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# Spatial autocorrelation of local patch extinctions drives recovery dynamics in metacommunities

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# Abstract

1

Human activities put ecosystems under increasing pressure, often resulting in local extinctions. 2  
However, it is unclear how local extinctions affect regional processes, such as the distribution of 3  
diversity in space, especially if extinctions show spatial patterns, such as being clustered. Therefore, 4  
it is crucial to investigate extinctions and their consequences in a spatially explicit framework. Using 5  
highly controlled microcosm experiments and theoretical models, we here ask how the number and 6  
spatial autocorrelation of extinctions interactively affect metacommunity dynamics. We found that 7  
local patch extinctions increased local ( $\alpha$ -) and inter-patch ( $\beta$ -) diversity by delaying the exclusion 8  
of inferior competitors. Importantly, recolonization dynamics depended more strongly on the spatial 9  
distribution than on the number of patch extinctions: clustered local patch extinctions resulted in 10  
slower recovery, lower  $\alpha$ -diversity and higher  $\beta$ -diversity. Our results highlight that the spatial 11  
distribution of perturbations should be taken into account when studying and managing spatially 12  
structured communities. 13

# Introduction

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Understanding the causes and consequences of local extinctions and how they affect biological systems at larger spatial scales lies at the heart of metapopulation and metacommunity ecology. Natural metapopulations and metacommunities — sets of local populations and communities linked by dispersal (Levins, 1969) — naturally experience local extinctions (Hanski & Kuussaari, 1995; Altermatt & 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 species 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 and basal species. As a consequence, prey species can benefit at the regional scale from local patch extinctions due to release from predation. In competitive communities with a competition-colonization trade-off occasional local patch extinctions can even prevent regional extinctions and increase regional diversity by allowing less competitive species to persist (Cadotte, 2007).

Clearly, the relationship between local processes, such as extinctions, and regional patterns, such as distributions of biodiversity, is non-trivial. This is because metacommunities consist of more or less independent units, patches, harbouring local communities, which are linked in space by dispersal events. The coupling of spatially distinct communities can reduce the effect of local extinctions if these are asynchronous: extinct patches can be recolonized from occupied ones. 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 such that local events have a regional effect (Gilarranz *et al.*, 2017; Zelnik *et al.*, 2019). For example, biomass could

decrease in unperturbed patches as they receive reduced biomass fluxes from perturbed patches, or their species composition could change if they exchange individuals with perturbed patches whose species composition differs during the recolonization process. At the metacommunity level, strong dispersal might homogenize the composition of perturbed and unperturbed patches, thus reducing inter-patch ( $\beta$ -) diversity.

One likely important factor that modulates the effects discussed above is the spatial distribution of local patch extinctions, that is, whether they are clustered in space or not. An increase in the spatial autocorrelation 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 & 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 these trends that foreshadow greater numbers and especially stronger spatial autocorrelation of climate-induced local extinctions, few studies have taken an appropriate, spatially explicit view of disturbances and their effects on metacommunity dynamics. This leaves a gap in our understanding of how spatially clustered extinctions may affect the dynamics of ecological systems.

Here, we investigate how the number and spatial distribution of local patch extinctions affect recolonization dynamics in metacommunities. We are particularly interested in the effects on local ( $\alpha$ -) and inter-patch ( $\beta$ -) diversity which act together to determine regional diversity. Previous theory on landscape moderation of biodiversity (Tscharntke *et al.*, 2012) led us to speculate that local extinctions could increase  $\beta$ -diversity if different species thrive in perturbed and unperturbed patches, and  $\alpha$ -diversity if mass effect dynamics take place between perturbed and unperturbed

patches with different species. Using a full factorial design crossing three levels of extinction 68  
numbers and two levels of spatial autocorrelation, we forced local patch extinctions in experimental 69  
and simulated metacommunities and followed metacommunity dynamics. We focused on the 70  
dynamics of the recolonization process (*i.e.*, shortly after the extinctions) to capture the transient 71  
effects of extinctions. We were able to show that local patch extinctions can increase both  $\alpha$ - and  $\beta$ - 72  
diversity, and that this effect depends strongly on the spatial autocorrelation of extinctions: dispersed 73  
extinctions increase  $\alpha$ -diversity more, while clustered extinctions increase mainly  $\beta$ -diversity. 74

## Methods 75

We used a combination of laboratory experiments with metacommunities of three freshwater ciliates 76  
(*Tetrahymena thermophila*, *Colpidium* sp. and *Blepharisma* sp.) in microcosm landscapes and 77  
mathematical modelling of metacommunities to address our main research question. To do so, we 78  
forced local patch extinctions (not sustained in time, *i.e.*, ‘pulse’ perturbations; see Bender *et al.* 79  
1984) in experimental microcosm landscapes (Altermatt *et al.*, 2015) and followed metacommunity 80  
recovery in terms of species diversity and biomass as a function of the intensity (amount of 81  
extinctions) and spatial distribution (clustered vs. dispersed) of the extinctions. Experiments and 82  
simulations followed the dynamics of metacommunities in landscapes made of 16 patches arranged 83  
in a square lattice and connected by tubes allowing active dispersal. We present here a summary 84  
description of our methods. A more detailed account is provided in the supplement S3. 85

## Experiments 86

Experimental landscapes were made of 16 vials (volume: 20 mL) arranged on a grid and connected 87  
to their 4 nearest neighbours, allowing individuals to disperse from one patch to another. Local 88  
patch extinctions consisted in removing all individuals of all species in a given patch. Each patch 89  
was initially inoculated with one of the three species at half its carrying capacity. Extinctions 90  
were implemented once, two weeks after inoculation to allow community assembly to have taken 91

