THE INTERACTIVE EFFECTS OF ENVIRONMENTAL WARMING

AND HABITAT FRAGMENTATION ON THE STRUCTURE OF

EXPERIMENTAL PROTIST COMMUNITIES

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SUMMARY

Global biodiversity is threatened by substantial and increasing human activity, such as human-induced environmental warming and habitat fragmentation. The effects of warming and fragmentation on biodiversity have been carefully studied, yet their potential interactive effects are less understood. Using freshwater protist communities subject to warming and fragmentation, I present the first experimental evidence of the interactive effects of warming and fragmentation on biodiversity. Somewhat unexpectedly, I found that fragmentation positively affected biodiversity. The magnitude of the effects of fragmentation, however, varied with the warming treatments. In one of our experimental communities (Combination B), fragmentation showed a much stronger positive effect on protist richness when warming was not conducted, but it showed a weaker but significant positive effect under a warming scenario. In other communities (from Combination C), however, fragmentation showed a stronger positive effect on richness when warming was present than when it was absent in experimental treatments. I further show that these long-term effects may be due to the alternation of individual species growth rate affected by warming, fragmentation and their interaction in short-term projections. Moreover, these findings of positive effects of fragmentation and interactions with warming can be useful for understanding conservation strategies, especially in areas where biodiversity is currently threatened or will be in the future.

CHAPTER 1

INTRODUCTION

Organisms affect their environment by seeking food and suitable chemical or physical conditions. We as humans are one such species that have drastically reshaped our environment (Tilman et al. 1997, Vitousek et al.1997, Wackernagel et al. 2002). Human activities have introduced many threats to biodiversity, including rapid climate change, habitat loss and degradation, overexploitation, species invasion, pollution and disease (Chapin et al. 1997, Daszak et al. 2000, Pimm et al. 1995, Wilcove et al. 1998). For example, the need for row-crop agriculture, industrialization and urbanization has transformed roughly 50% of lands accessible by humans (Vitousek et al. 1986, Vitousek et al.1997). This transformation degrades the original landscape with anthropogenic landscapes, which results in fragmentation (Andrén 1994, Saunders et al. 1991, Fahrig 2003). Fuel combustion in conjunction with human activities increased global temperatures $0.78℃$ on average over the twentieth century; the last 30 years (1983-2012) were the warmest decades of the past 14 centuries (IPCC 2013). Losing biodiversity will result in irreversible consequences that may change both biotic and abiotic global ecosystem processes (Chapin et al. 1997, Tilman et al. 1997). These combined threats result in rapid loss of biodiversity in the Earth's biosphere. The consequences of human activity have significantly increased the rate of species extinction worldwide (Heywood 1995, Pimm et al. 1995, Sala et al. 2000). Climate change in terms of environmental warming and habitat degradation including fragmentation are two of the most influential

factors that affect biodiversity and are driven by human activities (Parmesan & Yohe 2003, Sala et al. 2000, Thomas et al. 2004, Vitousek et al.1997).

Climate warming may induce extinction. In the Costa Rican cloud forest, a warming event in 1976 caused a drastic decline in the population of the golden toad (*Bufo periglenes*), eventually resulting in the complete extinction of this species by 1987 (Pounds et al. 1994; Pounds et al. 1997). However, single-species extinction is only a minute aspect of the diverse ecological consequences of climate warming; there are significantly community effects and interactions (Parmesan et al. 1999, Parmesan et al. 2000, Pounds et al. 1999, Root et al. 2003). Changes in community structure may follow changes in individual species traits, such as thermal sensitivity and multispecies interaction (Berg et al. 2010). Thermal sensitivity refers to how species alter their growth, behavior and reproduction in response to temperature change. Increased mean temperatures can reduce the probability of encountering a lower limit of species survival but increase the probability of experiencing an upper limit (Berg et al. 2010, Sheldon et al. 2011). If a species is sensitive to thermal changes, it will alter its previous traits to adapt, changing its life history, growth rate, or range (Berg et al. 2010). The interactions between competitors, predators, or prey may also change whether they have high thermal sensitivity or not, thus change the community structure (Post 1999, Pounds et al. 2006, Pounds et al. 2007). Moreover, mismatches in phenology may result in proportional community changes due to differences in the advancement of springtime, which may critically disturb previous community structure (Beebee 1995, Visser et al. 1998, Visser & Holleman 2001).

Land transformation by humans is a top threat to biodiversity (Chapin et al. 2000, Sala et al. 2000, Tilman et al 1994, Vitousek et al.1997) and is significantly related to urbanization and agriculture (Eppink et al. 2004; McKee et al. 2004; McKinny 2002). Transformation processes degrade the original habitat and create more isolated, smaller patches, resulting in habitat fragmentation, which is present in over half of available landscapes worldwide (Vitousek et al.1997). The reduction of natural habitats usually impacts biodiversity negatively (Haddad et al. 2015, Fahrig 2003). For example, smaller patches contain fewer species compared to undisturbed habitats because of the lack of resources, the available niche, and these patches are sometimes under the required size for some species (Díaz et al. 2000, Debinski & Holt 2000). Degraded patches also experience reduced species abundance and distribution and increased nest predation (Hartley & Hunter 1998, Schmiegelow & Mönkkönen 2002). Nevertheless, the effects of habitat fragmentation due to the separation of the habitat itself, were less understood even on the conceptual level, and are usually confounded with habitat loss (Fahrig 2003, Halia 2002). As reviewed by Fahrig (2003), the negative effects are likely due to whether species were restrained by impermeable non-habitat surroundings in small patches under an extinction threshold (Fahrig 2002, Gibbs 1998), or threatened by increased mortality due to negative edge effects of biotic interaction includig increased nest predation, parasitism, or abiotic microclimate changes (Chalfoun et al. 2002, Fahrig 2002). In contrast, the positive effects of fragmentation were even more ambiguous but common in mere-fragmentation studies (Fahrig 2003). For instance, for two competing species that were isolated by fragmentation instead of coexisting in a homogeneous habitat, the inferior competitor might survive by establishing in discrete patches while the superior

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competitor population is aggregated in certain clumped areas, assuming that fragmentation altered interactions within and between species enhancing their persistence, which may preserves biodiversity (Atkinson & Shorrocks 1981, Ives 1991, Ives & May 1985).

Dispersal has also been known to play an important role in the maintenance of biodiversity, particularly in landscapes where local habitats are fragmented. As the rate of dispersal increases, more species from the regional pool can be introduced in local habitats, resulting in increased biodiversity (Cadotte 2006, Durrett & Levin 1997, Mouquet & Loreau 2003). However, if the dispersal rate increases to an extremely high level, dispersal may reduce coexistence by homogenizing the community structure (Cadotte 2006, Mouquet & Loreau 2003). Dispersal may reduce biodiversity in fragmented habitats by decreasing the isolation of habitat patches and making fragmented communities more homogeneous in small or intermediate magnitudes (Cadotte 2006). Because of the unique role that dispersal plays in fragmented landscapes, I consider that the presence/absence of dispersal in fragmented habitats may also influence community structure.

