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Understanding Extinction and its Consequences: An Experimental Microcosm Model

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Abstract

Species extinction as one of a wide range of environmental changes poses serious threats to ecological systems. Society depends on biodiversity to sustain important ecological processes necessary for providing vital services to humanity. Loss of biodiversity has a potential to disrupt some of these important ecosystem processes. In addition, species extinction could also indirectly affect ecosystems via the ecological connections they are part of; meaning the extinction of a species could potentially cause massive changes to the abundance and composition of interacting species. Understanding the mechanisms and consequences of extinctions is critical to making predictions on extinction effects and devising mitigation strategies. This study utilized aquatic microcosms as experimental models to investigate the consequences of the removal of a ciliate *Blepharima japonicum* on the abundance of residual ciliates *Colpidium striatum* and *Paramecium caudatum* as well as total bacteria population. At low enrichment, *Blepharisma* excluded *Colpidium* to extinction prior to its removal; the removal of *Blepharisma* caused *Paramecium* to increase proportionately, but did not have any effect on its time of extinction. Bacterial population of communities where *Blepharisma* was removed were higher than where they were not. In the bacteria trophic level, *Serratia* appeared to outcompete the other bacteria species significantly. The results suggests that at low energy levels, the extinction of a species will likely cause an increase in the abundance of its competitor even though this increase will likely not guarantee its long term persistence. A species' extinction would also increase the abundance of its prey, which could cause a bloom, causing prey to use up available nutrients faster, which could potentially lead to rapid habitat collapse. Further research should utilize more trophic levels to determine the possibilities of detecting cascading effects of extinction across trophic levels. More in-depth protists-bacterial level research is also encouraged to provide insights on survival mechanisms, competition and co-existence and the factors affecting them; this will form the basis for more understanding on the fundamentals of matter and energy transfer across microbial trophic chains.

Keywords: Extinction; Environmental change; Removal experiments; Microcosms

Introduction

Earth is currently witnessing an era of rapid human--driven biological, hydrological and climatological changes with the potential to cause massive harm to ecological systems [1]. Flurries of scientific researchers have established series of case studies demonstrating diverse kinds of changes at different spatial scales [2-4]. Global climate is changing at unprecedented rates [4]; deforestation and biodiversity loss is increasing (Turner et al. 2011) [3,5,6]; changes in biogeochemical cycles are becoming more evident [2] etc. Environmental changes have several important drivers. One such driver of environmental change is extinction. Species extinction poses serious ecological/socioeconomic consequences. Diamond [7] famously described the 'Evil Quartet' of habitat destruction, over--exploitation, introduced species and cascading extinction as the major drivers of biodiversity loss. Hooper et al. [8] argued that the impacts of species extinctions could be as devastating for humans as air pollution and climate change. There are mounting evidences suggesting that extinctions may alter crucial processes necessary to maintain the sustainability and productivity of ecological systems [1]. If current rates of extinction continue to accelerate, changes in ecological processes will also likely accelerate to destructive proportions [9].

Environmental changes that accelerate extinction have intensified over the years; desertification, loss of tropical forests, pollution (MEA, 2005), but for most parts of the world and for most species, the rates of extinctions haven't been adequately quantified or haven't been quantified at all. Determining when the last individual of a species has died is an extremely difficult task [10] and monitoring the population trends of threatened species of small vertebrates/invertebrates is most times impossible [11].

This study seeks to improve understanding on the consequences of extinction on ecosystems.

Methods

Microcosms

The experiment utilized standard culture methods for protists [12] to set up simple microbial food chains in aquatic microcosms. Microcosms used in this experiment were covered 25ml Polystyrene Universal tubes. Tube lids were loosely covered to allow for air circulation but also to prevent any form of contamination. These tubes were filled with 10mL of supernatant from medium made from powdered freeze-dried Chlorella in mineral water at a concentration of 0.5g/L. Before use, the medium was autoclaved and inoculated with *Bacillus subtilis, Pseudomonas fluorescens, Serratia marcescens* and other unindentified bacteria filtered from the stock cultures of the protozoan species used in the experiment. Inoculations were done in a large sterile glass jar before distribution to the microcosm tubes.

