Spatial distribution of local patch extinctions drives recovery dynamics in metacommunities

Camille Saade*[1], Sonia Kéfi[1,2], Claire Gougat-Barbera[1], Benjamin Rosenbaum[3,4], and Emanuel A. Fronhofer*[1]

[1]ISEM, CNRS, Univ. Montpellier, IRD, EPHE, Montpellier, France

[2]Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA

[3]German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig

[4]Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany

*Corresponding authors: camille.saade@umontpellier.fr; emanuel.fronhofer@umontpellier.fr

Keywords: disturbance, spatial clumping, correlation, Moran effect, microcosm, protist, theory

Abstract

Human activities lead more and more to the disturbance of plant and animal communities with local extinctions as a consequence. While these negative effects are clearly visible at a local scale, it is less clear how such local patch extinctions affect regional processes, such as metacommunity dynamics and the distribution of diversity in space. Since local extinctions may not be isolated events in space but rather clump together, it is crucial to investigate their effects in a spatially explicit framework.

Here, we use experimental microcosms and numerical simulations to understand the relationship between local patch extinctions and metacommunity dynamics. More specifically, we investigate the effects of rate and spatial clumping of extinctions in a full factorial design. Experimentally, we found that local patch extinctions increased inter-patch (β-) diversity by creating differences between extinct and non-extinct patches and at the same time increased local (α-) diversity by allowing inferior competitors to persist. Most importantly, recolonization dynamics depended more strongly on the spatial distribution of patch extinctions than on the extinction rate per se. Clumped local patch extinctions reduced mixing between extinct and non-extinct patches which led to slower recovery, lower α-diversity in non-extinct patches and higher β-diversity. Results from a metacommunity model matched the experimental observations best when the model included a competition-colonization trade-off, giving a hint at the underlying mechanisms.

Our results highlight that local patch extinctions can increase the diversity within and between communities, that the strength of these effects depends on the spatial distribution of extinctions and that the effects of local patch extinctions can spread regionally, throughout a landscape. These findings are highly relevant for conservation and management of spatially structured communities under global change.

Introduction

Understanding the causes and consequences of local extinctions and how they affect biological systems at larger spatial scales lies at the heart of spatial ecology. Natural metapopulations and metacommunities – sets of local populations and communities linked by dispersal (Levins, 1969) – naturally experience local extinctions (Hanski and Kuussaari, 1995; Altermatt and Ebert, 2010; Fronhofer et al., 2012), for instance, due to demographic stochasticity, natural disasters or disease outbreaks. In addition, global changes – including climate change, habitat loss and fragmentation due to land-use changes, deforestation and urbanization – put increasing stress on ecological communities (Millennium Ecosystem Assessment, 2005; IPBES, 2019) which contributes to local patch extinctions.

Local patch extinctions, which we here define as the disappearance of all biomass from a patch, can have various consequences. In trophic systems, sustained local patch extinctions can induce regional species extinctions (Liao et al., 2017; Ryser et al., 2019) and thus reduce regional diversity. Top predators are more likely to go extinct than intermediate species, some of which can even benefit from local patch extinctions due to the release from predation pressure. However, microcosms experiments on a competitive community with a competition-colonization trade-off show that occasional local patch extinctions can prevent regional extinctions and increase regional diversity by allowing less competitive species to persist (Cadotte, 2007).

One important factor mitigating the effect of local patch extinctions is the fact that metacommunities are spatially structured. The coupling of spatially distinct communities can reduce the effect of local extinctions if individual local communities face them at different times: patches left empty by a local extinction event can be recolonized through dispersal of individuals from patches that are occupied. Finally, a spatially structured habitat can increase overall species diversity by allowing competitors to coexist at the scale of the landscape (Brown and Kodric-Brown, 1977; Hanski, 1983; Harrison, 1991). However, dispersal between local communities can also have detrimental effects by synchronizing populations and thereby decreasing spatial insurance effects (Abbott, 2011). Under strong dispersal, the effects of local extinctions can even spread throughout

a metacommunity (Gilarranz et al., 2017; Zelnik et al., 2019) such that local events have a regional effect.

One likely important factor that modulates the effects discussed above is the spatial distribution of local patch extinctions, for instance, whether they are clumped in space or not. An increase in the spatial clumping of local extinction events could have a destabilizing effect at the metacommunity scale by coupling local dynamics and thus increasing global extinction risk (Ruokolainen, 2013; Kahilainen et al., 2018). Indeed, climate models have predicted an increase in the spatial and temporal autocorrelation of temperature (Di Cecco and Gouhier, 2018), implying an increase in the environmental similarity between communities in space and time. This is expected to result in more climate extremes, such as heatwaves, droughts or frosts, affecting increasingly larger areas and for a longer time. Such climatic extremes can lead to local extinctions of populations of organisms sensitive to temperature changes, as seen in episodes of coral bleaching (Carpenter et al., 2008) or forest die-offs (Allen et al., 2010).

Despite this trend of climate data and predictions showing an increase in spatial and temporal correlation of temperature (Di Cecco and Gouhier, 2018) that could result in a greater number of climate-induced local extinctions and a stronger spatial clumping of these events, few studies have considered the spatial structure and extent of local extinctions, leaving a gap in our understanding of how spatially clumped extinctions may affect the dynamics of ecological systems.

Here, we investigate how the rate and spatial distribution of local patch extinctions affect recolonization dynamics in metacommunities. We were particularly interested in determining whether the effects of local patch extinctions can spread in space and have regional effects on metacommunities. Using a full factorial design crossing three levels of extinction rates and two levels of spatial clumping, we forced local patch extinctions in experimental and simulated metacommunities and followed community dynamics in each patch during the recolonization process. We were able to show that the effects of local patch extinctions on the metacommunity depend more on the spatial distribution of those extinctions than on their rate, and that local patch extinctions can increase both local (α-) and inter-patch (β-) diversity.

Material and methods

We used a combination of laboratory experiments with metacommunities of three freshwater ciliates (*Tetrahymena thermophila*, *Colpidium* sp. and *Blepharisma* sp.) in microcosm landscapes and mathematical modelling of metacommunities to address our main research question. To do so, we forced local patch extinctions (not sustained in time, i.e., 'pulse' perturbations; see (Bender et al., 1984)) in experimental microcosm landscapes (Altermatt et al., 2015) and followed metacommunity recovery in terms of species diversity and biomass as a function of the intensity (rate of extinctions) and spatial distribution (clumped vs. dispersed) of the extinctions. Experiments and simulations followed the dynamics of metacommunities in landscapes made of 16 patches arranged in a square lattice and connected by active dispersal.

Experiments

We used experimental landscapes made of 16 vials connected to their 4 nearest neighbours, allowing individuals to disperse from one patch to another. Local patch extinctions consisted in removing all individuals of all species in a given patch. Each patch was initially inoculated with one of the three species at half its carrying capacity. Extinctions were implemented once, two weeks after inoculation to allow for community assembly to have taken place. Subsequently, we then observed the recovery of the landscapes for two weeks. In order to explore the effects of the rate of local patch extinctions and their spatial clumping on the dynamics of metacommunities, we used a full factorial design crossing three levels of local patch extinctions (0, 4 or 8 simultaneous extinctions out of 16 patches) with two levels of spatial clumping (clumped: Fig. S1 landscapes 7-9 and 13-15; dispersed: Fig. S1 landscapes 4-6 and 10-12). This design yielded a total of 5 treatments (no extinction, 4 clumped extinctions, 4 dispersed extinctions, 8 clumped extinctions, 8 dispersed extinctions) that were each replicated in 3 landscapes, for a total of 15 landscapes and 240 patches. We followed the metacommunity dynamics through time by measuring the density of each species in each patch three times per week using video recording and analysis.

Species

We used three freshwater ciliate species commonly used in microcosms experiments (Diehl and Feissel, 2001; Cadotte, 2006; Worsfold et al., 2009): *Tetrahymena thermophila* (Tet) is a small (50 µm, Fig. S2) bacterivore, *Colpidium* sp. (Col) is a medium-sized (120 µm, Fig. S2) bacterivore and *Blepharisma* sp. (Ble) is a big (200 µm, Fig. S2) omnivore feeding on bacteria and a smaller ciliates. In this experimental system, all three species feed on the bacteria *Serratia marcescens* as a common resource and thus constitute a competition network. In addition, the biggest *Blepharisma* sp. individuals could also feed on *T. thermophila*. We determined the species demographic traits in preliminary single patch experiments: the species show differences in population growth rate (Tet $>$ Col $>$ Ble), carrying capacity (Tet $>$ Col $>$ Ble) (Fig. S3) and interspecific competitive ability (Tet $<$ Col $<$ Ble) (Fig. S4). Based on their population growth rates and competitive abilities, these species can be described as an ecological succession: *T. thermophila* density peaks after approximately two days, *Colpidium* sp. density peaks after approx. five days and *Bleparisma* sp. grows slowly and dominates the community after around 16 days (Fig. S4) in our experimental setting.

We did not quantify dispersal in isolation, but used movement speed observed *in situ* as a proxy of dispersal ability, as these two traits are usually well correlated (Fronhofer and Altermatt, 2015; Pennekamp et al., 2019). Generally, *Colpidium* sp. is faster than both *T. thermophila* and *Blepharisma* sp. – which move at roughly the same speed (Fig. S5).

Culture conditions

The species were kept in 20 mL of a standardized medium made of water (Volvic), dehydrated organic salad (1 g of salad for 1.6 L of water) and bacteria (*Serratia marcescens*) at 10% of their maximum density (obtained by a tenfold dilution of a one week old culture) as a common resource. The cultures were refreshed three times a week by replacing 2 mL of each culture with 2 mL of fresh, bacterized medium. The cultures were kept in a room with controlled temperature (20 °C). In order to exclude any potential confounding effects due to landscape positioning, the position

and orientation of landscapes was randomized and changed three times per week.

Landscape design

We used landscapes made of 16 vials (20 mL Sarstedt tubes) arranged in a square lattice and connected by silicon tubes (length: 6 cm, inner diameter: 4 mm). The silicon tubes were closed with clamps to control dispersal. The clamps were opened for 4 hours three times per week (after medium replacement) to allow dispersal. Each patch was initially inoculated with one of the three species at half of its carrying capacity at the beginning of the experiment. Initial species distributions were drawn at random so that one species initially occupied 6 patches and the two others occupied 5 patches in each landscape. We then followed community assembly for two weeks before forcing extinctions of all individuals of all species in selected patches and following the recolonization of those patches for two more weeks. Along with the landscapes, we also kept 9 monocultures (3 replicates per species) in single patches to provide a training data set for automated species identification (Pennekamp et al., 2017).

Extinction patterns

The extinction patterns (Fig. S1) were chosen to either maximize (clumped extinctions) or minimize (dispersed extinctions) the percentage of like adjacencies (pladj). The pladj is calculated as the proportion of connections in a landscape that link two patches of the same kind (i.e., extinct with extinct or non-extinct with non-extinct) and is a measure of the spatial clumping of the extinctions (pladj is close to 1 when extinctions are clumped, and close to 0 when they are dispersed). Because the landscapes are relatively small, the connectivity (i.e., the number of connections) of a patch varies depending on their position in the landscape. In order to minimize potential edge effects, we chose to draw the extinct patches only from the sets of patches with a mean connectivity of three, which is the mean connectivity of the landscape. This ensured that corners, edges and central patches were equally represented in clumped and dispersed treatments, making them similar in terms of position relative to the edge. The drawing of extinction patterns was done by *i)*

calculating the mean connectivity of all sets of 4 or 8 patches and keeping only those of connectivity 3, *ii)* calculating the pladj of the remaining sets and keeping only those with the highest pladj (for clumped extinctions) or lowest pladj (for dispersed extinctions) and *iii)* drawing an extinction pattern for each landscape among the remaining sets. We performed local patch extinctions by transferring the content of non-extinct patches to an identical new landscape in which extinct patches were not transferred and replaced by fresh bacterized medium instead.