Numerous studies have investigated the effects of environmental warming and habitat fragmentation on biodiversity, but they usually examine each threat individually or independently. Even when research focuses on a single threat, the effects were complicated and the mechanisms were highly variable on different biota and species (Parmesan 2006, Sala et al. 2000, Visser and Both 2005). However, considering their synchronicity, it is inadequate to estimate the consequence of multiple threats together without considering their potentially interactive effects, which may not be only addible.

Since there is an urgent need to conserve biodiversity, exploring the interactive effects of warming and fragmentation is critical. In one theoretical study, Travis (2003) suggested a disastrous outcome resulting from the interactive effects of climate change and habitat fragmentation using a model that considered the thresholds of these two threats, and assumed that habitat thresholds occur earlier under climate change (Travis 2003). In other studies, for example those conducted by Opdam & Wascher (2004) and Tylianakis et al. (2008), both based on reviews of existing empirical studies, the authors found potentially strong interactions among multiple environmental challenges. This evidence together demonstrates an urgent need to understand the interactive effects of multiple environmental factors on biodiversity (Thomas et al. 2001, Warren et al. 2001). Previous studies have assumed interactions by analyzing observational data using predictive models, which may cause ambiguity resulting from incontrollable factors, and indeed, interactions were mentioned to be critical but never clearly described (Opdam & Wascher 2004, Parmesan & Yohe 2003, Root et al. 2003, Sala et al. 2000, Tylianakis et al. 2008). In this study, I report the first experimental test of the interactive effects of warming and fragmentation on community structure. I used bacterivorous protists as model organisms, and introduced them simultaneously to manipulated warming processes and fragmentation conditions. I constructed freshwater communities of bacterivorous ciliated protists with short generation times, which ranged from approximately 30 to 150 generations during the eight-week experiment. Such different life cycles may reflect long-term dynamics of difference species and are not confounded by transient dynamics from the initiation of the experiment (Lawton 1995, McGrady-Steed et al. 1997, Naeem & Li 1997). By manipulating fragmentation and keeping the total habitat constant to

minimize the effects of habitat loss, I investigated the potential existence of the

interactive effects of warming and fragmented environments.

CHAPTER 2

MATERIRALS AND METHODS

The species pool for the experiment contained nine ciliated protist species:

Colpidium kleini, Halteria sp., *Loxocepholus sp.*, *Paramecium aurelia*, *Paramecium caudatum*, *Spirostomum ambiguum*, *Spirostomum teres*, *Tetrahymena thermophila* and *Uronema sp..* All of the species were bacterivores, isolated from freshwater ponds, or purchased from biological supply houses. I used three combinations of species, each of which contained five of the nine species, which were randomly selected from the species pool (Table 1).

Table 1 Species combinations of the three experimental communities.

Combination A	Combination B	Combination C
Paramecium aurelia	*Paramecium caudatum*	*Paramecium aurelia*
Colpidium kleini	*Tetrahymena thermophila*	*Paramecium caudatum*
Loxocepholus sp.	*Loxocepholus sp.*	*Colpidium kleini*
Spirostomum teres	*Spirostomum teres*	*Tetrahymena thermophila*
Spirostomum ambiguum	*Uronema sp.*	*Halteria sp.*

Microcosms were created in 25 mm × 150 mm Pyrex glass tubes filled with 24ml of a medium made from protozoan pellets (Carolina Biological Supply, Burlington, NC, USA; 0.55 g per 1L of deionized water). The medium was sterilized using an autoclave and inoculated with the three prey bacteria (*Bacillus cereus*, *Bacillus subtilis*, and *Serratia marcescens*) three days before the introduction of protists. Ten percent (10%) of the medium of each microcosm was replaced with a fresh, sterile medium every week.

A two-way factorial design was used for the experiment, with manipulation of the presence/absence of warming (constant versus a gradual warming environment) and habitat fragmentation (no fragmentation, fragmentation without dispersal, and fragmentation with dispersal). Each treatment was replicated three times. Beginning in the second week of the experiment, the temperature of the gradually warmed groups of tubes rose from 22℃ to 32℃, +2℃ per week or roughly +0.2℃ per generation, which corresponded to the increase over the past 100 years for long-lived organisms (Petchey et al. 1999). Temperatures remained at 32℃ from the beginning of the sixth to the end of the eighth week. Fragmentation began also during the second week. Each medium in the tube in the isolated-fragmented and connected-fragmented groups was separated and added to four 13 mm × 100 mm Pyrex glass tubes of 6ml each, as fragments totaling 162 tubes. Only the connected-fragmented groups were mixed as follows: on a weekly basis, ten percent (10%) of each of the four fragments were combined and added back to the original fragments immediately. Weekly sampling was conducted by inspecting the abundance of each protist species under microscopy (Figure 1).
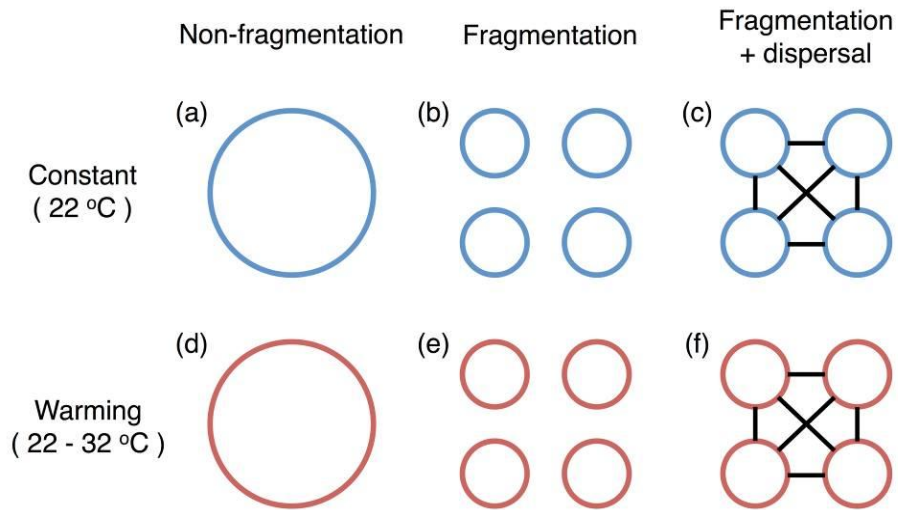
Figure 1 Experimental design. Large circles representing non-fragmentation and 24ml microcosms, small circle representing fragmented patches, 25% of the size of non-fragmentation and 6ml microcosms, and black lines representing dispersal between fragments with 10% mixing every week. Blue colors indicate constant temperature (22 ℃) and red indicate gradual warming (+2 ℃ per week, from 22 - 32℃).

