' five tenets of ecological genetics: experiments with bacteria at the interface of ecology and genetics. In *Ecology: Achievement and Challenge* (Press, M.C. *et al.*, eds), pp. 25–45, Blackwell Science
49 Reboud, X. and Bell, G. (1997) Experimental evolution in *Chlamydomonas*. III. Evolution of specialist and generalist types in environments that vary in space and time. *Heredity* 78, 507–514
50 Kassen, R. and Bell, G. (1998) Experimental evolution in *Chlamydomonas*. IV. Selection in environments that vary through time at different scales. *Heredity* 80, 732–741
51 Levins, R. (1968) *Evolution in Changing Environments*, Princeton University Press
52 Turchin, P. (2003) Evolution in population dynamics. *Nature* 424, 257–258
53 Yoshida, T. *et al.* (2003) Rapid evolution drives ecological dynamics in a predator–prey system. *Nature* 424, 303–306
54 Rainey, P.B. and Travisano, M. (1998) Adaptive radiation in a heterogeneous environment. *Nature* 394, 69–72
55 Levene, H. (1953) Genetic equilibrium when more than one ecological niche is available. *Am. Nat.* 87, 331–333
56 Schrag, S.J. and Mittler, J.E. (1996) Host–parasite coexistence: the role of spatial refuges in stabilizing bacteria-phage interactions. *Am. Nat.* 148, 348–377
57 Spiers, A.J. *et al.* (2002) Adaptive divergence in experimental populations of *Pseudomonas fluorescens*. I. Genetic and phenotypic bases of wrinkly spreader fitness. *Genetics* 161, 33–46
58 Swenson, W. *et al.* (2000) Artificial ecosystem selection. *Proc. Natl. Acad. Sci. U. S. A.* 97, 9110–9114
59 Grover, J.P. (2000) Resource competition and community structure in aquatic microorganisms: experimental studies of algae and bacteria along a gradient of organic carbon to inorganic phosphorus supply. *J. Plankton Res.* 22, 1591–1610
60 Rosenzweig, R.F. *et al.* (1994) Microbial evolution in a simple unstructured environment: genetic differentiation in *Escherichia coli*. *Genetics* 137, 903–917
61 Buckling, A. and Rainey, P.B. (2002) The role of parasites in sympatric and allopatric host diversification. *Nature* 420, 496–499
62 Buckling, A. and Rainey, P.B. (2002) Antagonistic coevolution between a bacterium and a bacteriophage. *Proc. R. Soc. Lond. Ser. B* 269, 931–936
63 Turner, P.E. and Chao, L. (1999) Prisoner's dilemma in an RNA virus. *Nature* 398, 441–443
64 Velicer, G.J. *et al.* (2000) Developmental cheating in the social bacterium *Myxococcus xanthus*. *Nature* 404, 598–601
65 Ackermann, M. *et al.* (2003) Senescence in a bacterium with asymmetric division. *Science* 300, 1920
66 Reboud, X. (2002) Response of *Chlamydomonas reinhardtii* to herbicides: negative relationship between toxicity and water solubility across several herbicide families. *Bull. Environ. Contam. Toxicol.* 69, 554–561
67 Bohannan, B.J.M. and Lenski, R.E. (1997) Effect of resource enrichment on a chemostat community of bacteria and bacteriophage. *Ecology* 78, 2303–2315
68 Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology* 42, 710–723
69 Boggs, C.L., *et al.* eds (2003) *Butterflies: Ecology and Evolution Take Flight* University of Chicago Press
70 Stiling, P. (2002) *Ecology: Theories and Applications*, 4th edn, Pearson Education
71 Dallinger, W.D. (1887) The president's address. *J. R. Microsc. Soc.* 7, 184–199
72 Woodruff, L.L. (1912) Observations on the origin and sequence of the protozoan fauna of hay infusions. *J. Exp. Zool.* 12, 205–264
73 Gause, G.F. (1934) *The Struggle for Existence*, Dover
74 Hardin, G. (1960) The competitive exclusion principle. *Science* 131, 1292–1297
75 Gorden, R.W. *et al.* (1969) Studies of a simple laboratory microecosystem: bacterial activities in a heterotrophic succession. *Ecology* 50, 86–100
76 Hairston, N.G. *et al.* (1968) The relationship between species diversity and stability: an experimental approach with protozoa and bacteria. *Ecology* 49, 1091–1101
77 Luckinbill, L.S. (1973) Coexistence in laboratory populations of *Paramecium aurelia* and its predator *Didinium nasutum*. *Ecology* 54, 1320–1327
78 Tilman, D. (1977) Resource competition between planktonic algae: experimental and theoretical approach. *Ecology* 58, 338–348
79 Dykhuizen, D. and Davies, M. (1980) An experimental model: bacterial specialists and generalists competing in chemostats. *Ecology* 61, 1213–1227

80 Hutchinson, G.E. (1978) *An Introduction to Population Ecology*, Yale University Press
81 Mertz, D.B. and McCauley, D.E. (1982) The domain of laboratory ecology. In *Conceptual Issues in Ecology* (Saarinen, E., ed.), pp. 229–244, Reidel
82 Ives, A.R. *et al.* (1996) Bottle or big-scale studies: how do we do ecology? *Ecology* 77, 681–685
83 Petersen, J.E. and Hastings, A. (2001) Dimensional approaches to scaling experimental ecosystems: designing mousetraps to catch elephants. *Am. Nat.* 157, 324–333

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