Experimental protocol

Microcosms consist of a mix of three known bacteria species (*B. subtilis, P. fluorescens* and *S. marcescens*), unidentified bacteria species and three protist species (*Blepharisma japonicum, Paramecium caudatum and Colpidium striatum* – all ciliates). *Blepharisma* is an omnivore that feeds on bacteria and other ciliates; *Paramecium* and *Colpidium* on the other hand are bacterivores feeding solely on bacteria. In the experiment, seven different food webs were created: all three protist species combined (B+P+C), all possible two protist species combination (B+C; B+P; P+C), and all three protist species singly (B; P; C) with bacteria. All food web combinations were replicated five times with the exception of B+P+C, B+P, and B+C which were replicated ten times (prior to removal of *Blepharisma*). This yielded a total of 50 microcosms. Microcosms were given unique ID number 1 – 50 (See Table 1) and incubated under constant experimental conditions (25°C). Initial stocking density was 20 each for all three ciliates per microcosm.

Table 1: Food web combinations for all 50 microcosms.

Food Web Combination	B + P + C	B + P	B + C	B + C	B	P	C
	1-10	11-20	21-30	31-35	36-40	41-45	46-50

B = *Blepharisma*, P = *Paramecium*, C = *Colpidium.*

Measuring abundance

The experiment lasted for 23 days. Population abundance count was done 4 times a week (Mondays, Tuesdays, Thursdays and Fridays) until the 23rd day after species introduction, corresponding to approximately 36 generations. Population densities were estimated by gently swirling microcosms to attain homogeneity, then sampling out known volumes of solution from each onto a sterile petri dish and counting the species. Sterile petri dishes used were left covered while counting, so that samples removed from microcosms can be returned with no contamination. In situations where species were too dense to count reliably, the samples were further divided into smaller portions and diluted with sterile media for a more convenient and reliable estimation. Efforts were taken to ensure microcosms were left out of experimental conditions (in this case 25°C) for as short a time as possible.

Removal experiments

Blepharisma spp. is widely regarded as photosensitive ciliates [13] and there have been widely reported cases of light-induced cell deaths at different levels of light intensity at specific durations (Takada and Matsuoka, 2009; Terazima et al., 1999). This research aims to use light to remove *Blepharisma* from aquatic communities, and to investigate the consequences on inherent community structure.

Removal experiment trial

With strong evidences to support its photosensitive tendencies, a trial experiment was carried out to ascertain the shortest time to completely kill *Blepharisma* with LED lights in a 10mL aquatic community and to investigate if LED light has any effect on *Paramecium* and *Colpidium,* The experiment was conducted using three ciliate species (*Blepharisma, Paramecium and Colpidium*) in combination with three known bacteria species (*B. subtilis, P. fluorescens* and *S. marcescens*) and unidentified bacteria species to form a food web in a 10mL microcosm. Microcosm experimental conditions were the same used in the main experiment setup. Food webs were subjected to LED lights at three different time treatments (10, 20 and 30 minutes) in three replicates making a total of 9 microcosms. Initial densities of ciliates were approximately *Blepharisma* 170, *Paramecium* 280, and *Colpidium* 900 per microcosm. Tube was held in place with a retort stand while LED lights were pointed from top and bottom of the tube. Tube was completely wrapped with foil so that light can bounce back and forth foil and remain within tube. After removal, known samples were removed from microcosms and counted before and after *Blepharisma* removal using standard techniques mentioned in section 4.3. Result showed that applying LED lights from underneath and above polystyrene universal tubes was effective in removing *Blepharisma* in 10, 20 and 30 minutes when in combination with *Paramecium* and *Colpidium* in a community.

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The result also suggested that there was no effect of the light treatment on the population of *Paramecium* and *Colpidium* an hour after the removal of *Blepharisma*. No difference in *Colpidium* population after light treatment in 10 minutes, 20 minutes and 30 minutes (Paired two--sample t--test: DF = 2, t = 2.92, p > 0.05). In the same vein, there was no difference in *Paramecium* population after light treatment in 10 minutes, 20 minutes and 30 minutes (Paired two--sample t--test: DF = 2, t = 2.92, p > 0.05).

Main removal experiment

Blepharisma removal was carried out on day 10 of the experiment. *Blepharisma* was removed from communities B+P+C, B+P, and B+C. Every one of these food webs were established in ten replicates prior to *Blepharisma* removal. For each of these food web combinations, five microcosms were randomly selected from the available ten replicates. These were exposed to the LED light treatment, following protocol enumerated in section 4.4.1. Selected microcosms were exposed to light for 20 minutes to ensure complete removal of *Blepharisma* from communities. Species abundance was measured before and after LED light inducement. Results of species count showed *Blepharisma* removal was successful and there were no effects of LED light on *Paramecium* and *Colpidium.* After *Blepharisma* removal, the experiment comprised of ten treatments in five replicates (Table 2).

