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Abstract
The intrinsic growth rate of nonselective microbivores increases asymptotically with increasing prey biomass, but we do not know how intrinsic growth rate is affected by prey richness. The objective of this experiment was to determine the effect of prey richness on the growth kinetics of nematode predators while grazing on mixed bacterial lawns. We found that the intrinsic growth rate of *Caenorhabditis elegans* in laboratory culture increased asymptotically with prey richness. The mechanism of this pattern was primarily due to the best available prey species in the mixture: the intrinsic growth rate of the consumer feeding on a mixture of prey was approximately equal to the intrinsic growth rate of the predator when feeding on the single best prey in monoculture. This was analogous to the selection effect observed in biodiversity-ecosystem functioning relationships. Generation time, and not reproductive output, was the life history trait component that was most consistent with the pattern of intrinsic growth rate. Our results suggest that in order to link invertebrate consumers' growth rates to their microbial species composition in the field, it will be necessary to determine the ability of microbivorous invertebrates to selectively forage in natural environments and to better understand the microscale distribution of microbial communities in their natural environments.

Keywords: nematodes, bacteria, polyculture, pathogenicity, community

Introduction

Consumers that feed on microbes regulate the abundance of their prey (Wardle et al. 1995), help to cycle nutrients in soil, sediment, and aquatic food webs (Anderson et al. 1981), and can even influence the community composition of their prey (Xiao et al. 2010). However, the mechanisms by which the microbial community affects its consumer community are not clear. Specifically, how might the composition of the microbial community affect the intrinsic growth rate of its consumers? For example, prey capture and consumption rates increase asymptotically with prey density (Holling 1959), much like how the growth rate of suspended microbial cells increases asymptotically with substrate concentration (Monod 1949). Similarly, the growth rate of nematode consumers increases asymptotically with prey density (Schiemer 1982a, b). Thus, microbivores tend to be most abundant around high concentrations of microbial prey. Furthermore, an optimal forager that is able to select prey should have higher intrinsic growth in patches of high prey quality (MacArthur and Pianka 1966). However, a filter or deposit feeder that does not, or is unable to, selectively harvest certain prey species may not necessarily have faster intrinsic growth rates when foraging in patches of high prey richness. An indiscriminate consumer also consumes prey of low quality, including those that are detrimental such as potential pathogens. Ultimately, we do not know how the richness of prey species affects the intrinsic growth rate of consumers that are indiscriminate consumers that are unable to select efficiently for the highest quality prey species. Examples of nonselective consumers include many of the classic ecological systems for model consumer-prey dynamics, such as rotifers, bivalves, and bacterivorous nematodes. Although these organisms can select for prey size (Gonzalez et al. 1990; Kirk 1991; Fang-Yen et al. 2009), can clear or excrete prey based on membrane rigidity or palatability (Bougrier et al. 1997; Dionisio Pires et al. 2004), and can selectively forage in defined patches of preferable prey (Coolon et al. 2009), it is not clear whether these consumers are able to selectively consume high- vs. low-quality prey items in well-mixed patches (Montagnes et al. 2008).

We can consider at least two ways in which the species richness of prey could influence indiscriminate consumers with a mixed diet. On one extreme, the intrinsic growth rate of the consumer feeding on a mixed diet could be equal to that of the consumer feeding on the single best prey item alone. This we call the "best of what's around" model, and is the expectation if the influence of forage quality on the consumer is primarily that of nutritional content, without complementarity, and not of adverse characteristics such as toxins or pathogenicity. Under this model, the pattern we would expect to see is that intrinsic growth rate of the consumer increases asymptotically with prey species richness, but levels off at approximately the same maximal growth rate of the consumer when grown in the single best prey species in monoculture (Fig. 1a). At the other extreme, the intrinsic growth rate of the consumer feeding on a mixed diet could be equal to that of the consumer feeding on the single worst prey item alone. This we call the "worst of what's around" model and is the expectation if forage quality is primarily a consequence of toxins, pathogenicity, or some other form of antagonism from the prey to the consumer. Under this model, the pattern we would expect to see is that intrinsic growth rate of the consumer decreases asymptotically with prey species richness but levels off at approximately the same growth rate of

the consumer when grown in the single worst prey species in monoculture (Fig. 1b). Of course, there are intermediate possibilities such as the "field average," where the intrinsic growth rate of the consumer feeding on a mixed diet could be equal to the average growth rate of the consumer feeding on each prey item individually (Fig. 1c). It is also possible that prey richness alone, possibly in combination with prey identity, could influence consumer growth rate. This could be the result of nutritional complementarity between multiple prey items that facilitates a greater consumer intrinsic growth rate than for any single prey item alone. The pattern we would expect to see might be a combination of the best of what's around model (intrinsic growth rate of the consumer decreasing asymptotically with prey species richness) but leveling off at a growth rate that is higher than for any species in monoculture (Fig. 1d).