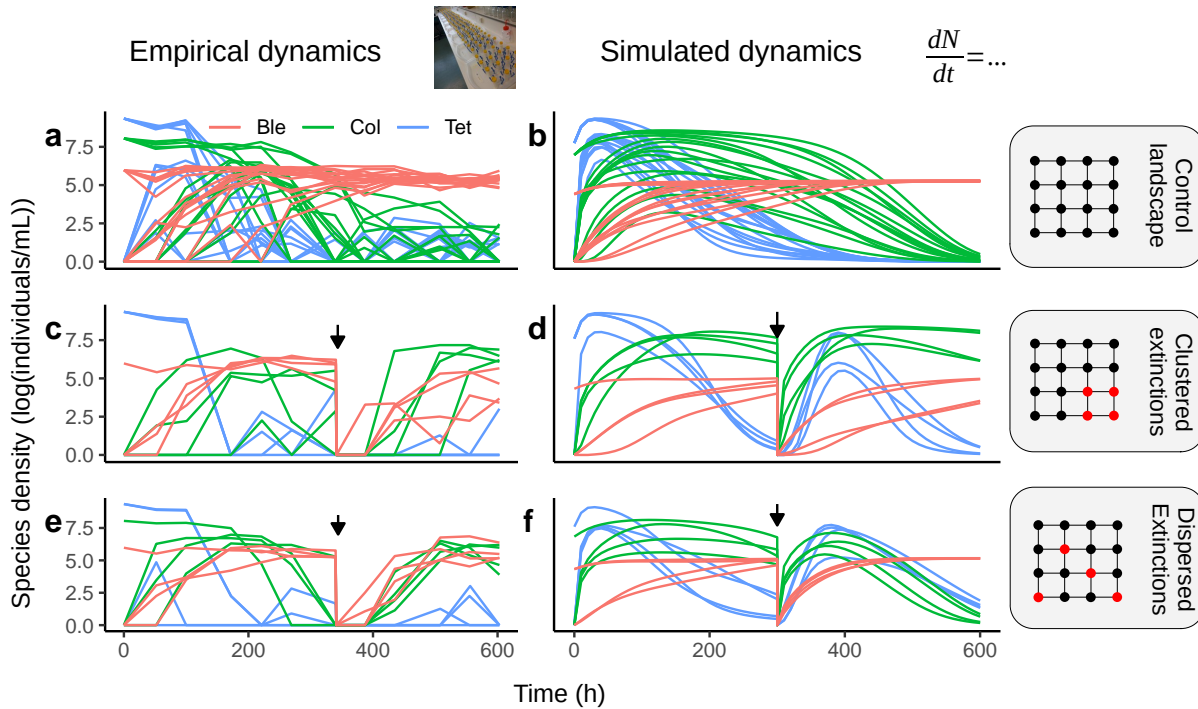


Figure 1: Overview of the experimental design: Species density over time of *Blepharisma* sp. (Ble, red), *Colpidium* sp. (Col, green) and *Tetrahymena thermophila* (Tet, blue), in experiments (a, c, e) and simulations under the “competition-colonization trade-off” scenario (b, d, f). (a, b) Dynamics in patches from control landscapes. (c, d) Dynamics in perturbed patches from landscapes with 4 clustered extinctions. (e, f) Dynamics in perturbed patches from landscapes with 4 dispersed extinctions. Black arrows represent the extinctions. Note that 2 treatments (8 clustered extinctions and 8 dispersed extinctions) are not shown here.

place. Subsequently, we observed the recovery of the landscapes (Fig. 1). Since we expected 92  
the extinctions to have only a transient effect before the metacommunity reached an equilibrium 93  
dominated by the best competitor (*Blepharisma* sp.), we followed the recovery dynamics just after 94  
the extinctions for a duration of two weeks (which is the time it takes for *Blepharisma* sp. to 95  
exclude the other species in a single patch co-culture; Fig. S1.12 h-j). In order to explore the 96  
effects of the number of local patch extinctions and their spatial autocorrelation on the dynamics of 97  
metacommunities, we used a full factorial design crossing three levels of local patch extinctions (0, 98  
4 or 8 extinctions out of 16 patches) with two levels of spatial autocorrelation (clustered: Fig. S1.8 99

landscapes 7-9 and 13-15; dispersed: Fig. S1.8 landscapes 4-6 and 10-12). This design yielded a total of 5 treatments (no extinction, 4 clustered extinctions, 4 dispersed extinctions, 8 clustered extinctions, 8 dispersed extinctions) that were each replicated in 3 landscapes, for a total of 15 landscapes and 240 patches.

We followed metacommunity dynamics through time by measuring the density of each species in each patch using automated video analysis. Three times per week, 2 mL of medium were sampled from all microcosms and replaced with fresh medium. For each microcosm, a subsample of 250  $\mu$ L was placed between two microscope slides (height: 500  $\mu$ m) and filmed using an optical stereo-microscope (Perfex Pro 10) coupled with a camera (Perfex SC38800) for 10 seconds (150 frames). We used the Bemovi R-package (version 1.0) (Pennekamp *et al.*, 2015) to extract individuals characteristics (shape, speed, size...) from the videos. We identified individuals from their characteristics 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 individuals with an identification confidence (proportion of trees leading to that identification) lower than 0.8 as a compromise between the number of observations discarded and the confidence of identification (Fig. S1.11).

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

All statistical analyses were conducted in R (version 4.0.2). To test the relative effects of spatial autocorrelation and number of local extinctions on metacommunity properties, we studied 4 metrics (biomass,  $\alpha$ -diversity,  $\beta$ -diversity and biomass recovery time) using mixed-effects models (R-package lme4 version 1.1-23) with the measurement point and landscape ID (for patch level metrics) as random effects to account for non-independence of measures taken the same day and measures taken within one landscape. Fixed effects were the autocorrelation of extinctions, the number of extinctions, as well as their interaction. We normalized the response variables using the



R-package `bestNormalize` (version 1.6.1): we used the function `bestNormalize` (which finds the best transformation to render some data Gaussian while losing the fewest degrees of freedom using a Pearson P statistic) on each response variable ( $\beta$ -diversity: no normalization needed;  $\alpha$ -diversity, biomass and recovery time normalized using the Ordered Quantiles technique, function `orderNorm`). 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 biomass higher than the 2.5% quantile of pre-extinction biomass 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 predictions for visualization.