Table 2: Community composition after *Blepharisma* removal.

Treatments	BPC	BPC*	BP	BP*	BC	BC*	PC	B	P	C

*B = *Blepharisma*, removal.

Bacteria density estimation

Bacteria density was estimated using the serial dilution and plate count method. This was done in the 22nd day of the experiment. Because bacterial densities are expected to be low after much grazing by protists, dilution was done 1/2 and 1/4. Serial dilution was carried out using a microtiter plate. 200µµl solution was removed from microcosms and put in the first well of the microplate plate. Subsequent wells were topped with 100µµl water. 100µµl of microcosm solution was removed from the first well (the whole) and diluted in the next well containing water; 100µµl of diluted solution was further transferred to the next well and mixed to achieve 1/4 dilution. This procedure was repeated for all 50 microcosms. 2µµl from each pocket was then transferred to LB agar plates; 5 microcosms samples per plate. To prepare LB agar, bactopeptone (10g/L), yeast extract (5g/L) and salt (5g/L) were measured and put into a 250ml duran flask, water was added to point 200ml and mixed. The pH was adjusted to 7.5, agar (1.5% of 250ml) was added to solution then water was topped to 250ml. The solution was autoclaved, allowed to cool then poured into 10 plates; approximately 25ml per plate.

Statistical analysis

To detect differences in population abundance of *Paramecium* and bacteria where *Blepharisma* extinction was induced and where it was not, a two--sample T--test assuming equal variances (homoscedasticity) was used, comparing the sample means at specific points in the growth curve. Also, a paired--sample T--test was used to ascertain if LED light treatments had any effects on *Paramecium* population by comparing abundance before and one hour after *Blepharisma* removal. The effect of competition on *Colpidium* was investigated using Analysis of variance (ANOVA) to compare *Colpidium* abundance across different combinations. Significant differences were tested at 95% confidence interval. All statistical analysis were carried out using MS Excel 2011 and StatPlus version 5.8.2.0

Results

Observations before removal of *Blepharisma*

All three ciliates (*Paramecium Colpidium* and *Blepharisma*) increased in abundance in all microcosms for the first few days. Growth rate was noticeably faster in microcosms with single ciliate species than it was in combination. This growth trend continued until day 7 when *Colpidium* (in communities BPC and BC) took a sharp decline till they completely went extinct on day 9. See Figure 1B.

Of the different food web combinations involving *Colpidium*, *Colpidium* significantly faired better when grown alone (ANOVA, DF = 3, 26, p < 0.05), followed by when in combination with *Blepharisma.* There was no significant difference in *Colpidium* population between communities PC and BPC (ANOVA, DF = 1, 13, p > 0.05). However, their population decreased significantly in communities where *Blepharisma* was present (BC and BPC) until they completely went extinct on day 9. *Paramecium* also subsequently outcompeted *Colpidium* for resources even though *Colpidium* growth went up in the earlier instance (see Figure 1C). Apparently, competition had an effect on *Colpidium* as it performed better when grown alone than it did when in combination with other ciliates.

Blepharisma on the other hand increased in all microcosms it was present, peaked on day 8 and remained stable prior to removal. *Blepharisma* however performed best when in combination with *Colpidium* (ANOVA, DF = 3, 31, p < 0.05), adequately outcompeting *Colpidium* in all microcosms that contained both species. *Blepharisma* alone, *Blepharisma* with *Paramecium* and *Blepharisma* in combination with *Colpidium* and *Paramecium* had similar abundance and growth rate. There was no significant difference in *Blepharisma* population abundance in these three food web combinations (ANOVA, DF = 2, 22, p > 0.05). See Figure 1.