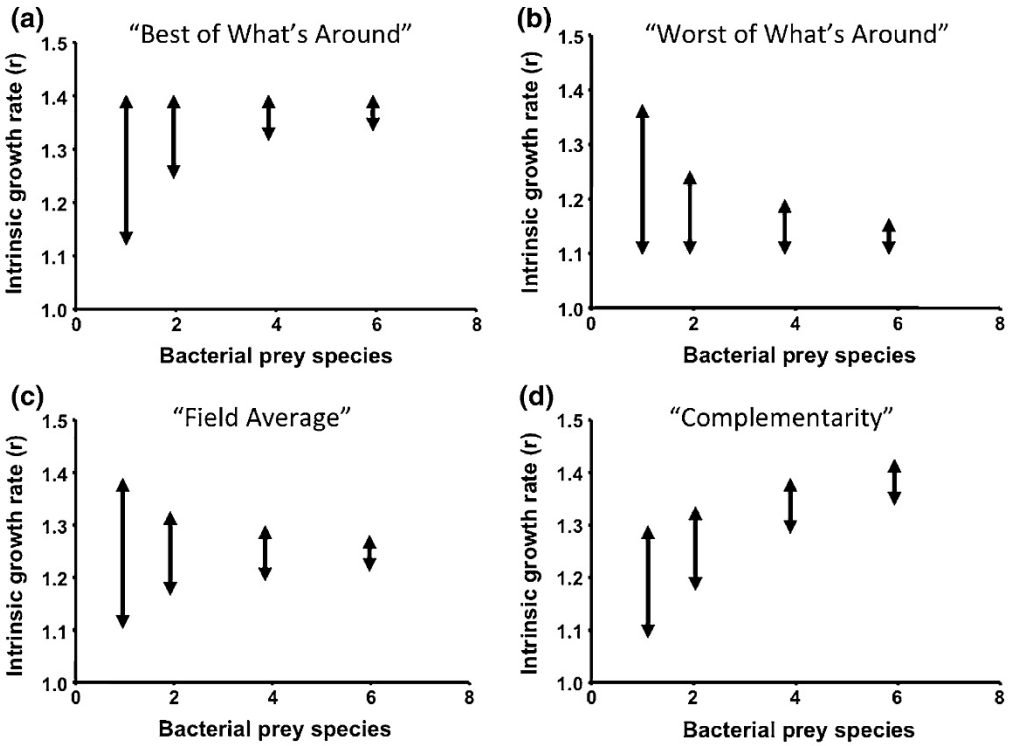

Figure 1. Hypothetical responses of consumer intrinsic growth rate to prey richness. (a) "Best of what's around" (consumer growth rate in mixed prey is equal to the growth rate of the consumer in the single most advantageous prey in monoculture), (b) "worst of what's around" (consumer growth rate in mixed prey is equal to the growth rate of the consumer in the single worst prey in monoculture), (c) "field average" (consumer growth rate in mixed prey is equal to the average growth rate of the consumer in prey in monoculture), and (d) combination of best of what's around plus "richness" effect (consumer growth rate in mixed prey is equal to the growth rate of the consumer in the single most advantageous prey in monoculture plus some complementary effect of bacteria in combination).