Because we use measurements taken at different times, the temporal autocorrelation of the data acquired in a patch could lead us to artificially increase our statistical power and report non-significant results as significant. To assess the robustness of our analysis, we reproduced it using a total pooling (McElreath, 2020) at the patch level by analyzing the average (Fig. S1.4) or the median (Fig. S1.5) of post-extinction data from a given patch. Both approaches are very conservative and free from issues of autocorrelation, yet they closely reproduce the patterns observed in the main text (Fig. 2).

The experimental data and the code for the statistical analysis are available on GitHub via Zenodo: <https://doi.org/10.5281/zenodo.6364903>.

## Metacommunity model

We also developed a metacommunity model to replicate and generalize the experiment *in silico*. 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  $k$ .

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

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

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

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

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

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

$$h(N_{i,\bullet}) = \sum_l \frac{m_i N_{i,l}}{c_l} \quad (4)$$

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

We used four different parameterizations (see supplement S3) to investigate which biological processes may explain the patterns observed experimentally, hereafter described as “scenarios of species interactions” (Tab. S2.7). The scenarios “**empirical interactions**” and “**competition-colonization trade-off**” use growth rate and interaction parameters fitted from experimental data (Fig. S1.12 and S1.27) with equal dispersal rates for all species in the former and dispersal rate inversely proportional to the competitive ability in the latter. The scenario “**randomized interactions**” used the same parameters as the “empirical interactions” scenario but with randomized interspecific interaction rates in order to test whether our results held for other community structures. Lastly, we used a scenario without competition (“**no interspecific interactions**”) as a null model. We also used this model to conduct sensitivity analysis on the

landscape size and dispersal rate in order to test the generality of our results. 169

The simulations were run in R (version 4.0.2), using the *ode45* solver from the library *deSolve* 170  
(version 1.30). We simulated dynamics using the same extinction plans as in the microcosm 171  
experiments with 100 replicates for each treatment. While the simulations are deterministic, the 172  
initial distribution of species was drawn randomly in each replicate of each treatment, leading to 173  
variability between replicates at a given timestep. To check that our integrator choice did not result 174  
in numerical errors, we also reproduced 10% of the simulations with a second integrator (*lsoda*) 175  
with very low error tolerance parameters ( $\text{rtol} = 10^{-9}$ ,  $\text{atol} = 10^{-9}$ ). These simulations (Fig. S1.6 176  
and S1.7) match the main simulations (Fig. 2 and 4), ruling out integrator-related numerical errors. 177

The model is available on GitHub via Zenodo: <https://doi.org/10.5281/zenodo.6364903>. 178

## Results 179

### The effect of the spatial distribution of extinctions 180

In the experiments, both local and regional effects of local patch extinctions were mainly 181  
determined by the spatial autocorrelation of extinctions. Except for  $\beta$ -diversity, the number of 182  
extinctions alone only had a marginal effect on the outcome of the experiment as indicated by 183  
model selection (Fig. 2; Tab. S2.3 and S2.5). For the local variables studied ( $\alpha$ -diversity, biomass 184  
and biomass recovery time), the autocorrelation of extinctions was found to be more important than 185  
the number of extinctions (Tab. S2.3 and S2.5). Both  $\alpha$ -diversity in unperturbed patches 186  
(Tab. S2.4b and S2.6b) and  $\beta$ -diversity (Tab. S2.3b and S2.5b) were mostly explained by the 187  
interaction between autocorrelation and number of extinctions (statistical models without the 188  
interactions had either a null (for  $\beta$ -diversity) or low (for  $\alpha$ -diversity) weight). 189

Numerical simulations of our metacommunity model with the same spatial configuration and 190  
extinctions patterns confirmed this important effect of the spatial arrangement of extinctions 191  
compared to that of their number for all competition scenarios (Fig. 3 and 5). 192

