

Effects of Adaptive Foragers on the Diversity and Functioning
of Assembled Model Communities

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

of the Requirements for the Degree of

Master of Science

by

William J. Tarantino

2008

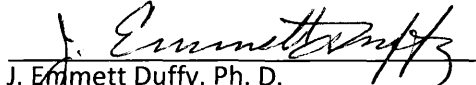
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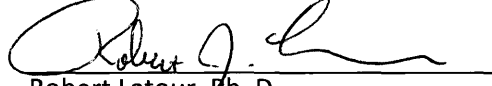


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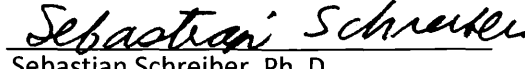
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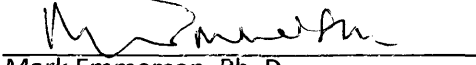
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ACKNOWLEDGEMENTS

I am extremely grateful to my two advisors, Drs. J. Emmett Duffy and Sebastian Schreiber for their patience and guidance over the course of this research. I would also like to thank the members of my committee for their flexibility and assistance in the choice of the topic, as well as their excellent suggestions and comments regarding the manuscript. In particular, I would like to thank Dr. Emmerson for agreeing to serve on my committee from across the Atlantic.

My lab-mates have been an invaluable source of entertainment and companionship, and I could not have gotten through this without them or the entire VIMS community. Their support and kindness were essential to my completion of this project. In addition, I would like to thank Kristen France, Rachael Blake, and James Douglass for substantive contributions to my project.

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ABSTRACT

Previous research suggests that prey-switching behavior by consumers (adaptive foraging) contributes to the stability of food web networks and may help explain the apparent contradiction between the complexity of natural ecosystems and theory that suggests such complex systems should be unstable. However, no previous study has explored the consequences of adaptive foraging behavior on ecosystem processes (or 'functioning'). I assembled communities from regional pools while varying searching efficiency, connectance, and the fraction of adaptive foragers in order to observe the effects these properties have on the diversity and functioning of the resultant communities. In general, pools with increased connectance, a higher fraction of adaptive foragers, and intermediate searching efficiencies yielded communities with greater diversity. However, while pools with high connectance and intermediate searching efficiencies tended to have higher ecosystem productivity, adaptive foragers decreased the overall productivity of the assembled communities. Unsurprisingly, adaptive foragers, connectance, and increased searching efficiency all led to higher rates of trophic transfer. These trends occurred alongside an overall positive correlation between diversity and the rates of these processes. In addition, the higher regional richness increased the per-species functioning of the assembled community. These results suggest that the diversity and structure of food web networks interact with the dynamics of trophic interactions to determine and maintain the properties and processes of ecological communities.

**THE EFFECT OF ADAPTIVE FORAGERS ON THE DIVERSITY
AND FUNCTIONING OF ASSEMBLED COMMUNITIES**

1. INTRODUCTION

The accelerating rate of global biodiversity loss [1, 2, 3], has brought increasing attention to the relationship between biodiversity and ecosystem functioning, and the potential consequences diversity loss has for services provided to the human population [4, 5, 6, 7]. This has triggered a charge to uncover the mechanisms by which diversity affects functioning, and the potential effects these mechanisms might have on ecosystem services. In addition, much of ecological theory focuses on reconciling the species-rich and highly connected communities found in nature with the fact that theoretical models attempting to represent these communities tend to be highly unstable. Although early heuristic arguments claimed that increased diversity and connectance should improve stability [8, 9], subsequent quantitative models consistently suggested that diversity could not be maintained in highly connected communities (e.g. [10, 11]). Suggested explanations have ranged widely: Food web models are ridiculously cartoonish and can not begin to approximate real ecosystems (e.g. [12]); most interactions are weak, facilitating dampening effects that encourage stability (e.g. [13]); sigmoidal functional responses (e.g. [14]) and plastic consumer behavior (e.g. [15]) reduce resource extinction risk; mutualistic interactions are more prevalent than is realized, increasing the stability of diverse communities (e.g. [16]). This relationship between complexity and stability could have large implications for the relationship between diversity and ecosystem functioning [17]. However, although these mechanisms help to maintain the stability of complex communities, their potential effects on the relationship between diversity and functioning has yet to be explored.

Although the response of species foraging behavior to a changing environment has been studied extensively [18], the potential effects of adaptive foraging behavior on the food web structure and dynamics are only recently being explored. This research has explored the effect of dynamic foraging strategies on the structure of food web interactions. Adaptive foraging behavior of consumers has been found to be particularly influential on food web stability ([15, 19, 20, 21]. For example, optimal foraging theory predicts the network structure of natural food webs [22], though the food web generated in the study is still static. In contrast, adaptive foraging theory allows for the evolution of network structure by facilitating prey-switching (see, e.g. [23, 24]). This behavior has been shown to facilitate the persistence of simple two-resource/one consumer model food webs [25]. Kondoh [15, 20] showed that allowing consumers to adjust their preferences for resources improves the stability of complex food webs. Subsequent, research discovered that simulations of model food webs with adaptive foragers results in fewer extinctions, and that these communities developed a diversity/connectance relationship similar to empirical food webs [21]. These studies suggest that adaptive foraging may be a mechanism determining the structure of food-web networks and maintaining their diversity.

Despite research showing that behavioral plasticity can have significant ecological consequences [26], the potential implications of adaptive foraging on ecosystem functioning have yet to be explored. Recent research has found that biodiversity can have important affects on ecosystem functioning [4, 6, 7], and adaptive food-web networks have the potential to influence this relationship in two ways. First, adaptive foragers help communities maintain greater diversity [21] [20]. Second, adaptive foraging behavior has the potential to significantly alter the effects of

increased biodiversity on ecosystem processes. The top down influence of consumers may have a disproportionately large effect on the relationship between biodiversity and ecosystem functioning ([27] [28]), and this could make the dynamics of trophic interactions particularly important to these relationships [29].

A potential limitation of many theoretical studies of food webs is that the initial species abundances used for simulations are often arbitrary. One possible solution to this problem is to create the communities using an assembly process. Assembly is the process through which species communities develop from a “void”. Theoretical ecologists have used a variety of methods to explore community assembly, most involving the sequential addition of species to communities governed by a system of Lotka-Volterra equations [30] [31] [32]. In addition, allowing adaptive consumer behavior may have profound effects on community assembly. Assembly history [33, 34] and processes such as invasion rates [32, 35] can have dramatic effects on community composition, and the presence of adaptive foragers during community assembly has the potential to influence the diversity of the assembled community and the structure of its affiliate food web network. Assembly acts as a sieve, limiting the community composition to one subset of the pool from which the community is assembled [36], and because interactions can have dramatic effects on the success of invading species [37] [38], it is probable that allowing species in the assembled community to adjust their foraging strategy will significantly impact their invasion success. Therefore, adaptive foragers have the potential to alter the composition of assembled communities, either by affecting their ability to invade, or by resisting/facilitating invasions of other species. In addition, the assembly history of a community can influence the resulting production-biodiversity relationship of the ecosystem [34], and invasion mechanisms help determine the relationships between biodiversity and additional processes [34] [39] [40].

In this study I use an assembly process to investigate how food web complexity and adaptive foraging behavior interact to determine the diversity and functioning of ecological communities. I found that (1) community diversity is enhanced by a strong interactive effect between higher numbers of food-web connections and a higher fraction of adaptive foragers, that (2) ecosystem productivity was maximized in highly connected communities with intermediate searching efficiency, and that (3) transfer of biomass to higher trophic levels was maximized in highly connected communities with high searching efficiency. In addition, the effects of increased connectance and more adaptive foragers on community diversity and functioning is largely dependant on consumers’ searching efficiency.

2. THE MODEL AND METHODS

In order to simulate an assembly process, we first generated a food web representing a regional species pool containing n species. Species in the pool were selected randomly and allowed to invade a local community at exponentially distributed intervals with mean length μ (the invasion period). Species were removed from the community at any time their biomass dropped below a threshold density ($X_0 = 0.001$), which also served as the propagule size for invasions. We independently manipulated the threshold value and the propagule size by an order of magnitude and found that neither affected the results. Between invasions, the population dynamics of species in the local community were simulated by an adaptive-foraging model. The biomass and preferences of each species were monitored throughout the simulation, which allowed the ecosystem processes in the model to be measured as well.

