

# The dynamics of community assembly under sudden mixing in experimental microcosms

GEORGE LIVINGSTON,<sup>1,3</sup> YUEXIN JIANG,<sup>1</sup> JEREMY W. FOX,<sup>2</sup> AND MATHEW A. LEIBOLD<sup>1</sup>

<sup>1</sup>*Section of Integrative Biology, University of Texas at Austin, 1 University Station C0930, Austin, Texas 78712 USA*

<sup>2</sup>*Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2L 1Z3 Canada*

**Abstract.** Landscape connectivity has been shown to alter community assembly and its consequences. Here we examine how strong, sudden changes in connectivity may affect community assembly by conducting experiments on the effects of “community mixing,” situations where previously isolated communities become completely connected with consequent community reorganization. Previous theory indicates that assembly history dictates the outcome of mixing: mixing randomly assembled communities leads to a final community with random representation from the original communities, while mixing communities that were assembled via a long history of colonizations and extinctions leads to strong asymmetry, with one community dominating the other. It also predicts that asymmetry should be stronger in the presence of predators in the system. We experimentally tested and explored this theory by mixing aquatic microcosms inhabited by a complex food web of heterotrophic protists, and algae. Our results confirm the prediction that long assembly history can produce asymmetry under mixing and suggest these dynamics could be important in natural systems. However, in contrast to previous theory we also found asymmetry weaker under mixing of communities with more complex trophic structure.

**Key words:** biotic interchange; community assembly; competitive interactions; connectivity; meta-community; microcosms; trophic interactions.

## INTRODUCTION

Spatial effects are increasingly recognized to be important to community assembly at local and regional scales (Leibold et al. 2004, Holyoak et al. 2005). A central finding is that the degree of connectivity among local communities in a metacommunity can alter patterns of diversity, composition, and food web and ecosystem attributes (Logue et al. 2011, Massol et al. 2011). To date, most of this work has focused on cases where connectivity is fixed in time. However connectivity can change due to both natural and anthropogenic factors. Although some attention has been given to altered fragmentation corresponding to rapidly decreased connectivity (Didham et al. 2012), a largely unexplored and interesting possibility is the reverse: a sudden increase in connectivity through “community mixing.”

Community mixing occurs when previously isolated communities merge into one. The phenomenon is likely widespread in nature, but it is difficult to identify cases of mixing because field data is not typically collected with a delineation of past community isolation or of changes in connectivity across time. However, community mixing does occur. For example, over long geologic

time scales macroecological events such as the collision of landmasses or the merging of ocean or river basins (Vermeij 1991, Wilkinson et al. 2006) provide opportunities for community mixing. On decadal time scales, defragmentation processes may also represent contemporary mixing (e.g., reforestation; Sitzia et al. 2010, Didham et al. 2012). Seasonally, recurrent rainfall events induce rivulets to form among rock pool communities and this dispersal mode accounted for the majority of dispersal volume of invertebrates in one system (Vanschoenwinkel et al. 2008). Even on daily time scales, tidal action floods and re-isolates coastal water bodies (Larkin et al. 2008) and the mixing of some microbial communities may occur at even higher frequency (Gonzalez et al. 2012).

What is the outcome of such events? Tilman (2011) reviewed cases of the historical merging of “biogeographic realms.” In general, coexistence was the predominant outcome and wholesale extinctions of taxa from either of the two source realms did not occur, nor did the overall extinction rate among both groups of taxa increase. A notable exception to this pattern comes from the extinction of 12 of 20 genera of South American ungulates after the collision of the North and South American landmasses, possibly due to direct or apparent competition with Northern taxa (Webb 1976). Although these examples provide patterns, it is extremely difficult to determine the processes responsible. Possible processes involve pre-contact evolutionary

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<sup>3</sup> E-mail: glivingston@utexas.edu

community assembly like character displacement, coevolution, phylogenetics, species range evolution (Urban et al. 2008), and trade-off surfaces (Tilman 2011), or post-contact ecological community assembly involving rapid reassembly through species interactions and environmental heterogeneity among the previously isolated realms.