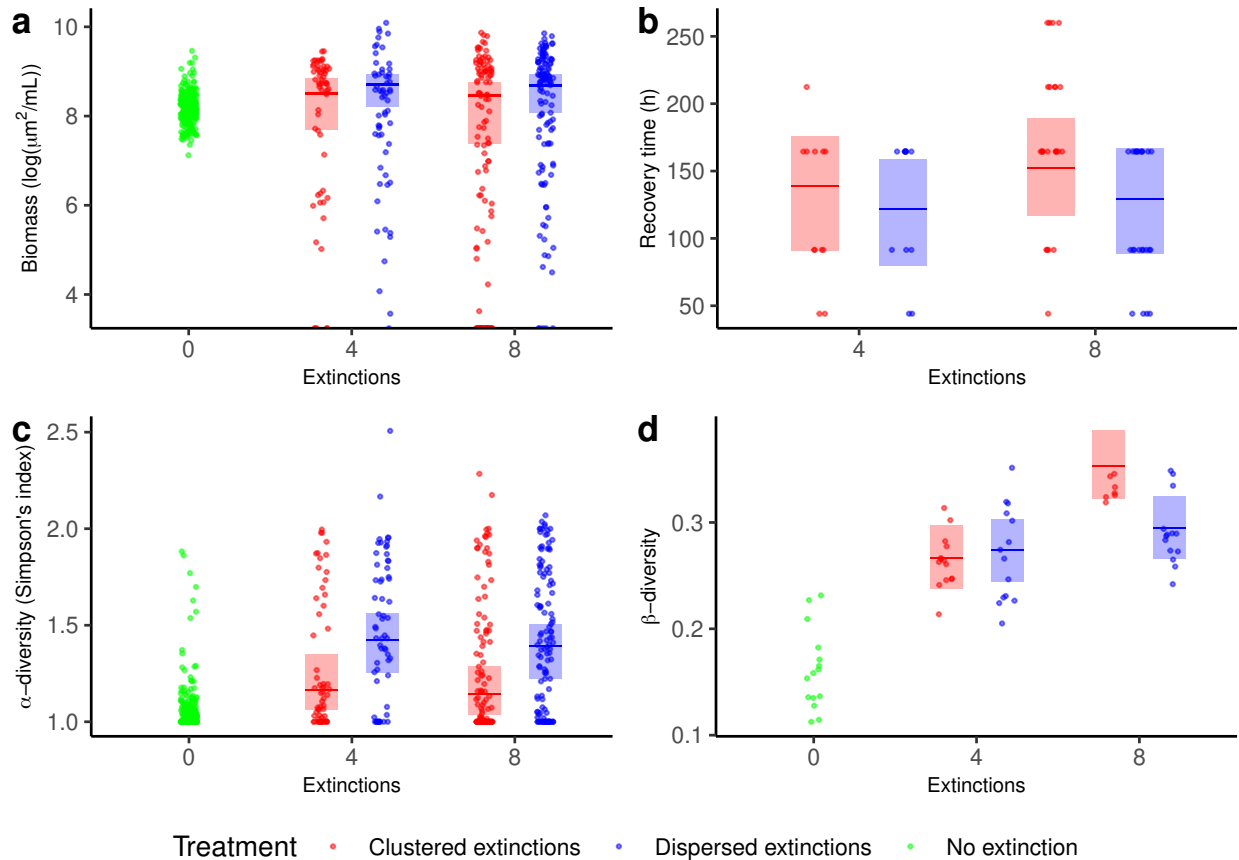


Figure 2: Observed response variables in the experiments (dots) and averaged mixed model predictions (medians and 95% confidence intervals; Tab. S2.3) from the extinction events to the end of the experiments. (a) Biomass in perturbed patches (blue: dispersed extinctions, red: clustered extinctions) and patches from landscapes with no extinctions (green), (b) biomass recovery time in perturbed patches, (c)  $\alpha$ -diversity (measured as Simpson's index) in perturbed patches and patches from landscapes with no extinctions and (d)  $\beta$ -diversity in all landscapes.

## Direct effects — recolonization dynamics in perturbed patches

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### Biomass

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The biomass in a given patch after local patch extinctions was slightly higher in perturbed patches from landscapes with dispersed extinctions than in perturbed patches from landscapes with clustered extinctions (Fig. 2a; median predictions :  $6076 \mu\text{m}^2 \text{mL}^{-1}$  vs.  $4855 \mu\text{m}^2 \text{mL}^{-1}$ , 5-95% quantiles:  $4274 - 7436 \mu\text{m}^2 \text{mL}^{-1}$  vs.  $2224 - 6372 \mu\text{m}^2 \text{mL}^{-1}$ ). 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. S2.3). The recovery time needed to reach a biomass higher than the 2.5% quantile of the pre-extinction

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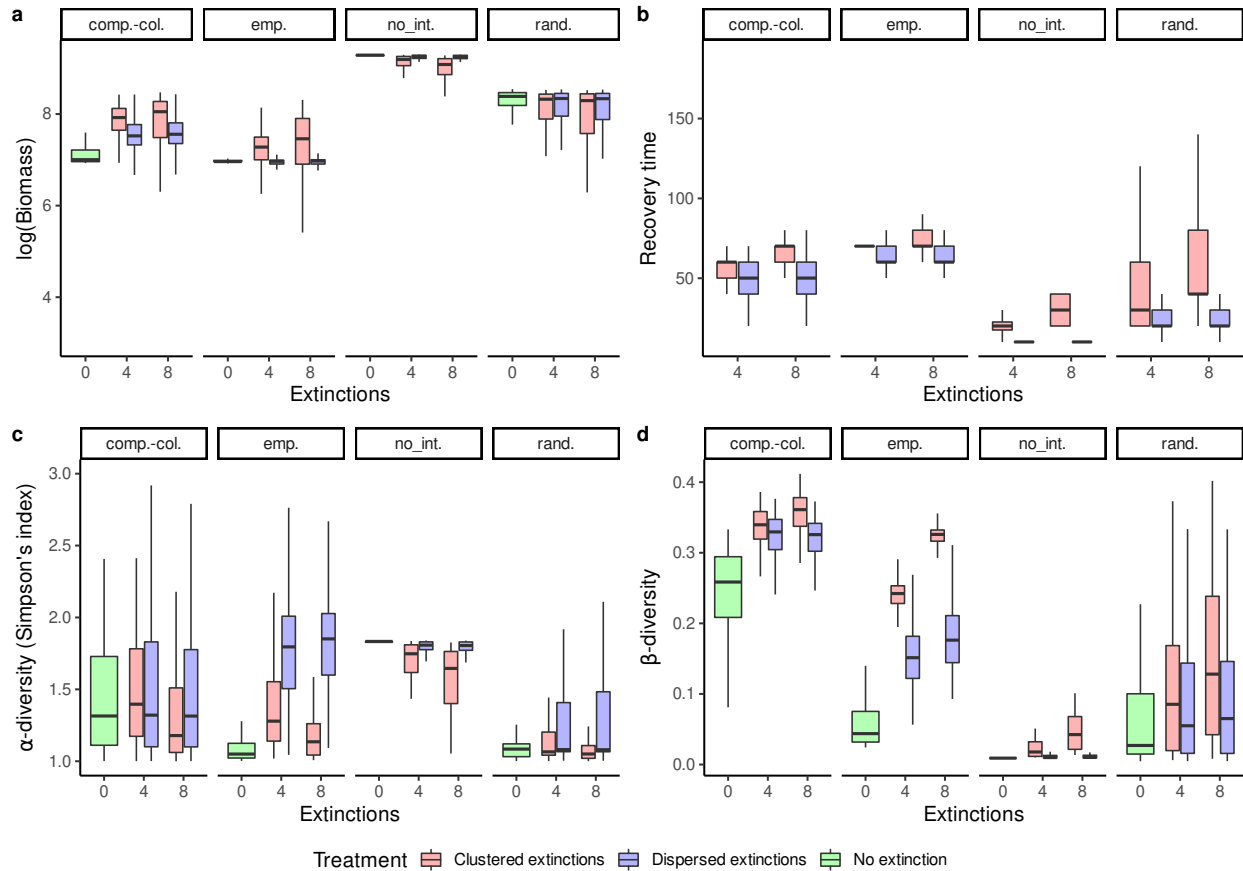