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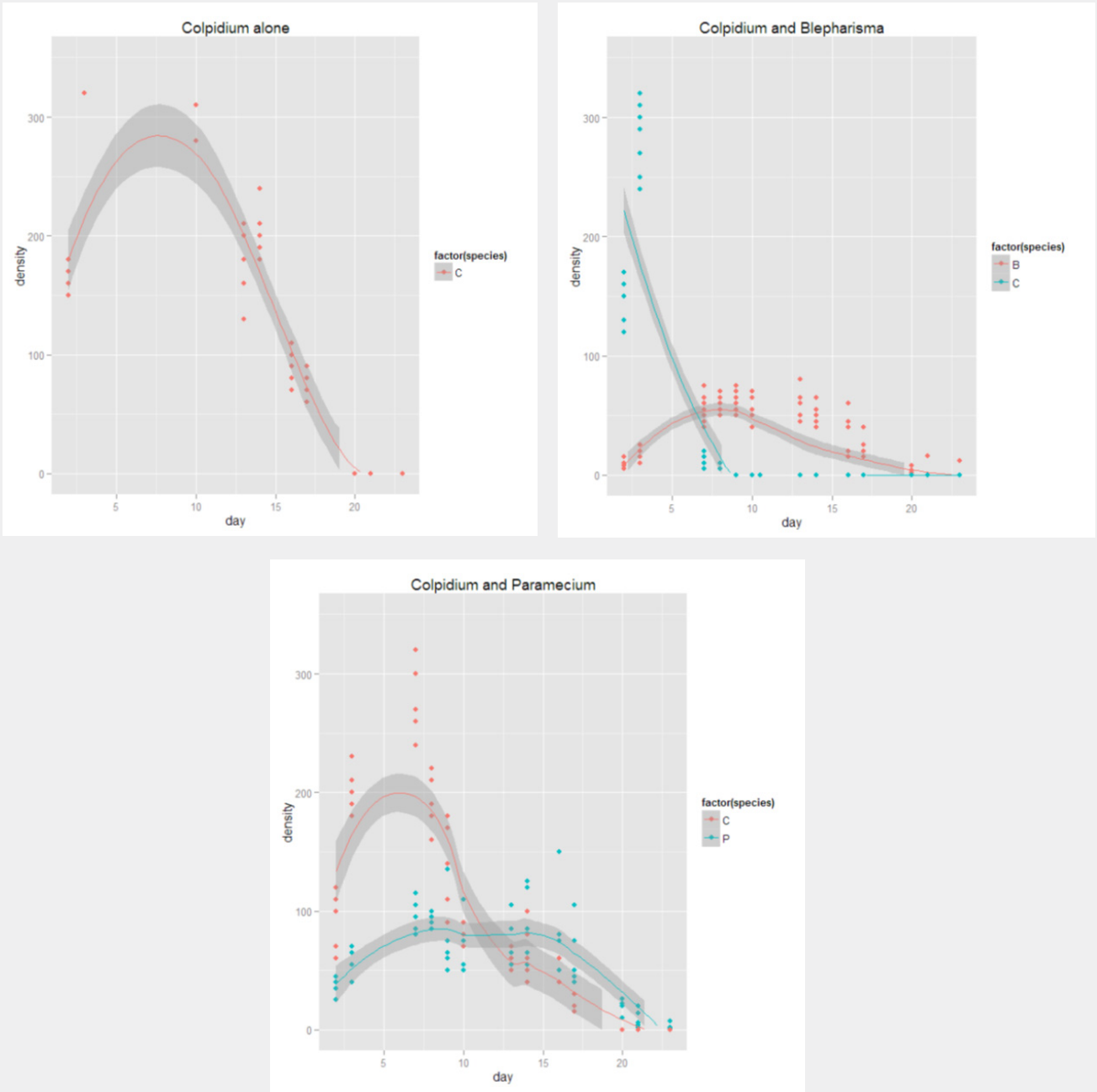

Figure 1: Population abundance trends of (A) Colpidium alone (red); (B) Colpidium (green) and Blepharisma (red); (C) Colpidium (red) and Paramecium (green) plotted through time. The y-axis range panel represents number of individuals per ml; the x-¬□ axis represents time in days. Dots represents microcosm numbers. Each dot stands for one microcosm. B = Blepharisma, P= Paramecium, C = Colpidium.

Paramecium also increased in abundance in all communities but performed best in when grown alone and when grown in combination with *Colpidium* (ANOVA, DF = 3, 26, $p < 0.05$). There was no significant difference in *Paramecium* abundance between communities BP and BPC (ANOVA, DF = 1, 18, $p > 0.05$). Generally, the growth rate of *Paramecium* was relatively stable. Day 10 saw *Paramecium* begin to decline in communities where they were in combination with *Blepharisma*

Observations following removal of *Blepharisma*

There was no effect of the 20 minutes LED light treatment (used to remove *Blepharisma* from the randomly selected

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communities) on the population of *Paramecium* an hour after the removal of *Blepharisma.* This observation was consistent for the BPC and BP communities (Paired two sample test: DF = 2, t = 2.131847, p > 0.05). *Blepharisma* went extinct in every community where it was exposed to LED light treatment.