Simple assembly models based on competition can aid interpretation of the general pattern of coexistence observed in biogeographic contexts. These models reveal the expected consequences of community mixing under simple, widely applicable, ecological scenarios. Gilpin (1994) used Lotka-Volterra models to show that after mixing, one community could mostly or entirely replace the other, much as in the partial replacement of the South American mammal fauna by the Northern. He contrasted situations where the initial communities were “random” vs. “nonrandom.” The random ones were created by drawing species at random from a species pool and finding sets of species that could stably coexist but were subject to no other mechanisms of community assembly. The nonrandom communities were those that initially contained an unstable set of species, but collapsed under deterministic extinctions to a smaller subset of species that could stably coexist. He found that mixing two random communities usually resulted in a final community that comprised roughly equal numbers of species from the two initial communities. In contrast, he found that mixing of two nonrandom communities resulted in final communities that were often completely or partially biased to contain species only from one or the other of the initial ones (asymmetry). The results illustrate that nonrandom communities are likely to have a set of species with a more globally stable species composition (across many possible species combinations) and can thus “trap” mixed communities more than do random ones with local stability (across few possible species combinations). However, only 29% of mixes among nonrandom communities produced asymmetry, indicating that the occurrence of asymmetry is sensitive to the composition of mixed communities. Subsequent theoretical work also showed that communities with few species tend to overtake more species-rich communities (Toquenaga 1997).

Incorporating trophic structure by adding a trophic level to communities enhances asymmetry due to the increased global stability imposed by the predator relative to competitors (Wright 2008). This increased global stability occurred because the effects imposed by predators on their prey tended to be larger than the interaction coefficients among competitors. Under the mixing of nonrandom communities with predators, asymmetry in the final community is further enhanced by the need for the prey from each initial community to coexist with a novel predator and for those predators to coexist with one another (Wright 2008). Although unexplored theoretically, mixing a single-trophic-level

community with a two-level community could produce similarly enhanced asymmetry.

Although intriguing, this theory is poorly developed, being represented by only the three related simulation studies summarized above. Conversely, examples from natural systems suffer from a lack of control that hinders interpretation of patterns. An experimental approach can complement theory and observations from nature, reveal if asymmetric outcomes of mixing are possible in communities comprised of real (as opposed to theoretical) organisms, and allow causation to be attributed to the mixing event (as opposed to, e.g., pre-mixing evolutionary history).

We use multi-trophic aquatic microbial communities to explore the dynamics resulting from assembly in isolation followed by sudden mixing. Microbial microcosms are a powerful model system for bridging the gap between theory and nature (Lawler and Morin 1993, Morin 1999, Cadotte et al. 2005, Fox et al. 2011). We used a well-characterized food web involving producers, herbivores, omnivores, and predators. To address the effect of trophic structure, communities included interaction networks whose species composition was manipulated to produce either mostly competitive (C) or trophic (predator-prey; T) interactions among species. We mixed two competitive communities (CC), two trophic communities (TT), and one of each (TC) in replicated pairs.

We tested two hypotheses about the mixing of two isolated communities: ( $H_1$ ) asymmetric outcomes (one community largely or entirely replaces the other) occur more often than expected by chance; and ( $H_2$ ) asymmetry is more frequent in TT and TC than in CC mixes. We explored potential biological mechanisms underlying the mixing process using an analysis of asymmetry within each of six trophic guilds used in our experiment: bacterivores, inedible algae, edible algae, herbivores, predators, and omnivores.

## MATERIALS AND METHODS

### *Experimental design*

The 52 species in the experiment included edible algae, inedible algae, bacterivores, omnivores, herbivores, and predators. We generated 132 eight-species communities divided equally into two types: communities that were dominated by trophic interactions (T); and communities that were dominated by competitive interactions (C). Like Gilpin (1994) and Wright (2008), we choose to initiate our communities with equal numbers of species. Unlike Wright's (2008) model, both C and T communities include trophic and competitive interactions, however, we varied the ratio of trophic to competitive species in an analogous way to Wright's method of substituting one prey for a predator.

We then paired communities in three ways: 22 pairs of competitive communities (CC), 22 pairs where one community was a competitive community and the second was a trophic community (TC), and 22 pairs in