Figure 3: Observed response variables in numerical simulations of the metacommunity model displaying different metrics after the extinction events (all biomass and diversity values of all perturbed patches between  $T_{extinction} + 50$  and  $T_{extinction} + 150$ ). (a) Biomass in perturbed patches (blue: dispersed extinctions, red: clustered extinctions) and patches from landscapes with no extinctions (green), (b) biomass recovery time in perturbed patches, (c)  $\alpha$ -diversity (measured as Simpson's index) in perturbed patches and patches from landscapes with no extinctions and (d)  $\beta$ -diversity in all landscapes. 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 was shorter in case of dispersed extinctions compared to clustered extinctions, and it slightly 201  
increased with the number of extinctions (Tab. S2.3 and S2.5, Fig. 2b and S1.2; median (5-95% 202  
quantiles) mixed model predictions: 4 dispersed: 122 h (85-152), 8 dispersed: 129 h (94-164), 4 203  
clustered: 139 h (100-172), 8 clustered: 152 h (122-185)). 204

In simulations of the metacommunity model, recovery times (Fig. 3b) qualitatively matched 205  
the experimental patterns in all scenarios. Quantitatively, the recovery times were much shorter 206  
(less than 100 time units) than what we found experimentally, probably because dispersal in the 207

experiments happened over discrete time intervals (4 h periods, three times per week) resulting in a lag in recolonization dynamics.

In simulations with fitted interaction terms (“empirical interactions” and “competition-colonization trade-off”), the biomass of perturbed patches during the recolonization process was on average higher than the biomass of patches from control landscapes (fig. 3a) because of the fast recolonization and higher carrying capacity of the less competitive species (*T. thermophila* and *Copidium* sp.) compared to the most competitive species (*Blepharisma* sp.). In the other simulations, the biomass during recolonization did not differ much between the perturbed patches and the patches from control landscapes (fig. 3a) and was only slightly lower in perturbed patches.

### **$\alpha$ -diversity**

In patches from control landscapes,  $\alpha$ -diversity increased at first as species dispersed between patches but quickly fell to 1 as *Blepharisma* sp. finally excluded the two other species and dominated the community (Fig. S1.1). In perturbed patches of the landscapes with extinction treatments,  $\alpha$ -diversity was higher during the recolonization process in comparison to patches from control landscapes since the species were present in more even densities in the former (Fig. 2c and S1.1). This effect was stronger for dispersed extinctions than for clustered extinctions (Fig. 2c).

In simulations from the metacommunity model, the empirical  $\alpha$ -diversity pattern was best recaptured by the “empirical” and “randomized” scenarios (Fig. 3c), as well as transiently in the “competition-colonization trade-off” scenario (Fig. S1.23). In the absence of interspecific interactions, all species coexisted locally and the  $\alpha$ -diversity was high in all patches.

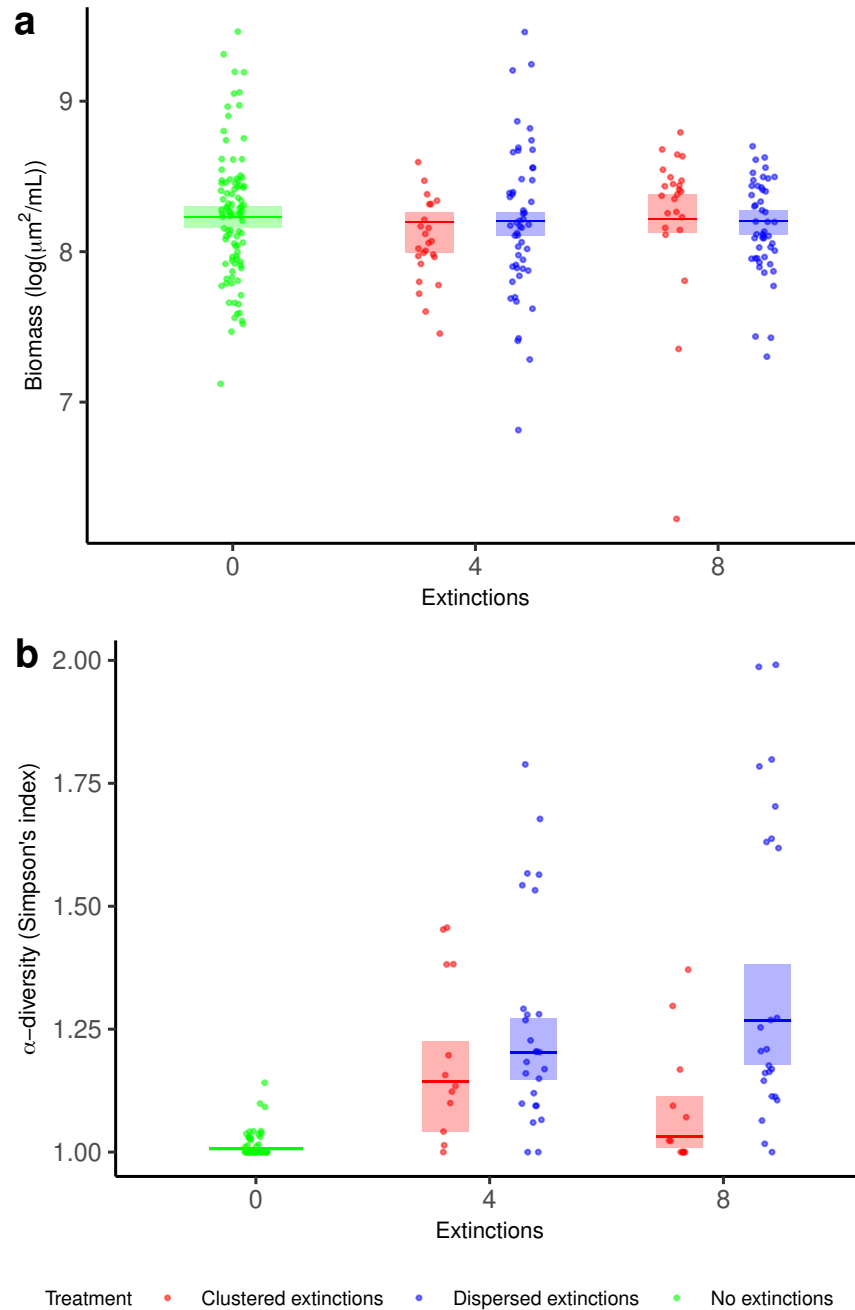


Figure 4: Observed response variables in the experiments (dots) and averaged mixed model predictions (medians and 95% confidence intervals; Tab. S2.4) in unperturbed patches adjacent to at least one perturbed patch (blue: dispersed extinctions, red: clustered extinctions) and in control landscapes (green). (a) biomass in unperturbed patches (for the two measurements following the extinctions), (b)  $\alpha$ -diversity (measured as Simpson's index) in unperturbed patches at the last two measurements.