The effect of prey species richness on the intrinsic growth rate of their consumers is relevant to understanding the community composition and distribution of species that are used as indicators of their environments. For example, nematodes and other invertebrates have been proposed as biological indicators of soil and aquatic health (Neher 2001). The distribution of nematode species is constrained by abiotic components of their environment, such as temperature, moisture, texture, and soil pH (Wilson and Kakouli-Duarte 2009), but it has been challenging to define the relevant biotic component of the soil environment that is predictive of nematode species distributions. Species in the enrichment-type functional guild families (such as Rhabditidae) are most abundant in soils that have been recently enriched with a high-nutrient content substrate that results in an increased density of prey bacteria. Conversely, basal-type bacterivores (such as Cephalobidae) tend to be present at relatively constant abundance regardless of bacterial densities. We know that fecundity, developmental rate, and generation time increase asymptotically with bacterial prey density (Schiemer 1982a, b), but we do not know whether the growth rate of the bacterivores necessarily increases asymptotically with prey richness, or if it is some other function of prey composition. Bacterial-feeding nematodes exhibit different life history traits when grown on different bacterial species (Grewal 1991; Venette and Ferris 1998). Although bacteria are a necessary prey item, some bacterial species are also potential pathogens that shorten the lifespan or result in a reduced or delayed reproductive output for some nematodes. Thus, palatability, nutrition, and pathogenicity are all potential ways in which bacteria as food items can influence their nematode predators. The combination of these effects can be experimentally measured by determining the post-juvenile lifespan and reproductive output of nematodes under constant exposure to particular bacteria (Tan et al. 1999). Many of the bacteria on which *Caenorhabditis elegans* has the lowest lifespan and fecundity are also known human pathogens, such as *Enterococcus faecalis, Pseudomonas aeruginosa*, or *Staphylococcus aureus*, but shortened lifespan is not necessarily characteristic of all bacteria encountered by nematodes in the soil.

The objective of this experiment was to determine the effect of prey richness on growth kinetics of consumers on mixed microbial lawns. We used the nematode *C. elegans*, which is in the family Rhabditidae and is characteristic of enrichment-type bacterial-feeding consumers that have a comparatively short generation time and high reproductive output. *C. elegans* proliferate in highly enriched substrates, like compost or decaying fruit, and disperse by phoresy on a variety of invertebrates, such as snails, slugs, millipedes, isopods, and insects (Félix and Braendle 2010). We exposed *C. elegans* to multiple bacteria, in monoculture and then in polyculture, and tested the relationship between prey richness and intrinsic growth rate. Intrinsic growth rate is an appropriate population metric to study for *C. elegans* because they are an *r*-selected species (sensu Pianka 1970) characteristic of enrichment-type nematodes associated with a short-lived "boom-and-bust" lifestyle (Ferris and Bongers 2006). We explicitly tested four main models: best of what's around (Fig. 1a), worst of what's around (Fig. 1b), field average (Fig. 1c), and richness (Fig. 1d).

Materials and methods

Experimental setup

Caenorhabditis elegans strain N2 was grown on six different species of bacteria from a broad range of phyla (all isolated from Konza Prairie Long-Term Ecological Research Network, Kansas, USA): *Variovorax paradoxus* 10-1 (β-Proteobacteria), *Arthrobacter luteolus* D-4 (Actinobacteria), *Pseudomonas putida* W-1 (γ-Proteobacteria), *Flavobacterium* sp. D-6 (Bacteroidetes), *Bacillus thuringiensis* W-5 (Firmicutes), and *Stenotrophomonas maltophilia* JCMS (γ-Proteobacteria). To prepare bacterial treatments, overnight cultures of these bacteria [in Luria-Bertani (LB) broth] were combined in all two-, four-, and six-way combinations in equal biomass ratios as determined by optical density. This resulted in 37 bacterial treatments: 6 monocultures, 15 pair-wise combinations, 15 four-way combinations, and 1 six-way combination. Each bacterial treatment was contained in a 2-ml aliquot of LB broth and stored at 4°C until use. To prepare experimental nematodes, bleach-synchronized cohorts of *C. elegans* N2 eggs were grown on *Escherichia coli* OP50 for 48 h, and fourth-stage juveniles were picked onto a plate that had been seeded with the appropriate bacterial treatment, ten individuals per plate. The plates were seeded by adding 500 μl of the mixed or monoculture bacterial treatment in the middle of the petri dish; the initial inoculum contained approximately 108 cells and became concentrated overnight as the liquid media evaporated or was absorbed by the agar. Each plate was monitored daily for survival and fecundity. Each day, gravid females were transferred to new plates that had been freshly seeded with the same bacterial treatment 24 h prior to use. This entire experiment was performed on three independent batches, each with unique overnight cultures of bacteria, and unique bleach-synchronized cohorts of *C. elegans* N2. Fecundity and post-juvenile survivorship schedules were used in standard life table analysis (Gotelli 2001) to estimate mean lifespan (i.e., life expectancy, following exposure to bacterial treatment) and intrinsic rate of increase [$r \approx \ln(R_0)/\mathrm{GT}$] as a function of reproductive output (R_0) and generation time (GT).