Following removal of *Blepharisma*, a declining *Paramecium* population began to increase significantly in communities that had both species in the (Figure 2 & 3). They also performed significantly better than communities were *Blepharisma* was not removed (Two sample test: DF = 8, t = 1.86, p < 0.05). Nothing can be said of the *Blepharisma+Colpidium* communities because *Colpidium* went extinct before *Blepharisma* was removed from the community. *Paramecium* continued to decline in communities where *Blepharisma* was not removed but decline rates were slow and stable. See Figure 2 & 3.

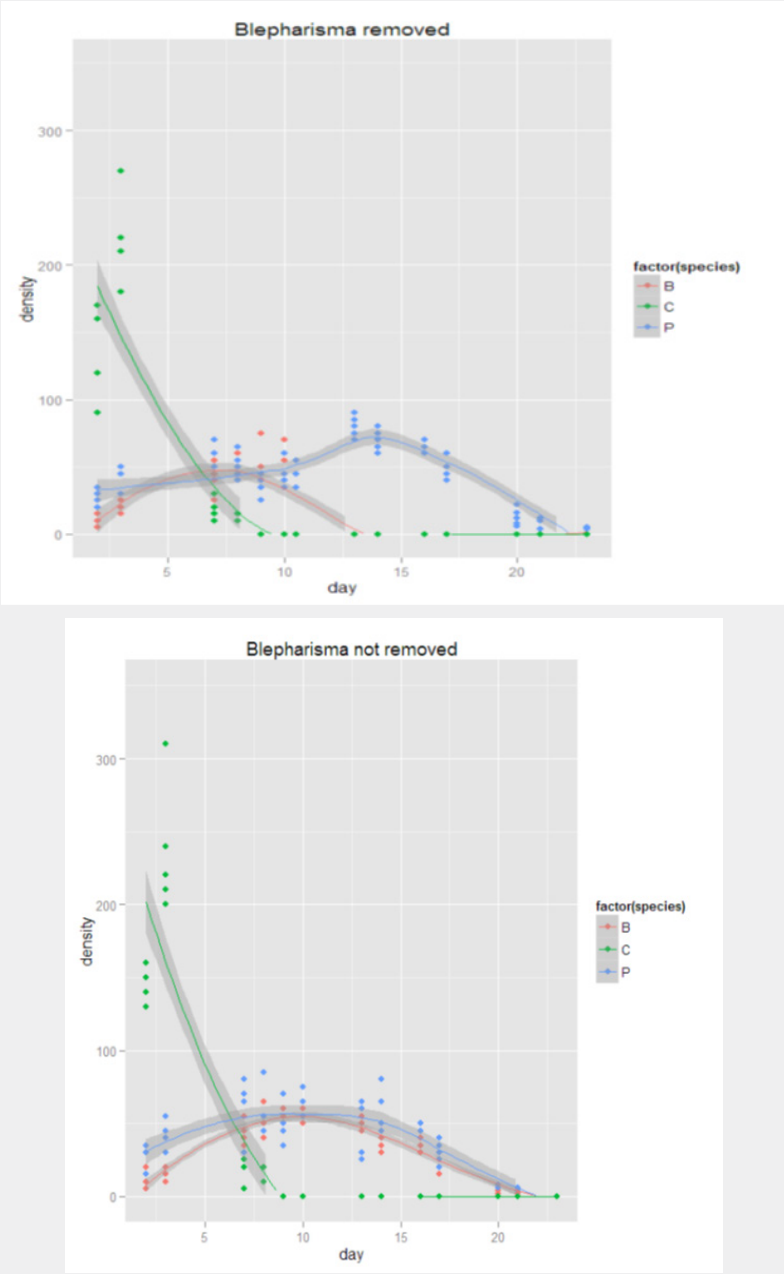

Figure 2: Population abundance trend of Blepharisma (red), Colpidium (green) and Paramecium (blue) before and after Blepharisma removal. (A) Population trends in BCP microcosms where Blepharisma was removed (B) Population trends in BCP microcosms where Blepharisma was not removed. The y-axis range panel represents number of individuals per ml; the x-axis represents time in days. Dots represent microcosm numbers. Each dot stands for one microcosm. B = Blepharisma, P= Paramecium, C = Colpidium.