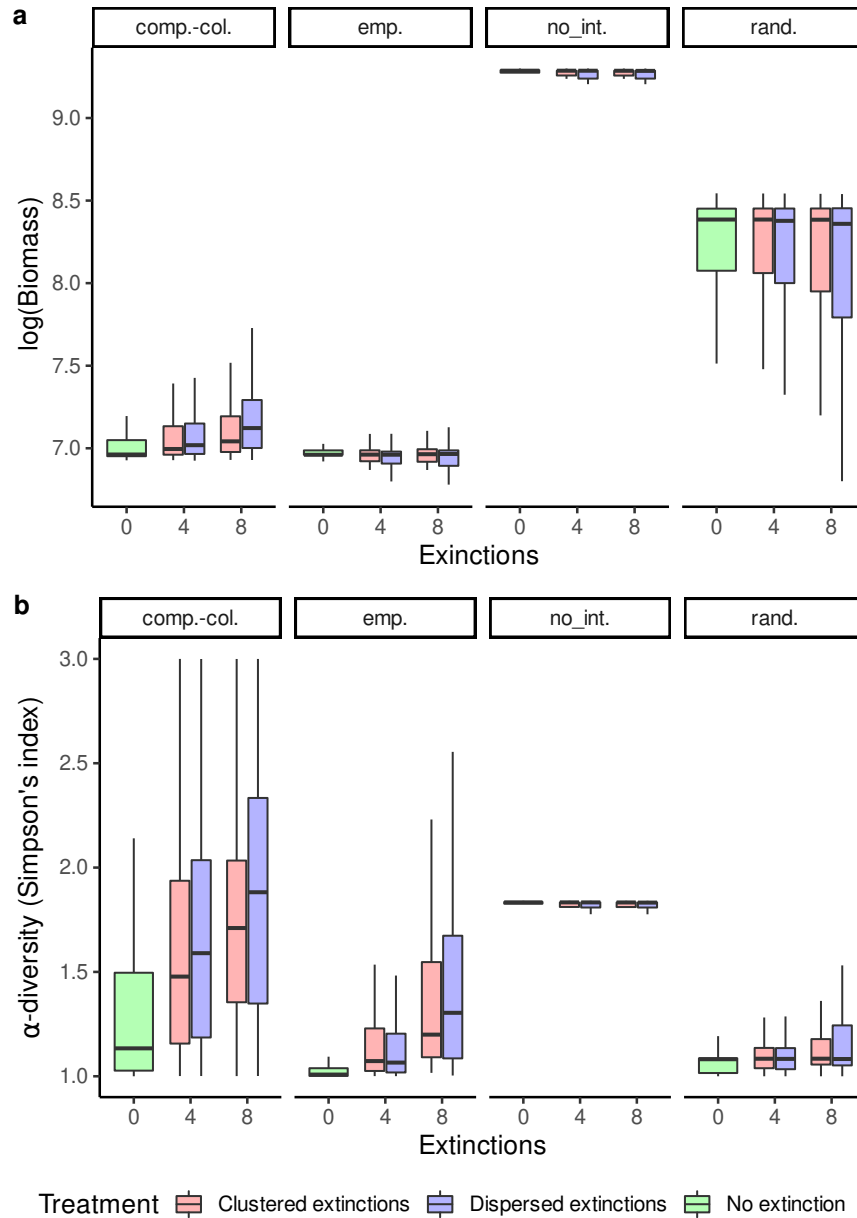


Figure 5: Observed response variables in numerical simulations of the metacommunity model showing biomass (a) and  $\alpha$ -diversity (measured as Simpson's index) (b) in unperturbed patches adjacent to at least one perturbed patches (blue: Dispersed extinctions, red: clustered extinctions) and in control landscapes (green) after extinction events (all biomass and diversity values of all unperturbed patches adjacent to a perturbed patch between  $T_{extinction} + 50$  and  $T_{extinction} + 150$ ). 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".

## Indirect effects — spread of extinctions effects to unperturbed patches and at the regional scale 229 230

### Biomass 231

In both experiments and simulations, we observed no strong difference in biomass between 232



## $\alpha$ -diversity

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Experimentally,  $\alpha$ -diversity was higher in unperturbed patches than in patches from control landscapes, particularly for dispersed extinctions (Fig. 4b and S1.28d-f). Most of the variation between treatments was explained by the spatial autocorrelation of extinctions rather than the number of extinctions (Tab. S2.4b and S2.6b). Interestingly, the effect of the number of extinctions depended on their spatial organization: under clustered extinctions, the  $\alpha$ -diversity in unperturbed patches decreased with the number of extinctions but it increased under dispersed extinctions (Fig. 4b and S1.28d-f). Note that this was not observed in simulations. This discrepancy could be due to either condition-dependant dispersal not accounted for in simulations, or to the low statistical power when it comes to indirect effect.

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In simulations lacking interspecific competition,  $\alpha$ -diversity levels were similar in unperturbed patches (across all treatments) and patches from control landscapes. In all simulations that included interspecific competition,  $\alpha$ -diversity increased with both the number of extinctions and their spatial autocorrelation (Fig. 5b). Nevertheless, the effect sizes were variable: empirical interactions yielded effect sizes consistent with the experimental results (according to qualitative visual inspection), while randomized interactions yielded smaller effects and the “competition-colonization trade-off” scenario yielded stronger effects.