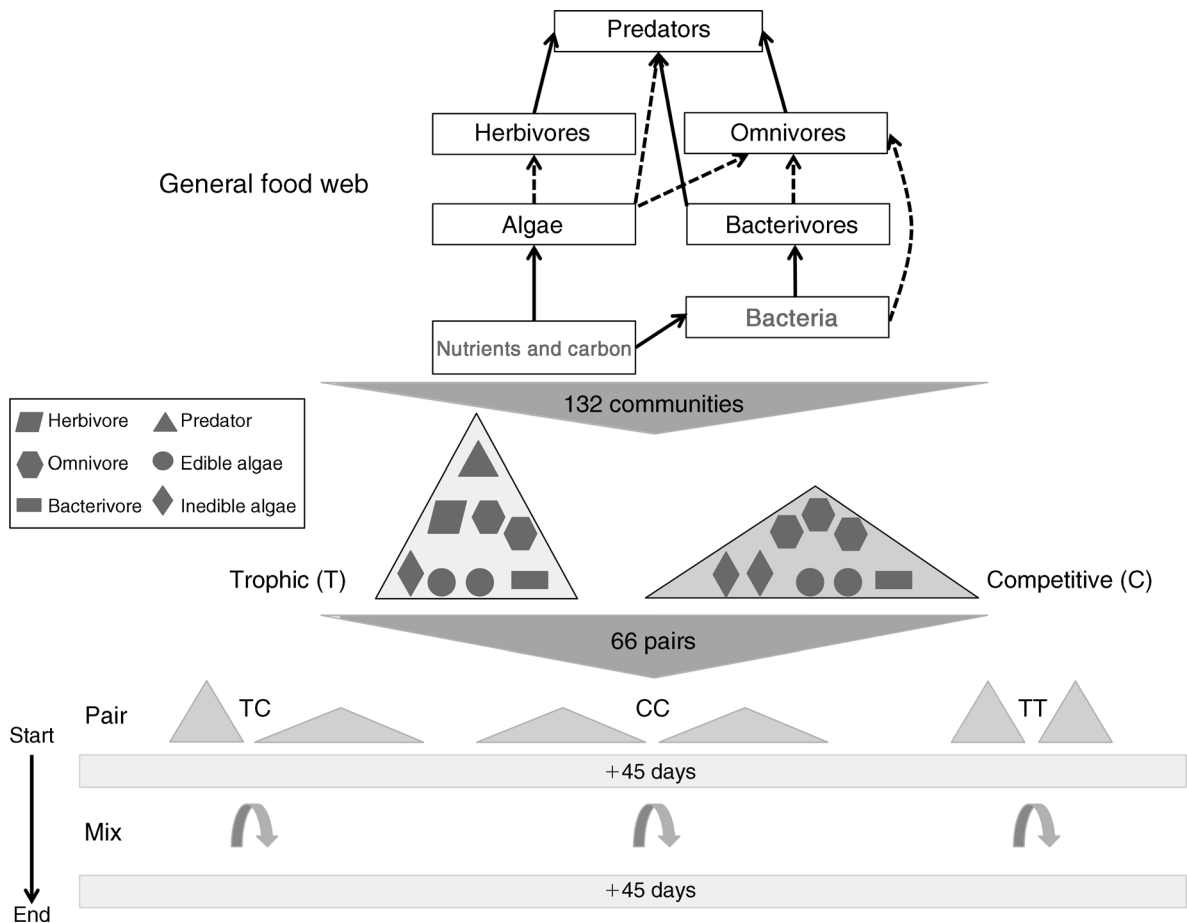


FIG. 1. Schematic of experimental design. The general food web was adapted from the feeding trial (Appendix B) and Petchey et al. (1999). Dashed lines indicate context-dependent feeding links. A total of 132 trophic (T) and competitive (C) communities each with eight species were randomly generated and paired in TC, CC, and TT combinations (66 total pairs and 22 of each type, see *Methods*). These communities were assembled for 45 days, mixed, and assembled for another 45 days until the end of the experiment.

which both were trophic (TT; 66 total pairs, Fig. 1). Each community in the experiment contained a unique species composition and there was no overlap in composition between paired communities. We mixed community pairs 45 days after establishment and allowed the mixed communities to reassemble for an additional 45 days. These periods are similar to previous microcosm assembly experiments (Fox 2008) and represent approximately 90 generations by the end of the experiment for mid-trophic-level species (other groups have longer or shorter generation times).

#### *Trophic and competitive community assembly*

Trophic communities were inoculated with one species each of bacterivore, inedible algae, edible globular algae, edible non-globular algae, herbivore, predator, and two omnivore species. In competitive communities, we increased the frequency of competitive interactions by removing the herbivore and predator and adding an additional omnivore and inedible algae

species. Competitive communities were inoculated with one each of bacterivore, edible globular algae, edible non-globular algae, two inedible algae, and three omnivore species (Fig. 1). Edibility of algae was determined by size (Appendix A and methods in Appendix B). We classified the majority of heterotrophic species into trophic categories based on a combination of feeding trials (Appendix B and C), mouthpart size, and published observations (see references in Appendix A). Although precise feeding relationships were context dependent, all herbivores, predators and omnivores used in the experiment are considered to be generalists.