Data acquisition

The 2 mL of medium taken out of the patches and monocultures during medium replacement were used as samples to estimate the density of each species in each patch. For each patch and monoculture, 250 µL were put between two microscope slides (height: 500 µm) and filmed — using an optical stereo-microscope (*Perfex Pro 10*) coupled with a camera (*Perfex SC38800*) — for 10 seconds (150 frames).

Species identification

The three species differ in size, shape and behavior which allows for automated species identification (Pennekamp et al., 2017). The videos were analyzed with the Bemovi R-package (version 1.0) (Pennekamp et al., 2015) to track individuals and characterize their shape and trajectories (speed, size). The individuals were then identified from their characteristics (entire output of bemovi analysis) using a random forest algorithm (R-package randomForest version 4.6-14) trained on videos of the monocultures filmed on the same day (Pennekamp et al., 2017). We rejected all the individuals with an identification confidence (proportion of trees leading to that identification) lower than 0.8 as a good compromise between the number of observations discarded and the confidence of identification (Fig. S6).

Diversity measures

α-diversity was measured as the inverse of the Simpson's index, which represents an effective number of species (Jost, 2006), and takes the relative abundance of different species into account. We used the function beta.div.comp (R-package adespatial version 0.3-8, Ruzicka-based index) to compute the total β-diversity among the patches of a landscape (Legendre and De Cáceres, 2013).

Statistical analyses

All statistical analyses were conducted in R (version 4.0.2). To test the relative effects of spatial clumping and rate of local extinctions on metacommunitiy properties, we studied 4 metrics (biomass, α-diversity, β-diversity and biomass recovery time) using mixed-effects models with measure point and landscape ID (for patch level metrics) as random effects to account for the non-independence of measures taken the same day and measures taken within one landscape. Fixed effects were clumping of the extinctions, extinction rate as well as their interaction. Response variables were normalized using the R-package bestNormalize (version 1.6.1). The biomass in each patch was estimated using the bioarea per volume, a measure of the total surface of organisms visible in a video divided by the volume of medium in the camera field. The biomass recovery from extinction was estimated as the time needed to reach a bioarea per volume higher that the 2.5% quantile of pre-extinction bioarea in a given patch. This time span is hereafter referred to as recovery time.

For each statistical model, we performed AICc-based model selection on all models from the intercept to the full model. We used the weighted average of the model selection for predictions and quantified the relative importance of each predictor variables to assess their importance on the observed patterns.

Metacommunity model

We developed a mathematical model describing the dynamics of a competitive metacommunity of n species characterized by demographic and interaction parameters in landscapes similar to those used experimentally (i.e., a square lattice of 4 by 4 patches). We used Bayesian inference of demographic parameters on times series from the experimental single-patch cultures to parameterize the model (see below for details). We simulated dynamics using the same extinction plans as in the microcosm experiments with 100 replicates of each treatment.

Metacommunity dynamics

We used a set of ordinary differential equations to describe the dynamics of metacommunities (Eq. 1), where the terms describe the local dynamics (f), the emigration (g) and the immigration (h) of species i in patch k, with $N_{i,k}$ as the density of species i in patch k.

$$\frac{dN_{i,k}}{dt} = f(N_{\bullet,k}) - g(N_{i,k}) + h(N_{i,\bullet}) \tag{1}$$

The local dynamics are described by a competitive Lotka-Volterra equation (Eq. 2) were $N_{i,k}$ grows logistically (r_i: growth rate, $\alpha_{i,i}$: intraspecific competition) and is down-regulated by interspecific competition ($\alpha_{i,j}$).

$$f(N_{\bullet,k}) = r_i\, N_{i,k} - \sum_{j=1}^{n} \alpha_{i,j}\, N_{i,k}\, N_{j,k} \tag{2}$$

The number of individuals emigrating from a patch k is defined by a constant dispersal rate m_i (Eq. 3).

$$g(N_{i,k}) = m_i\, N_{i,k} \tag{3}$$

In analogy, we obtain the number of individuals immigrating into patch k as follows (Eq. 4) :

$$h(N_{i,\bullet}) = \sum_{l} \frac{m_i \, N_{i,l}}{n_links_l} \tag{4}$$

where l are the patches adjacent to k and n_links_l is the number of connections leaving the patch l.

Parameterization of the model

We used four different sets of parameters (hereafter referred to as "scenarios of species interactions") to investigate which processes may be responsible for the patterns observed experimentally. Two scenarios of species interactions ("empirical interactions" and "competition-colonization trade-off") used demographic parameters (population growth rates r_i and competitive abilities $\alpha_{i,j}$) fitted from empirical time series and were expected to most closely reproduce the experimental data. One scenario ("randomized interactions") used the same competitive abilities but randomly shuffled between species in order to investigate whether the results were specific to our experimental community or if they could arise in other competitive communities with a different structure but similar overall interactions strength. The last scenario ("no interspecific interactions") ignored interspecific interactions altogether and was thought of as a control scenario.

Empirical interactions We parameterized the model using single-patch time series of mono-, bi- (cultures of *Blepharisma* sp. with *T. thermophila)* and of *Blepharisma* sp. with *Colpidium* sp.) and tri-specific cultures from the experiments (three replicates of each culture). We fitted competitive Lotka-Volterra equations to the data using Bayesian inference (R-package Rstan version 2.19.3) (Rosenbaum et al., 2019; Feng et al., 2020). We fitted a single set of parameters (three r_i and a 3 by 3 matrix of $alpha_{i,j}$) over all replicates of all single-patch cultures (one curve per culture, with different initial conditions N_0 for each culture), using lowly informative priors (Tab. S1) and assuming a negative binomial distribution of the residuals. We fit the model using the No U-Turn Sampler (NUTS) with three chains each of total length 10 000 (of which 2 000 steps were discarded as warm-up). We used default parameters for the sampler, except for the control

parameters ”adapt_delta” (set at 0.9) and ”max_treedepth” (set at 12). The average fit can be found for visual inspection in Fig. S7.

This allowed us to infer values of population growth rates (r_i) and interaction strengths ($\alpha_{i,j}$) for which the model yields dynamics that are quantitatively similar to the dynamics of the experimental community. We used the same dispersal rates for all three species ($m_i = 1/100$).

Competition-colonization trade-off We used the fitted values from the experimental results for the Lotka-Volterra parameters (r_i, $\alpha_{i,j}$) and used different dispersal rates for each species ($m_i = \{1/50, 1/100, 1/500\}$) with the most (resp. least) competitive species having the lowest (resp. highest) dispersal rate, resulting in a trade-off between competition and colonization.

Randomized interactions We used the same parameters as in the “empirical interactions” scenario but we randomized interspecific interactions (i.e., the off-diagonal terms of the competition matrix: $\alpha_{i,j},\ i \neq j$). We randomly changed the position of the interaction terms while keeping each $\alpha_{i,j}$ associated to the same $\alpha_{j,i}$.

No interspecific interactions We used the same parameters as in the “empirical interactions” scenario but we set the interspecific interaction terms ($\alpha_{i,j},\ i \neq j$) to be zero. This results in a community where species do not experience interspecific competition.

Results

The role of the spatial distribution of extinctions

In the experiments, both local and regional effects of local patch extinctions were mainly determined by the clumping of extinctions or by the interaction between clumping and rate of extinctions, while the extinction rate alone only had a marginal effect on the outcome of the experiment as indicated by model selection (Fig. 1; Tab. 1 and S2). For the local variables studied (α-diversity, bioarea and bioarea recovery time), the clumping of extinctions was found to be more important

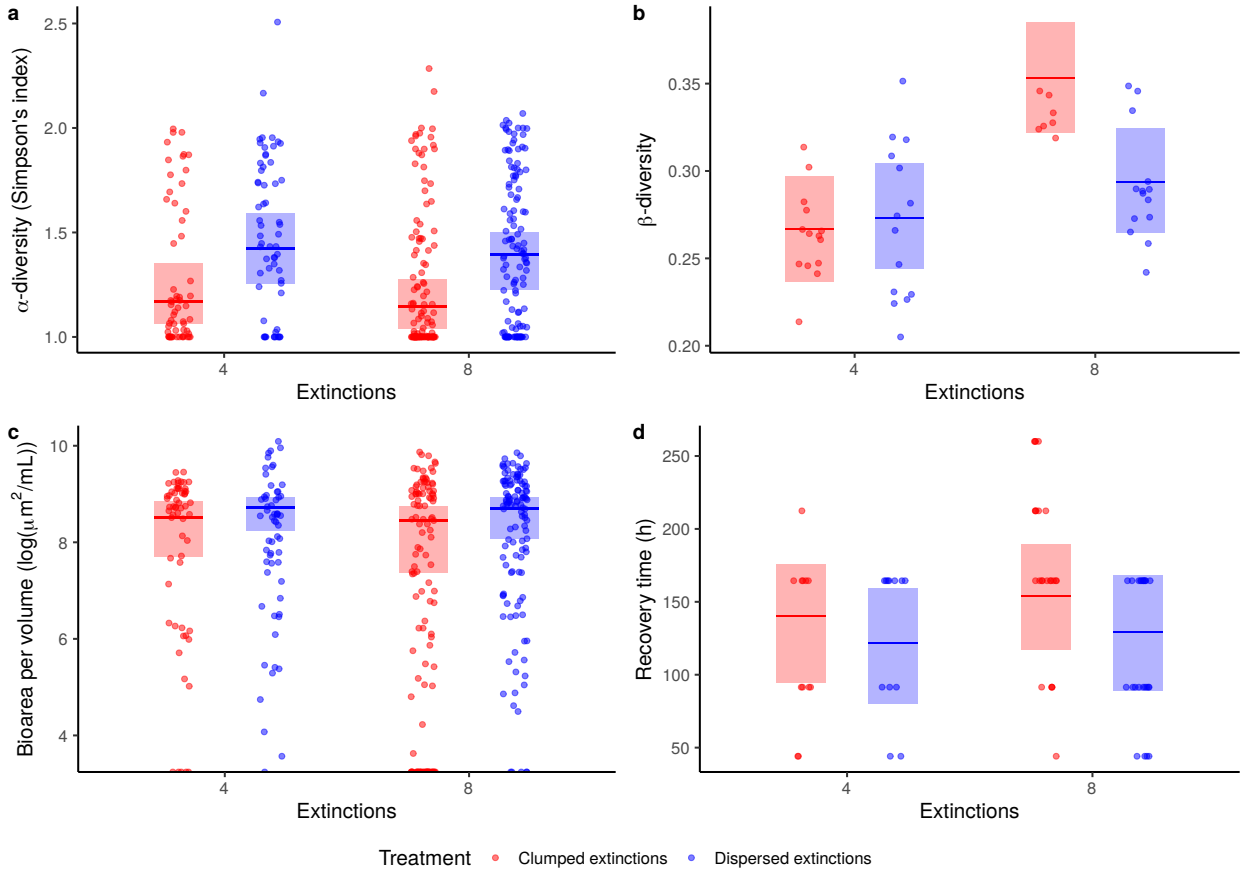

Figure 1: Observed response variables in the experiments (dots) and averaged mixed model predictions (medians and 95% confidence intervals; Tab. 1 and S2) from the extinction events to the end of the experiments. (a) α-diversity (measured as Simpson's index) in extinct patches, (b) β-diversity in landscapes with extinction, (c) Bioarea in extinct patches and (d) biomass recovery time in extinct patches.

than the extinction rate (Tab. 1). Both α-diversity in non-extinct patches (Tab. 2 and S3b) and β-diversity (Tab. 1 and Tab. S2b) were mostly explained by the interaction between clumping and extinction rate (statistical models without the interactions had either a null (for β-diversity) or low (for α-diversity) weight).