2.1. The Adaptive Foraging Model. The adaptive foraging model accounts for the biomass and behavioral dynamics of all species simultaneously [15]. The biomass dynamics are described by Lotka-Volterra predator-prey equations modified to include a saturating (type II) functional response [41]. The dynamics of species j 's biomass (X_j) is given by

$$(1) \quad \dot{X}_j = X_j \left(r_j \left(1 - \frac{X_j}{K}\right) - d_j + \sum_{i=1}^n \theta_{ij} P_{ij} f_{ij} F_j X_i - \sum_{i=1}^n P_{ji} f_{ji} F_i X_i \right)$$

where primary producers have a per-biomass reproductive rate (r_i), and they all have the same habitat size K . Every species j has a respiration rate, d_j . The f_{ij} is the efficiency of species j (the consumer) searching for species i (the resource); it determines the ability of i to exploit j . θ_{ij} is the conversion efficiency of j preying on i , and depends on whether i is a plant ($\theta_{ij} = 0.5$) or an animal ($\theta_{ij} = 0.85$), as suggested by Yodzis and Innes [42]. F_j is the fraction of consumer j that is free to actively search for resources,

$$(2) \quad F_j = \frac{1}{1 + H_j \sum_{i=1}^n P_{ij} f_{ij} X_i}$$

where $F_j f_{ij} X_i$ corresponds to a type II functional response [43] [44] and H_j is species j 's handling time.

P_{ij} is the fraction of time consumer j spends searching for resource i . The preferences of an adaptive forager are allowed to change in response to availability of its resources. We assume that the preferences of an adaptive forager move in the direction that most rapidly increases its intake rate, while ensuring that the sum of its preferences remains one (i.e. $\sum_{i=1}^n P_{ij} = 1$). This direction is calculated using a gradient with respect to the Shashahani metric, a metric used extensively in evolutionary game theory (e.g., see Hofbauer and Sigmund [45]). Under this set of assumptions, we show in appendix A that the preference dynamics are given by

$$(3) \quad \dot{P}_{ij} = g_j P_{ij} F_j^2 \left(\frac{\theta_{ij} f_{ij} X_i}{F_j} - (H_j f_{ij} X_i + 1) \sum_{k=1}^n \theta_{kj} P_{kj} f_{kj} X_k \right)$$

where g_i scales the rate at which species i adjusts its foraging rates (preferences). The fraction of species that are allowed to adapt (adaptability) determines the number of species which have a non-zero g , which is the same for all adaptive species. We set $g = 0.3$ for most simulations and, as in previous studies, the actual value of g had negligible influence over the results. Equation (3) provides a natural generalization of Kondoh’s original preference equation [15]. However, ensuring that adaptive foragers are maximizing their intake causes equation (3) to differ from the equations of Brose et al. [41] and subsequent studies [19] [20] [21].

2.2. Food Web Structure and Allometric Scaling. The food web network describing the potential interactions between species in the regional pool is represented by the n by n matrix f . The location of the l non-zero entries in f are determined by the niche model, which has been shown to produce networks with structural properties similar to those of empirically determined food-webs [46]. The niche model assumes that species can be ordered along a one-dimensional gradient, or “niche dimension” [47]. The model generates the structure of f by assuming consumers can eat every species within a contiguous range R_i , where the center of R_i is a randomly determined point in the niche dimension below species i and its breadth is determined by the food web’s connectance, the fraction of potential links in the food web that are actually realized ($\frac{c}{n^2}$). For consistency with previous literature, all non-zero searching efficiencies are assumed to be identical.

The one-dimensional niche gradient used to generate the food web is often assumed to be a representation of body size [31] [46] [48]. We retain this convention, using uniformly distributed random variables between 0 and 1 as the body size of each species [46] [48] and using allometric scaling to determine the production rates, r_i , handling times H_i , and respiration rates, d_i [49] [42] [50].

Previous work has showed that the interaction between connectance, adaptability and diversity can be confounded when the niche model is used because, traditionally, producer diversity is inversely correlated with connectance [41] [20]. To avoid this complication, we kept the fraction of primary producers fixed at 0.4. Food web research has reported fractions ranging from 0.04 to 0.5 [46] [51], however, fractions of basal species reported in the lower range are likely an artifact of increased aggregation of species in lower trophic levels [51]. In any case, lowering the fraction of basal species to as low as 0.1 did not affect the main results.

2.3. Simulation and Data Analysis. In the majority of the simulations (79380) the manipulated input variables included the fraction of adaptive foragers (adaptability, or A), the connectance of the regional food web used to assemble the community (C), the period between invasions (μ), and the mean searching efficiency of the species (f) in order to investigate how these properties interact to determine the final diversity and functioning of the assembled communities. The values of the input variables in these simulations were: for A (adaptability), 21 values from 0 to 1; for C (connectance), 21 values from 0 to 0.45; for f , (mean searching efficiency) $f = 0.3, 0.03, \text{ or } 0.003$; and for μ , (invasion period) $\mu = 1, 10^{0.5}, \text{ or } 10$, yielding a total of 3969 input treatments. Twenty simulations were run with each combination of variables, in which 20 species were included in the regional pool. 13230 additional simulations were run to investigate the importance of regional richness. Half with a 10 species regional pool, and half with 40 species.

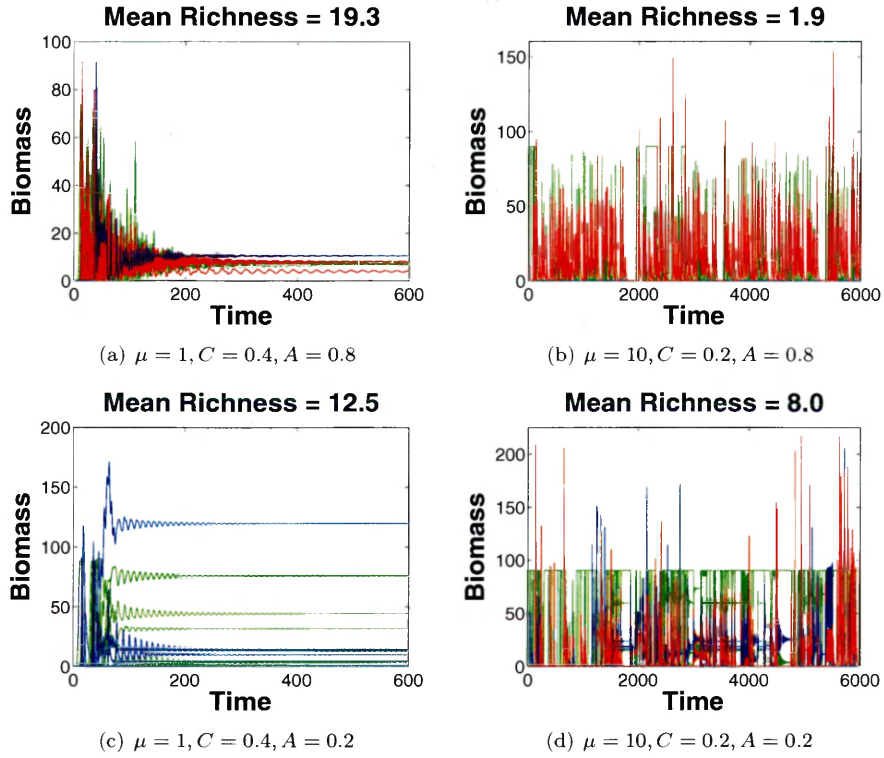
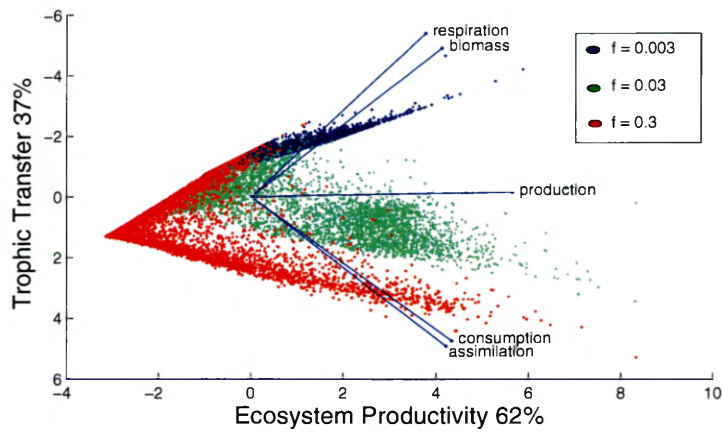