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## $\beta$ -diversity

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In control landscapes,  $\beta$ -diversity was fairly low because the patches ended up being homogeneous and dominated by *Blepharisma* sp. (Fig. S1.1).  $\beta$ -diversity was higher in landscapes with extinctions than in control landscapes because of differences in species composition and density between perturbed and unperturbed patches (Fig. S1.1). This effect was stronger for 8 extinctions than for 4 extinctions, particularly for clustered extinctions (Fig. 2d).

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In simulations of the metacommunity model, these results held qualitatively for all scenarios (Fig. 3d). These effects were strong and on par with experimental effect sizes for realistic interaction matrices (scenarios “empirical interactions” and “competition-colonization trade-off”).

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They were weaker for randomized interaction matrices and negligible in the absence of interspecific interactions. 260  
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## **Sensitivity to landscape size and dispersal rates** 262

The simulations on larger landscapes (16\*16 patches) yielded results (Fig. S1.13 and S1.14) 263  
remarkably consistent with those discussed above. Our results were more sensitive to dispersal 264  
rates, but most qualitative patterns described for the “empirical interactions” and “competition- 265  
colonization trade-off” scenarios (e.g., stronger influence of the spatial autocorrelation than the 266  
number of extinctions, higher  $\beta$ -diversity for clustered extinctions, higher  $\alpha$ -diversity spillover and 267  
faster biomass recovery for dispersed extinctions) were coherent for dispersal rates up to 2 times 268  
stronger/weaker than our standard simulations (Fig. S1.15 to S1.22). 269

## **Discussion** 270

### **The role of the spatial distribution of the extinctions** 271

We found that the spatial autocorrelation of extinctions had a stronger effect than the number 272  
of extinctions *per se* on all metrics measured, both in experiments and in simulations. Since 273  
our simulations suggest that this effect is independent of community structure, this result must 274  
be explained by the connectivity and distance between perturbed and unperturbed patches: if 275  
extinctions are dispersed, perturbed patches are closer and better connected to unperturbed patches 276  
than when extinctions are clustered (Tab. S2.2; Fig. S1.2 and S1.3). 277

The analysis of the simulations of large landscapes indicates that patch-level metrics in perturbed 278  
patches (recovery time and  $\alpha$ -diversity; Fig. S1.24 and S1.25) depend only on the distance to the 279  
closest unperturbed patch and not on the connectivity to unperturbed patches. This is coherent 280  
with our experimental results, where perturbed patches that were two links away from unperturbed 281  
patches had a longer recovery time (Fig. S1.2, in red) and a lower  $\alpha$ -diversity (Fig. S1.3, in red) 282

than the patches adjacent to at least one unperturbed patch. These findings also explain why the number of extinctions had a marginal effect in dispersed treatments compared to clustered treatments (Fig. 2 and 3): increasing the number of extinctions did not increase the distance from perturbed to unperturbed patches for dispersed extinctions (Tab. S2.2). On the contrary, more clustered extinctions resulted in larger clusters and thus in a greater distance from perturbed to unperturbed patches (Tab. S2.2).

## Direct effects of extinctions

### Biomass recovery

Experimental data and simulations support the conclusion that simultaneously increasing the number and autocorrelation of extinctions increases the time needed for a metacommunity to recover its pre-extinction biomass (Fig. 2b and 3b). These results were surprisingly consistent between the experiments and the various simulations scenarios, highlighting that this pattern does not depend on species interactions but rather on the geometry of the patches to be recolonized. A high number of spatially clustered extinctions increases the recovery time by creating large areas of perturbed patches, thus increasing the average distance and reducing the average connectivity between perturbed and unperturbed patches (Tab. S2.2). Clustered extinctions therefore result in what Zelnik *et al.* (2019) have termed “rescue recovery regime” where biomass recovery relies mainly on local population growth and is thus slower.

Additionally, both experimentally and in model simulations, perturbed patches had a slightly higher biomass after recovery than patches from unperturbed landscapes (Fig. 2a and 3a). This is because unperturbed patches mainly had the better competitor left (*Blepharisma* sp., Fig. S1.1), while all three species persisted in perturbed patches. Since poorly competitive species (especially *Colpidium* sp.) reached a higher biomass than *Blepharisma* sp., perturbed patches had a higher 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, 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).

### **$\alpha$ -diversity**

Local patch extinctions generally increased  $\alpha$ -diversity as delayed competitive exclusion of inferior competitors. The persistence of less competitive species in perturbed 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. These results are similar to the 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 successional 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-successional species should exhibit the  $\alpha$ -diversity increase observed here, while metacommunities skewed towards late-successional species (as in Cadotte, 2007) should see  $\alpha$ -diversity decrease with local patch extinctions.

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

## Indirect effects

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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 unperturbed patches (Gilarranz *et al.*, 2017; Zelnik *et al.*, 2019).

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## $\alpha$ -diversity

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Unperturbed patches in landscapes with extinctions had a higher  $\alpha$ -diversity than unperturbed patches from control landscapes (Fig. 4b). This is because dispersal of less competitive species (*T. thermophila* and *Colpidium* sp.) from perturbed patches, where they were present in high density during the recolonization process, allowed persistence in both patches (Fig. S1.1) with perturbed patches acting as sources and unperturbed patches as sinks. These source-sink dynamics correspond to the cross-habitat spillover hypothesis discussed by Tschardt *et al.* (2012). The increase of  $\alpha$ -diversity was stronger in unperturbed patches from dispersed extinction treatments, as these patches were connected to more perturbed patches and thus received an increased number of less competitive dispersers than unperturbed patches from clustered extinction treatments.

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The patterns observed experimentally were recovered in all simulations that included interspecific competition (Fig. 5b), showing that local diversity maintenance by local extinctions is not restricted to our particular experimental community but can occur as long as some species excludes others.

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It is worth noting that the increase in  $\alpha$ -diversity was only observed in patches adjacent to perturbed patches, which could be described as an edge effect. This means that isolated extinction events don't have large scale effects in our setting, as perturbed patches only have an effect on their local neighbourhood. Indirect effects, however, can affect large proportions of the landscape if extinctions are numerous and spatially dispersed. Dispersed extinctions thus have both a stronger effect on unperturbed patches and affect a greater number of unperturbed patches.