Numerical simulations of our metacommunity model with the same spatial configuration and extinctions patterns reproduced these results for all competition scenarios (Fig. 2 and 4).

Direct effects — recolonization dynamics in extinct patches

We first consider the recolonization dynamics of biomass and α-diversity in extinct patches.

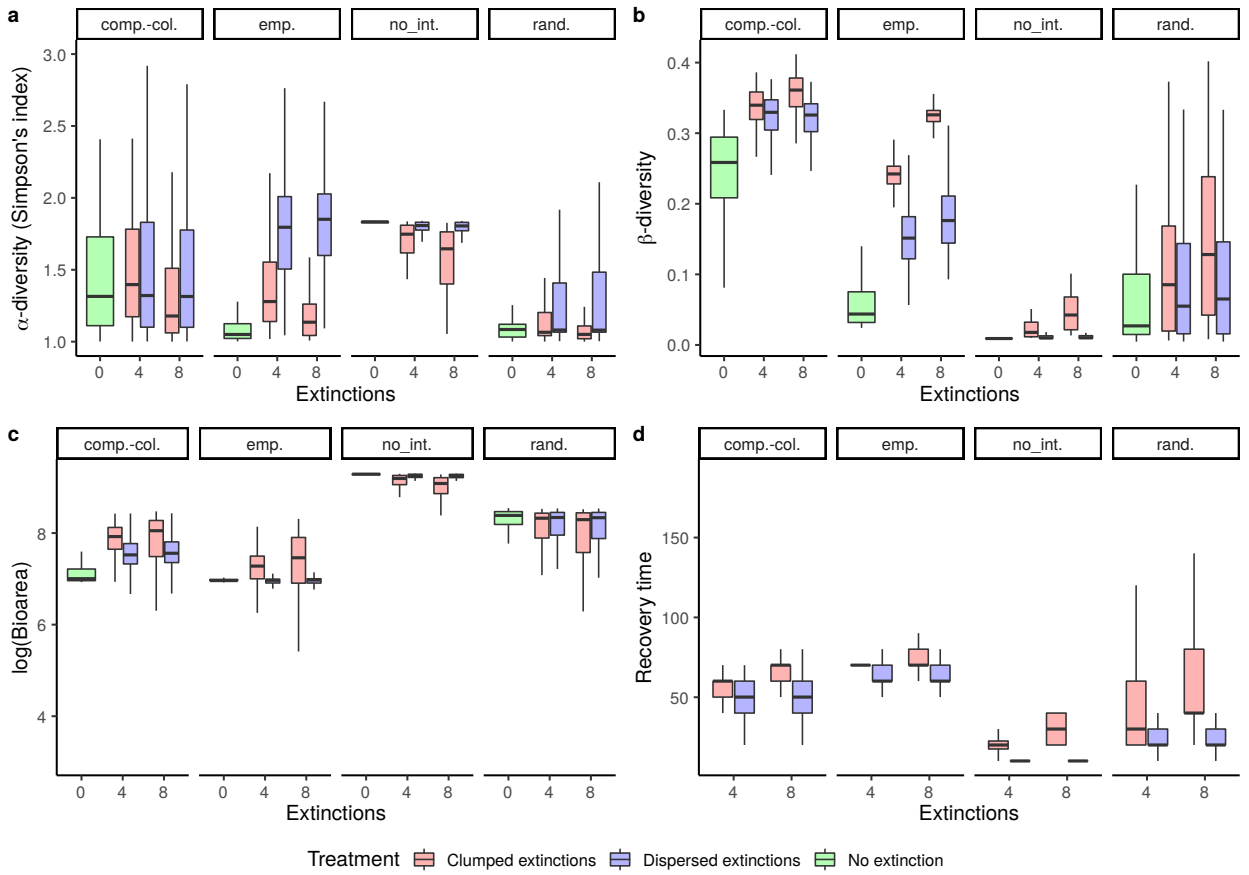

Figure 2: Observed response variables in numerical simulations of the metacommunity model displaying different metrics after the extinction events. (a) α-diversity (measured as Simpson's index) in extinct patches, (b) β-diversity in landscapes with extinction, (c) biomass in extinct patches and (d) biomass recovery time in extinct patches. The top labels denote the scenarios of species interactions: "emp." for "empirical interactions", "comp.-col." for "competition-colonization trade-off", "rand." for "randomized interactions" and "no int." for "no interspecific interactions".

Biomass

The bioarea per volume, as proxi for biomass in a given patch, after local patch extinctions was slightly higher in extinct patches from landscapes with dispersed extinctions than in landscapes with clumped extinctions (Fig. 1c, median predictions : $\sim 6000\,\mu m^2\,mL^{-1}$ vs. $\sim 5000\,\mu m^2\,mL^{-1}$). Note that this effect is weak as indicated by model selection which ranks the intercept model second with an AICc weight of 0.27 (Tab. S2). The recovery time needed to reach a bioarea higher than the 2.5% quantile of the pre-extinction bioarea was shorter in case of dispersed extinctions compared to clumped extinctions, and it slightly increased with the number of extinctions (Tab. S2 and Fig. 1d; median mixed model predictions: 4 dispersed: 122 h, 8 dispersed: 130 h, 4 clumped: 139 h, 8 clumped: 134 h).

In simulations of the metacommunity model, recovery times (Fig. 2d) depended greatly on the scenario of species interactions: it was shorter in the absence of interspecific interactions (scenario: "no interspecific interactions") and with randomized interactions ("randomized interactions"), and longer for fitted interaction terms ("empirical interactions" and "competition-colonization trade-off"). However, the differences between treatments were qualitatively similar between all interaction scenarios: the recovery times were shorter for dispersed extinctions than for clumped extinctions. In landscapes with dispersed extinctions, the recovery times were not affected by the number of extinctions. By contrast, in landscapes with clumped extinctions, the recovery times increased with the number of extinctions. It is noteworthy that, in general, the recovery times were much shorter (less than 100 time units) than what we found experimentally, probably because dispersal in the experiments happened over discrete time interval (4 h periods, three times per week) resulting in a lag in recolonization dynamics.

α-diversity

In patches from control landscapes (i.e., landscapes without any patch extinctions), α-diversity increased at first as species dispersed between patches but quickly fell to 1 (the minimal value) as *Blepharisma* sp. finally excluded the two other species and dominated the community. In

Table 1: Relative importance of explanatory parameters in the mixed models explaining all four response variables (α-diversity, β-diversity, bioarea per volume and recovery time) in extinct patches.

	α-diversity	β-diversity	Bioarea	Recovery time
Spatial clumping	0.95	1	0.62	0.67
Extinction rate	0.43	1	0.37	0.52
Spatial clumping * Extinction rate	0.11	1	0.1	0.23

extinct patches of the landscapes with extinction treatments, α-diversity was higher during the recolonization process in comparison to the control landscapes since all three species were present in more even densities (Fig. 1a). This effect was stronger for dispersed extinctions than for clumped extinctions (Fig. 1a, Tab. 1).

In simulations from the metacommunity model, α-diversity patterns depended on the scenario of species interactions (Fig. 2a). In the absence of interspecific interactions ("no interspecific interactions"), the three species could coexist locally and the α-diversity stayed high in patches from control landscapes. In extinct patches, the α-diversity was 1 right after extinction but quickly came back to pre-extinction levels as all species recolonized (Fig. S8). This recovery was faster for dispersed than for clumped extinctions and in landscapes with 4 rather than 8 extinctions. In all three other scenarios ("empirical interactions", "randomized interactions" and "competition-colonization trade-off"), interspecific interactions resulted in competitive exclusion. As a consequence, α-diversity was fairly low in control landscapes (Fig. 2a). In the extinct patches of the landscapes with extinction treatments, α-diversity during the recolonisation process was higher (for all treatments) than in the patches from control landscapes. α-diversity was highly variable in time during the recolonization process (Fig. S8). In all scenarios, α-diversity in patches from dispersed extinction treatments was higher early in the recolonization process but then decreased quickly. Later in the recolonisation process, α-diversity was higher in patches from clumped extinction treatments than in patches from dispersed extinction treatments.

Table 2: Relative importance of explanatory parameters in the mixed models explaining bioarea and α-diversity in non-extinct patches.

	Bioarea	α-diversity
Spatial clumping	0.32	1
Extinction rate	0.38	0.86
Spatial clumping * Extinction rate	0.15	0.81

Indirect effects — spread of extinctions effects to non-extinct patches and at the regional scale

As local events can spread in space and have regional consequences, we now focus on the indirect effects of local patch extinctions on undisturbed patches (biomass and α-diversity) and on regional effects (β-diversity).

Biomass

We observed no strong difference in bioarea per volume between treatments (Fig. 3b). Although the bioarea predictions from the mixed model are slightly higher in non-extinct patches than in patches from control landscapes, both empirical data and the statistical models predictions are largely overlapping between treatments.

α-diversity

Experimentally, α-diversity was higher in non-extinct patches than in patches from control landscapes, particularly for dispersed extinctions (Fig. 3a). Most of the variation between treatments was explained by the spatial clumping of extinctions rather than extinction rates (Tab. 2 and Tab. S3b). Interestingly, the effect of extinction rates depended on the spatial organization of extinctions: under clumped extinctions, the α-diversity in non-extinct patches decreased with the number of extinctions but it increased under dispersed extinctions (Fig. 3a).