Stock cultures were obtained from biological supply companies and contributions from other microbiological labs (see Appendix A). We inoculated communities from high-density stock cultures grown under similar conditions for 10 days prior to the start of the experiment. Bacterivores, omnivores in pure culture, and algae were added as 250- $\mu$ L inocula. *Spirogyra* sp., a filamentous alga, was added as a single strand. For

omnivores, herbivores, and predators, we isolated five individuals for inoculation by serial dilution. Food webs were assembled from the base up, with bacterivores and algae added at 7 d, and omnivores, herbivores, and predators added at 14 d.

#### *Microcosm conditions*

We used deep  $100 \times 25$  mm petri dishes as microcosms filled with 39 mL of COMBO culture medium (Kilham et al. 1998), on which all species exhibited vigorous growth. Lids were vented allowing gas exchange. To initiate bacterial populations we inoculated autoclaved wheat seeds (carbon source) with a mixture of three unknown bacterial strains that were isolated from cultures of bacterivorous protists. We then added two of these wheat seeds to each microcosm. Our cultures were not axenic, and other unknown bacterial species and possibly nanoflagellates were unavoidably introduced. However, additions of these unknown organisms were consistent across replicates and are unlikely to confound our results (Fox 2008).

Microcosms were placed under a single fluorescent tube light in a growth chamber with a 16:8 light dark cycle at 20°C. Each week we replaced 11% of culture volume with fresh sterile medium to prevent the accumulation of toxic metabolites. Trays of 18 petri dishes were rotated weekly within the growth chamber to ensure uniform lighting conditions, but all community pairs were placed adjacent to each other to assure that each pair was subject to identical conditions.

#### *Mixing and sampling procedures*

Mixing involved pouring the contents (including wheat seeds) of both petri dishes simultaneously into a single new sterile dish. A sterile cell scraper was used to transfer attached biofilms. Mixing doubled the volume in each microcosm to 78 mL.

We sampled communities at mixing and at the end of the experiment. Communities were placed under a stereomicroscope and scanned until all species were accounted for or a maximum of 10 minutes. Preliminary trials and other studies (Fox 2008) demonstrate that this length of time is sufficient to find all species present. Because of logistical constraints we only sampled species abundances for 24 community pairs (distributed evenly across treatments). If supplemented with abundance data, presence/absence provides sufficient information to address our main hypotheses. Thus, for the remaining 42 community pairs we scanned communities for presence/absence only. To check if extinctions were still occurring at mixing, we scanned 13 communities selected at random for extinctions at 28 d.

For those communities where abundance was estimated, 300  $\mu$ L was extracted using a micropipette after swirling the dish and counted under a stereoscope (Fox 2002). Algae that were either too abundant or too small to count using this method were estimated by transferring approximately 30  $\mu$ L to a haemocytometer for

counting under a compound scope. High-density samples were diluted until they reached countable densities.

#### *Statistical analyses*

We calculated asymmetry in composition as the absolute value of the difference in post-mixing extinction rates from each initial community within a mixed pair. Let  $A$  represent asymmetry and  $e_1$  and  $e_2$  represent the proportion of species present at the time of mixing that went extinct after mixing in communities 1 and 2. The equation for asymmetry is thus:  $A = |e_1 - e_2|$ . This method controls for variation in species richness between each community in a pair prior to mixing and allowed us to look at both the randomness of the overall distribution of asymmetry outcomes as well as the outcome for any particular pair of communities.

Our core results involve comparing the mean, variance and skew of our observed asymmetry in composition with that predicted by a null model. We make comparisons overall, within treatments, and to aid interpretation of community-level results, within guilds. Skew is only reported for the overall distribution because among treatments and guilds it never significantly deviated from the null model. For our guild-level analysis, we calculated asymmetry separately for each guild within paired communities. We calculated asymmetry using the same general equation presented above, but only for those cases where both communities contained at least one species in a given guild.

We neither expected nor observed all species to persist in all microcosms because of species interactions and demographic stochasticity. This allowed us to analyze our results using a null model. We used each species' pre-mixing persistence probabilities to simulate extinctions in observed communities from the time of mixing until the end of the experiment. The pre-mixing persistence probability for each species was calculated as the number of communities with that species present after 45 d divided by the total number of communities inoculated with that species (probabilities are reported in Appendix A). This model assumes that species persistence probabilities are unaffected by mixing, i.e., that persistence probabilities are the same during the first and last 45 d of the experiment. We test this assumption by correlating pre and post-mixing persistence probabilities. After 1000 simulation runs, we inferred the likelihood of observing symmetric vs. asymmetric outcomes by generating confidence intervals (mean, variance, skew of distributions, and deviance of asymmetry values from expected for each mixed pair of communities).