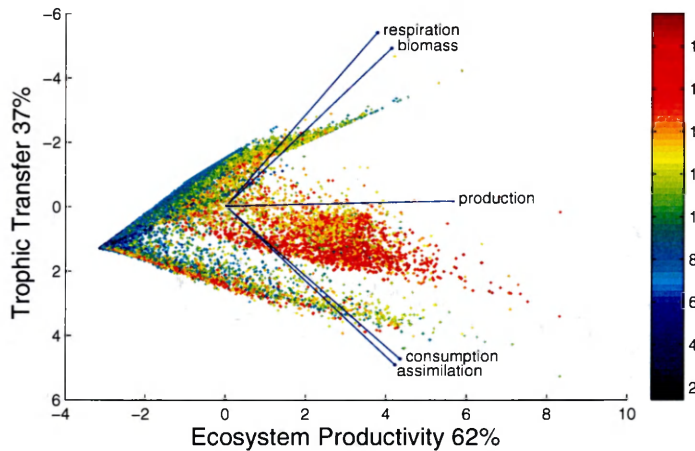
FIGURE 1. Examples of biomass dynamics for four sets of parameter values: a ($f = 0.3, \mu = 1, C = 0.4, A = 0.8$), b ($f = 0.3, \mu = 10, C = 0.2, A = 0.8$), c ($f = 0.3, \mu = 1, C = 0.4, A = 0.2$), d ($f = 0.3, \mu = 10, C = 0.2, A = 0.2$). Green indicates producer species, blue indicates non-adaptive consumer species, and red indicates adaptive foragers.

Each simulation was run until species in the regional pool have invaded an average of 30 times (time $T \approx 30n\mu$, see fig. 1). Quantities tracked throughout each simulation include the time each species has spent in the community, total biomass of each species in the community (\bar{X}), and the preference values contained in the n by n matrix \mathbf{P} . The simulation outputs were calculated from these quantities. They included the average richness and biomass ($\sum_i X_i$) of the community, as well as the average rates of four ecosystem processes (“functions”), productivity ($r \cdot X$), respiration ($d \cdot X$), assimilation ($\sum_j X_j \sum_i \theta_{ij} P_{ij} f_{ij} F_j X_i$), and consumption ($\sum_i X_i \sum_j P_{ij} f_{ij} F_j X_j$).

Often, the biomass dynamics began to approach an equilibrium after a mean of 15 invasions for each species (e.g. figs. 1a, c). However the assembled community’s dynamics occasionally failed to stabilize through the entire simulation (e.g. figs. 1b, d). In these communities, the diversity of the local community, the biomass of individual species, and the strength of particular interactions could vary greatly (see appendix B). Therefore, the values of the response variables were averaged over the last half of each simulation.



(a) Color shows searching efficiency (f)



(b) Color shows the community's richness

FIGURE 2. Biplots showing the relative contribution of each functioning variable on the two main principal components from a PCA that included every simulation. The scatter plot show the component values of 20,000 simulations colored according to (a) the searching efficiency, f , or (b) community richness. The percent of total variation explained by each component is shown on the axes.

3. RESULTS

3.1. Functioning components and overall trends. In order to obtain metrics of ecosystem “functioning”, we performed a principal component analysis (PCA) on the four rate variables (productivity, respiration, consumption and assimilation) and the mean total biomass of the assembled communities ([52]). The first two principal components explained 99% of the total variation of these variables (fig. 2). The first component (62%) is a weighted average of the five variables; it is most dependent on overall productivity. In contrast, the second functioning component (37%) separates communities in which the productivity is predominantly respired from those with large amounts of trophic transfer (i.e. consumption and assimilation). Hereafter we refer to communities with high values on the first component as communities with high “ecosystem productivity”, and to communities with high values on the second component as having high “trophic transfer”.

Overall, there is a positive correlation between the diversity of an assembled community and both its ecosystem productivity and trophic transfer (table 1). In addition, regional pools with increased connectance, higher fractions of adaptive foragers and shorter periods between invasions (lower μ) tended to promote higher diversity and increased trophic transfer in the assembled communities. Connectance generally increased ecosystem productivity (table 1), but more adaptive foragers and faster invasion rates tended to lower ecosystem productivity (table 1). Despite these broad trends, there were a number of exceptions and qualifications due to subtle interactive effects. Like the correlations in table 1, all of the results mentioned below are statistically significant with p-values far below $p = 0.01$. Therefore, we do not include p-values when discussing these results.

3.2. Diversity of the Assembled Community. Regional pools with high connectance and a high proportion of adaptive foragers produce the most diverse communities (fig. 3 and table 1). This is mostly due to a consistent positive interaction between the two variables. This interaction is easily observable in communities assembled with intermediate searching efficiencies (figs. 3d-f). This pattern probably arises in part because adaptive foraging offers a greater advantage to consumers with multiple resources.

Although increased connectance and adaptability always interact to produce greater diversity, the community’s searching efficiency determines how these two variables’ effects on diversity are influenced by the period between invasions and each other. For example, in communities with high searching efficiency ($f = 0.3$), the effect of adaptive foragers on diversity switches from neutral (fig. 3a) to negative (fig. 3c) in communities with longer invasion periods (μ) and low to intermediate connectance. In communities with high connectance, however, the interaction between adaptive foragers and connectance maintains a positive adaptability/diversity relationship. The lower diversity in these communities with high searching efficiencies is probably due to overexploitation, indicated by the loss of basal species in these communities (see appendix D, fig. 9). Slowing the assembly process may enhance this exploitive effect by giving adaptive foragers time to focus their consumption and drive their resource (and thus themselves) extinct before alternative resources appear. As a result, the community is unable to build up a “critical mass” of species richness that would be sustainable. The extremely high variability in the richness of these communities supports this hypothesis (see appendix B, fig. 7c).

TABLE 1. Correlation Coefficients of diversity, ecosystem productivity (PC1) and trophic transfer (PC2) with adaptability, connectance, μ , and each other for different searching efficiencies (f). All of the non-zero relationships are significant ($p < 0.05$). Note that, although PC1 and PC2 are orthogonal ($r^2 = 0$), there are fairly high correlations between the two among communities with the same searching efficiency.