The results from the simulations of the metacommunity model depended on the scenarios of species interactions (Fig. 4a): in the absence of interspecific competition ("no interspecific interactions"), α-diversity levels were similar in non-extinct patches (across all treatments) and

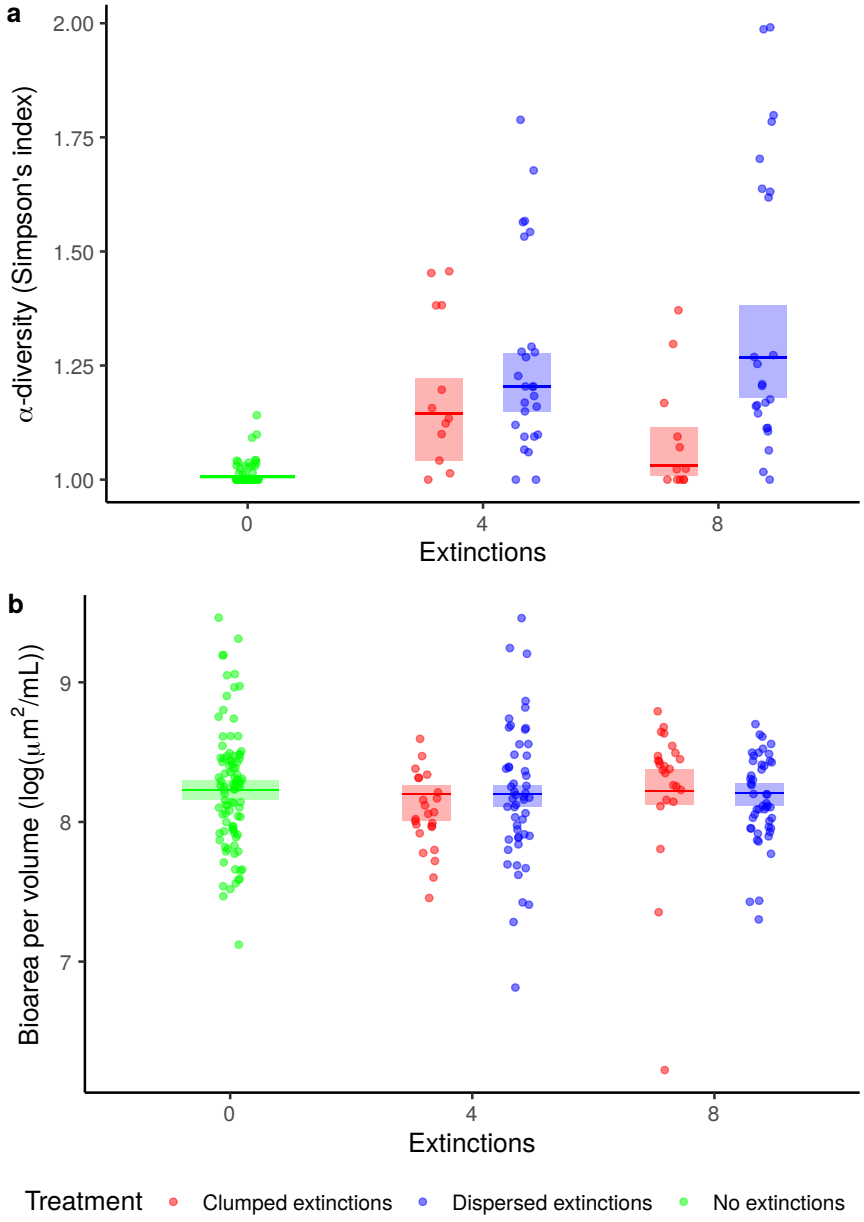

Figure 3: Observed response variables in the experiments (dots) and averaged mixed model predictions (medians and 95% confidence intervals; Tab. 2 and S3) in non-extinct patches adjacent to at least one extinct patch (blue, red) and in control landscapes (green). (a) α-diversity (measured as Simpson's index) in non-extinct patches at the last two measurement points, (b) bioarea in non-extinct patches (for the two measurement points following the extinctions).

patches from control landscapes. In every other scenario ("empirical interactions", "randomized interactions" and "competition-colonization trade-off"), α-diversity was higher in non-extinct patches than in patches from control landscapes. In line with experimental results, α-diversity was higher for treatments with dispersed extinctions. α-diversity also increased with the number of extinctions. Although these results were qualitatively similar across the scenarios that included interspecific competition ("randomized interactions", "empirical interactions" and "competition-colonization trade-off"), the effect sizes were highly variable: randomized interactions yielded smaller effects while the "competition-colonization trade-off" scenario yielded stronger effects, more consistent with experimental results.

β-diversity

In control landscapes, β-diversity was fairly low because the patches ended up being homogeneous (not shown). β-diversity was higher in landscapes with extinctions than in control landscapes because of differences in species composition and density between extinct and non-extinct patches. This effect was stronger for 8 extinctions than for 4 extinctions, particularly for clumped extinctions (Fig. 1b).

In simulations of the metacommunity model, these results held qualitatively for all competition scenarios (Fig. 2b): β-diversity was higher in landscapes with extinctions than in control landscapes. Among landscapes with extinctions, β-diversity generally increased with spatial clumping and extinction rate. These effects were strong and on par with experimental effect sizes for realistic interaction matrices (scenarios "empirical interactions" and "competition-colonization trade-off"). They were weaker for randomized interaction matrices ("randomized interactions" scenario) and negligible in the absence of interspecific interactions ("no interspecific interactions" scenario).

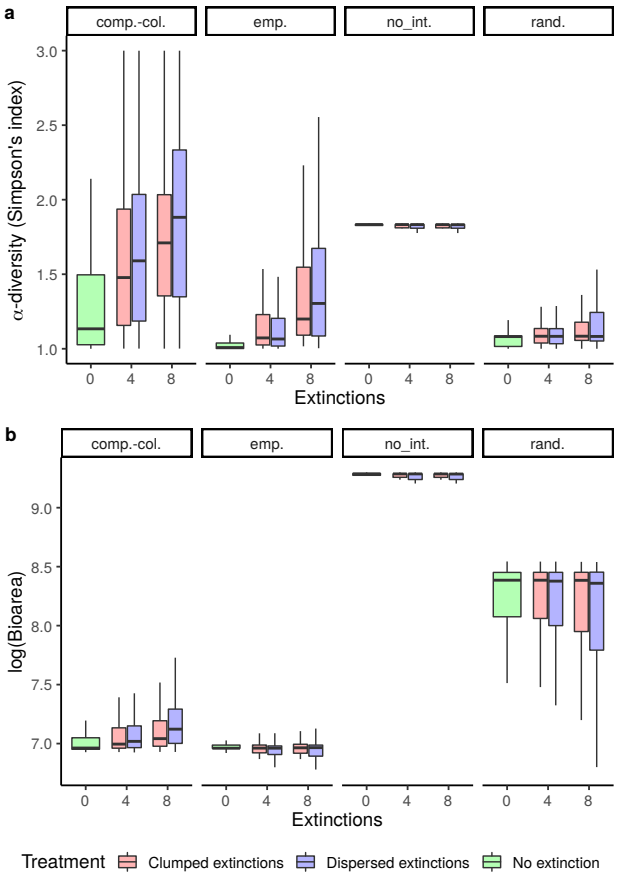

Figure 4: Observed response variables in numerical simulations of the metacommunity model showing Simpson's index (a) and biomass (b) in non-extinct patches adjacent to at least one extinct patches (blue, red) and in control landscapes (green) after extinction events. The top labels denote the scenarios of species interactions: "emp." for "empirical interactions", "comp.-col." for "competition-colonization trade-off", "rand." for "randomized interactions" and "no int." for "no interspecific interactions".

Discussion

The role of the spatial distribution of the extinctions

Our work clearly shows that recovery from extinctions depends more on the spatial features of local patch extinctions (such as the connectivity between extinct and non-extinct patches) than on interspecific interactions or on the number of patches affected. More specifically, our experiments clearly showed that the spatial clumping of extinctions had stronger effects than extinction rates per se on all metacommunity metrics measured, including biomass, recovery time, α- and β-diversity (Tab. 1 and S2). These empirical findings were confirmed by our theoretical model, regardless of the specific scenario. The main factor driving these results can be linked to the connectivity of extinct to non-extinct patches: in the dispersed extinction treatments, extinct patches were adjacent to more non-extinct patches (on average 3) than in the clumped extinction treatments (on average 1 (4 clumped extinctions) and 0.5 (8 clumped extinctions)), which modulated recovery speed. These results can be inerpreted as differences in recovery regimes across spatial treatments: clumped extinctions, characterized by a weak connectivity between extinct and non-extinct patches, result in what Zelnik et al. (2019) described as a "rescue recovery regime", while dispersed extinctions, characterized by a strong connectivity between extinct and non-extinct patches, result in a "mixing recovery regime". Under the "rescue" regime, dispersal between extinct and non-extinct patches is marginal compared to local dynamics. Extinct and non-extinct patches are strongly differentiated, and the recovery dynamics mainly rely on local growth. Under the "mixing" regime, dispersal between extinct and non-extinct patches is on par with local dynamics. Extinct and non-extinct patches are well mixed, and both local growth and dispersal from extinct patches participate substantially to the recovery.

Direct effects of extinctions

Biomass recovery

Experimental data and simulations support the conclusion that simultaneously increasing the rate and clumping of extinctions increases the time needed for a metacommunity to recover its pre-extinction biomass (Fig. 1d and 2d). Experimentally, increasing only the rate of extinctions or transitioning from dispersed to clumped extinctions had no effect on the recovery time (Fig. 1d). In simulations of the metacommunity model, recovery time always increased with spatial clumping (Fig. 2d). Extinction rate had no effect on recovery time under dispersed extinctions treatments, but it increased the recovery time under clumped extinctions. These results were surprisingly consistent for the different scenarios of species interactions, highlighting that this pattern does not depend on species interactions but rather on the geometry of the patches to be recolonized. A high rate of spatially clumped extinctions increases the recovery time by creating large areas of extinct patches, thus increasing the average distance and reducing the average connectivity between extinct and non extinct patches. As above, this can be discussed from a recovery regime perspective (Zelnik et al., 2019): dispersed extinctions result in a "mixing recovery regime" where extinct and non extinct patches are well mixed and dispersal, in combination with local population growth, qualitatively participates to biomass recovery. Clumped extinctions result in a "rescue recovery regime" where biomass recovery relies mainly on local population growth and is thus slower.

Additionally, both experimentally and in model simulations, extinct patches had a slightly higher biomass after recovery than patches from unperturbed landscapes (not shown). This is because unperturbed patches only had the better competitor left (*Blepharisma* sp.), while all three species persisted in extinct patches. Since poorly competitive species (*Colpidium* sp. and *T. thermophila*) reached a higher biomass than *Blepharisma* sp., unperturbed patches had a lower biomass. This result should hold for communities dominated by highly competitive but slowly reproducing species that do not reach high densities (e.g., if there is a trade-off between population growth rate and competitive ability rather than the often assumed trade-off between population

growth rate and carrying capacity; for a discussion, see Mallet 2012) or when populations are able to overshoot their equilibrium density. This should however not be the case for communities where the dominant species happens to reach higher equilibrium densities, as it is the case in forests, for instance, where transiently recolonising species (e.g., grasses or shrubs) do not accumulate biomass and are slowly replaced by dominant species that do (trees).

α-diversity

Local patch extinctions generally increased α-diversity: experimentally, unperturbed patches reached a state where *Blepharisma* sp. was largely dominant, sometimes to the point where *T. thermophila* and *Colpidium* sp. were locally excluded. In control landscapes, this resulted in the extinction of *T. thermophila* at the landscape scale. As a result, α-diversity was low in control landscapes and in non-extinct patches (Fig. 3a). In extinct patches, all three species persisted during the recolonization process, resulting in higher α-diversity (Fig. 1a) compared to non-extinct patches from the same landscapes or from control landscapes (Fig. 3a). This result was also observed in all simulations of the metacommunity model, except in the absence of interspecific competition ("no interspecific interactions" scenario) since no competitive exclusion occurs in that case (Fig. 2a). The persistence of less competitive species in extinct patches during the recolonisation process can be explained both by the decrease in population density and by a competition-colonization trade-off across the three species: the low population density after extinction events decreases the intensity of competition, while the competition-colonization trade-off delays the recolonization by *Blepharisma* sp., both processes resulting in the delay of competitive exclusion. Since the increased α-diversity was observed in simulations without a competition-colonization trade-off (i.e., scenarios "randomized interactions" and "empirical interactions"; Fig. 2a), such a trade-off is not necessary for local extinctions to increase α-diversity, even though the trade-off increased α-diversity even more. These results are similar to effect described in the intermediate disturbance hypothesis which predicts that some degree of perturbation should result in a higher local and regional biodiversity by reducing the abundance of competitively dominant species and allowing

the persistence of early succesional species (Wilkinson, 1999; Shea et al., 2004). However, previous experiments on similar systems found that local patch extinctions decreased local diversity (Cadotte, 2007). This can be explained by differences in metacommunity composition: metacommunities skewed towards early-succesional species should exhibit the α-diversity increase observed here, while metacommunities skewed towards late-succesional species (as in Cadotte 2007) should see α-diversity decrease with local patch extinctions.