To better understand the effects of warming and medium volume on each species, I performed a short-term experiment with a two-way factorial design (22°C and 32°C; 6mL and 24mL microcosms) on the effects of these factors on the growth rate of each study species. During a one week period, I sampled the microcosms twice a day to determine the abundance of each protist species, with an initial abundance set to 1 individual per ml. I used the data collected during the exponential growth phase to calculate the intrinsic growth rate, following:

$$r = \frac{[\ln(Abundance_{T_1} + 1) - \ln(Abundance_{T_0} + 1)]}{T_1 - T_0}$$

where T_0 and T_1 represent the time when the exponential growth phase began and ended.

All of the protist communities reached equilibrium before week 6. Therefore, my analysis was based on the data from the final sampling on week 8. To determine the effects of warming and fragmentation on community structure for each combination, I performed multivariate analysis of variance (MANOVA), using warming and fragmentation as the independent variables and the abundance of each species of each combination as the dependent variables, followed by an analysis of variance (ANOVA) to test the effect of these two factors on the abundance of each species. I calculated Eta-square in to determine the effect size of fragmentation in each warming condition in ANOVA. To determine the effects of warming and fragmentation on species richness, I implemented a generalized linear model (GLIM), in which species richness was considered a discrete dependent variable with a Poisson distribution and calculated pseudo-R^2 to determine the effect size of fragmentation in each warming condition. To determine the effects of these two factors on community structure and richness over time, repeated measures MANOVA and GLIM were also performed. All statistical analysis was conducted using SPSS 21.

CHAPTER 3

RESULTS

Community Structure

In all combinations, warming and habitat fragmentation had strong interactive effects on the structure of protist communities (Table 2 and Figure 2). In all communities, warming resulted in lower abundance of protist species. Habitat fragmentation, on the other hand, led to higher community abundance. The interaction term of warming and habitat fragmentation was also significant in all combinations, resulting in weaker effects of fragmentation on the community structure of gradually warmed treatments than treatments incubated in the constant environment. There were weaker effects of fragmentation on species richness of treatments that experienced warming (partial-η^2 = 0.31, 0.86 and 0.75 in Combination A, B and C, respectively) than treatments incubated in the constant environment (partial-η^2 = 0.97, 0.97 and 0.97 in Combination A, B and C, respectively). ANOVA results indicated warming and fragmentation showed strong effects on individual species (shown in Table A1). Repeated measures MANOVA across the eight week experimental time was summarized in Table A2. The main effects of warming, fragmentation and time, and all their interaction effects were significant except the warming-fragmentation interaction in combination C.

Table 2 Summary of MANOVA on the effects of warming and fragmentation on protist community structure. Significant values are highlighted in bold.

| Source	df	Wilk's λ	F	*p* value
Combination A				
Warming	5,8	<0.01	5855.85	**<0.001**
Fragmentation	10,16	0.04	6.10	**<0.001**
Warming × Fragmentation	10,16	0.04	6.17	**0.001**
Combination B				
Warming	5,8	0.01	222.51	**<0.001**
Fragmentation	10,16	0.01	12.88	**<0.001**
Warming × Fragmentation	10,16	0.03	7.05	**<0.001**
Combination C				
Warming	5,8	0.01	268.00	**<0.001**
Fragmentation	10,16	0.04	9.08	**<0.001**
Warming × Fragmentation	10,16	0.11	4.47	**0.004**
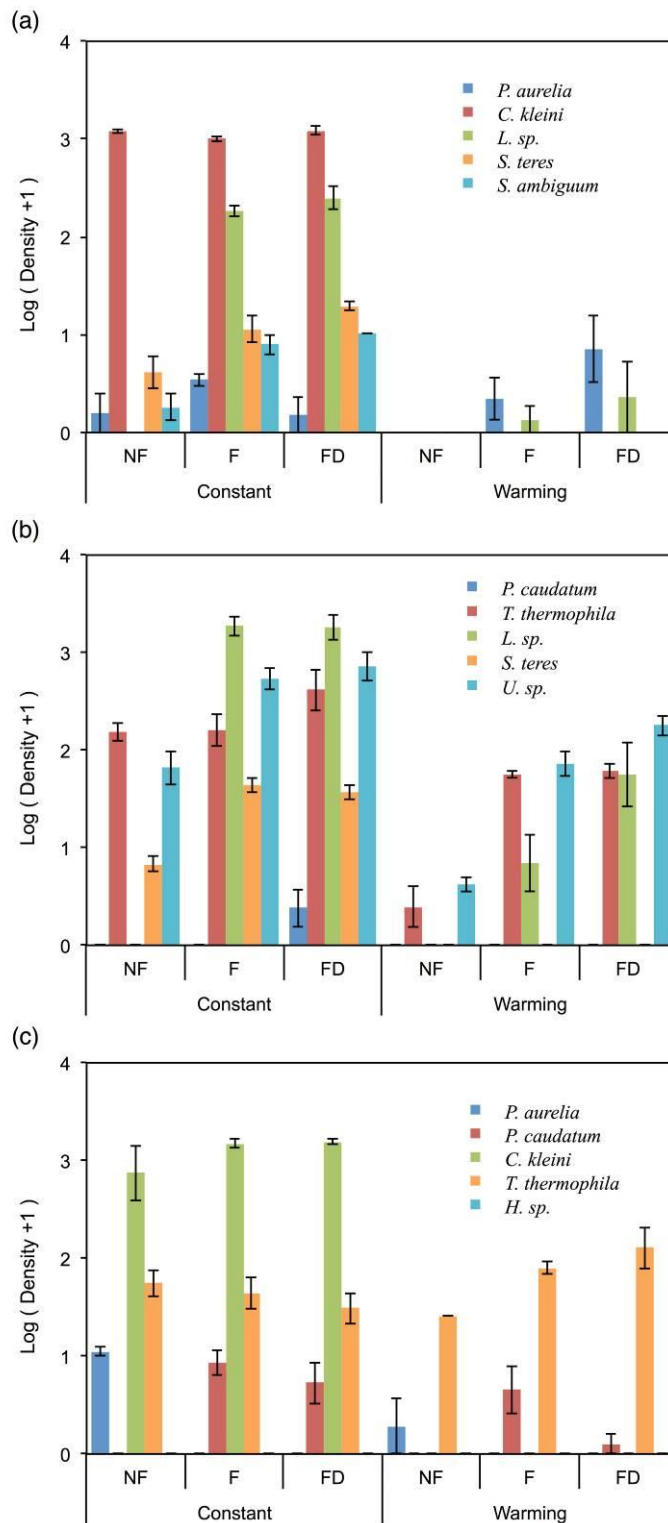
Figure 2 Bar chart of the abundance of each species from the final week of the experiment. From top, Combination A (A), Combination B (B), and Combination C (C) Different colored bars correspond to different species. The values are means±standard errors. NF, non-fragmentation; F, fragmentation without dispersal; FD, fragmentation with dispersal.