Data analysis

The four life history traits (intrinsic growth rate, generation time, reproductive output, and lifespan) were first analyzed with a mixed linear model (PROC MIXED; SAS Institute, Cary, North Carolina) comparing four independent variables: maximum, minimum, average, and richness. Richness was simply the number of bacterial species in the mixture, while maximum, minimum, and average were computed from the results of *C. elegans* grown on the single bacteria in monoculture. For example, minimum lifespan is equal to the lifespan of *C. elegans* when grown on the bacteria (of those species in the given combination) that causes the lowest lifespan of *C. elegans* in monoculture. If the average lifespan of *C. elegans* is 8, 9, and 10 days when grown on bacterium A, B, and C, individually, then the value of minimum lifespan when *C. elegans* is grown on bacteria B and C together would be 9 and the value of maximum lifespan would be 10. In this case, richness would be 2. Thus, the variable minimum can be described as the worst of what is available, maximum is the best of what is available, and average is the arithmetic mean of all available. In all models, the unit of replication was each individual plate ($n = 3$, $N = 111$).

Secondly, we applied stepwise selection (PROC GLMSELECT; SAS Institute) to determine the best selection of independent variables (alone or in combination) to model each of the dependent variables. Stepwise selection was forward (with optional backward selection) and the criterion for inclusion or exclusion of each parameter was the Swartz Bayesian information criterion (SBC; where a lower value indicates a better model fit). This means that the model begins with no independent variables and selects the single most explanatory variable for first inclusion. At each subsequent cycle, the best remaining (most explanatory) independent variable that is not currently in the model is added only if inclusion would decrease SBC, and the least explanatory variable currently in the model is removed if exclusion would decrease SBC. Model selection is complete when no further inclusion or removal of a variable is available to decrease SBC. The stepwise selection model was performed for each of four dependent life history trait response variables: intrinsic rate of increase, reproductive output, generation time, and lifespan. In all models, the unit of replication was each individual plate ($n = 3$, $N = 111$).

Results

The life history traits of *C. elegans* when grown in monoculture differed between the bacteria prey on which it was grown (Table 1), although the rank order of bacteria was not the same across all life history traits. Among the six bacteria in monoculture, the intrinsic rate of increase was negatively correlated with generation time ($R^2 = 0.989$), positively correlated with reproductive output ($R^2 = 0.567$), and not correlated with lifespan ($R^2 = 0.088$).

Table 1. Intrinsic growth rate (r), generation time (GT), reproductive output (R_0), and mean lifespan of *Caenorhabditis elegans* grown on monocultures of six different bacteria

Abbreviations	Species	r	GT	R_0	Lifespan
Vp	*Variovorax paradoxus* 10-1	1.41	4.03	290	12.2
Pp	*Pseudomonas putida* W-1	1.37	4.12	279	8.4
Sm	*Stenotrophomonas maltophilia* JCMS	1.38	4.12	299	7.8
Fv	*Flavobacterium* sp. D-6	1.33	4.26	296	10.4
Al	*Arthrobacter luteolus* D-4	1.15	4.79	246	12.0
Bt	*Bacillus thuringiensis* W-5	1.09	5.11	259	6.2

Intrinsic growth rate increased asymptotically with bacterial prey richness (Fig. 2a), while generation time decreased asymptotically with bacterial prey richness. (This is consistent with intrinsic growth rate because generation time is considered to be inversely related to intrinsic growth rate.) Linear models determined that maximum intrinsic rate of increase was the best single variable intrinsic growth rate (Table 2), and this was the only independent variable to remain in the model after stepwise selection. Similarly, minimum generation time was the best predictor of generation time (Table 2) and was the only dependent variable to remain after stepwise selection. Reproductive output (Fig. 2c) was best modeled by richness, but this was not the independent variable kept by the stepwise selection model (which was the poorest fit of all models, with an SBC value of 906.8). In contrast, lifespan (Fig. 2d) was best modeled by a combination of richness plus maximum

reproductive output, and these were the two variables kept by stepwise selection. Overall, the final model for intrinsic growth rate had the best fit statistics (as determined by SBC), followed by generation time, then lifespan, then reproductive output.