For the 48 communities with abundance data, we calculated asymmetry in Raup-Crick dissimilarity to address the possibility that focusing on presence/absence data missed important patterns using the vegan package in R (Oksanen et al. 2013). Asymmetry was calculated as the difference in dissimilarity of the communities in each pair relative to the final mixed community. This asks if,



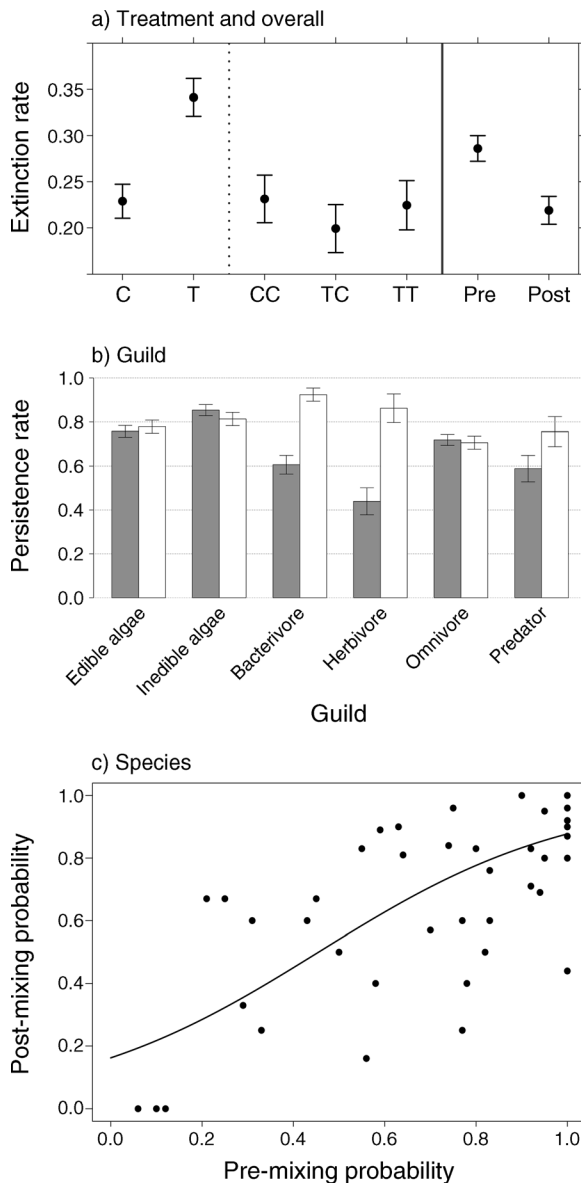


FIG. 2. Pre- and post-mixing effects on extinction/persistence rates. Error bars show standard error. (a) Mean extinction by treatment. C stands for competitive; T, trophic; CC, TC, TT are mixes. Pre and post are overall rates before and after mixing, respectively.  $N = 1056$  populations in pre and  $N = 748$  populations in post. The differences between C and T and between pre and post are significant (GLM,  $P < 0.001$ ,  $df = 1055$ ,  $\chi^2 = 885.29$ , and  $P < 0.01$ ,  $df = 1806$ ,  $\chi^2 = 1629.34$ , respectively), but not among mixing types. (b) Mean persistence by guild. There is a significant effect of guild on persistence rate before (GLM,  $P < 0.00001$ ,  $df = 1055$ ,  $\chi^2 = 782.69$ ) and after mixing (GLM,  $P < 0.001$ ,  $df = 743$ ,  $\chi^2 = 625.64$ ). (c) Mean pre- and post-mixing persistence for all species present at both times ( $N = 48$  populations), fitted with a binomial GLM ( $P < 0.01$ ,  $df = 47$ ,  $\chi^2 = 23.32$ ).

in terms of Raup-Crick dissimilarity, the final community is more similar to one of the two pre-mixing communities. The Raup-Crick index was used to avoid confounding effects of differing species richness among communities (Chase et al. 2011).

We explored two mechanisms that could have determined the identity of dominant communities. For the first, we asked if the presence of particular species was associated with communities showing significantly higher or lower asymmetry than expected under the null model. For the second, we asked if the pre-mixing extinction rate in each community correlated with the post-mixing extinction rate or with asymmetry using a GLM with a logit link function. The simulations and all statistical analyses were implemented in R (v2.14.1; R Development Core Team [2012]; Supplement).