Species Richness

Overall, warming decreased species richness but fragmentation, both with or without dispersal, increased species richness in all combinations. In species combination B, there was a weaker effect of fragmentation on species richness of treatments that experienced warming (pseudo-$R^2 = 0.77$) than treatments incubated in the constant environment (pseudo-$R^2 = 0.88$). On the other hand, in combination C there was a stronger effect of fragmentation on species richness of treatments that experienced warming (pseudo-$R^2 = 0.36$) than other treatments which displayed no effect when incubated in the constant environment (pseudo-$R^2 < 0.001$). The results were shown in Table 3 and Figure 3. Repeated-measure GLIM across eight weeks of experimental time was summarized in Table A3. The interaction effects of warming and fragmentation were significant in all combinations.

Table 3 Summary of GLIM on the effects of warming and fragmentation on species richness. Significant values are highlighted in bold.

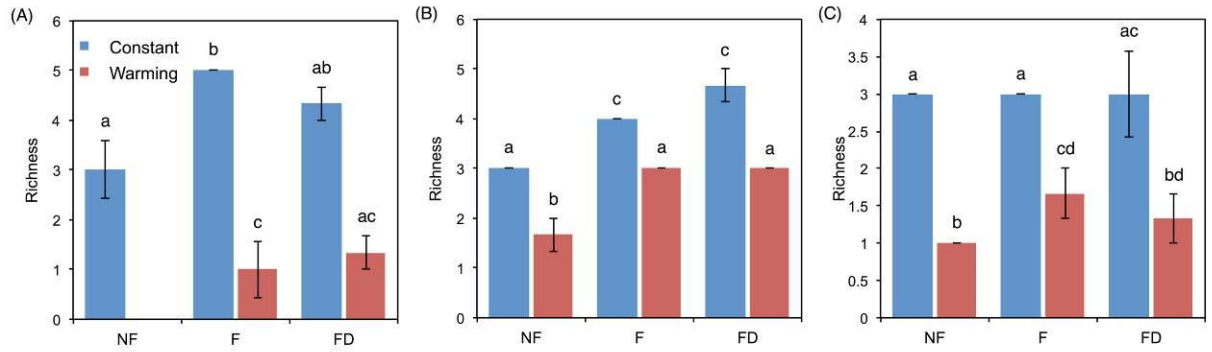| Source	df	Wald χ^2	p value
Combination A			
Warming	1	29.02	**<0.001**
Fragmentation	2	7.56	**0.023**
Warming × Fragmentation	2	0.69	0.405
Combination B			
Warming	1	57.71	**<0.001**
Fragmentation	2	35.73	**<0.001**
Warming × Fragmentation	2	10.36	**0.006**
Combination C			
Warming	1	67.04	**<0.001**
Fragmentation	2	11.03	**0.004**
Warming × Fragmentation	2	11.03	**0.004**

Figure 3 Bar chart of species richness from the final week of the experiment. From left, Combination A (A), Combination B (B), and Combination C (C). The values are means±standard errors. Bars with the same letters are not significantly different (p > 0.05), while those with different letters are significantly different (P≦0.05). NF, non-fragmentation; F, fragmentation without dispersal; FD, fragmentation with dispersal.

Individual Growth Rate under Different Volume and Temperature

Temperature and patch volume had strong interactive effects on most of the study species (Table 4 and Figure 4). For *Loxocepholus sp.*, there was a stronger effect of patch volume on growth rate in treatments incubated under 32°C ($\eta^2 = 0.97$) than 22°C ($\eta^2 = 0.56$), resulting in higher growth rates in 24ml volume at 32°C. For *P. aurelia*, there was a weaker effect of patch volume on growth rate in treatments incubated at 32°C ($\eta^2 = 0.83$) than 22°C ($\eta^2 = 0.94$), resulting in higher growth rates in 6ml volume at 32°C. *P. caudatum* showed growth only at 22°C, in the 24 ml condition. *S. ambiguum* showed greater growth rates in 6ml than 24ml at 22°C, and no growth at 32°C. For *Uronema sp.*, there was a stronger effect of patch volume on growth rate in treatments incubated at 32°C ($\eta^2 = 0.99$) than 22°C ($\eta^2 = 0.31$) resulting in higher growth rates in 24ml volume at 32°C.

Table 4 Summary of ANOVA on the effects of temperature and patch volume on the growth rate of each species. Significant values are highlighted in bold.

| Species	Source	df	F	p value
C. kleini	Temperature	**1**	**556.10**	**<0.001**
	Patch volume	**1**	4.97	0.056
	Temperature × Patch volume	1	4.97	0.056
L. sp.	Temperature	**1**	**10.15**	**0.013**
	Patch volume	**1**	**14.20**	**0.005**
	Temperature × Patch volume	**1**	**58.83**	**<0.001**
P. aurelia	Temperature	1	2.66	0.141
	Patch volume	**1**	**9.53**	**0.015**
	Temperature × Patch volume	1	**33.12**	**<0.001**
P. caudatum	Temperature	**1**	**317.37**	**<0.001**
	Patch volume	**1**	**317.37**	**<0.001**
	Temperature × Patch volume	**1**	**317.37**	**<0.001**
S. ambiguum	Temperature	**1**	**720.39**	**<0.001**
	Patch volume	1	**6.42**	**0.035**
	Temperature × Patch volume	**1**	**6.42**	**0.035**
S. teres	Temperature	**1**	**139.71**	**<0.001**
	Patch volume	1	4.43	0.068
	Temperature × Patch volume	**1**	4.43	0.068
T. thermophila	Temperature	**1**	1.14	0.317
	Patch volume	**1**	**18.28**	**0.003**
	Temperature × Patch volume	**1**	3.66	0.092
U. sp.	Temperature	1	**115.89**	**<0.001**
	Patch volume	1	**43.90**	**<0.001**
	Temperature × Patch volume	**1**	**16.43**	**0.004**
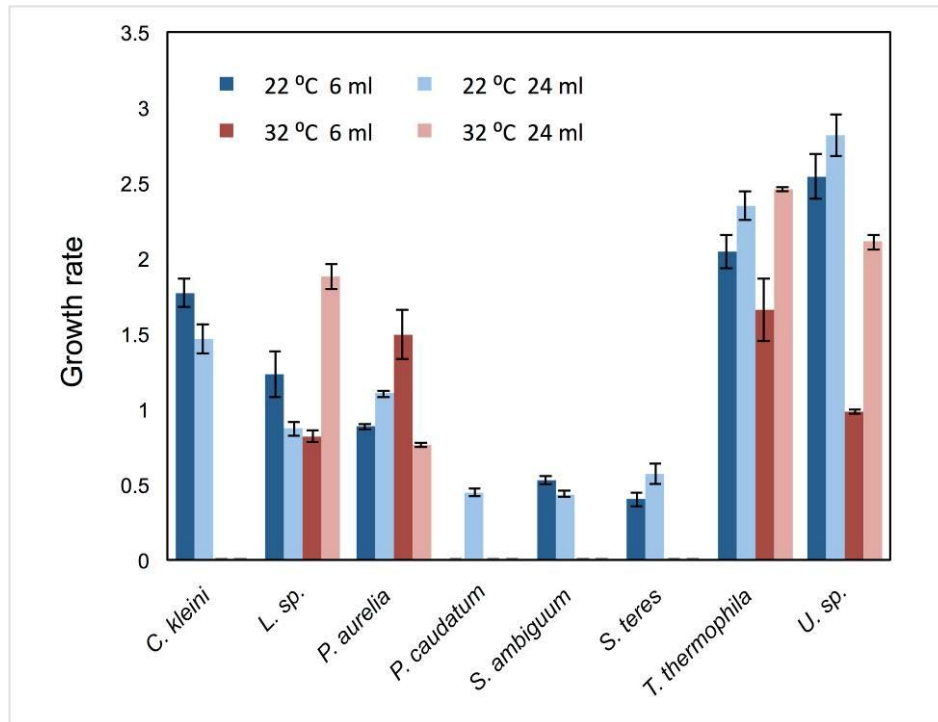
Figure 4 Growth rate of each species under different temperatures and patch volumes. The values are means±standard errors. Blue: 22°C, 6ml. Azure: 22°C, 24ml. Red: 32°C, 6ml. Pink: 32°C, 24ml.