Component	f	PC1	PC2	Diversity	Adaptability	Connectance	mu
Ecosystem	all	-	0	0.59	-0.10	0.24	0.04
Productivity (PC1)	0.3	-	0.46	0.39	-0.27	0.18	-0.05
	0.03	-	0.62	0.58	-0.02	0.61	-0.02
	0.003	-	-0.97	0.28	-0.03	-0.11	0.37
Trophic	all	0	-	0.12	0.01	0.30	-0.03
Transfer (PC2)	0.3	0.46	-	0.41	-0.01	0.67	-0.01
	0.03	0.62	-	0.63	0.17	0.60	0.01
	0.003	-0.97	-	-0.18	0.03	0.12	-0.33
Diversity	all	0.59	0.12	-	0.16	0.32	-0.14
	0.3	0.39	0.41	-	0.11	0.42	-0.32
	0.03	0.58	0.63	-	0.36	0.51	-0.10
	0.003	0.28	-0.18	-	0.10	0.12	0.07

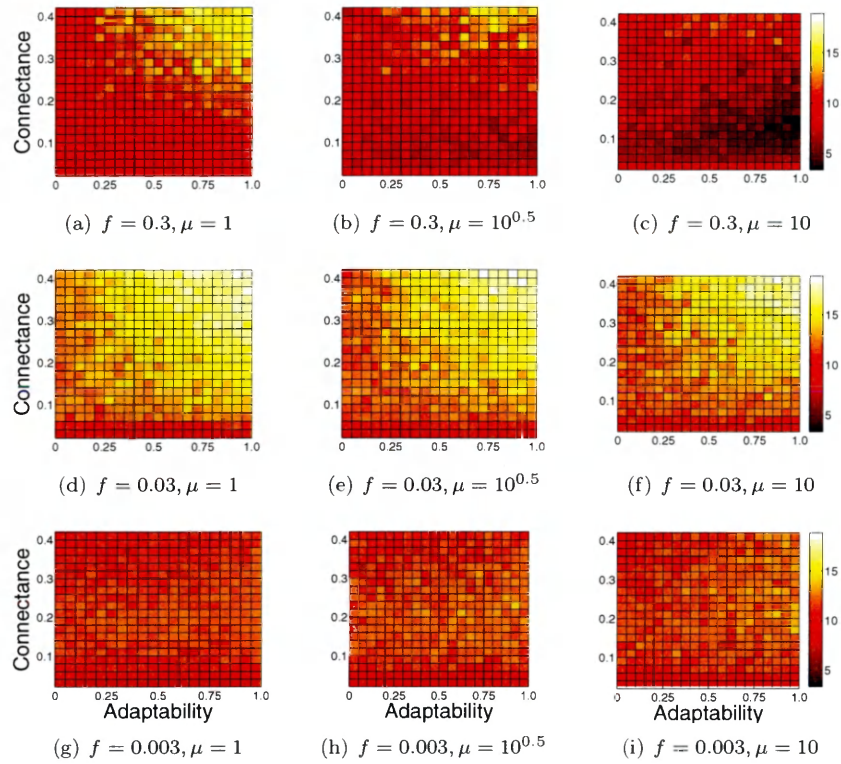


FIGURE 3. Each panel shows mean richness (scale is the same for each panel, indicated by the colorbars) as a response to manipulating Adaptability along the X axis (20 values from 0 to 1), and Connectance along the Y axis (20 values from 0 to .45), with a particular invasion rate (columns, $\mu = 1, 10^{0.5}$, or 10) and searching efficiency (rows, $f = 0.3, 0.03$, or 0.003). Every value is from an average of twenty independent simulations with the same input parameters.

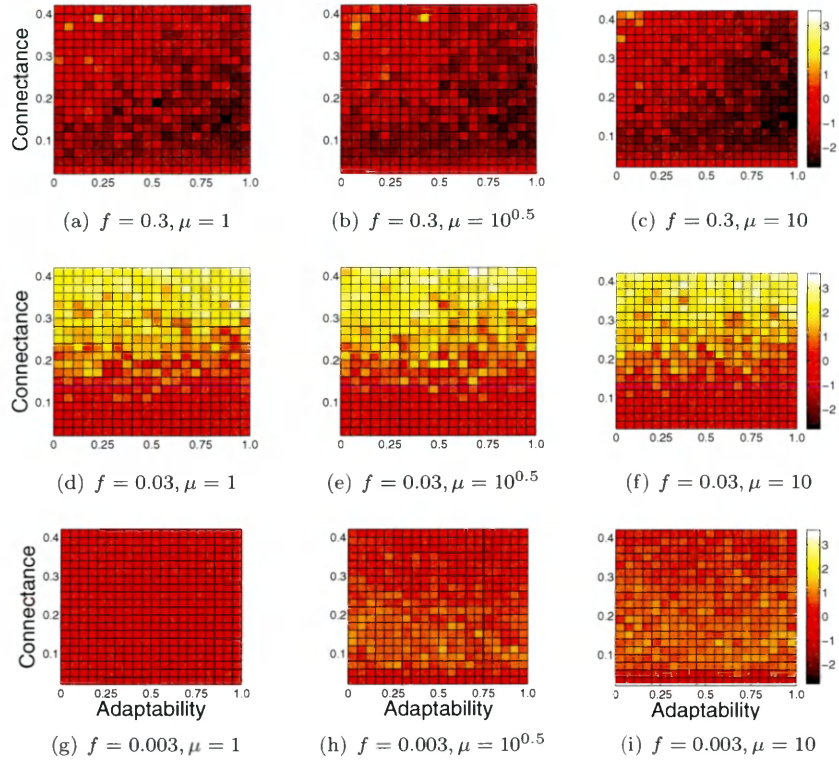


FIGURE 4. Each panel shows mean ecosystem productivity (i.e. PC1 from the PCA in 2) as a response to manipulating Adaptability along the X axis (20 values from 0 to 1), and Connectance along the Y axis (20 values from 0.0 to 0.45), with a particular invasion rate (columns, $\mu = 1, 10^{0.5}$, or 10) and searching efficiency (rows, $f = 0.3, 0.03$, or 0.003). Every value is from an average of twenty independent simulations with the same input parameters.

In contrast, when searching efficiencies are low ($f = 0.003$), diversity is maximized at intermediate connectance (fig. 3g), although the connectance-adaptability interaction switches this to a positive effect of connectance in slowly assembled communities (fig. 3i). This effect of high connectance on richness may be because splitting a higher level consumer’s potential effort among so many resources leads to an inability to gather sufficient resources to support more than one extra trophic level. However, because simulations last longer when the invasion period is slower ($\mu > 1$), they have extra time to adjust their preferences and build biomass that supports additional consumers. Indeed, the total biomass increases with invasion period only when $f = 0.003$ (appendix C fig. 8).

3.3. Functioning of the Assembled Community. Overall, there was a positive correlation between ecosystem productivity (PC1) and diversity (table 1). This is probably because both richness and ecosystem productivity were maximized by high connectance and intermediate searching efficiency of consumers (figs. 3, 4). However, in contrast to species richness, adaptive foraging and faster invasions affected ecosystem productivity negatively (table 1 and fig. 4). Also, there is no indication of a consistent increase in functioning due to a connectance/adaptability interaction.

As would be expected, the relative importance of trophic transfer is increased by higher searching efficiency and connectance (fig. 5). In addition, searching efficiency was the principal factor determining how adaptability, connectance, and invasion period affected ecosystem productivity and the importance of trophic transfer.

In communities with intermediate searching efficiencies ($f = 0.03$), both increased connectance and a larger proportion of adaptive foragers increased the importance of trophic transfer (figs. 5d-f). The latter trend mirrors the diversity result (figs. 3d-f). Consumers with intermediate searching efficiencies ($f = 0.03$) were able to slightly reduce the number of basal species (see appendix D fig. 9), but basal richness was maintained by higher connectance and/or a higher fraction of adaptive foragers (appendix D fig. 9). This suggests that spreading foraging effort among multiple resources and allowing prey-switching stabilizes resource diversity, facilitating an increase in diversity at higher trophic levels. The resulting increase in the number of consumer species increases the fraction of biomass moving into higher trophic levels, indicated by the increase in the relative importance of trophic transfer (figs. 5d-f).

Ecosystem productivity of communities with intermediate searching efficiencies is enhanced by the increase in connectance. The increase in productivity may be facilitated by lowering basal biomass below the carrying capacity, $K \frac{(r-d)}{r}$ (appendix D fig. 10). However, if connectance is not high enough, adaptive foragers lower basal biomass further (appendix D fig. 10), resulting in a slight drop in ecosystem productivity (fig. 4d-f).