Clearly, these effects may be relevant in the context of ecosystem management: while local perturbations (here in their most extreme form, the extinction of all species) decrease biomass, they can also allow the persistence of species that would otherwise be excluded and lead to an increased local diversity.

Indirect effects

Besides the direct effects discussed above, local patch extinctions may also have indirect effects at the regional scale by altering species densities and composition in non-extinct patches (Gilarranz et al., 2017; Zelnik et al., 2019).

Biomass

Biomass in non-extinct patches was mainly unaffected by local patch extinctions. Experimentally, the biomass in non-extinct patches was fairly similar to the biomass in patches from control landscapes (Fig. 3b). This was also the case in simulations: biomass distributions largely overlapped between treatments (Fig. 4b). Despite reduced fluxes from extinct patches, the density in non-extinct patches did not decrease. This can be explained by local dynamics (population growth) being faster than spatial dynamics (dispersal). In this case, the adverse effect of local extinctions (decreased biomass) does not spread to non-extinct patches. However, in metacommunities with strong dispersal, non-extinct patches should also experience reduced biomass. While we did not observe a decrease of biomass in non-extinct patches, probably because local dynamics were too fast for spatial dynamics to have an effect on these patches, previous theoretical work predicts that

a local biomass reduction could spread in space if dispersal rates were high enough (Zelnik et al., 2019).

α-diversity

Experimentally, non-extinct patches in landscapes with extinctions were not dominated by *Blepharisma* sp. This is because dispersal of *T. thermophila* and *Colpidium* sp. from extinct patches, where they were present in high density during the recolonization process, allowed these species to persist in non-extinct patches. Their persistence increased α-diversity in non-extinct patches compared to patches from control landscapes that were mainly monospecific (Fig. 3a). The increase of α-diversity was stronger in non-extinct patches from dispersed extinction treatments, as these patches were connected to more extinct patches and thus received an increased amount of less competitive dispersers than non-extinct patches from clumped extinction treatments.

The increase of α-diversity following extinctions did not occur in the metacommunity model in the absence of interspecific competition (Fig. 4a; scenario "no interspecific interactions"), because competitive exclusion did not occur and therefore all three species were present in all patches. However, the patterns observed experimentally were recovered in all simulations that incorporated interspecific competition (Fig. 4a; scenarios "randomized interactions", "empirical interactions" and "competition-colonization trade-off"), showing that local diversity maintenance by local extinctions is not restricted to our particular experimental community but can occur as long a some species excludes others.

β-diversity

Both in experiments and theoretically, β-diversity was higher in landscapes that experienced local patch extinctions in comparison to control landscapes (Fig. 1b and 2b). More precisely, this result holds in theory as long as interspecific competition is included (Fig. 2b, scenarios "randomized interactions", "empirical interactions" and "competition-colonization trade-off"). In the simulations without interspecific competition (Fig. 2b; scenario "no interspecific interactions"),

β-diversity increased only marginally because all three species quickly recolonized the patches in the same proportion as in non-extinct patches. The increase in β-diversity following local patch extinctions (in experiments and in simulations with interspecific competition) can be explained by the fact that extinct patches had a different species composition than non-extinct patches. In non-extinct patches communities were mainly composed of *Blepharisma* sp., while extinct patches allowed for less competitive species to persist during the recolonization process. While we find a strictly increasing relationship between extinctions rate and β-diversity (Fig. 1b and 2b), Cadotte (2007) found a unimodal relationship between β-diversity and local patch extinction rates. While this seems contradictory, it is also possible that we did not cover enough extinction rate values to uncover a unimodal relationship, as β-diversity could decrease at higher extinction rates.

By crossing the extinction rates and spatial clumping treatments, we were able to show that the relationship between β-diversity and local patch extinctions rates is strongly dependant on the spatial distribution of extinctions: the increase in β-diversity was higher when extinctions were clumped than when they were dispersed in space. When extinctions were clumped, the connectivity between extinct and non extinct patches was fairly low, resulting in a strong differentiation between extinct and non-extinct patches. When extinctions were dispersed, extinct and non-extinct patches were well connected, resulting in a stronger mixing of communities between patches and a lower β-diversity.

Perspectives

Clearly, we have used a number of simplifying assumptions in our metacommunity model as well as in the experimental work that could provide some interesting directions for future research. Firstly, we consider only competitive interactions between species while natural communities consist of more diversified interactions, including predation, mutualism and parasitism, for example (Kéfi et al., 2012, 2015). These interactions could complicate the response (Kéfi et al., 2016) and affect the consequences of extinctions on ecological communities. Moreover, the sensitivity of species to local extinctions could depend on their trophic level, as demonstrated for habitat destruc-

tion (Liao et al., 2017; Ryser et al., 2019): top predators (or parasites) could be more vulnerable as they suffer both from the perturbation and from the reduction of their prey (or host) density. Specialized predators and parasites may also take longer to recolonize since they cannot return to perturbed patches while their prey (or host) is not present at a high enough density. Vice versa, other species could benefit from local extinctions through decreased predator or parasite pressures. Secondly, we ignore evolutionary processes although natural populations can readily adapt to environmental change. Increased local patch extinction rates should select for higher dispersal rates (Bowler and Benton, 2005; Ronce, 2007), but increased spatial clumping of extinctions could select for lower dispersal rates and longer dispersal distances (Fronhofer et al., 2014), which could result in opposite selective pressures if both increase at the same time. This could have implications for the dynamics of biodiversity because dispersal can mediate species coexistence (Hanski, 1983), diversity patterns (Laroche et al., 2016) and speciation (Pellissier, 2015). In particular, increased dispersal could synchronize metacommunities, making them more prone to global extinctions. Metacommunity synchrony could also be increased by the increasing spatial synchrony of climatic events (Di Cecco and Gouhier, 2018), as observed in the metapopulation of *Melitaea cinxia* (Kahilainen et al., 2018). On the other hand, evolutionary rescue could buffer the effects of disturbances, allowing metacommunities to persist in increasingly harsher environments (Bell and Gonzalez, 2011).

Conclusion

Overall, our study shows that the effects of local patch extinctions in metacommunities strongly depend on the spatial distributions of extinctions. Local patch extinctions can increase both α-diversity and β-diversity by allowing weak competitors to persist in the metacommunity and by forcing a differentiation between extinct and non-extinct patches.

Dispersal and connectivity between patches are central to recovery as they allow the recolonization of extinct patches but also a mixing between extinct and non-extinct patches, which can

result in the spread of local extinction effects to unperturbed patches. In our setting, this spread was characterised by an increase in α-diversity in unperturbed patches through dispersal from species-rich, previously extinct patches to species poor, previously non-extinct patches.

By determining the connectivity between extinct and non-extinct patches, the spatial clumping of extinctions modulates the dynamics after the extinction events: when extinctions are clumped, extinct and non extinct patches are weakly connected. This results in a slower biomass recovery, a weak spread of α-diversity and a high β-diversity as extinct and non-extinct patches are differentiated. On the contrary, dispersed extinctions imply higher connectivity between extinct and non-extinct patches which translates into a faster biomass recovery, a stronger spread of α-diversity and a lower β-diversity as extinct and non-extinct patches are better mixed.

Our highly controlled experiment in combination with the theoretical model provide a proof-of-concept for the importance of taking into account the spatial distribution of disturbances in biodiversity research. Of course, applying our findings to specific, real-world ecosystems will require a combination of field data and system-specific models to better estimate the effects of local extinctions in more realistic settings. Nevertheless, our work highlights the importance of the spatial distribution of local extinctions when doing so.

References

Abbott, K. C. 2011. A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. Ecology letters, **14**:1158–1169.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, E. T. Hogg, et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest ecology and management, **259**:660–684.

Altermatt, F. and D. Ebert. 2010. Populations in small, ephemeral habitat patches may drive dynamics in a daphnia magna metapopulation. Ecology, **91**:2975–2982.

Altermatt, F., E. A. Fronhofer, A. Garnier, A. Giometto, F. Hammes, J. Klecka, D. Legrand, E. Mächler, T. M. Massie, F. Pennekamp, et al. 2015. Big answers from small worlds: a user's guide for protist microcosms as a model system in ecology and evolution. Methods in Ecology and Evolution, **6**:218–231.

Bell, G. and A. Gonzalez. 2011. Adaptation and evolutionary rescue in metapopulations experiencing environmental deterioration. Science, **332**:1327–1330.

Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology, **65**:1–13.

Bowler, D. E. and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews, **80**:205–225.

Brown, J. H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology, **58**:445–449.

Cadotte, M. W. 2006. Metacommunity influences on community richness at multiple spatial scales: a microcosm experiment. Ecology, **87**:1008–1016.

Cadotte, M. W. 2007. Competition–colonization trade-offs and disturbance effects at multiple scales. Ecology, **88**:823–829.

Carpenter, K. E., M. Abrar, G. Aeby, R. B. Aronson, S. Banks, A. Bruckner, A. Chiriboga, J. Cortés, J. C. Delbeek, L. DeVantier, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science, **321**:560–563.

Di Cecco, G. J. and T. C. Gouhier. 2018. Increased spatial and temporal autocorrelation of temperature under climate change. Scientific reports, **8**:1–9.

Diehl, S. and M. Feissel. 2001. Intraguild prey suffer from enrichment of their resources: a microcosm experiment with ciliates. Ecology, **82**:2977–2983.

Feng, Y., S. Soliveres, E. Allan, B. Rosenbaum, C. Wagg, A. Tabi, E. De Luca, N. Eisenhauer, B. Schmid, A. Weigelt, et al. 2020. Inferring competitive outcomes, ranks and intransitivity from empirical data: A comparison of different methods. Methods in Ecology and Evolution, **11**:117–128.

Fronhofer, E. A. and F. Altermatt. 2015. Eco-evolutionary feedbacks during experimental range expansions. Nature communications, **6**:6844.

Fronhofer, E. A., A. Kubisch, F. M. Hilker, T. Hovestadt, and H. J. Poethke. 2012. Why are metapopulations so rare? Ecology, **93**:1967–1978.

Fronhofer, E. A., J. M. Stelz, E. Lutz, H. J. Poethke, and D. Bonte. 2014. Spatially correlated extinctions select for less emigration but larger dispersal distances in the spider mite tetranychus urticae. Evolution, **68**:1838–1844.

Gilarranz, L. J., B. Rayfield, G. Liñán-Cembrano, J. Bascompte, and A. Gonzalez. 2017. Effects of network modularity on the spread of perturbation impact in experimental metapopulations. Science, **357**:199–201.

Hanski, I. 1983. Coexistence of competitors in patchy environment. Ecology, **64**:493–500.

Hanski, I. and M. Kuussaari. 1995. Butterfly metapopulation dynamics. Population dynamics: new approaches and synthesis, **8**:149–171.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological journal of the Linnean Society, **42**:73–88.

IPBES. 2019. Global assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn, Germany. URL `https://www.ipbes.net/news/ipbes-global-assessment-summary-policymakers-pdf`.

Jost, L. 2006. Entropy and diversity. Oikos, **113**:363–375.