## RESULTS

### Pre-mixing assembly

Species persistence probabilities prior to mixing ranged widely from 0% to 100% (Appendix A). Trophic communities had significantly higher pre-mixing extinction rates than competitive communities (Fig. 2a). Persistence probabilities differed significantly among guilds, being highest for inedible algae and lowest for predators and herbivores (Fig. 2b). The average number of extinctions among pre-mixing communities ranged from zero to six with an average of  $2.3 \pm 1.2$  (mean  $\pm$  SD). The weekly extinction rate during the first 28 d of assembly was 5.5% and between 28 and 45 d of assembly it was 5%. This indicates the extinction rate was not increasing and may have attained levels reflecting background stochasticity prior to mixing.

### Post-mixing assembly

After mixing, the extinction rate among species from the 13 communities during the first 28 d was 3.5%, but dropped to 0.01% between 28 and 45 d. This indicates that extinctions had stabilized by the final sample. Species persistence probabilities again ranged from 0% to 100% and were significantly correlated with pre-mixing probabilities (Fig. 2c, Appendix A). Overall the extinction rate was significantly lower post-mixing and CC, TC, and TT mixes had similar post-mixing extinction rates (Fig. 2a). Among guilds, three (bacterivores, herbivores, and predators) exhibited significantly lower extinction rates after mixing (Fig. 2b). These reduced extinction rates occurred because two bacterivore species, three herbivore species, and two predators had extremely low or zero pre-mixing persistence probability (Appendix A) and were thus eliminated before mixing. The number of post-mixing extinctions per community again ranged from zero to six with an average of  $2.5 \pm 1.4$ .

### Asymmetry

We observed significantly greater overall mean asymmetry and also greater variance relative to the null

TABLE 1. Summary statistics by treatment and guild for asymmetry in composition.

Treatment and statistic	Observed	Simulated	SD	95% CI
Overall				
Mean	<b>0.215</b> <sup>†</sup>	0.182	0.017	0.149–0.216
Variance	<b>0.036</b>	0.023	0.005	0.014–0.032
Skew	0.838	0.838	0.321	0.210–1.467
CC				
Mean	<b>0.235</b>	0.167	0.026	0.116–0.218
Variance	<b>0.032</b>	0.018	0.006	0.006–0.030
TC				
Mean	0.224	0.193	0.034	0.128–0.259
Variance	<b>0.048</b>	0.024	0.008	0.009–0.040
TT				
Mean	0.188	0.196	0.032	0.134–0.258
Variance	0.032	0.025	0.009	0.008–0.042
Bacterivores				
Mean	0.105	0.212	0.062	0.090–0.334
Variance	0.099	0.165	0.037	0.093–0.238
Edible algae				
Mean	<b>0.367</b>	0.200	0.035	0.131–0.269
Variance	0.143	0.108	0.018	0.072–0.144
Herbivores				
Mean	<b>0.333</b>	0.025	0.015	–0.004–0.055
Variance	0.333	0.026	0.015	–0.003–0.054
Inedible algae				
Mean	<b>0.282</b>	0.079	0.026	0.028–0.130
Variance	<b>0.137</b>	0.061	0.020	0.021–0.101
Omnivores				
Mean	0.372	0.322	0.043	0.238–0.406
Variance	0.097	0.104	0.016	0.073–0.136
Predators				
Mean	<b>0.857</b>	0.084	0.027	0.031–0.138
Variance	<b>0.143</b>	0.077	0.023	0.032–0.122

Notes:  $N = 66$  pairs of communities overall,  $N = 22$  pairs for each mix type, and  $N = 19, 60, 55, 3, 52$ , and 7 pairs for bacterivores, edible algae, inedible algae, herbivores, omnivores, and predators, respectively. C stands for competitive; T, trophic; CC, TC, TT are mixes. Boldface type highlights those observed statistics that are significantly higher ( $P < 0.05$ ) than expected under the null model. Simulations were run for 1000 times.

<sup>†</sup>  $P = 0.05$ .

model (Table 1), supporting  $H_1$ . Comparing the frequency distributions shows a fatter tail of high asymmetry communities in the observed data (Fig. 3). By analyzing individual pairs of pre-mixing communities, we found 10 pairs of communities deviated from predicted with significantly greater asymmetry (Fig. 4). Asymmetry was significantly greater than expected in CC mixes, but not in TC or TT, failing to support  $H_2$  (Table 1, Fig. 4). Disregarding the null model, observed asymmetry among CC, TC, and TT treatments did not differ significantly. Among guilds, we found significantly greater asymmetry than expected under the null model for all groups except bacterivores and omnivores (Table 1). Asymmetry in Raup-Crick dissimilarity is correlated with asymmetry in extinction rate (Appendix D).