In communities with high searching efficiencies ($f = 0.3$) the overexploitation of resources leads to lower ecosystem productivity (figs 4a-c). As in the case with intermediate searching efficiency, this is mitigated somewhat by increased connectance. However, although an increased fraction of adaptive foragers helps to maintain diversity (fig. 3 and see appendix D), the heightened effectiveness of these consumers still decimates the biomass of the basal species (appendix D fig. 10) and dramatically lowers ecosystem productivity. Unsurprisingly, trophic transfer dominates in these communities as long as connectance is high enough to allow significant

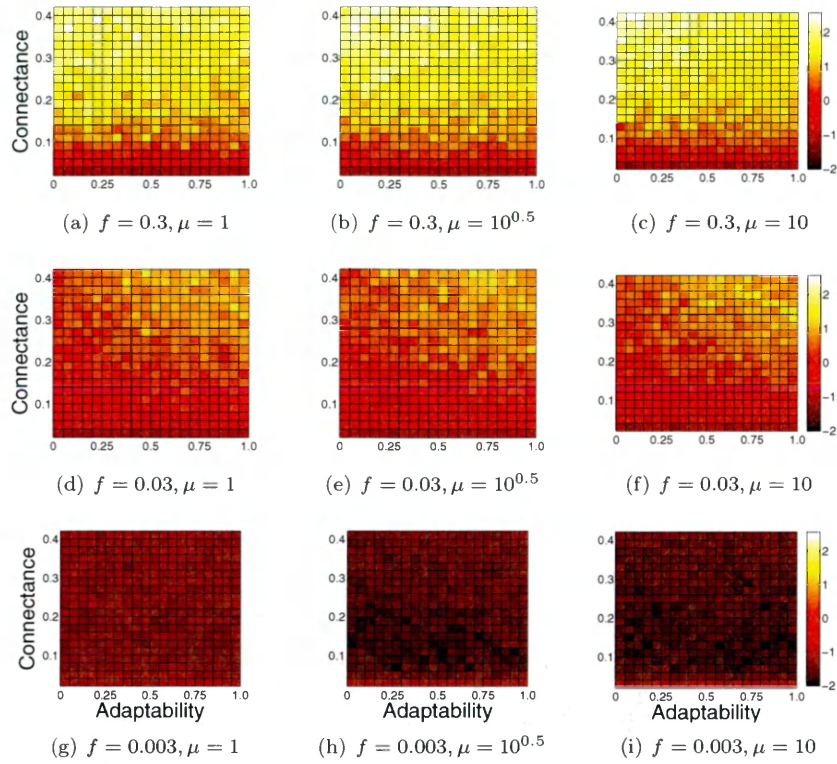


FIGURE 5. Each panel shows mean trophic transfer (-PC2) as a response to manipulating Adaptability along the X axis (20 values from 0 to 1), and Connectance along the Y axis (20 values from 0.0 to 0.45), with the invasion rate (μ) and the searching efficiency (f) shown. Every value is from an average of twenty independent simulations with the same input parameters.

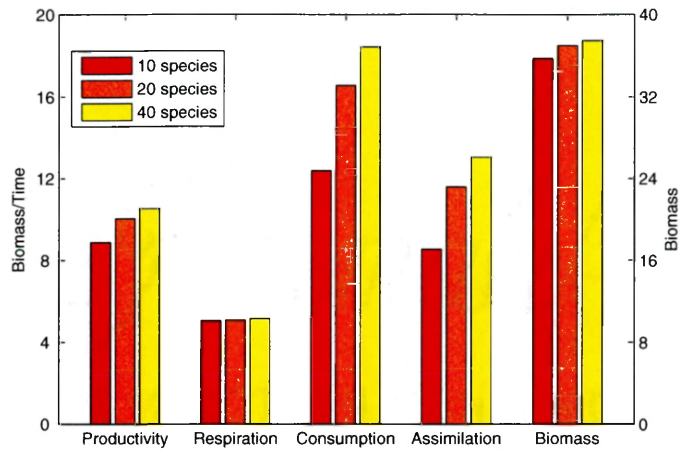
consumption by consumers (fig. 5a-c). Less expected, adaptability actually decreases the trophic transfer component. This is probably because there is so little ecosystem productivity in these communities that the amount of trophic transfer is constrained, i.e. the range of PC2 depends on the score along PC1 (see fig. 2). Surprisingly, although a longer invasion period triggers the negative effect of adaptive foragers on both overall (fig. 3c) and basal (see appendix D fig. 9c) diversity, functioning (figs 4 and 5) and the biomass of basal species (appendix D fig. 10) are relatively unaffected.

Unsurprisingly, communities with low searching efficiencies ($f = 0.003$) have minimal trophic transfer (figs. 5g-i). When assembly is rapid ($\mu = 1$) both ecosystem productivity and trophic transfer are the same as in communities only containing basal species (figs. 4g and 5g). Interestingly, when assembly slows down ($\mu > 1$) in communities with low searching efficiencies, those with intermediate connectance ($C \approx 0.15$) have higher ecosystem productivity and less trophic transfer (figs. 4g-i and 5g-i). This suggests that, in communities with low searching efficiency, lower trophic transfer values are more an indicator of high biomass/respiration than of low consumption/assimilation (see fig. 2). This is also consistent with the diversity trend in (fig. 3g-i), which we suggested could be due to the increased potential for biomass buildup in longer simulations (i.e. $\mu > 1$ see appendix C fig. 8g-i), allowing for successful invasions of higher trophic level species.

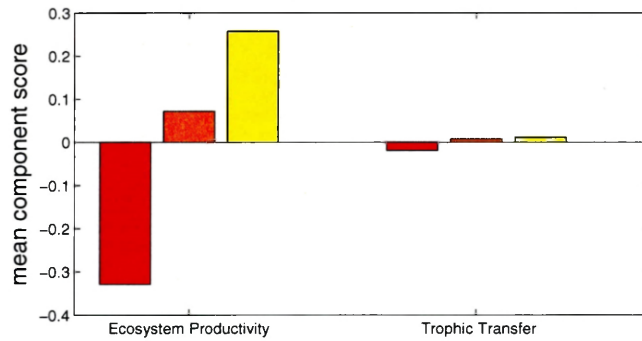
3.4. Adaptation speed, basal species, and regional diversity. The above influences of adaptability (A), connectance (C), searching efficiency (f), and invasion period (μ) on the assembled community’s richness, ecosystem productivity, and trophic transfer were unaffected by the maximal adaptation rate g (see eq. (3)). Coefficients for the principal components were also maintained. However, there was one notable effect, g alters the invasion speed (μ) required to see any interactive effects between μ and adaptability. For example, when foraging changes happen slowly ($g \approx 0.03$ or less) the negative effect of adaptability on diversity when μ and f are high and connectance is low (fig. 3c) requires even slower invasions (increased μ). Perhaps due to the relatively minimal effect of invasion period on the two functioning components, changing g has no notable effect on either. These results are consistent with previous research suggesting that the magnitude of g is not important as long as it is sufficiently positive [15].

The fraction of basal species in the pool had a somewhat larger effect on the assembled community. In addition to decreasing the total biomass of assembled communities, a lower fraction of basal species decreased the richness of assemblages, and vice versa. This is consistent with a similar effect found previously [20]. The fraction of basal species also had notable effects on the functioning variables. Although the relationships between the input variables (A , C , f , and μ) and the functioning components (ecosystem productivity and trophic transfer) were maintained, communities assembled from pools with more producers had higher values for each of the five functioning variables.

The effects of adaptability, connectance, searching efficiency and invasion period on the diversity and functioning of the assembled community were unaffected by the diversity of the regional pool. Indeed, an average 66% of species in the regional pool were in the assembled communities regardless of regional diversity. However, despite no proportional change in the average richness of the assembled community, the diversity of the regional pool had an obvious positive effect on the



(a) Functional Variables



(b) Principal Components

FIGURE 6. The effect of regional pool size on mean per-species functioning. The mean of the five functioning variables in each community, divided by the regional richness (a), and a comparison of the two main components of a PCA done using these adjusted values (b). In (a), values of the four rate variables are indicated by the left axis, and values for biomass are shown on the right axis.

per-species functioning of the assembled communities (fig. 6). Since there is no direct competition between producers in this model, an increase in functioning merely proportional to the increase in pool diversity would be explained by the increase in the total potential productivity. However, communities built from regional species pools with either 10 or 40 species had either lower or higher per-species functioning, respectively, than communities assembled from 20 species pools (fig. 6). The trend held for all five of the functional variables (fig. 6a) and for the two principal components of an analysis done on the functioning variables normalized to the richness of the regional pool (fig. 6b).