Kahilainen, A., S. van Nouhuys, T. Schulz, and M. Saastamoinen. 2018. Metapopulation dynamics in a changing climate: Increasing spatial synchrony in weather conditions drives metapopulation synchrony of a butterfly inhabiting a fragmented landscape. Global change biology, **24**:4316–4329.

Kéfi, S., E. L. Berlow, E. A. Wieters, L. N. Joppa, S. A. Wood, U. Brose, and S. A. Navarrete. 2015. Network structure beyond food webs: mapping non-trophic and trophic interactions on chilean rocky shores. Ecology, **96**:291–303.

Kéfi, S., E. L. Berlow, E. A. Wieters, S. A. Navarrete, O. L. Petchey, S. A. Wood, A. Boit, L. N. Joppa, K. D. Lafferty, R. J. Williams, et al. 2012. More than a meal… integrating non-feeding interactions into food webs. Ecology letters, **15**:291–300.

Kéfi, S., V. Miele, E. A. Wieters, S. A. Navarrete, and E. L. Berlow. 2016. How structured is the entangled bank? the surprisingly simple organization of multiplex ecological networks leads to increased persistence and resilience. PLoS biology, **14**:e1002527.

Laroche, F., P. Jarne, T. Perrot, and F. Massol. 2016. The evolution of the competition–dispersal trade-off affects α-and β-diversity in a heterogeneous metacommunity. Proceedings of the Royal Society B: Biological Sciences, **283**:20160548.

Legendre, P. and M. De Cáceres. 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. Ecology letters, **16**:951–963.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. American Entomologist, **15**:237–240.

Liao, J., D. Bearup, Y. Wang, I. Nijs, D. Bonte, Y. Li, U. Brose, S. Wang, and B. Blasius. 2017. Robustness of metacommunities with omnivory to habitat destruction: disentangling patch fragmentation from patch loss. Ecology, **98**:1631–1639.

Mallet, J. 2012. The struggle for existence. how the notion of carrying capacity, k, obscures the links between demography, darwinian evolution and speciation. Evolutionary Ecology Research.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being, volume 5. Island press Washington, DC.

Pellissier, L. 2015. Stability and the competition-dispersal trade-off as drivers of speciation and biodiversity gradients. Frontiers in Ecology and Evolution, **3**:52.

Pennekamp, F., J. Clobert, and N. Schtickzelle. 2019. The interplay between movement, morphology and dispersal in tetrahymena ciliates. PeerJ, **7**:e8197.

Pennekamp, F., J. I. Griffiths, E. A. Fronhofer, A. Garnier, M. Seymour, F. Altermatt, and O. L. Petchey. 2017. Dynamic species classification of microorganisms across time, abiotic and biotic environments—a sliding window approach. PloS one, **12**:e0176682.

Pennekamp, F., N. Schtickzelle, and O. L. Petchey. 2015. Bemovi, software for extracting behavior and morphology from videos, illustrated with analyses of microbes. Ecology and Evolution, **5**:2584–2595.

Ronce, O. 2007. How does it feel to be like a rolling stone? ten questions about dispersal evolution. Annu. Rev. Ecol. Evol. Syst., **38**:231–253.

Rosenbaum, B., M. Raatz, G. Weithoff, G. F. Fussmann, and U. Gaedke. 2019. Estimating parameters from multiple time series of population dynamics using bayesian inference. Frontiers in Ecology and Evolution, **6**:234.

Ruokolainen, L. 2013. Spatio-temporal environmental correlation and population variability in simple metacommunities. PloS one, **8**:e72325.

Ryser, R., J. Häussler, M. Stark, U. Brose, B. C. Rall, and C. Guill. 2019. The biggest losers: Habitat isolation deconstructs complex food webs from top to bottom. Proceedings of the royal society B, **286**:20191177.

Shea, K., S. H. Roxburgh, and E. S. Rauschert. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecology letters, **7**:491–508.

Wilkinson, D. M. 1999. The disturbing history of intermediate disturbance. Oikos, pages 145–147.

Worsfold, N. T., P. H. Warren, and O. L. Petchey. 2009. Context-dependent effects of predator removal from experimental microcosm communities. Oikos, **118**:1319–1326.

Zelnik, Y. R., J.-F. Arnoldi, and M. Loreau. 2019. The three regimes of spatial recovery. Ecology, **100**:e02586.

Author contributions

C.S., S.K. and E.A.F. conceived the study. C.S. and C.G.B. conducted the experiments. C.S. performed the statistical analyses. C.S., B.R. and E.A.F. performed the model fitting. C.S. analysed the mathematical model. C.S., S.K. and E.A.F. wrote the manuscript and all authors commented on the draft.

Acknowledgements

The study was funded by a grant of the ENS to C.S. and CNRS funds to E.A.F. B.R. acknowledges the support of iDiv funded by the German Research Foundation (DFG–FZT 118, 202548816). This is publication ISEM-YYYY-XXX of the Institut des Sciences de l'Evolution – Montpellier.

Data availability

Data and code are available on GitHub via Zenodo: https://doi.org/10.5281/zenodo.4297535

Supplementary Material

Supplementary Figures

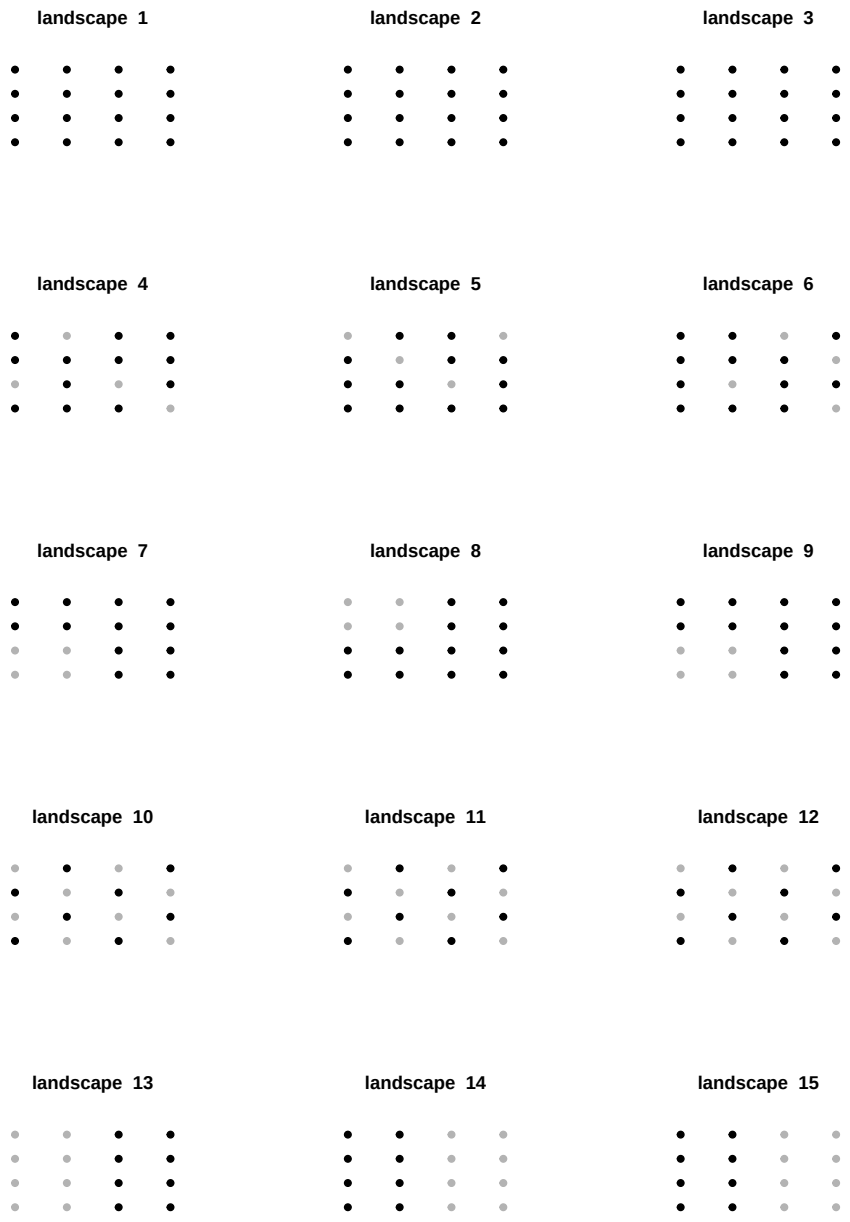

Figure S1: Positions of the extinctions (grey) in each landscape in the experimental setting. Landscapes 1-3: no extinction, landscapes 4-6: 4 dispersed extinctions, landscapes 7-8: 4 clumped extinctions, landscapes 10-12: 8 dispersed extinctions, landscapes 13-15: 8 clumped extinctions.

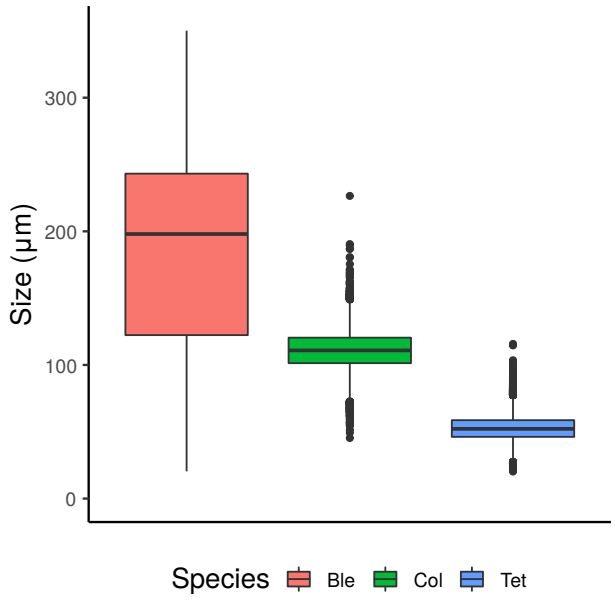

Figure S2: Size distributions of *T. thermophila* (Tet), *Colpidium* sp. (Col) and *Blepharisma* sp. (Ble) in monocultures.