CHAPTER 4

DISCUSSION

Environmental warming and habitat fragmentation are two major threats to ecological communities. Previous studies (Chapin et al. 1997, Parmesan & Yohe 2003, Sala et al. 2000, Tilman et al. 1997, Vitousek et al.1997) have shown that both of these two factors can considerably alter the structure of communities and therefore the functioning of these communities. Thomas et al. (2004) explored the estimated probability of extinction, and assumed that 18-35% of 1,103 species in their study will become extinction due to climate warming by the year 2050. In another study, Fahrig (2003) reviewed over 1,600 papers studying habitat fragmentation, and concluded that fragmentation had diverse effects on biodiversity. One topic that remains unclear is the interactive effect of warming and habitat fragmentation on the structure of communities. In this study, I describe an experiment that manipulated both warming and habitat fragmentation simultaneously and achieved three novel findings. First, habitat fragmentation had strong positive effects on biodiversity. Species were less likely driven to extinction in the fragmented habitats that those without fragmentation. Second, along with the overall negative effects of warming on biodiversity, there is a strong interaction between warming and habitat fragmentation. Protist communities were less affected by warming in fragmented habitats than in those without fragmentation. Third, over the short-term, I found that the growth rate of protist species was also interactively affected by warming and fragmentation.

In this experiment, warming strongly altered the community structure and reduced species richness. This effect may contribute to the destruction of ecosystems at global scale (Parmesan & Yohe 2003). Zogg et al. (1997) found that warming altered the microbial community structure as well as their metabolism and shifted soil decomposition functions. Walker et al. (2006) performed a study in which they found that warming increased shrub cover while decreased the cover of mosses and lichens, which resulted in an altered community structure and decline of biodiversity in the tundra biome, implying that warming changed ecological processes. Klanderud and Totland (2007) suggested that climate warming decreased resident diversity by increasing interspecific competition which increased the establishment of invasive species in alpine regions. In my study, warming not only decreased biodiversity but also changed the dominant species both at the end and during the experiment (Figure 2, A1, A2 & A3). This may be due to the effect of warming on the species growth rate of protists. For example, *T. thermophila* and *Uronema sp.* dominated because they retained high growth rates while *C. kleini* and *Loxocepholus sp.* suffered in warming groups (Figure 2bc & 4), likely a result of their individual responses to thermal sensitivity (Berg et al. 2010).

Fragmentation altered community structure and species richness in this study, preventing community disassembly, a non-random species loss process. This effect was unlike most current fragmentation research (Fahrig 2003). Indeed, not every component of a community responds to the same level fragmentation, as Robinson et al. (1992) mentioned in their forest experiment in which only bird communities showed extinction rate that were positively associated with levels of fragmentation. Moreover, Golden and Crist (1999) demonstrated that different feeding guilds of canopy insects had different

responses to levels of habitat fragmentation during the summer yet during the winter

abundance was not affected but richness declined through the loss rare species. A

simulation conducted by Obstfeld and LoGiudice (2003) concluded that different orders

of community disassembly during habitat fragmentation may have opposite consequences

of decreasing biodiversity, with the successive spread of Lyme disease from wild

vertebrates to humans only accomplished when extinction followed the order from largest

to smallest body mass, as differences in disassembly order altered biodiversity-ecosystem

function. As pointed out by Fahrig (2002), fragmentation may reduce biodiversity when

the size of each remnant patch was below 20-30% of the original size, which was

predicted from amphibian and avian studies, whereas it may also result in positive effects

on biodiversity when the effect of fragmentation is modified by complex interspecific

interactions. This unique characteristic distinguishes habitat fragmentation from other

forms of habitat loss. For example, Ives (1991) tested a model in which intraspecific

aggregation may occur between competing species by carrion flies, and showed that

different patterns of ovipositing behavior increased coexistence. In this study,

fragmentation increased community abundance and richness (Figure 2&3) and drove

community dynamics to equilibrium (Figure A1, A2 & A3), which contradicted previous

research. One possibility is that smaller patches of fragmentation provide benefits to sub-

dominant species, which decreased competition. For example, *Loxocepholus sp.* became

dominant or secondarily dominant only in fragmented treatments while it went extinct in

non-fragmentation treatments (Figure 2) and may be explained by fragmentation-

increased growth rates (Figure 4). *P. caudatum*, which surprisingly benefited from

fragmentation in combination C, while showed no growth in a patch-size monoculture

(Figure 2 & 4), may have benefitted from fragmentation in a mixed culture due to changes in bacterial assemblage. *P. aurelia*, in contrast, went extinct in combination C fragmented groups, but was able to grow in monoculture (Figure 2 & 4). In this case, competition between *P. caudatum* and *P. aurelia* may have been altered because they didn't coexist (Figure A3). However, there were no signs of the effect of dispersal between the two different fragmentation treatments observed even provided the strong dispersal rate (10% per week). This is likely because all communities were transitive, with hierarchy competition, and dispersal did not result in the rotation of dominant species over time which reduces the extinction rate (Kerr et al. 2002). The effect of fragmentation could be important to biodiversity in a positive way as well as have obviously negative effects since humans have transformed about 50% of available land (Vitousek et al. 1986).

