




LETTER

How pulse disturbances shape size-abundance pyramids

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Abstract

Ecological pyramids represent the distribution of abundance and biomass of living organisms across body-sizes. Our understanding of their expected shape relies on the assumption of invariant steady-state conditions. However, most of the world's ecosystems experience disturbances that keep them far from such a steady state. Here, using the allometric scaling between population growth rate and body-size, we predict the response of size-abundance pyramids within a trophic guild to any combination of disturbance frequency and intensity affecting all species in a similar way. We show that disturbances narrow the base of size-abundance pyramids, lower their height and decrease total community biomass in a nonlinear way. An experimental test using microbial communities demonstrates that the model captures well the effect of disturbances on empirical pyramids. Overall, we demonstrate both theoretically and experimentally how disturbances that are not size-selective can nonetheless have disproportionate impacts on large species.

Keywords

Body-size, community size structure, disturbance frequency, disturbance intensity, extreme events, metabolic theory, perturbations, protist communities, size spectrum.

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INTRODUCTION

Ecological pyramids, which represent the distribution of abundance and biomass of organisms across body-sizes or trophic levels, reveal one of the most striking regularities among communities (Elton 1927; Lindeman 1942; Trebilco *et al.* 2013). Several types of pyramids have been reported in ecological research, as well as distinct underlying mechanisms to explain their shape. For example, trophic pyramids describe the distribution of abundance or biomass along discrete trophic levels (Fig. 1a). The inefficiency in energy transfer from resources to consumers as well as strong self-regulation within trophic levels provide the main explanation for their shape (Lindeman 1942; Barbier & Loreau 2019). Alternatively, size-abundance pyramids (Fig. 1b and c), also known as the pyramid of numbers (Elton 1927), the Damuth law (Damuth 1981) or the abundance size spectrum (Sprules & Barth 2016), describe the distribution of abundance across body-sizes and can be studied both within and across trophic guilds (Elton 1927; Trebilco *et al.* 2013). The energetic equivalence rule, along with the metabolic theory of ecology, provide theoretical expectations regarding the shape of such size-abundance pyramids: in a community where all individuals feed on a common resource (i.e. within a trophic group), population abundance should be proportional to $M^{-0.75}$, where M is body-size, and biomass should be proportional to $M^{0.25}$ (Damuth 1981; Brown *et al.* 2004; White *et al.* 2007).

As with most concepts in ecology, these relationships correspond to theoretical baselines that are predicted under steady-state conditions, which are rarely met in nature (DeAngelis & Waterhouse 1987; Hastings 2004, 2010). Most natural

ecosystems and communities are exposed to a wide range of environmental fluctuations and disturbances, ranging from harvesting to extreme weather events. Furthermore, many of these disturbances are expected to increase in frequency and intensity in the context of global change, as illustrated by recent large-scale wildfires, floods or hurricanes (Coumou & Rahmstorf 2012; Hughes *et al.* 2017; Harris *et al.* 2018). Such disturbances increase population mortality and could trigger even faster changes in community structure and dynamics than gradual changes in average conditions (Jentsch *et al.* 2009; Wernberg *et al.* 2013; Woodward *et al.* 2016).

Despite the extensive literature on disturbance ecology (Sousa 1984; Yodzis 1988; Petraitis *et al.* 1989; Fox 2013; Dantas *et al.* 2016; Thom & Seidl 2016), the effects of disturbances on community structure and biomass distribution remain poorly understood (Donohue *et al.* 2016). On the one hand, ecologists have often focused on the consequences of environmental disturbances on species richness (Huston 1979; Haddad *et al.* 2008; Bongers *et al.* 2009) and the coexistence of competing species (Violle *et al.* 2010; Miller *et al.* 2011; Fox 2013), rather than on body-size and biomass distribution (but see Woodward *et al.* (2016)). As such, the specific identity of species resistant (or not) to disturbances has received ample attention, with various definitions of disturbance-resistant species groups (Sousa 1980, 1984; Lavorel *et al.* 1997). These studies have pointed out key demographic traits, notably population growth rate and carrying capacity, that determine species' capacities to persist in a disturbed environment (McGill *et al.* 2006; Haddad *et al.* 2008; Enquist *et al.* 2015; Woodward *et al.* 2016). On the other hand, the metabolic theory of ecology uses the scaling of metabolic rate with body-