#### Mechanisms

We observed that the presence of four species, *Anabaena* sp., *Campylomonas reflexa*, *Loxocephalus*

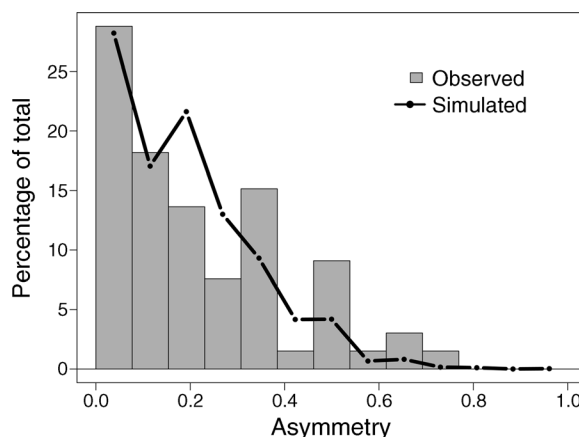


FIG. 3. Histogram of asymmetry in composition.  $N = 66$  mixes for observed data, and  $N = 66,000$  mixes for simulation results. The figure shows observed and simulated composition asymmetry.

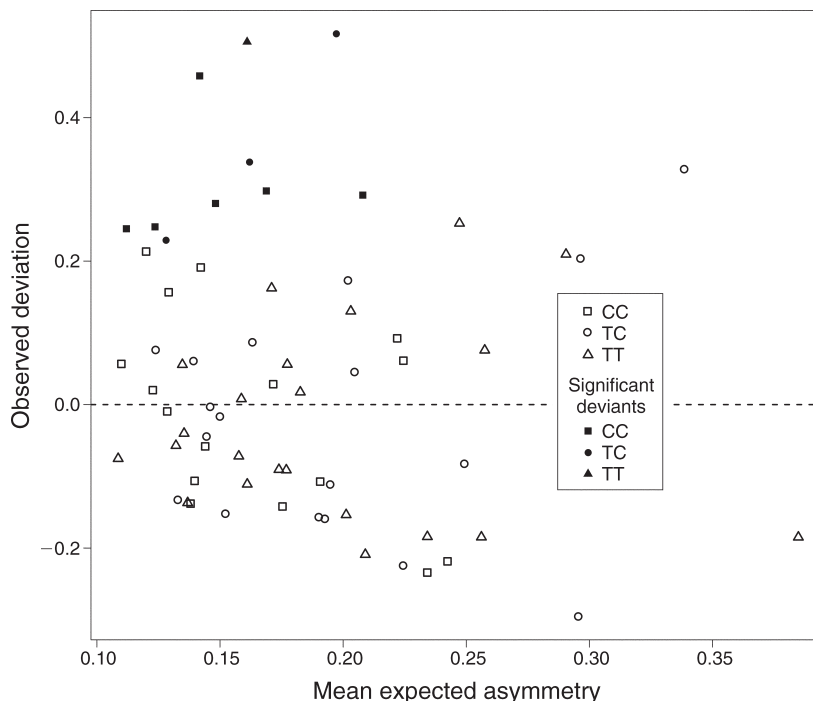


FIG. 4. Scatterplot of observed and expected asymmetry by community. The observed deviation represents the difference between the mean expected asymmetry (simulated) and the observed value for each of the 66 post-mixing communities. Significant deviants are calculated at the  $P < 0.05$  level.

sp., and *Tetrahymena pyriformis*, before or after mixing was associated with asymmetry in composition ( $P < 0.05$ , none after Bonferroni correction), but there was no tendency for these species to be associated with the dominant final community. More extinctions prior to mixing did not affect the chances a community would dominate another after mixing, or the likelihood of extinctions post-mixing.

#### DISCUSSION

Community mixing resulted in asymmetrical outcomes more often than expected under our null model, supporting  $H_1$ . Asymmetry occurred despite the fact that pre-mixing communities did not differ in their evolutionary history or environment, were assembled and paired at random, and that “winning” and “losing” communities were not consistently associated with the presence of particular species. Although our experiment did not include unmixed control communities, similar overall and per species extinction rates pre and post-mixing suggest that the microcosm environment was largely unaffected by mixing and our null model is a reasonable approximation. Significant asymmetry in composition occurred in 18% of 66 mixes. By comparison, Gilpin (1994) observed asymmetry in 29% of simulated mixes among communities structured only by competition and Wright (2008) observed this number to be 38% when including predation. However, these percentages are sensitive to arbitrary choices of model

parameters, so that no particular value is necessarily expected.