Significant interaction of warming and fragmentation were observed whether in a single time point or across the whole experimental time, both at the species and community level. When temperatures were constant, fragmentation increased biodiversity while in gradual warming conditions; the effects of fragmentation still promoted biodiversity but could be increase or decrease. Recently, Mantyka–Pringle et al. (2012) presented the first global-terrestrial meta-analysis of warming and fragmentation and found that the effects of fragmentation were the greatest with the highest maximum temperature, which accelerated the lost of biodiversity, and lowest where precipitation increased (Travis 2003; Opdam & Wascher 2004). In other words, the most vulnerable fragmented landscapes are areas of increased temperatures and decreased rainfall over the past century (Mantyka–Pringle et al. 2012). For instance, tree

harvesting indirectly increased warming and as warming can increase the extinction rate of trees in tropical areas (Chapin et al. 2000, Thomas et al. 2004, Tylianakis et al. 2008, Walther et al. 2002). These were contradictory to my results. Three reasons why warming did not accelerate the loss of biodiversity in fragmented treatments in this study may be: (1) the size of fragmented patches did not develop overall negative effects under $32^{o}C$. Gibbs (1997) showed that resistant patterns of species to fragmentation with lower or no obvious habitat threshold were the species with the greatest density. Since fragmentation increased abundance of low-frequency species instead, this decreased the threshold; (2) warming could increase the growth rate of bacterial prey for protists which maintained their coexistence. Petchey et al. (1999) reported increased bacterivore biomass and decomposition in gradual warming conditions, but bacterial biomass had no difference to constant temperature treatments; (3) the interspecies competitions were no more significant under warming than in constant condition in this study.

Conclusion

Results of this study indicate novel effects of habitat fragmentation and evidence of its interaction with environmental warming. Fragmentation did not always affect biodiversity negatively; long-term and diverse interactive effects may conserve biodiversity in fragmented habitats. By understanding these interaction effects, combined with other findings in further studies, new prediction models could be built to reinforce current efforts to restore and conserve of biodiversity (Benayas et al. 2009, Melo et al. 2013).

Table A1 Summary of ANOVA of the effects on the abundance of each species from the last week of the experiment. Significant values are highlighted in bold.

Source	Species	df	F	p value
Combination A				
Warming	*P. aurelia*	1	0.35	0.567
	C. kleini	**1**	**26235.75**	**<0.001**
	L. sp.	**1**	**106.08**	**<0.001**
	S. teres	**1**	**190.33**	**<0.001**
	S. ambiguum	**1**	**159.97**	**<0.001**
Fragmentation	*P. aurelia*	2	2.49	0.125
	C. kleini	2	1.95	0.185
	L. sp.	**2**	**41.12**	**<0.001**
	S. teres	**2**	**7.74**	**0.007**
	S. ambiguum	**2**	**16.81**	**<0.001**
Warming × Fragmentation	*P. aurelia*	2	3.17	0.079
	C. kleini	2	1.95	0.185
	L. sp.	**2**	**26.56**	**<0.001**
	S. teres	**2**	**7.74**	**0.007**
	S. ambiguum	**2**	**16.81**	**<0.001**
Combination B				
Warming	*P. caudatum*	1	3.97	0.070
	T. thermophila	**1**	**74.64**	**<0.001**
	L. sp.	**1**	**69.33**	**<0.001**
	S. teres	**1**	**957.44**	**<0.001**
	U. sp.	**1**	**75.98**	**<0.001**
Fragmentation	*P. caudatum*	**2**	**3.97**	**0.048**
	T. thermophila	**2**	**21.36**	**<0.001**
	L. sp.	**2**	**96.02**	**<0.001**
	S. teres	**2**	**35.00**	**<0.001**
	U. sp.	**2**	**64.50**	**<0.001**
Warming × Fragmentation	*P. caudatum*	**2**	**3.97**	**0.048**
	T. thermophila	**2**	**11.11**	**0.002**
	L. sp.	**2**	**20.18**	**<0.001**
	S. teres	**2**	**35.00**	**<0.001**
	U. sp.	2	2.77	0.102
Combination C				
Warming	*P. aurelia*	**1**	**32.97**	**<0.001**
	P. caudatum	1	2.05	0.178
	C. kleini	**1**	**58435.27**	**<0.001**
	T. thermophila	1	0.27	0.611
	H. sp.	1		

Fragmentation	*P. aurelia*	**2**	**27.86**	**<0.001**
	P. caudatum	**2**	**5.02**	**0.026**
	C. kleini	2	1.29	0.311
	T. thermophila	**2**	**5.83**	**0.017**
	H. sp.	2		
Warming × Fragmentation	*P. aurelia*	**2**	**27.86**	**<0.001**
	P. caudatum	2	0.63	0.550
	C. kleini	2	1.29	0.311
	T. thermophila	**2**	**13.12**	**0.001**
	H. sp.	2		

Table A2 Summary of repeated measures MANOVA on the effects on community structure.
Significant values are highlighted in bold.

Source	df	Wilk's λ	F	*p* value
Combination A				
Warming	5, 8	209.99	429.64	**<0.001**
Fragmentation	10, 16	79.88	7.21	**<0.001**
Time	35, 339	255.82	52.85	**<0.001**
Warming × Fragmentation	10, 16	7.29	1.02	**0.026**
Warming × Time	35, 339	161.01	23.54	**<0.001**
Fragmentation × Time	70, 385	52.65	3.76	**<0.001**
Warming × Fragmentation × Time	70, 385	13.02	2.60	**0.001**
Combination B				
Warming	5, 8	0.01	200.39	**<0.001**
Fragmentation	10, 16	0.01	13.31	**<0.001**
Time	35, 339	<0.01	29.23	**<0.001**
Warming × Fragmentation	10, 16	0.14	2.74	**0.035**
Warming × Time	35, 339	0.10	7.05	**<0.001**
Fragmentation × Time	70, 385	0.03	6.21	**<0.001**
Warming × Fragmentation × Time	70, 385	0.11	3.22	**<0.001**
Combination C				
Warming	5, 8	<0.01	1958.55	**<0.001**
Fragmentation	10, 16	0.04	9.51	**<0.001**
Time	35, 339	<0.01	152.21	**<0.001**
Warming × Fragmentation	10, 16	0.39	1.33	0.289
Warming × Time	35, 339	<0.01	51.51	**<0.001**
Fragmentation × Time	70, 385	0.12	4.20	**<0.001**
Warming × Fragmentation × Time	70, 385	0.12	4.15	**<0.001**

Table A3 Summary of repeated measures GLIM on the effects on species richness.
Significant values are highlighted in bold.