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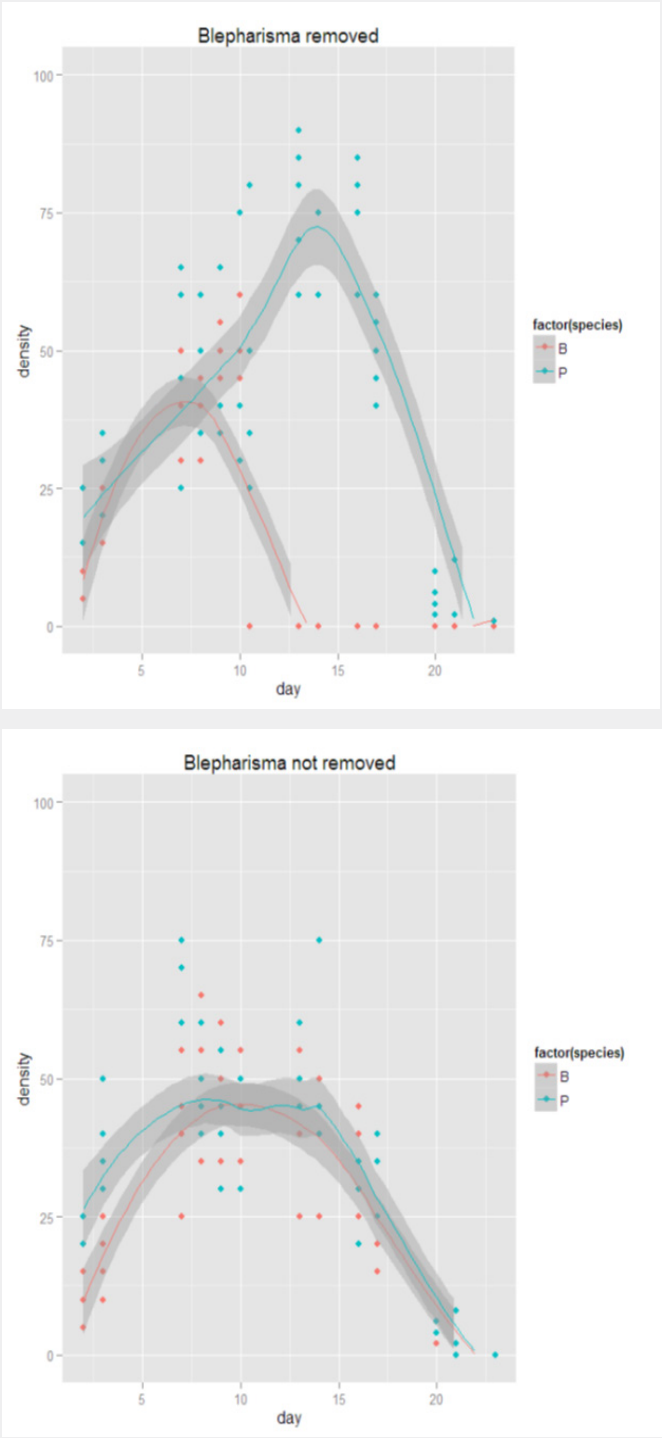

Figure 3: Population abundance trend of Blepharisma (red), and Paramecium (green) before and after Blepharisma removal. (A) Population trends in BP communities where Blepharisma was removed (B) Population trends in BP communities where Blepharisma was not removed. The y-¬□ axis range panel represents number of individuals per ml; the x-¬□ axis represents time in days. Dots represent microcosm numbers. Each dot stands for one microcosm. B = Blepharisma, P= Paramecium.

Where *Blepharisma* was not removed, *Paramecium* went completely extinct on day 23. However, time of extinction of *Paramecium* did not differ significantly for the both treatments (*Blepharisma* and *Blepharisma*) (Two sample test: DF = 8, t = 1.86, $p > 0.05$) even though *Paramecium* was still present in two of the five replicates in the BCP (B) community and present in one of five replicates in the BP (B) community at day 23 (last day of the experiment). See Figure 2 & 3.

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Observations in combinations with no removal

In 4 combinations (20 microcosms) where *Blepharisma* was not removed at all, certain observations were also recorded: *Colpidium* continue to decline in communities where they were grown alone and in combination with *Paramecium* until they went completely extinct in both communities on day 20. *Blepharisma* when grown alone declined slowly after peaking at day 13 until it went completely extinct on day 20. *Paramecium* also slowly declined in population when grown alone and when in combination with *Colpidium* after peaking on day 13. *Paramecium* however persisted the longest in all communities it was part of, albeit in low numbers. Of the 50 microcosms used for the experiment, only 10 did not go extinct as at day 23 of the experiment.