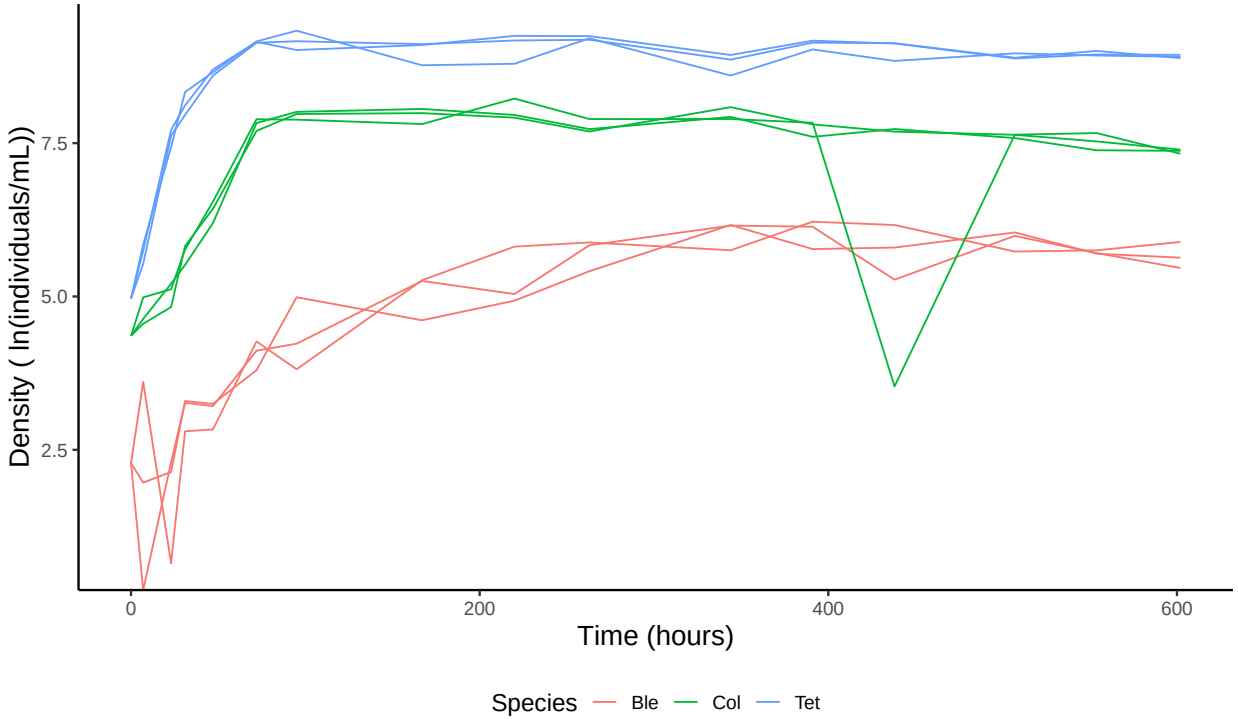

Figure S3: Densities of *T. thermophila* (Tet), *Colpidium* sp. (Col) and *Blepharisma* sp. (Ble) over time in single patch monocultures.

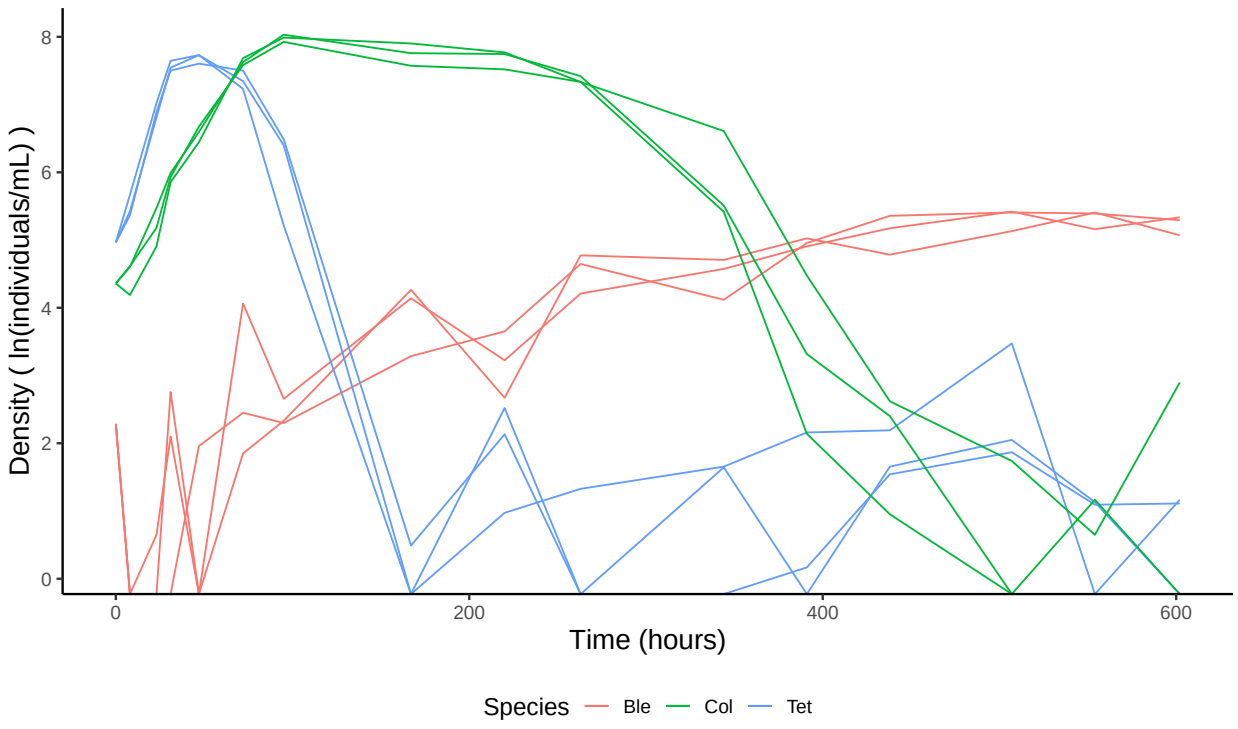

Figure S4: Densities of *T. thermophila* (Tet), *Colpidium* sp. (Col) and *Blepharisma* sp. (Ble) over time in single patch co-cultures.

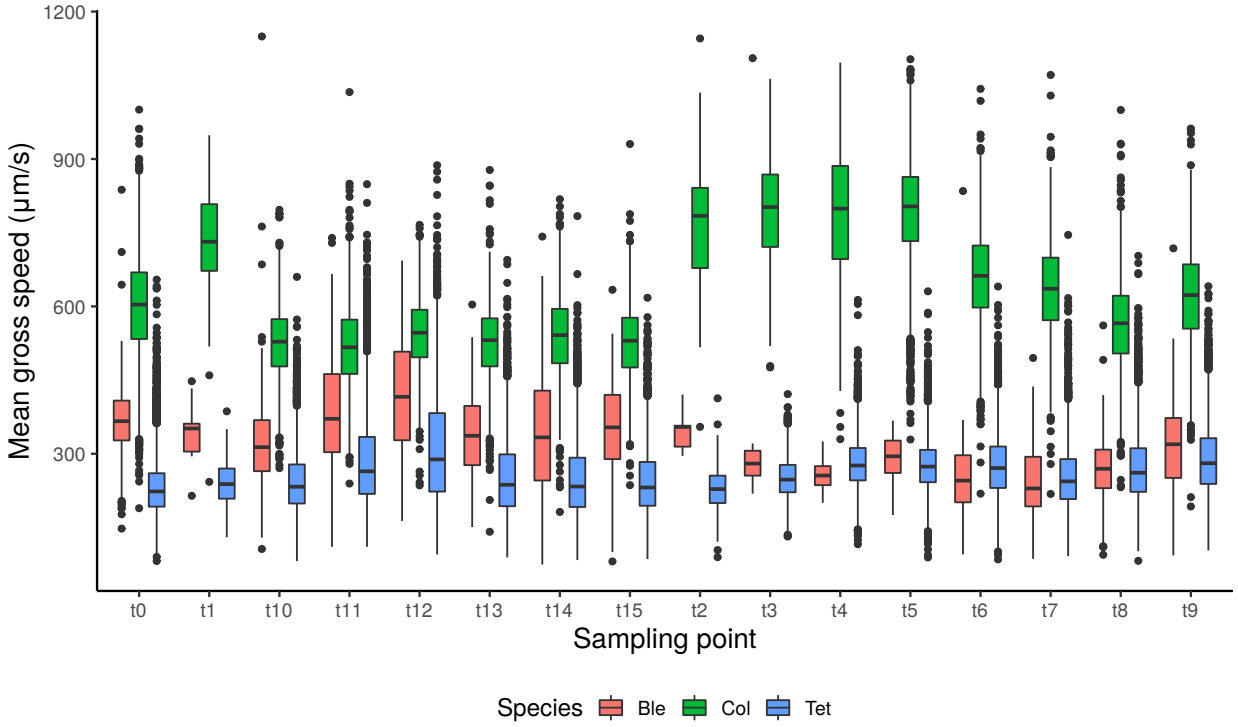

Figure S5: Gross speeds of *T. thermophila* (Tet), *Colpidium* sp. (Col) and *Blepharisma* sp. accross sampling points in single-patch mono-culutures.

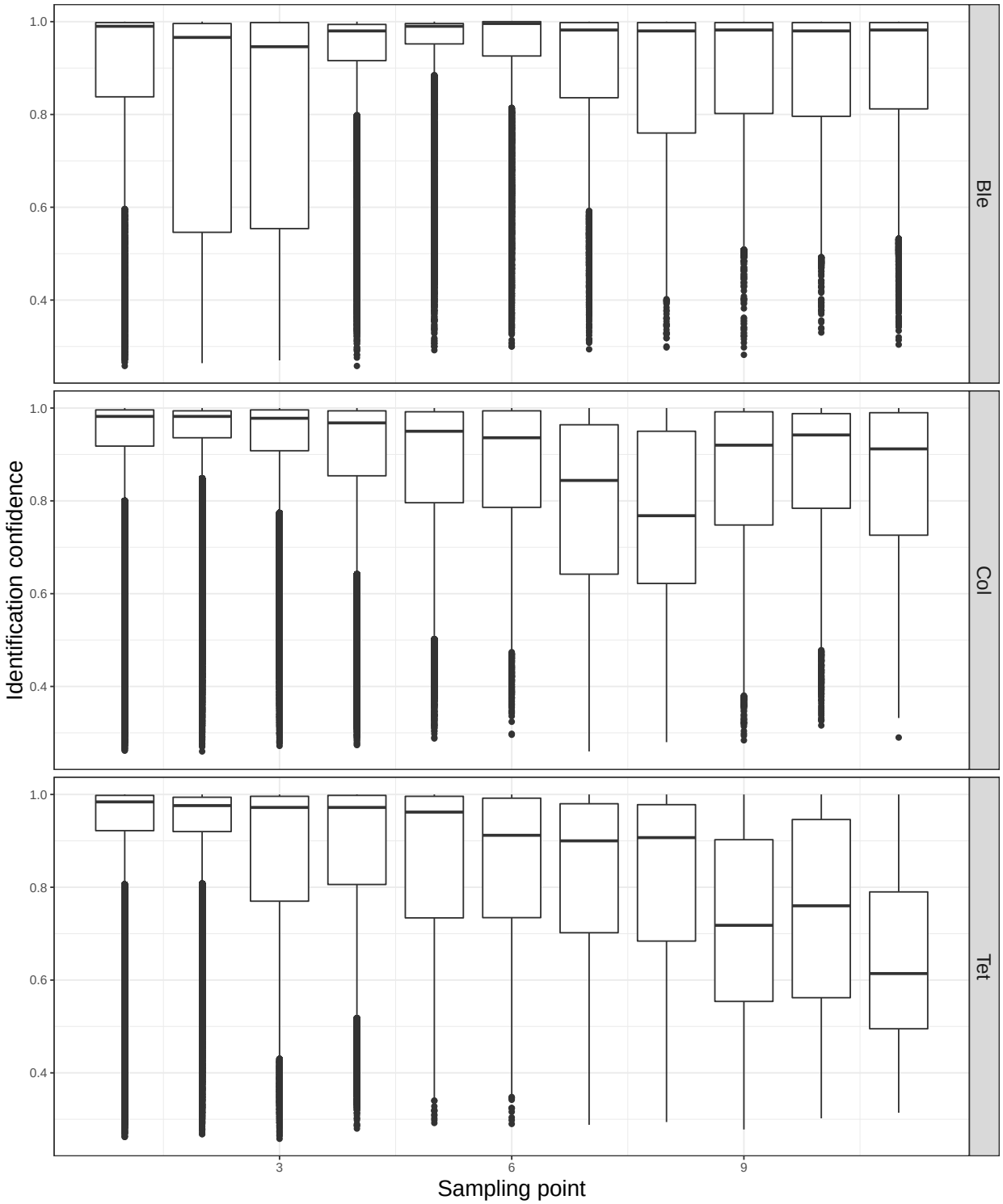

Figure S6: Identification confidence for individuals identified as *Blepharisma* sp. (Ble), *Colpidium* sp. and *T. Thermophila* at each sampling point of the experiment.