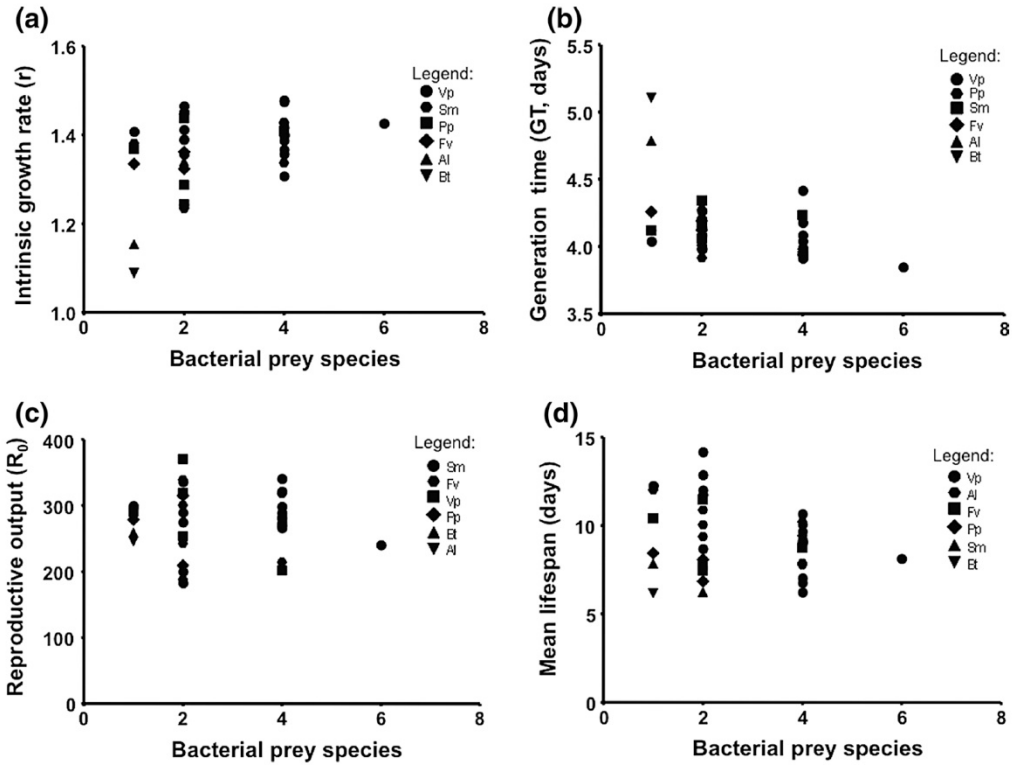

Figure 2. (a) Intrinsic growth rate, (b) generation time (days), (c) reproductive output, and (d) mean lifespan (days) of *Caenorhabditis elegans* feeding on six different bacterial isolates grown individually or in two-, four-, and six-way combinations. *Symbols* indicate the bacterial species present in the polyculture treatment that had the maximum value of intrinsic growth rate, reproductive output, or lifespan when grown in monoculture (or minimum value in the case of generation time).

Table 2. Summary statistics of linear models for *r*, GT, R_0, and mean lifespan

Model	Source	*df*	*F*-value	*p* > *F*
Intrinsic growth rate	Richness	1,107	0.59	0.4454
(SBC of final stepwise model −543.5)	Minimum	1,107	0.45	0.5055
	Maximum[a]	1,107	3.31	0.0716
	Average	1,107	1.62	0.2055
Generation time	Richness	1,107	0.01	0.9081
(SBC of final stepwise model −305.9)	Minimum[a]	1,107	3.85	0.0524
	Maximum	1,107	1.15	0.2870
	Average	1,107	2.12	0.1478
Reproductive output	Richness	1,107	3.36	0.0697
(SBC of final stepwise model 906.8)	Minimum	1,107	1.98	0.1618
	Maximum[a]	1,107	0.00	0.9704
	Average	1,107	1.36	0.2463
Lifespan	Richness[a]	1,107	12.83	0.0005
(SBC of final stepwise model 129.4)	Minimum	1,107	0.38	0.5411
	Maximum[a]	1,107	6.18	0.0145
	Average	1,107	0.01	0.9388

SBC Swartz Bayesian information criterion; for other abbreviations, see Table 1

a. Independent variables that were included in the final stepwise selection model (with the SBC information criteria as indicated for each dependent variable, where a *lower value* indicates a better model fit)