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## $\beta$ -diversity

$\beta$ -diversity was higher in landscapes that experienced local patch extinctions in comparison to control landscapes, both in experiments and in simulations including interspecific competition (Fig. 2d and 3d). This can be explained by the fact that perturbed patches had a different species composition than unperturbed patches. In unperturbed patches communities were mainly composed of *Blepharisma* sp., while perturbed patches allowed less competitive species to persist during the recolonization process. While we find a strictly increasing relationship between the number of extinctions and  $\beta$ -diversity (Fig. 2d and 3d), Cadotte (2007) found a unimodal relationship between  $\beta$ -diversity and local patch extinction number. While this seems contradictory, it is also possible that we did not use enough extinctions to reveal a unimodal relationship, as  $\beta$ -diversity could decrease when extinctions affect more patches.

## Perspectives

The strong effect of the spatial distribution of extinctions we report can be interpreted as differences in recovery regimes across spatial treatments: clustered extinctions, characterized by a weak connectivity between perturbed and unperturbed patches, result in what Zelnik *et al.* (2019) described as a “rescue recovery regime”, while dispersed extinctions, characterized by a strong connectivity between perturbed and unperturbed patches, result in a “mixing recovery regime”. Under the “rescue” regime, dispersal between perturbed and unperturbed patches is marginal compared to local dynamics. Perturbed and unperturbed patches are strongly differentiated, and the recovery dynamics mainly rely on local growth. Because of this strong differentiation,  $\beta$ -diversity was higher than in the “clustered extinctions” treatment, but the high  $\alpha$ -diversity of perturbed patches did not spill over much to unperturbed patches. Under the “mixing” regime, dispersal between perturbed and unperturbed patches is on a par with local dynamics. Perturbed and unperturbed patches are well mixed, and both local growth and dispersal from perturbed patches participate substantially to the recovery. Because of the mixing between perturbed and unperturbed patches,  $\alpha$ -diversity in the “dispersed extinctions” treatment in unperturbed patches increased greatly (due to dispersal from

perturbed patches), but  $\beta$ -diversity was lower than in the “clustered extinctions” treatment. 382

Strictly speaking, our experimental settings, with discrete patches, homogeneous conditions and 383  
only three non-redundant species, may be thought to conform best to the patch dynamics paradigm 384  
(Leibold *et al.*, 2004), making extrapolations potentially difficult. However, as Thompson *et al.* 385  
(2020) point out, metacommunity dynamics are more complex than what is captured by the four 386  
archetypes described by Leibold *et al.* (2004). Here, by looking at the transient recolonization 387  
dynamics, we were able to observe patterns consistent with both species sorting (good competitors 388  
are found mainly in unperturbed patches, good colonizers in perturbed patches), and mass effects 389  
(perturbed patches act as a source of less competitive species), highlighting that these mechanisms 390  
may often act simultaneously (Fournier *et al.*, 2017). Our work also showcases the importance 391  
of transient dynamics in shaping biodiversity patterns, especially when we consider that local 392  
patch extinctions in nature should be recurring and asynchronous, leaving patches at different 393  
stages of recolonization and potentially enhancing metacommunity stability (Fox *et al.*, 2017) 394  
and  $\beta$ -diversity. Moreover, the spatial treatment strongly influenced which patterns we observed 395  
during the recolonization: landscapes with clustered extinctions verged more on species sorting 396  
while landscapes with dispersed extinctions were more in line with the mass effects paradigm 397  
because the spatial autocorrelation of extinctions decreased the overall dispersal between perturbed 398  
and unperturbed patches. The spatial patterns of local perturbations can thus deeply alter the 399  
functioning of a metacommunity, here driving it from one metacommunity paradigm to another. 400  
This is particularly concerning when we consider that climate change could increase the spatial 401  
and temporal autocorrelation of climatic events (Di Cecco & Gouhier, 2018), as observed in the 402  
metapopulation of *Melitaea cinxia* (Kahilainen *et al.*, 2018). Our study thus warrants the inclusion 403  
of finer processes into existing metacommunity theory in order to better understand how the 404  
spatial structure of perturbations and the following transient dynamics affect the functioning of 405  
metacommunities. 406

## Conclusion

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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  $\alpha$ -diversity and  $\beta$ -diversity by allowing weak competitors to persist in the metacommunity and by forcing a differentiation between perturbed and unperturbed patches.

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Dispersal and connectivity between patches are central to recovery as they allow the recolonization of perturbed patches but also a mixing between perturbed and unperturbed 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  $\alpha$ -diversity in unperturbed patches through dispersal from species-rich, previously perturbed patches to species poor, unperturbed patches.

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By determining the connectivity between perturbed and unperturbed patches, the spatial autocorrelation of extinctions modulates the dynamics after extinction events: when extinctions are clustered, perturbed and unperturbed patches are weakly connected. This results in a slower biomass recovery, a weak spread of  $\alpha$ -diversity and high  $\beta$ -diversity as perturbed and unperturbed patches are differentiated. On the contrary, dispersed extinctions imply higher connectivity between perturbed and unperturbed patches which translates into a faster biomass recovery, a stronger spread of  $\alpha$ -diversity and a lower  $\beta$ -diversity as perturbed and unperturbed patches are better mixed.

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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 obtain better estimates of the effects of local extinctions in more realistic settings. Nevertheless, our work highlights the relevance of the spatial distribution of local extinctions when doing so.

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## **Author contributions**

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C.S., S.K. and E.A.F. conceived the study. C.S. and C.G.B. conducted the experiments. C.S. 435  
performed the statistical analyses. C.S., B.R. and E.A.F. performed the model fitting. C.S. analysed 436  
the mathematical model. C.S., S.K. and E.A.F. wrote the manuscript and all authors commented on 437  
the draft. 438

## **Data availability**

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Data and code are available on GitHub via Zenodo: <https://doi.org/10.5281/zenodo.6364903>. 440

## **Conflict of interest disclosure**

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The authors of this article declare that they have no financial conflict of interest with the content of 442  
this article. 443

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