| Source	df	Wald χ^2	p value
Combination A			
Warming	1	188.91	**<0.001**
Fragmentation	2	77.32	**<0.001**
Time	1	214.61	**<0.001**
Warming × Fragmentation	2	10.74	**0.005**
Warming × Time	1	150.43	**<0.001**
Fragmentation × Time	2	55.07	**<0.001**
Warming × Fragmentation × Time	2	15.16	**0.001**
Combination B			
Warming	1	1.75	0.186
Fragmentation	2	1.57	0.456
Time	1	11.61	**0.001**
Warming × Fragmentation	2	7.00	**0.030**
Warming × Time	1	2.62	0.106
Fragmentation × Time	2	8.81	**0.012**
Warming × Fragmentation × Time	2	2.26	0.323
Combination C			
Warming	1	23.23	**<0.001**
Fragmentation	2	5.35	0.069
Time	1	176.36	**<0.001**
Warming × Fragmentation	2	8.78	**0.012**
Warming × Time	1	73.64	**<0.001**
Fragmentation × Time	2	9.59	**0.008**
Warming × Fragmentation × Time	2	15.85	**<0.001**
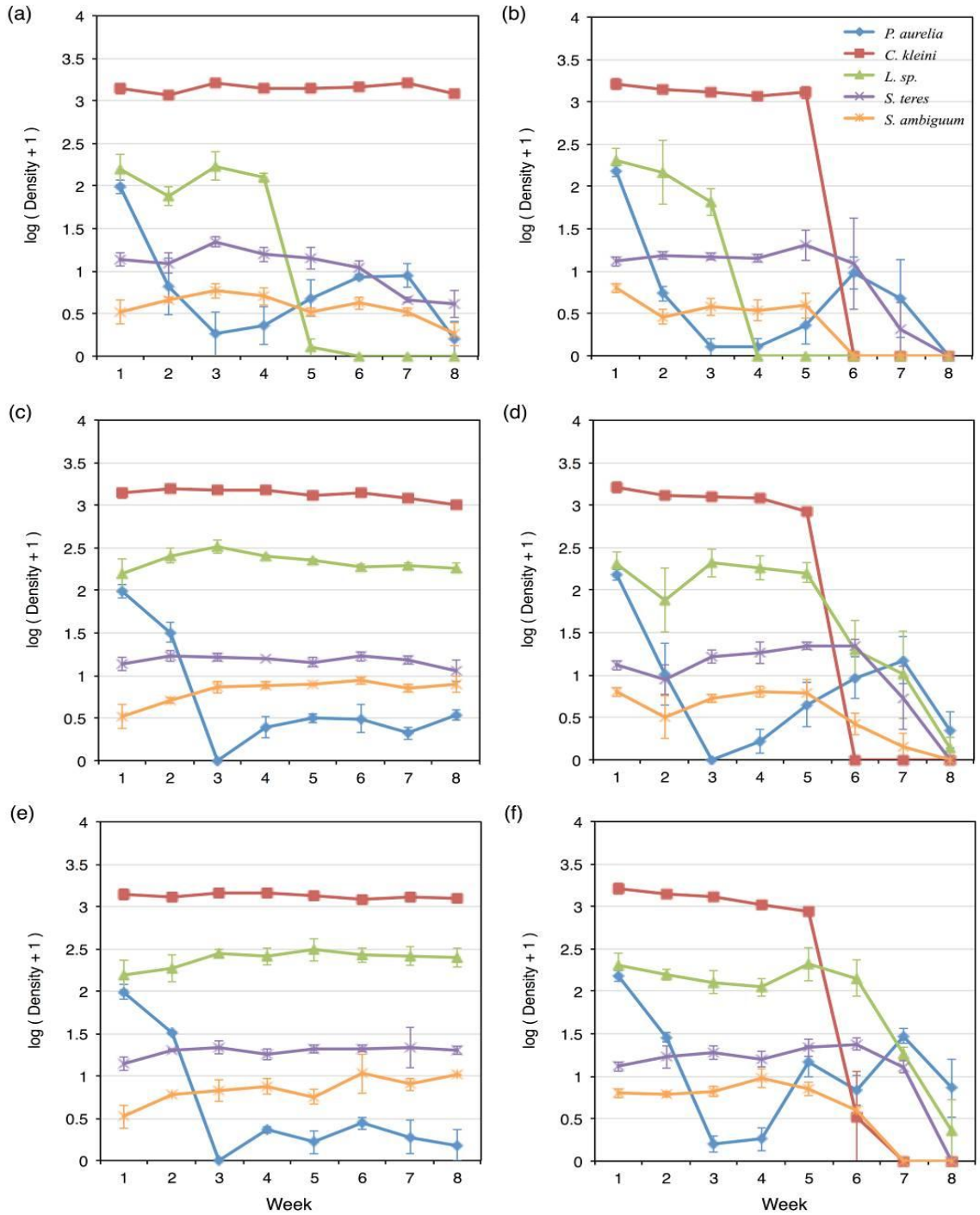