4. DISCUSSION

This study supports the conclusion of previous research that adaptive foraging behavior facilitates high diversity in ecological communities [15, 21, 53]. However, in our study this result is dependant on a complex set of interactions between the searching efficiency of consumers, the invasion period, and the connectance (fig. 3). In particular, diversity is maximized in communities with a high fraction of adaptive foragers, high connectance, a rapid assembly process, and intermediate searching efficiencies. Many recent studies [13, 17, 54, 49] suggest that the strength of trophic interactions can be an influential determinant of community stability. We further show that consumer efficiency alters how connectance and the fraction of adaptive foragers affect community diversity. For example, the diversity of slowly assembled communities with highly efficient consumers is negatively affected when the consumers exhibit adaptive behavior.

Despite the prevalence of complex relationships like this, diversity is always maximized by intermediate searching efficiencies. This result confirms previous work suggesting that high interaction strengths destabilize communities [13, 54]. In addition, many studies have found that variation in interaction strength may increase stability [17, 54, 49], especially if there are a few strong interactions and many weak ones. Indeed, it has been suggested that community stability is more dependant on the variance of interaction strengths than their mean [54, 55, 53]. I propose that adaptive foraging behavior may be a source of this variation. Because a consumer's total foraging effort is fixed (preferences always sum to 1), allowing consumers to increase their preference for a valuable resource will make their other interactions weaker. Thus, in communities with high connectance and a high fraction of adaptive foragers, consumer species will have a few (relatively) strong interactions and many weak interactions. Distinguishing between the stabilizing effects of adaptive behavior and skewed interaction strengths requires additional study.

Although this resultant heterogeneity in the strength of a consumer's interactions may partially explain how adaptive foragers interact with high connectance to yield diverse communities, the fact that diversity is highest in communities with intermediate searching efficiency even when there are no adaptive foragers requires an alternate explanation. Potentially, high searching efficiencies allow for the overexploitation of resources. Adaptive foragers with few resources would be particularly susceptible, especially when there is a long period between invasions (see fig. 3c). On the other hand, exceptionally low searching efficiencies dramatically limits the ability of high trophic level consumers to invade, perhaps because their potential resources have not accumulated enough biomass to support them. In this case, a slow assembly process would allow for enough biomass accumulation by low-level consumers to facilitate the invasion of higher trophic levels, especially in communities with high adaptability and connectance (fig. 3i).

There is a positive correlation between increased richness and increased ecosystem productivity of the assembled community (table 1). However, the strength of this relationship and whether it is coincident with an increase in the importance of trophic transfer depends highly on the searching efficiency of consumers in the community. While adaptive foragers are typically able to stabilize and maintain community diversity, in communities with high or intermediate searching efficiency ($f \geq 0.03$) the increased effectiveness of these consumers lowers ecosystem productivity. When searching efficiency is high ($f = 0.3$) this effect is large enough

to lower trophic transfer as well. In contrast, the additional consumers in communities with weak interactions increase functioning by increasing the biomass in the community, as opposed to increasing trophic transfer. This is consistent with research suggesting that the relationship between diversity and functioning is more complex in multitrophic systems [56].

Although assembly processes that produce more diverse communities do not always produce communities with greater functioning, assembled communities from more diverse regional pools exhibit functioning proportionately greater than the increase in regional diversity. This may be another example of scale altering diversity/function relationships. This is similar to previous studies done on invasion success [57] [58]. The studies showed that the same properties of communities that encourage diversity facilitate exotic invasions among different ecosystems. Therefore, there is often a correlation between diversity and invasion success across large spatial scales, however, among similar communities (typically at smaller scales) higher diversity inhibits the success of invaders. In this study, the properties of the species pool (e.g. connectance, adaptability, searching efficiency) that enhance diversity usually increase functioning as well, but not necessarily. On the other hand, if these properties are the same in two different regional pools, but the pools contain different numbers of species, the more diverse pool will produce communities with higher per-species functioning. In other words, whether the biodiversity determines ecosystem functioning or both are jointly determined by regional properties may depend the scale at which the ecosystems being compared differ.

This study has shown that the diversity and functioning of assembled communities depends on consumer behavior, which in this case facilitated the food-web network's ability to evolve. For example, the effects of high searching efficiencies (strong interactions) on overall diversity or ecosystem productivity could be dramatically underestimated if the community has a significant number of adaptive foragers (figs. (4)a-f), and trophic transfer rates would be overestimated (figs. (5)a-c). As a consequence, before attempting to make predictions with food web models, it is essential to attempt an accurate description of consumer behavior, whatever it may be.

APPENDIX A. ADDITIONAL MODEL DETAILS

As discussed in the methods (section 2.1), The adaptive foraging model used is a modified Lotka-Volterra predator-prey model that allows interactions to change in strength. The assumption is that a consumer species is given a fixed amount of time that it can spend searching for (and handling, if a type II response is included) resources and that it can only actively search for one type of resource at any particular time [15] [59]. This assumption applies in many situations where an organism needs to change its location and/or behavior in order to exploit different resources. The equations are based on a prey-switching model presented by Kondoh [15]. The biomass dynamics (eq. 1 described in section 2.1) are shown below, F_j is a Holling type 2 functional response [43] [44].

$$\dot{X}_j = X_j \left(r_j \left(1 - \frac{X_j}{K} \right) - d_j + \sum_{i=1}^n \theta_{ij} P_{ij} f_{ij} F_j X_i - \sum_{i=1}^n P_{ji} f_{ji} F_i X_i \right)$$

$$F_j = \frac{1}{1 + \sum_{i=1}^n H_{ij} f_{ij} P_{ij} X_i}$$

From eq. (1) we derive eq. (3) by first making two assumptions regarding j 's preferences, \vec{P}_j : 1) \vec{P}_j must evolve to maximize j 's biomass intake rate, $I_j = \sum_{i=1}^n \theta_{ij} P_{ij} f_{ij} F_j X_i$ which is a function of \vec{P}_j , given $X(t)$; 2) the sum of the components of P_j is one ($\sum_i P_{ij} = 1$). To maintain the first assumption, we take the gradient of I_j with respect to P_j , in order to maintain the second we use a gradient system with respect to the Shashahani metric [45].

$$\dot{\vec{P}}_j = \vec{P}_j \circ \left(\nabla I_j - \vec{P}_j \cdot \nabla I_j \right)$$

As stated in the methods, ∇I_j is the gradient of I_j with respect to P_j ,

$$\nabla I_j = \left[\frac{\partial I_j}{\partial P_{1j}} \quad \frac{\partial I_j}{\partial P_{2j}} \quad \dots \quad \frac{\partial I_j}{\partial P_{nj}} \right]$$

and after defining $H(\hat{k}) = H_{kj} f_{kj} X_k$ and $\theta(\hat{k}) = \theta_{kj} f_{kj} X_k \dots$

$$\begin{aligned} \frac{\partial I_j}{\partial P_{ij}} &= \frac{\partial}{\partial P_{ij}} \left(F_j \sum_{k=1}^n \theta(\hat{k}) P_{kj} \right) \\ &= F_j^2 \left(\frac{\theta(\hat{i})}{F_j} - H(\hat{i}) \sum_{k=1}^n \theta(\hat{k}) P_{kj} \right) \end{aligned}$$

and because $F_j = \frac{1}{1 + \sum_i H(i) P_{ij}}$ we get

$$\begin{aligned}
\vec{P}_j \cdot \nabla I_j &= \sum_k P_{kj} \frac{\partial I_j}{\partial P_{kj}} \\
&= F_j^2 \left(\sum_k P_{kj} \theta(\hat{k}) (1 + \sum_{l=1}^n H(\hat{l}) P_{lj}) + \sum_k P_{kj} H(\hat{k}) \sum_{l=1}^n \theta(\hat{l}) P_{lj} \right) \\
&= F_j^2 \left(\sum_k P_{kj} \theta(\hat{k}) + \left(\sum_k P_{kj} \theta(\hat{k}) \right) \sum_k P_{kj} H(\hat{k}) - \left(\sum_k P_{kj} H(\hat{k}) \right) \sum_k P_{kj} \theta(\hat{k}) \right) \\
&= F_j^2 \sum_{k=1}^n P_{kj} \theta_{kj} f_{kj} X_k
\end{aligned}$$

finally, after adding the adjustable adaptation rate (g), we have eq. (3)

$$\begin{aligned}
\dot{P}_{ij} &= g P_{ij} \left(\frac{\partial I_j}{\partial P_{ij}} - \sum_k P_{kj} \frac{\partial I_j}{\partial P_{kj}} \right) \\
&= g P_{ij} F_j^2 \left(\frac{\theta_{ij} f_{ij} X_i}{F_j} - (H_{ij} f_{ij} X_i + 1) \sum_{k=1}^n \theta_{kj} P_{kj} f_{kj} X_k \right)
\end{aligned}$$