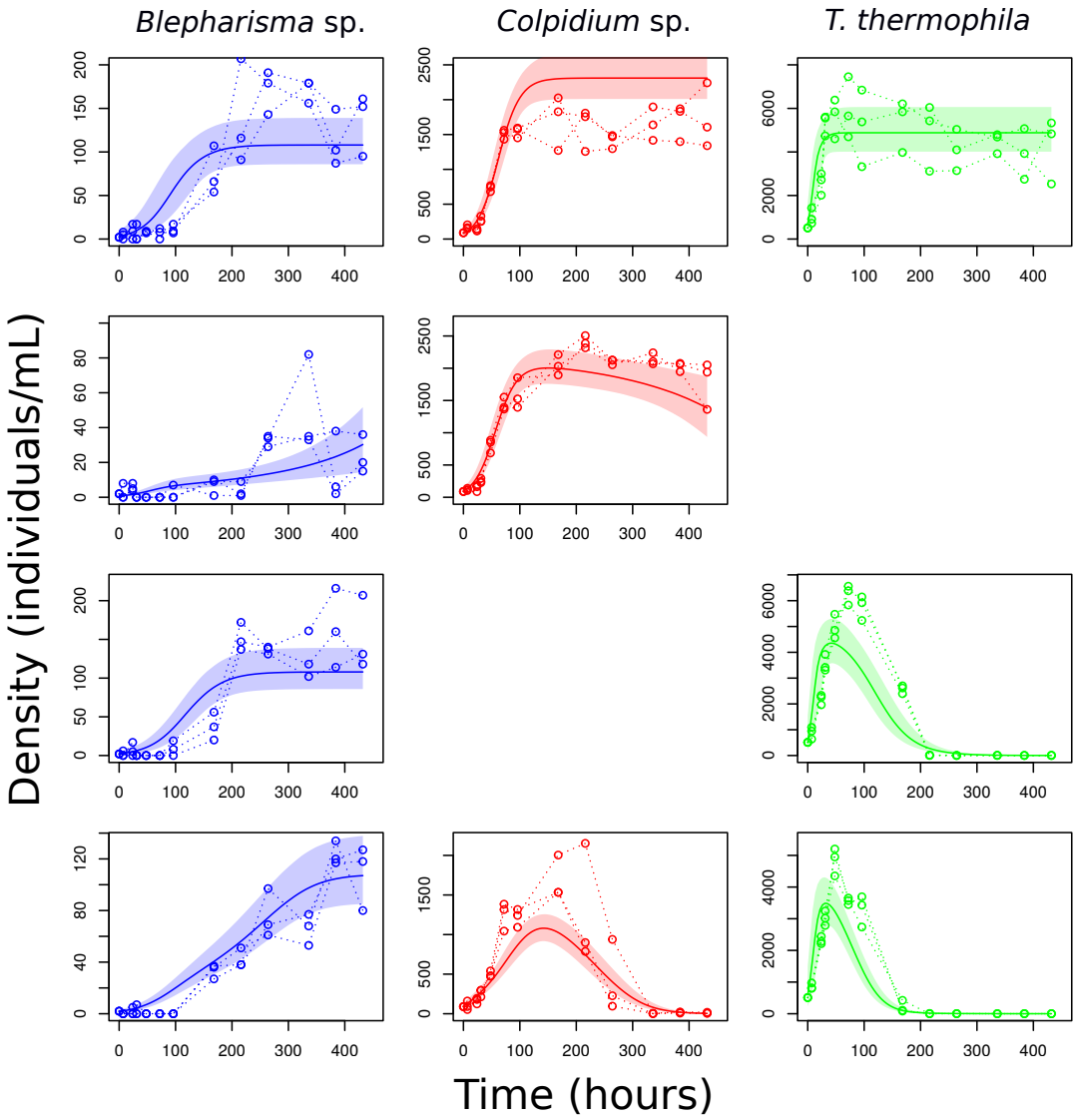

Figure S7: Fit of a competitive Lotka-Volterra model to experimental time series data obtained in single patch cultures of *Blepharisma* sp. (blue), *Colpidium* sp. (red) and *T. thermophila* (green). The curves and shaded areas show the posterior model predictions (median and 95% CI), the points and dashed lines show the experimental densities. The first line shows the monoculture of each species. The second and third lines show co-cultures of *Blepharisma* sp. with *Colpidium* sp. (second line) and *Blepharisma* sp. with *T. thermophila* (third line). The fourth line shows the co-culture of all three species together.

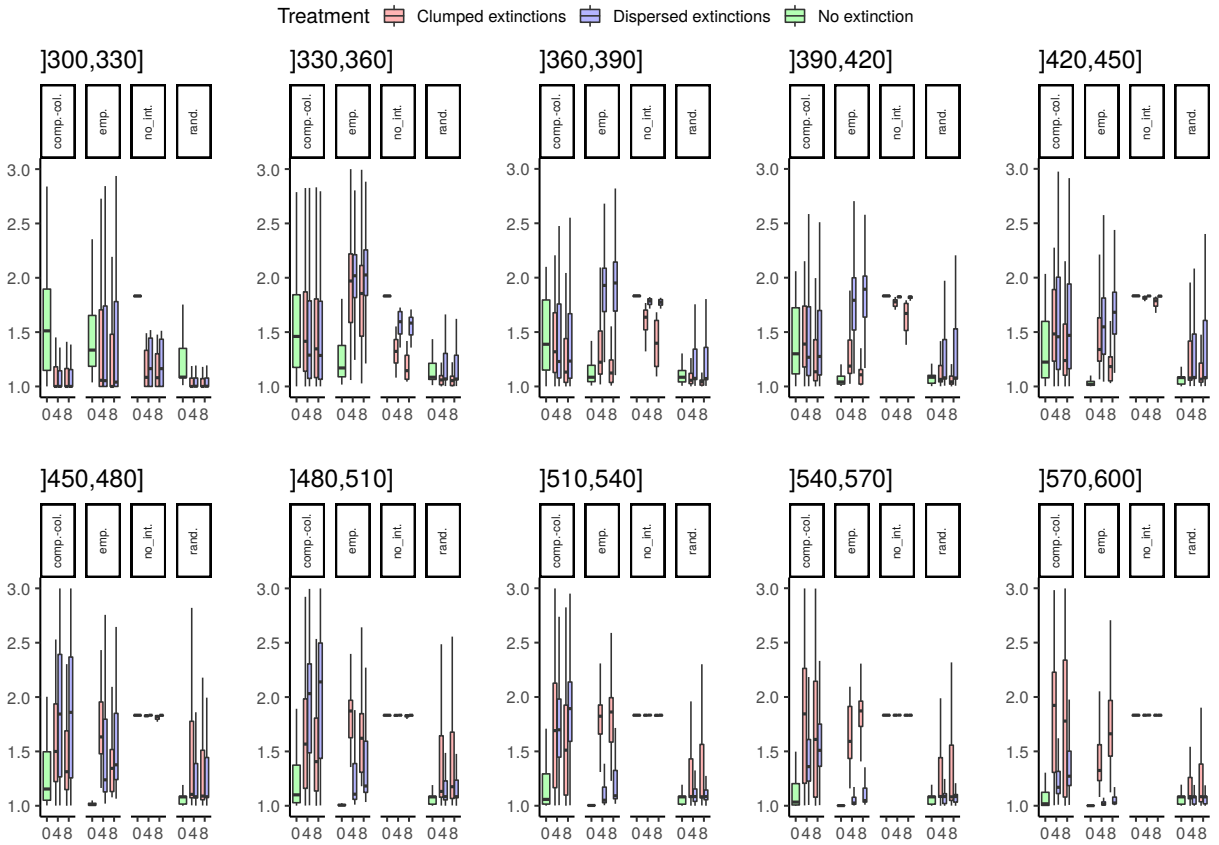

Figure S8: α-diversity in extinct patches in numerical simulations of the metacommunity model over moving time windows from the extinction time (300 time units) to the end of the simulation (600 time units). The bottom labels denote the number of extinctions (0, 4, 8). The top labels denote the scenarios of species interactions: ”emp.” for ”empirical interactions”, ”comp.-col.” for ”competition/colonization trade-off”, ”rand.” for ”randomized interactions” and ”no_int.” for ”no interspecific interactions”.

Supplementary Tables

669

Table S1: Priors used to fit a competitive Lotka-Volterra model on experimental time series. We used the same growth rates (r_i, one per species) and competition strengths (one intraspecific term ($\alpha_{i,i}$) per species and 6 interspecific terms ($\alpha_{i,j;\ i\neq j}$)) over all replicates. We fitted unique initial densities (N_0) on each species in each replicate.

Parameters	Meaning	prior
r_i	Growth rates	lognormal(-2, 1)
$\alpha_{i,j}$	Competition strengths	gamma(2, 1)
N_0	Initial densities	*Blepharisma* sp.: normal(0,10) *Colpidium* sp.: normal(0,100) *T. thermophila*: normal(0,1000)

Table S2: **Tables of model comparison** for local effects in extinct patches (α-diversity, bioarea and recovery time) and β-diversity. For each variable, we compared all mixed models between the full model (Spatial clumping * Extinction rate) and the intercept using AICc. Models not displayed – for β-diversity (b) – had a negligible weight.

(a) Alpha diversity model comparison.

Model	ΔAICc	Weight
Spatial clumping	0.00	0.542
Spatial clumping + Extinction rate	1.15	0.302
Spatial clumping * Extinction rate	3.23	0.108
Intercept	5.71	0.031
Extinction rate	7.16	0.015

(b) Beta diversity model comparison.

Model	ΔAICc	Weight
Spatial clumping * Extinction rate	0.00	1
Spatial clumping + Extinction rate	20.44	0.00

(c) Bioarea model comparison.

Model	ΔAICc	Weight
Spatial clumping	0.00	0.362
Intercept	0.62	0.265
Spatial clumping + Extinction rate	1.70	0.155
Extinction rate	2.32	0.113
Spatial clumping * Extinction rate	2.48	0.105

(d) Recovery time model comparison.

Model	ΔAICc	Weight
Spatial clumping	0.00	0.271
Spatial clumping * Extinction rate	0.31	0.232
Intercept	0.50	0.211
Spatial clumping + Extinction rate	0.93	0.170
Extinction rate	1.69	0.117

Table S3: **Tables of model comparison** for bioarea and $\alpha-$diversity in non-extinct patches adjacent to at least one extinct patch. For both variables, we compared all mixed models between the full model (Spatial clumping * Extinction rate) and the intercept using AICc. Models not displayed – for α-diversity (b) – had a negligible weight.

(a) Bioarea model selection.

Model	ΔAICc	Weight
Intercept	0.00	0.515
Extinction rate	2.23	0.169
Spatial clumping * Extinction rate	2.43	0.153
Spatial clumping	3.19	0.104
Spatial clumping + Extinction rate	4.35	0.059

(b) α-diversity model selection

Model	ΔAICc	Weight
Spatial clumping * Extinction rate	0.00	0.806
Spatial clumping	3.43	0.145
Spatial clumping + Extinction rate	5.62	0.049