Previous models of community mixing found both an effect of assembly history and a combinatorial effect (Gilpin 1994, Toquenaga 1997, Wright 2008). This is because even mixing among random communities could sometimes produce asymmetry due to the rarity of multi-species attractors in phase space just as with the nonrandom communities. Our experiment does not include random communities. This is because, in an experimental setting, it is not possible to generate randomly assembled communities since the effect of deterministic assembly history cannot be eliminated. This is not a shortcoming of our approach, but rather it is an indication of the probable rarity of completely randomly assembled communities in nature. Furthermore, several lines of evidence suggest that asymmetry at the community and guild level were influenced by assembly history ( $H_1$ ) and were not random. First, although cases of asymmetry occurred in TT and TC, we found significant overall asymmetry only among CC mixes that included guilds with more species per guild than in TC or especially TT mixes. This is concordant with Gilpin's simulations, in which competition-driven extinctions during assembly enhanced the likelihood of asymmetry under mixing. Second, extinctions were quite frequent during the assembly process. We did not observe any consistent effects of extinction rate during assembly on the outcome of mixing, but the timing,

order, and species identity of extinctions and density changes likely had strong effects (Drake 1990, Lundberg et al. 2000, Fukami 2004) analogous to the assembly method in Gilpin's model.

The significant trend toward asymmetry is a robust result because our experimental system both maintained key features of theoretical models and incorporated substantial novel complexity. Consequently, we also find evidence for effects that have not been considered by theory. In contrast to our results that found lower asymmetry in TT and TC than CC mixes, Wright (2008) found substantially more asymmetry when simulating mixing of simple trophic communities than mixing competitive communities ( $H_2$ ). Our failure to support  $H_2$  may be explained by three complexities that are absent from Wright's model relating to the guild structure of our trophic communities. First, Wright's model did not include unsaturated communities. Our trophic communities have fewer species in the omnivore and algae guilds, making it more likely that under mixing a "niche-filling" process occurs on resource heterogeneity (Davies et al. 2009). This could reduce post-mixing competition and enhance persistence. A role for niche-filling is suggested by nonsignificant asymmetry for bacterivores (a guild likely not to be saturated at two species [Davies et al. 2009]). Second, the traits of species in Wright's model were fixed. However, species may show adaptive feeding responses (behavior or plasticity) to mixing in trophic communities that reduce resource competition and enhance persistence (Petchey 2000). Supporting this possibility, we found that omnivores (generally most flexible in diet) show nonsignificant asymmetry despite containing relatively more species than other guilds. Third, Wright's model included only a predator and prey guild, whereas our experiment included up to six guilds. Trophic and competitive communities differ in their capacity to "swap" guild modules rather than individual component species. Upon mixing, TT or TC mixes can, for example, maintain the omnivores from one community but the herbivores and predators from another. Mean asymmetry is often high within guilds (higher than the overall community-level asymmetry in four of five guilds; Table 1) suggesting that between-guild interaction is more intense under sudden mixing than interactions between whole communities.

Although asymmetry may seem only marginally more common than under our null model, it is important to emphasize that even the occasional occurrence of a highly asymmetric outcome of mixing can be a major event that produces the complete replacement of local community composition. Our experiment has only considered the mixing of environmentally identical patches, however, in nature, synergistic or antagonistic interactions between communities and environmental heterogeneity among patches could affect asymmetry or the composition of dominant communities. Further, the frequency of asymmetry might be higher under other

assembly scenarios, such as those involving concurrent and directional environmental change (deterministically favoring one community over another [Croft 2001]) or interactions involving direct and obligate facilitative or parasitic interactions (producing linked extinctions [Goodnight 2011]). Last, study of anthropogenic interaction with ecosystems has focused on the effects of lowered connectivity while the role of increased connectivity is less well understood in contexts like species introductions producing invasive communities and invasional meltdown (Simberloff 2006), canal and corridor construction, or restoration projects requiring enhanced connectivity (Gilpin 1994, Lockwood et al. 2005). Theoretical frameworks like sudden mixing theory are urgently needed in the context of rapid anthropogenic change to ecosystem connectivity.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Summary table of species used in the experiment ([Ecological Archives E094-267-A1](#)).

### Appendix B

Methods for feeding trials and characterization of trophic structure ([Ecological Archives E094-267-A2](#)).

### Appendix C

Heat map of feeding trial growth rates and the general experimental food web ([Ecological Archives E094-267-A3](#)).

### Appendix D

Scatterplot of asymmetry in species composition ([Ecological Archives E094-267-A4](#)).

### Supplement

R script with annotations for simulation and analysis of simulation output ([Ecological Archives E094-267-S1](#)).