Under the assumptions made in Kondoh's initial study [15] ($H_j = 0$ and $\theta_{1j} = \theta_{2j} = \dots \theta_{nj}$) this reduces to

$$\dot{P}_{ij} = g P_{ij} \left(\theta f_{ij} X_i - \sum_{k=1}^n \theta P_{kj} f_{kj} X_k \right)$$

which corresponds to the preference equation in that study. However, under the assumptions used in subsequent studies (i.e. $H_{1j} = H_{2j} = \dots H_{nj}$ and $\theta_{1j} = \theta_{2j} = \dots \theta_{nj}$), we get

$$\dot{P}_{ij} = g F_j^2 P_{ij} \left(\theta f_{ij} X_i - \sum_{k=1}^n \theta P_{kj} f_{kj} X_k \right)$$

which is weighted by an additional F_j term. This adjustment only affects the speed of adaptation, and because the g term has been shown to have minimal influence, it is unlikely to appreciably influence the results. However, we do not assume equivalent θ 's. Without that assumption, previous formulations could potentially move \vec{P}_j in a different direction than eq. (3).

APPENDIX B. COEFFICIENT OF VARIATION

Variability in the richness of the communities through time was maximized in high searching-efficiency communities with long invasion periods, a high fraction of adaptive foragers, and low-intermediate connectance (fig. 7). These coincide with the low-diversity communities in fig. 3c. These patterns may be because the consumer species in the community rapidly over-exploit their resources. This results in communities with extremely low richness in which invading consumers quickly drive their resources (and thus themselves) extinct, and a resource only lasts until one of its consumers arrives (e.g. fig. 1b).

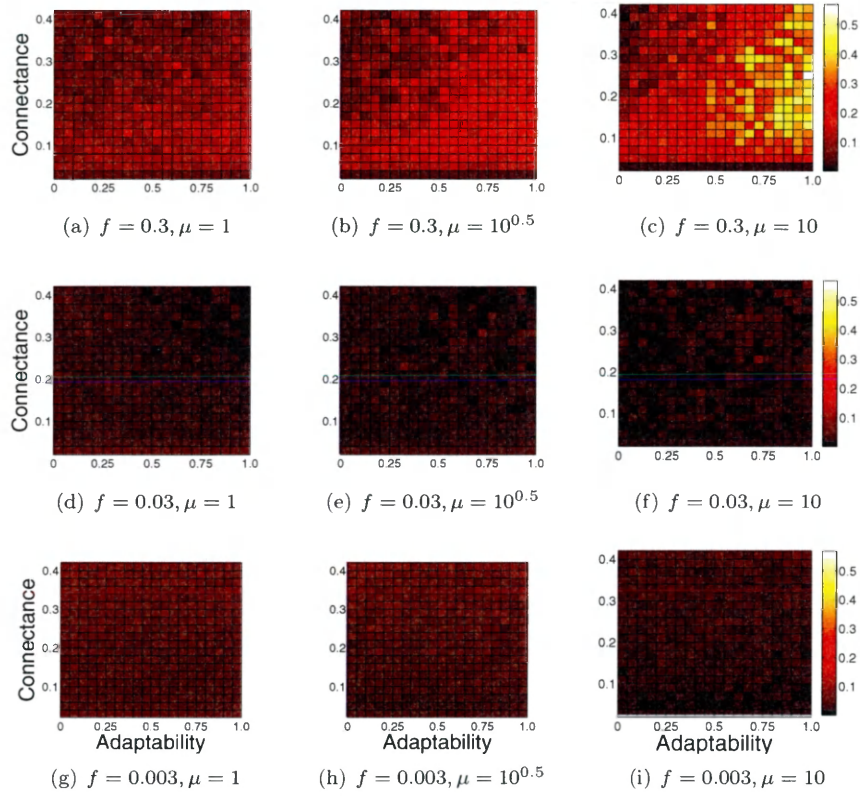


FIGURE 7. Each panel shows mean coefficient of variation of species richness as a response to manipulating Adaptability along the X axis (20 values from 0 to 1), and Connectance along the Y axis (20 values from 0 to .45), with a particular invasion rate (columns, $\mu = 1, 10^{0.5},$ or 10) and searching efficiency (rows, $f = 0.3, 0.03,$ or 0.003). Every value is averaged over twenty independent simulations with the same input parameters.

APPENDIX C. TOTAL COMMUNITY BIOMASS

As with diversity and the two composite functioning variables, the effects of adaptive foragers and connectance on the assembled community's total biomass depended on the searching efficiency (fig. 8). In fact, total biomass and ecosystem productivity (PC1) had very similar patterns. Both were negatively affected by adaptive behavior when consumers were highly efficient ($f = 0.3$, figs. 3a-c and 4a-c) and, to a lesser extent, with intermediate search efficiencies as well ($f = 0.03$, figs. 3d-f and 4d-f). Also like ecosystem productivity, biomass in communities with low searching efficiencies was only affected by connectance and the invasion period. However, although the total biomass in low searching efficiency communities was (on average) greater than in communities with intermediate searching efficiency (fig. 8), the reverse was true for ecosystem productivity, with intermediate searching efficiency communities generally having much higher scores on the first principal component (fig. 4). This suggests that biomass may be a reasonable measure of "functioning" in the same types of communities, but that using biomass to compare different types of communities may be misleading. As might be expected, using biomass to compare the trophic transfer of different kinds of systems would be even more problematic; total biomass in the community increased with searching efficiency (fig. 8), but the amount of that biomass making it into the higher trophic levels decreased dramatically (fig. 5).

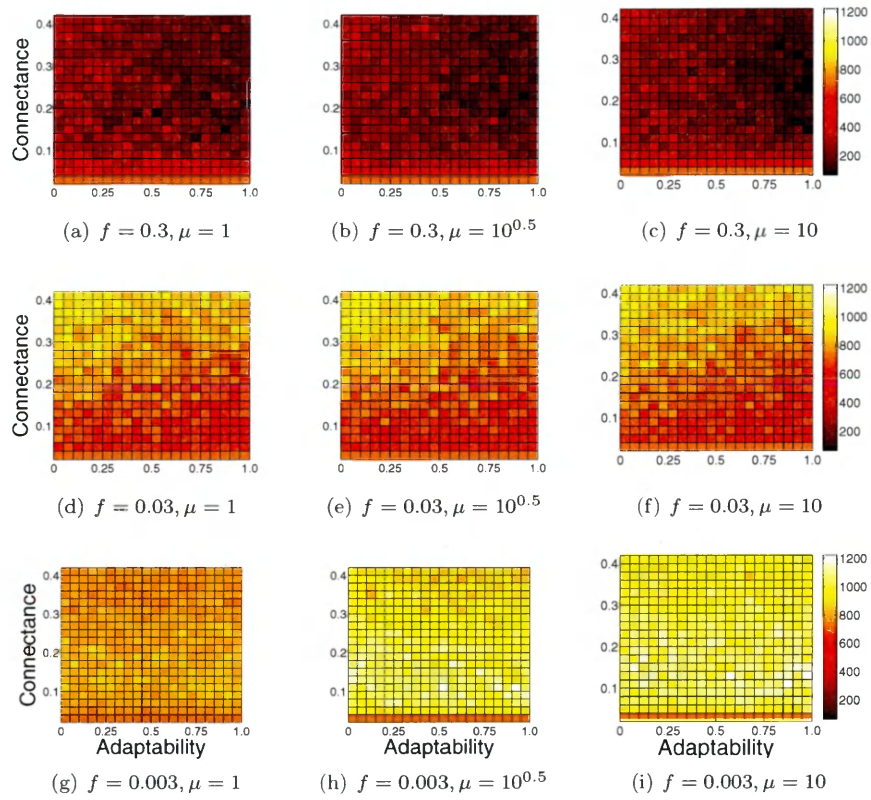


FIGURE 8. Each panel shows average total biomass as a response to manipulating Adaptability along the X axis (20 values from 0 to 1), and Connectance along the Y axis (20 values from 0 to .45), with a particular invasion rate (columns, $\mu = 1, 10^{0.5}$, or 10) and searching efficiency (rows, $f = 0.3, 0.03$, or 0.003). Every value is averaged over twenty independent simulations with the same input parameters.