Observation of bacterial density following Blepharisma removal

There was clearly an effect of *Blepharisma* removal on bacterial population as total bacterial densities in communities where *Blepharisma* was removed were significantly higher than in communities where *Blepharisma* was not removed. This observation was consistent for the 3 communities BPC, BP and BC ($DF = 8$, $t = 1.85955$, $p < 0.05$) where *Blepharisma* removal was induced (see Figure 3). Also, observations from plate count showed evidence of only two types of bacteria colonies present (*S. marcescens* and another) even though three bacterial species in addition with potentially unknown bacterial species were used to set up the communities. Plate counts showed *S. marcescens* significantly outcompeted the other bacteria ($DF = 8$, $t = 1.8594$, $p < 0.05$) in all three communities (see Figure 3) and this dominance increases with decreasing dilutions. In other microcosms, bacterial densities were highest in communities where *Colpidium* was grown alone, followed by when in combination with *Paramecium*, and then followed by *Paramecium* alone. *Blepharisma* when grown alone had the lowest bacterial density of all combinations made.

Discussion

Effect of competition on *Colpidium* population

The competitive exclusion principle propounded by Gause [14] states that two species competing for same resource cannot coexist stably without one having an advantage over the other till it gradually drives it to extinction in the long run. The result enumerated in section 5.1 showed how *Colpidium* was rapidly excluded in all microcosms in which it has a competitor, especially by *Blepharisma.* Competition in this scenario may have been heightened by resource availability factors given that the enrichment level of the aquatic communities in which they thrive is relatively low. It is important however to recognize that bacterial density counts suggested that under the research experimental conditions, *Blepharisma* in the single species microcosms reduced bacterial densities the most. Fox [15] opined that in monocultures, ciliates that reduced bacterial densities the most are the dominant competitor. *Blepharisma* in this scenario may have driven *Colpidium* to extinction via this mechanism. Grazing abilities may not be the most ideal competition gradient to judge from as competing species with varying grazing capacities have been shown to coexist in stable equilibrium [15] and competing species with analogous grazing capacities may sometimes exclude each other [16]. However, grazing capacity is a very useful and popular compass to determine a dominant competitor. It is also of utmost importance to note that *Colpidium* was excluded very rapidly by an omnivore (The intraguild predator *Blepharisma*). The mechanisms and conditions for intraguild predation are still not completely understood. A number of theories and assumptions have been propounded for these kinds of interactions: Holt & Polis [17] opined that an intraguild prey must demonstrate competitive superiority for resource to achieve stable equilibrium. The single species bacteria density results may have suggested this criterion was not met, as *Blepharisma* appeared to have grazed the most bacteria and so may be the dominant competitor. Diehl & Feissel [18] suggested that since the intraguild prey is both a competitor and a prey, it has the capacity to enhance or inhibit the intraguild predator. Enhancement of the intraguild predator can be attained if growth rate gain from consumption of intraguild prey is more than the growth rate loss from low density of resource where the intraguild prey is present. The opposite can be said for the inhibition criteria. This theory suggests the intraguild predator is expected to thrive at low enrichment levels and will achieve its highest densities in the presence of an intraguild prey than in its absence. The result agrees with this theory as *Blepharisma* thrived at low enrichment in the presence of an intraguild prey *Colpidium.* In direct contrast to findings of this research, Morin (1999) reported that *Blepharisma* was an inferior competitor for bacterial resource at low enrichment in comparison to *Colpidium,* but with higher bacterial density, the reverse was the case. In another report, Diehl & Feissel [19] also reported intraguild predator, *Blepharisma* dominance on prey following enrichment of their resources.

There is however no clear evidence of feeding trade--offs made by *Blepharisma* between intraguild prey and bacteria but the effect its presence had on *Colpidium* at low enrichment level is significant and could be as a result of any of the scenarios highlighted. It is also worthy of note that *Paramecium* also outcompeted *Colpidium* subsequently even though at a much slower pace.

Consequences of Blepharisma removal on Paramecium population

Among a considerable number of extinction consequences, one prominent consequence is the effect it may pose on interacting species' population [20]. This assertion is supported strongly by the extinction cascade theory, which states that the impact of the extinction of a primary species has the potential to cause secondary extinctions by virtue of co--extinctions of very

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dependent species [21,22]. The result of this experiment however suggested that this theory is likely not applicable with competing species within the same trophic level as there is no evidence of any interdependency relationship between competitors *Blepharisma* and *Paramecium*. In fact, the population of *Paramecium* increased markedly following the removal of its competitor *Blepharisma.* With low energy levels in the aquatic community.