Discussion

The objective of this experiment was to determine the effect of prey richness on the growth kinetics of a nonselective consumer. Initially, we found that the intrinsic growth rate of our consumer (*C. elegans*) increased asymptotically with increasing prey species richness (Fig. 2a). Upon further examination, we found that this pattern was best explained by a best of what's around model: the intrinsic growth rate of our indiscriminate consumer feeding on mixed prey was approximately equal to the intrinsic growth rate of the consumer when feeding on the single best prey in monoculture. Thus, the significant finding of this study is that the intrinsic rate of increase of the consumer was more influenced by the composition of prey (or, more specifically, the single most advantageous prey) rather than by prey richness itself. To better understand the biological mechanism, we also tested the effect of prey composition on reproductive output and generation time, separately. Generation time, and not reproductive output, was most consistent with the best of what's around model that was observed for intrinsic growth rate (Fig. 2b). Generation time also resulted in better overall model-fit statistics than reproductive output (Table 2). Because intrinsic growth rate is maximized by low values of generation time and high values of reproductive output, both intrinsic growth rate and generation time followed the best of what's around model. We interpret this to mean that the "best around" bacterium maximizes intrinsic growth rate by reducing consumer generation time rather than by increasing reproductive output. Life history trait trade-offs are common when resources are limited, and our results are consistent with other reports that diet can influence the balance of life history traits such as generation time and reproductive output (Jervis et al. 2007; Geister et al. 2008; Twombly et al. 1998; Urabe and Waki 2009; Zimmer and Topp 1997; Lardies et al.

2004; Chen et al. 2010). Although intrinsic growth rate was not correlated with lifespan in this experiment, this does not mean that lifespan is not an ecologically relevant parameter for enrichment-type microbivores such as *C. elegans*. We expect that the agar petri dish environment with unlimited food allows this species to have a longer post-reproductive lifespan, and potentially shorter egg-to-median-egg generation time than it might experience in its natural environment (such as soil, compost, and decaying fruit).

The relationship we observed between prey richness and consumer growth rate is similar in pattern to the relationship between plant biodiversity and plant biomass or cover (Tilman et al. 1997). This pattern was also observed between ciliate evenness and bacterial prey richness (Saleem et al. 2013) and between predator richness and prey diversity (Saleem et al. 2012). We cannot say that the ecological mechanism is necessarily the same because we do not consider nematode intrinsic growth rate to be an "ecosystem function" of bacterial richness. However, we can draw an analogy between the mechanisms that drive biodiversity-ecosystem functioning and the relationship between prey richness and consumer growth rates. The relationship between plant richness and ecosystem functioning can be separated into two additive partitions: selection effects (SE) and complementarity effects (CE) (Loreau and Hector 2001). SE reflect the tendency for a plant community's yield to be comparable to that of the individual species with the most extreme trait values when in monoculture. CE reflect the niche partitioning or facilitative interactions between species. In communities that are dominated by SE, the overall average yield will appear to increase with richness, but in fact maximal yield can still be achieved with particular combinations of species even at low diversity as long as they contain one of the extreme-yielding species (Hooper et al. 2005). In communities that are dominated by CE, yield will increase asymptotically with species richness but some species combinations may over-yield relative to what any individual species will yield in monoculture. We cannot calculate SE and CE because we cannot partition the "yield" of predator intrinsic growth rate due to each individual prey species separately, but we can draw an analogy between the SE and CE that drive the plant relationships between richness and biomass and the best of what's around model that drives the relationship between prey richness and predator growth rate. Both SE and CE appear to be present in our data, but our analysis suggests that the relationship between prey richness and predator growth rate is dominated by a mechanism more analogous to SE rather than CE. The intrinsic growth rate of predators in mixed culture reflects the intrinsic growth rate of predators in a monoculture of the single best prey species. Maximal predator growth rate can still be achieved with particular combinations of species even at low prey richness as long as they contain one of the "best," most advantageous, species. However, CE appears to occur in our data as well. Specifically, for each life history trait, certain two- and in some cases four-way bacterial combinations produced values that exceeded that observed for any individual bacterium. However, these interactions were much less significant components of the models than was the overall effect of the species with the dominant effect on the predator when in monoculture.

Although we interpret the results of intrinsic growth rate to be most similar to the SE component of diversity-function relationships, the exact biological mechanism is still unclear and may depend on the selectivity of feeding by *C. elegans* in this environment. On the one hand, our observations could be explained as the nematode actively selecting the