Figure A1 Population dynamics of each species in six treatments in Combination A: (a,b) Non-fragmentation; (c,d) Fragmentation without dispersal; (e,f) Fragmentation with dispersal; (a,c,e) constant temperature; (b,d,f) warming. The values are means±standard errors.
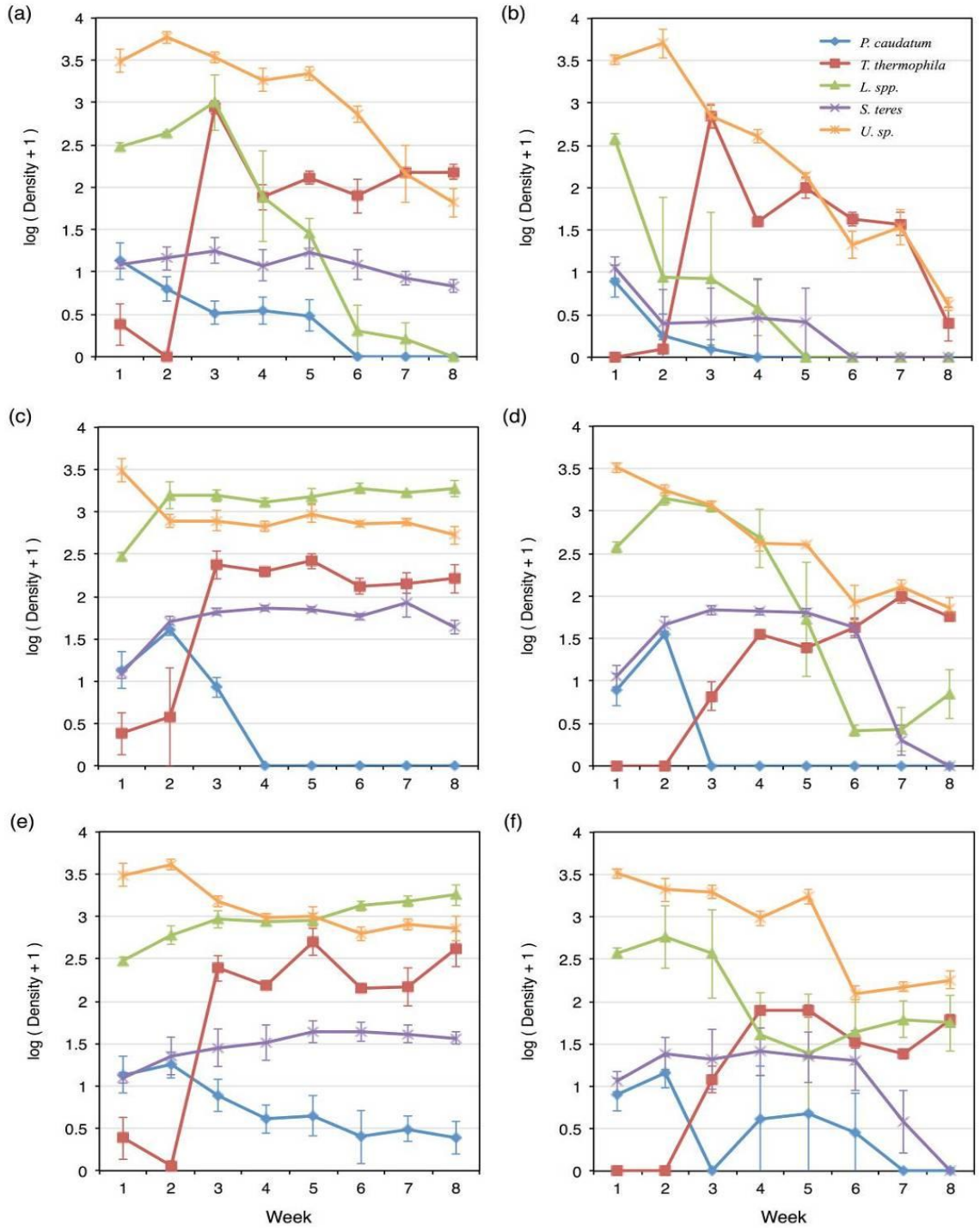
Figure A2 Population dynamics of each species in six treatments in Combination B: (a,b) Non-fragmentation; (c,d) Fragmentation without dispersal; (e,f) Fragmentation with dispersal; (a,c,e) constant temperature; (b,d,f) warming. The values are means±standard errors.
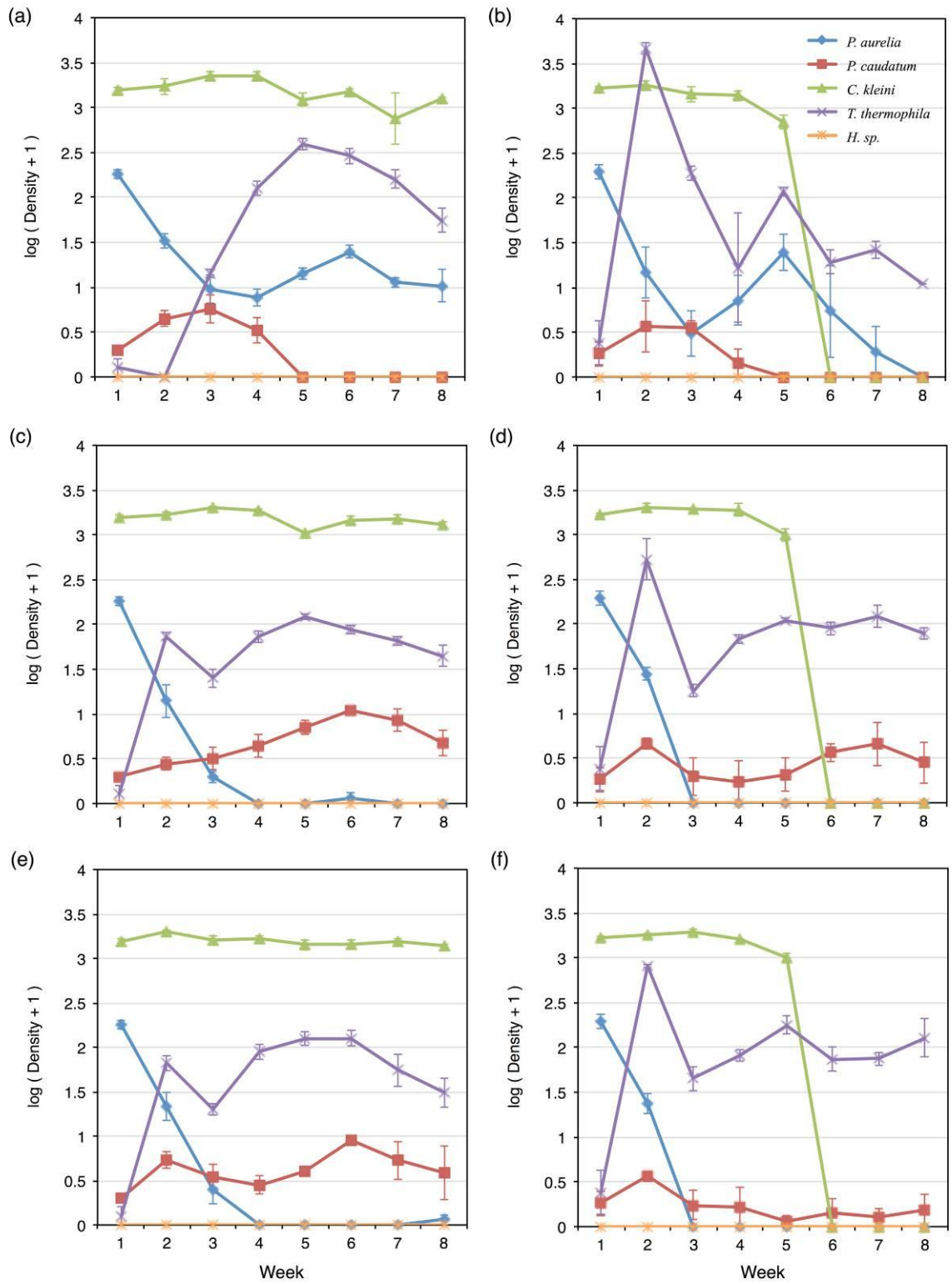
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Figure A3 Population dynamics of each species in six treatments in Combination C: (a,b) Non-fragmentation; (c,d) Fragmentation without dispersal; (e,f) Fragmentation with dispersal; (a,c,e) constant temperature; (b,d,f) warming. The values are means±standard errors.

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