Blepharisma may have been exerting competitive pressure on the population of *Paramecium.* Its removal from the community facilitated the resurgence of *Paramecium.* It would have been interesting to monitor the interaction between *Colpidium* and *Paramecium* following the removal of *Blepharisma* but *Colpidium* went extinct before *Blepharisma* removal. Given the low energy levels, perhaps *Blepharisma* should have been removed two days earlier. Also, the presence of a top predator would have provided the dependence criteria needed to adequately understand the dynamics of extinction consequences across trophic levels. However, the study provided important insights on extinction and how it could have positive impacts on competitors within the same trophic levels. Alternatively, a scenario where the extinction of a species from a community will reduce the population of its competitor could also be possible depending on the dynamics of the interaction strengths/weaknesses between the two competing species and their preys [23], but this is hardly the case here in similar single trophic level interaction patterns.

Effects of *Blepharisma* removal on time of extinction of *Paramecium*

In this study, comparing time of extinction of *Paramecium* in microcosms where a competition interaction between Blepharisma and Paramecium was sustained with microcosms where *Blepharisma* extinction was induced provided insights on the veracity of this theory. The results showed that even though *Paramecium* increased following the removal of its competitor *Blepharisma,* the overall extinction time of *Paramecium* in both treatments did not differ significantly. This suggests that despite lack of competition for *Paramecium*, low energy levels of the aquatic community still couldn't sustain their populations far long enough to go extinct a little later. This study is in conformity with the findings of Ferguson & Ponciano [24]. In summary, the research deduced that with low enrichment, the extinction of a species' competitor would not extend the time of extinction of the species.

Effects of Blepharisma removal on bacterial prey densities

Evidence from the results of this study suggested the extinction of a bacterial predator *Blepharisma* from the protists trophic level might have led to a relative increase in total bacterial densities. Apparently, a combination of *Blepharisma* and *Paramecium* exerts more top--down pressure on the bacterial population; removal of one reduced this top--down influence. With a reduced protistan predator influence, bacterial prey reproduced relatively faster, thus using up scarce nutrients faster, this could be an explanation for the generally fast rate of community collapse. In conformity with findings of this research, Bell et al. [25] reported total bacterial population increase in the absence of predators. However, their study revealed that the increase in bacterial population did not lead to a corresponding increase in bacterial diversity. Diversity is often times the biodiversity gradient used to measure the stability of ecological systems [26-47].

Conclusion

As the reviews in section 1.1.3 to 1.1.5 suggest, extinctions have been predicted to pose serious threats to ecological systems both directly and indirectly. Probable cases and scenarios of direct consequences of extinction are well documented in peer--reviewed journals, newspaper articles, magazines and popular literature. Indirectly, extinctions have also been predicted to disrupt ecosystems via the interacting links which species are part of. This research showed that within a simple single trophic level ecosystem involving protists and bacteria, the consequences of extinction of *Blepharisma* wasn't totally disastrous for interacting species. A competing *Paramecium* species increased proportionately with *Blepharisma* extinction due to the removal of its competitor and the bacterial population where *Blepharisma* extinction was induced showed higher densities compared to where *Blepharisma* was present due to the removal of one of their predators. There was no evidence of extinction cascading effects as a consequence of *Blepharisma* extinction. Also, there was no evidence of any effect of *Blepharisma* extinction on the time of extinction of its competitor.

These findings however showed patterns that emerge within a single trophic level-primary producers community. Most real world natural processes in aquatic systems occur in very complex food web interactions, connecting multiple trophic levels (Polis and Strong 1996). The patterns of reaction to extinction may differ markedly with more trophic levels, as one would be able to monitor how dependent species would react to loss of their food source and how this will affect overall species composition, ecosystem structure and functioning. Further research should focus on detecting cascading effects of extinction across trophic levels to really grasp the concept of extinction beyond competition interactions. It may also be interesting to understand the role of temperature in these types of interaction both at the protist and the bacteria trophic levels.

Also, the patterns observed at the bacterial trophic level poses lots of questions on predation preferences, survival mechanisms, competition and co--existence and the factors affecting them. Understanding the patterns of these interactions will aid predictions on how protists graze on bacteria which is an important process that will form the basis of more understanding on the fundamentals of matter and energy transfer across microbial trophic chains. More research is encouraged.

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Declaration

Author contribution statement

Amabogha O. developed, designed the experiments and analyzed, interpreted the data and also wrote the paper.

Amabogha B. did correction of the write up.

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Data availability statement

Data included in article/supp. material/referenced in article.

Declaration of interest's statement

The authors declare no conflict of interest.

Additional information

No additional information is available for this paper.

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