single best prey item from the mixture, and thus the intrinsic growth rate would reflect growth on just that best prey item. However, we do not believe that our experimental set up necessarily allowed the nematode (*C. elegans*) to be a selective forager. *C. elegans* does selectively forage on lawns of optimal bacteria that are either separated in space or in homogeneous patches that are wider than the nematode's head (Shtonda and Avery 2006; Zhang et al. 2005; Coolon et al. 2009). In an experimental environment, these patches are either implemented manually (by selective placement of droplets of bacterial monocultures), or allowed to develop in time (as differential growth of bacteria from a well-mixed polyculture will start to form patches after 2–3 days). However, in our experimental set up, individuals were moved to new plates daily to prevent the formation of the monoculture patches that would allow for selective feeding, and it is not clear to us that the lips of the mouth region are capable of selecting individual bacterial cells when they are well mixed. For example, De Ley (1992) tested the hypothesis that the variable lip structure and labial probolae of the bacterial-feeding Cephalobidae select for bacterial cells on the basis of size or shape. Ultimately there was no clear data to support this hypothesis, and it would seem to be even less likely for the rounded-lipped *C. elegans*. Freyth et al. (2010) tested feeding selectivity in *C. elegans* using a combination of green fluorescent protein-expressing *E. coli* and fluorescent in situ hybridization to screen for consumed bacteria. They found that after 3 days of foraging in a mixture of two bacteria, a majority of individual nematodes had both prey species in their intestines, but some individuals had only one of the two bacterial species present. Although the authors interpret their data to indicate selective foraging, we actually interpret their data to mean that *C. elegans* still is relatively unable to selectively forage when their prey is well mixed. Only when their prey are allowed to grow into distinct patches (such as after 3 days of undisturbed growth) can *C. elegans* selectively forage for optimal prey. The feeding selectivity of bacterial-feeding nematodes still deserves additional clarification, but we think that our observations (that the intrinsic growth rate was most consistently affected by the best prey around) were most likely not because of selective feeding on the part of *C. elegans* but rather by an unknown mechanism of acquiring sufficient nutrients after consumption.

Since intrinsic growth rate is a key determinant of the distribution of enrichment-type bacterivores in the soil environment, we can ask whether the best of what's around model presented here can be used to predict the composition of nonselective predators in an environment of mixed quality prey. If so, this would allow us to predict the composition of certain consumers that are often indicator species of their respective habitats, such as rotifers in aquatic environments or bacteria-feeding nematodes in a soil environment. We observed a slight convergence upon an upper asymptote for per capita growth rate (Fig. 2a), although a maximum richness of only six bacteria was tested. Grasslands can contain more than 1,000 bacterial operational taxonomic units in just 1 g of soil (Nacke et al. 2011). The best of what's around model would predict that the best species available (for nematode consumers) in two microbial communities with different assemblages of 1,000 species should still result in a similar intrinsic growth rate for their nematode consumers by chance alone. (The best bacterial species out of one set of the 1,000 species is likely to be about as high quality for the consumer as the best bacterial species out of a different set of 1,000

species.) However, this does not mean that the composition of bacteria is irrelevant to nematode fitness or community composition in the field. There are a few reasons that we might still be able to apply the functions observed in this present laboratory study to field situations. Firstly, nematode movement is constrained in tortuous, nonsaturated soils. Secondly, bacterial cells can occur in local micropatches that are less diverse than a well-mixed bulk sample. These two factors mean that a single nematode might consume or encounter only a few different bacterial species in a given period of time. Thus, microbial consumers may not be saturated by bacterial species richness in the field environment and the best of what's around model may still be applicable to understanding the intrinsic growth rate of predators in their natural environment. The analogy of SE vs. CE as discussed above might be extended here to think about the relative contribution of SE and CE mechanisms in productivity gradients. In a 10-year biodiversity experiment, Fargione et al. (2007) found that complementarity increased through time. This was interpreted to be the result of high plant nitrogen pools (in the plots with legumes), or greater nitrogen use efficiency (in the plots without legumes). If resource availability affects the relative contribution of SE and CE, it might also affect the relative balance of the analogous mechanism in consumer-prey dynamics in the environment. We found little complementarity in the consumer-prey relationship when the consumer was fed unlimited prey, but it is possible that complementarity dynamics may be more influential in the soil environment where prey are expected to be much less abundant. Clearly it is necessary to have a better understanding of how consumers perceive and relate to their microbial prey on a micro-scale in order to sort out the relative contributions of these analogous mechanisms in consumer–prey dynamics.