APPENDIX D. BASAL SPECIES DATA

For communities with high or intermediate searching efficiencies ($f = 0.3, 0.03$), the mean richness of the basal species (figs. 9a-f) followed almost the same pattern as total community richness (figs. 3a-f). Adaptability and connectance interacted to increase the number of basal species that successfully established themselves in the local community. This is consistent with the suggestion that the interaction between these variables increased richness by allowing consumers to switch resources before one went extinct. As with overall diversity, a longer period between invasions lowered basal diversity in high searching efficiencies. Communities containing consumers with low searching efficiency always had a full complement of basal species (fig. 9), consistent with the suggestion that these consumers are unable to affectively take advantage of their resources.

In communities with high searching efficiency, the combined biomass of the basal species dropped with connectance and adaptability (figs 10a-c). The negative effect of adaptive foragers on basal biomass was present even when the connectance of the community was helping to maintain basal richness (figs 9a-c). This suggests that adaptive consumer behavior makes consumers more effective at exploiting resources, but that when they have enough choices they are less likely to drive them extinct.

The biomass of the basal species is decreased by adaptive foragers in communities with intermediate searching efficiencies, but it is increased by high connectance. This could indicate that consumers with intermediate searching efficiencies are better able to maintain their resources at relatively high levels when they are generalists (figs 10d-f). These biomass densities could explain the high levels of ecosystem productivity in these communities (figs. 4d-f), due to the primary producers compensation for consumption when their biomass drops slightly below carrying capacity, $K \frac{(r-d)}{r}$.

Like total biomass, community richness, and both functioning components, the variable with the largest influence on basal biomass was invasion period (figs 10g-i). Basal species had lower biomass in communities with a slower assembly process ($mu = 10^5, 10$). This indicates that the gain in total biomass in these communities (figs 8g-i) was due to an accumulation of biomass by consumers.

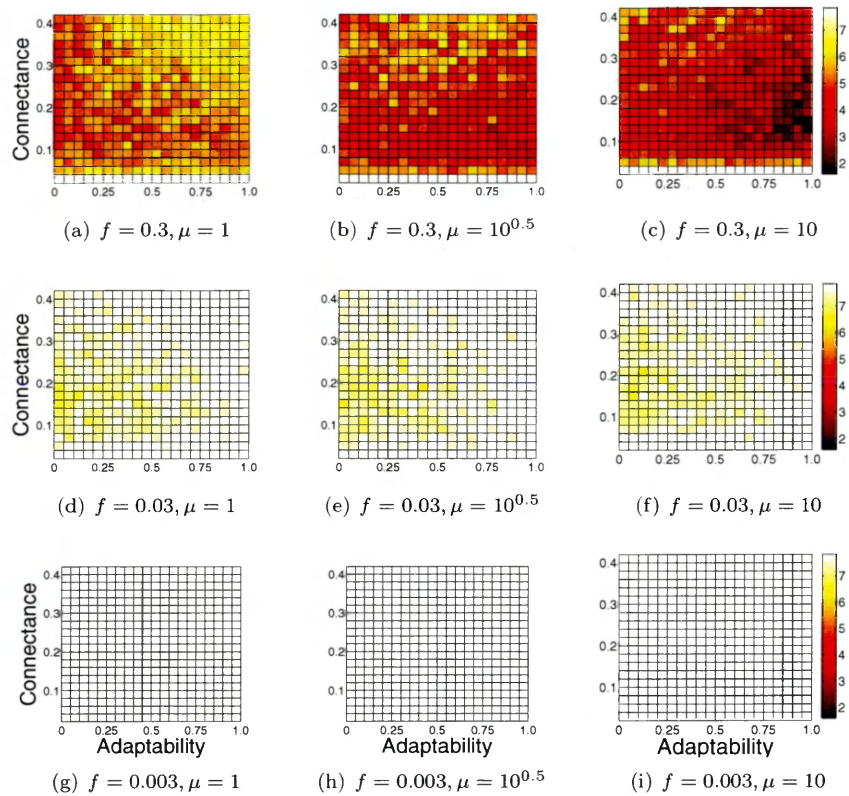


FIGURE 9. Each panel shows average richness of basal species as a response to manipulating Adaptability along the X axis (20 values from 0 to 1), and Connectance along the Y axis (20 values from 0 to .45), with a particular invasion rate (columns, $\mu = 1, 10^{0.5}$, or 10) and searching efficiency (rows, $f = 0.3, 0.03$, or 0.003). Every value is averaged over twenty independent simulations with the same input parameters.

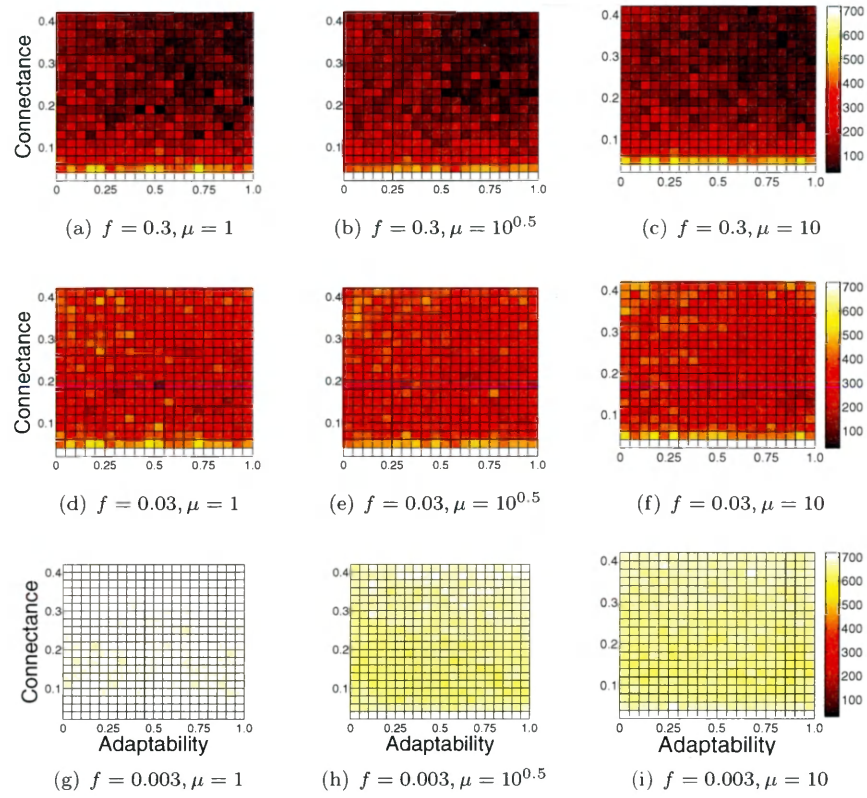


FIGURE 10. Each panel shows average biomass of the basal species as a response to manipulating Adaptability along the X axis (20 values from 0 to 1), and Connectance along the Y axis (20 values from 0 to .45), with a particular invasion rate (columns, $\mu = 1$, $10^{0.5}$, or 10) and searching efficiency (rows, $f = 0.3$, 0.03, or 0.003). Every value is averaged over twenty independent simulations with the same input parameters.

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