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	(presence/absence of bacteria species)						(treatment means, n = 3)									
	Variovorax paradoxens	Arthrobacter luteolus	Pseudomonas putida	Flavobacterium sp.	Bacillus thuringiensis	Stenotrophomonas maltophila										
NumSpecies	Vp	Al	Pp	Fv	Bt	Sm	mGrowthRate	mGT	mR0	lifespan	minLifespan	avgLifespan	maxLifespan	minGrowth	avgGrowth	maxGrowth
1	1	0	0	0	0	0	1.41	4.03	290	12.2	12.2	12.2	12.2	1.41	1.41	1.41
1	0	1	0	0	0	0	1.15	4.79	246	12.0	12.0	12.0	12.0	1.15	1.15	1.15
1	0	0	1	0	0	0	1.37	4.12	279	8.4	8.4	8.4	8.4	1.37	1.37	1.37
1	0	0	0	1	0	0	1.33	4.26	296	10.4	10.4	10.4	10.4	1.33	1.33	1.33
1	0	0	0	0	1	0	1.09	5.11	259	6.2	6.2	6.2	6.2	1.09	1.09	1.09
1	0	0	0	0	0	1	1.38	4.12	299	7.8	7.8	7.8	7.8	1.38	1.38	1.38
2	1	1	0	0	0	0	1.45	3.98	319	14.1	12.0	12.1	12.2	1.15	1.28	1.41
2	1	0	1	0	0	0	1.35	4.08	253	8.7	8.4	10.3	12.2	1.37	1.39	1.41
2	1	0	0	1	0	0	1.41	4.13	339	12.8	10.4	11.3	12.2	1.33	1.37	1.41
2	1	0	0	0	1	0	1.39	4.26	370	11.7	6.2	9.2	12.2	1.09	1.25	1.41
2	1	0	0	0	0	1	1.46	3.98	335	12.0	7.8	10.0	12.2	1.38	1.39	1.41
2	0	1	1	0	0	0	1.44	4.01	315	9.4	8.4	10.2	12.0	1.15	1.26	1.37
2	0	1	0	1	0	0	1.36	4.19	300	10.0	10.4	11.2	12.0	1.15	1.24	1.33
2	0	1	0	0	1	0	1.34	4.31	319	10.9	6.2	9.1	12.0	1.09	1.12	1.15
2	0	1	0	0	0	1	1.39	4.06	274	9.4	7.8	9.9	12.0	1.15	1.27	1.38
2	0	0	1	1	0	0	1.24	4.21	188	7.7	8.4	9.4	10.4	1.33	1.35	1.37
2	0	0	1	0	1	0	1.29	4.15	209	6.8	6.2	7.3	8.4	1.09	1.23	1.37
2	0	0	1	0	0	1	1.45	3.91	289	8.1	7.8	8.1	8.4	1.37	1.37	1.38
2	0	0	0	1	1	0	1.32	4.12	243	11.5	6.2	8.3	10.4	1.09	1.21	1.33
2	0	0	0	1	0	1	1.23	4.34	199	7.4	7.8	9.1	10.4	1.33	1.36	1.38
2	0	0	0	0	1	1	1.24	4.16	182	6.2	6.2	7.0	7.8	1.09	1.23	1.38
4	1	1	1	1	0	0	1.48	3.91	319	7.0	8.4	10.8	12.2	1.15	1.32	1.41
4	1	1	1	0	1	0	1.36	3.91	202	6.7	6.2	9.7	12.2	1.09	1.25	1.41
4	1	1	1	0	0	1	1.47	3.92	321	9.6	7.8	10.1	12.2	1.15	1.33	1.41
4	1	1	0	1	1	0	1.31	4.41	318	10.6	6.2	10.2	12.2	1.09	1.25	1.41
4	1	1	0	1	0	1	1.40	4.08	298	10.0	7.8	10.6	12.2	1.15	1.32	1.41
4	1	1	0	0	1	1	1.40	4.17	340	8.9	6.2	9.6	12.2	1.09	1.26	1.41
4	1	0	1	1	1	0	1.37	3.94	214	6.2	6.2	9.3	12.2	1.09	1.30	1.41
4	1	0	1	1	0	1	1.42	3.96	269	9.0	7.8	9.7	12.2	1.33	1.37	1.41
4	1	0	1	0	1	1	1.40	3.99	265	9.1	6.2	8.7	12.2	1.09	1.31	1.41
4	1	0	0	1	1	1	1.39	4.04	270	9.2	6.2	9.2	12.2	1.09	1.30	1.41
4	0	1	1	1	1	0	1.41	3.98	268	7.8	6.2	9.3	12.0	1.09	1.24	1.37
4	0	1	1	1	0	1	1.43	3.96	282	9.4	7.8	9.7	12.0	1.15	1.31	1.38
4	0	1	1	0	1	1	1.43	3.93	273	7.9	6.2	8.6	12.0	1.09	1.25	1.38
4	0	1	0	1	1	1	1.34	4.23	288	10.2	6.2	9.1	12.0	1.09	1.24	1.38
4	0	0	1	1	1	1	1.43	3.94	280	8.7	6.2	8.2	10.4	1.09	1.29	1.38
6	1	1	1	1	1	1	1.42	3.84	240	8.1	6.2	9.5	12.2	1.09	1.29	1.41