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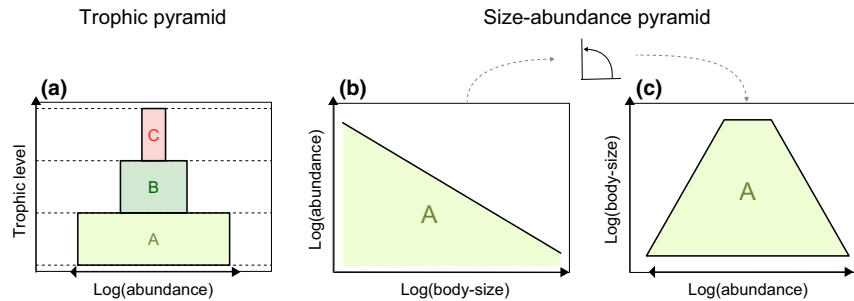


Figure 1 A trophic pyramid (a) describes the distribution of biomass along discrete trophic levels, and assumes that all species within a trophic level have the same functional traits. The community size structure (b) and the size-abundance pyramid (c) are equivalent size-centric representations of ecological communities and are the focus of this study. They describe the distribution of abundance across body-sizes and can be studied both within and across trophic levels. (b) The community size structure depicts $\log(\text{body-size})$ on the x-axis and $\log(\text{abundance})$ on the y-axis, while (c) the size-abundance pyramid shows $\log(\text{abundance})$ on the x-axis and $\log(\text{body-size})$ on the y-axis. Note that the area A is the same in both panels. We use the community size structure representation throughout the paper as it facilitates comparisons between theory and experimental data, but see Fig. 6 for a synthesis of our findings using the pyramid representation.

size to predict a set of structural and functional characteristics across biological scales (Brown *et al.* 2004). At the community level, it demonstrates how size-abundance pyramids emerge from the scaling of population growth rate and abundance with body-size (Trebilco *et al.* 2013). Surprisingly, a formal integration of the theory on disturbances with the metabolic theory of ecology is still lacking, but would allow ecologists to generalise and predict the effect of environmental disturbances on the shape of size-abundance pyramids.

Here, we integrate these two disconnected fields by developing a size-based model for population persistence, assuming that the scaling of population growth rate with body-size is the leading mechanism determining the response of size-abundance pyramids to disturbances. We predict the shape of size-abundance pyramids within a trophic guild in response to repeated pulse disturbances of varying frequency and intensity affecting all species in a similar way, regardless of their size. Such disturbances represent a wide range of environmental pressures that increase species mortality, such as floods, wildfires or hurricanes. They differ from the disturbance studies developed in fishery science, that specifically addressed the effect of a press, size-selective disturbance (i.e. fishing) on the abundance size spectrum (Jennings *et al.* 2002; Shin *et al.* 2005; Petchey & Belgrano 2010; Sprules & Barth 2016). We then experimentally tested the predicted responses of size-abundance pyramids and standing biomass to disturbances, using microbial communities composed of aquatic species with body-sizes and populations densities varying over several orders of magnitudes. We finally discuss the general implications of our findings for the structure and functioning of communities exposed to environmental disturbances.

MATERIALS AND METHODS

A model for size-abundance pyramids exposed to disturbances

We build a mechanistic model to predict how disturbance frequency and intensity modulate the shape of size-abundance pyramids and community total biomass. We describe the dynamics of population abundance N with a logistic model:

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (1)$$

where r is population growth rate and K is population carrying capacity. We model a disturbance regime, corresponding to a recurrent abundance reduction, of intensity I (fraction of abundance) and frequency f or period $T = 1/f$ (time between two disturbances, Fig. 2a). We can demonstrate that a population persists in a disturbed environment only if its growth rate balances the long-term effect of the disturbance regime (adapted from Harvey *et al.* 2016), that is:

$$r > - \frac{\ln(1 - I)}{T} \quad (2)$$

From eqn (2), we can predict the set of disturbance regimes a population can sustain according to its growth rate (Fig. 2b), as well as predict the minimum generation time ($1/r$) needed to maintain a viable population (Fig. S1). We then use the allometric relationship between population growth rate r and average body-size M , that is $r = c \times M^a$ with $a = -1/4$ (Brown *et al.* 2004; Savage *et al.* 2004) and c a positive constant, to derive the following size-specific criterion for population persistence under a disturbance regime:

$$M \leq \left(\frac{\ln(1 - I)}{T \times c} \right)^{-4} \quad (3)$$

Eqn (3) indicates that a species can persist in a disturbed environment only if its average body-size is below a certain value. Note that this analytical criterion is applicable to any biological and temporal scale. Indeed, the disturbance frequency and population growth rate are expressed with the same time unit and can range from hours (e.g. fast-growing microbial organisms) to years (e.g. slow-growing organisms such as large mammals). To investigate the effect of disturbances on the shape of size-abundance pyramids, we derive the mean abundance at dynamical equilibrium \bar{N} of a population under a given disturbance regime (i.e. averaged over a time period, see Appendix S1 for detailed steps), that is:

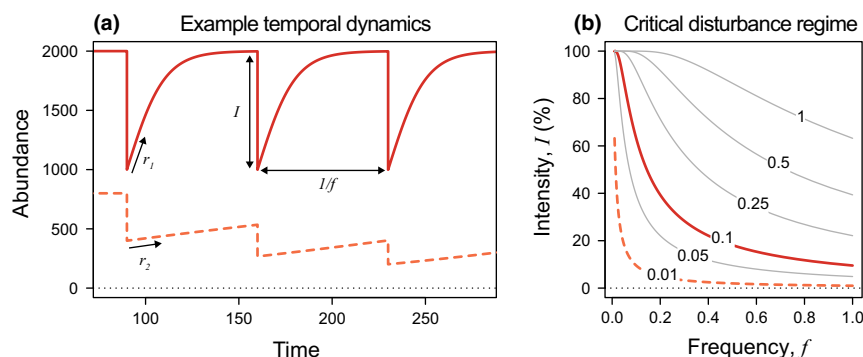


Figure 2 Population dynamics and persistence according to disturbance regime. (a) Temporal dynamics of two species experiencing the same disturbance regime. Species 1 has a smaller body-size and therefore a higher growth rate than species 2. A population can persist only if its growth rate balances the long-term effect of the disturbance regime. We derive in eqn (4) the mean abundance at dynamical equilibrium (i.e. temporal mean) of the persisting species experiencing varying disturbance regimes. (b) Isoclines of the persistence criterion in the disturbance regime landscape according to population growth rate (numbers): on and above the line, the population of a given growth rate goes extinct. Lines with the same colour code as in panel (a) correspond to the same growth rate.

$$\bar{N} = K \left(\frac{\ln(1-I)}{T \times r} + 1 \right) \quad (4)$$

where K corresponds to the carrying capacity of the population, which also scales with body-size on a logarithmic scale (Brown & Gillooly 2003; Brown *et al.* 2004): $\ln(K) = a_K \ln(M) + b_K$, where a_K and b_K are normalising constants. We use this allometric relationship to express mean abundance as a function of mean population body-size and finally obtain:

$$\ln(\bar{N}) = a_K \ln(M) + b_K + \ln \left(\frac{\ln(1-I)}{T e^{a_K \ln(M) + b_K} r} + 1 \right) \quad (5)$$

The formula is valid when the expression in parentheses in the right-hand term is positive, which corresponds to the persistence criteria given in eqns (2) and (3). We express population biomass, B , as the product of mean abundance at dynamical equilibrium, \bar{N} , and the average individual body-size in the population, M , that is $B = \bar{N}M$.

We extend this approach to multispecies assemblages composed of potentially hundreds of co-occurring species with different body-sizes (see detailed method in Appendix S2 and Table S1 for parameter values). We assume that all species' populations follow a logistic growth and are constrained by intraspecific competition only (an assumption relaxed in Appendix S3). From eqns (3) and (5), we expect that disturbances will decrease the maximum size observed in the community as well as total biomass. We use this analytical approach to explore how community size structure, a more tractable representation of abundance distribution across size classes compared to pyramids (Fig. 1b), and total community biomass will respond to a whole landscape of disturbance frequencies and intensities (Fig. 3).

Disturbance experiment on microbial communities

We conducted an experiment in aquatic microcosms inoculated with 13 protist species and a set of common freshwater bacteria as a food resource. The protist species cover a wide

range of body-sizes (from 10 to $10^3 \mu\text{m}$) and densities ($10\text{--}10^5$ individuals/ml, Giometto *et al.* 2013). General laboratory procedures follow the protocols described in Altermatt *et al.* (2015), and build upon previous work on pulse disturbance effects on diversity (Altermatt *et al.* 2011; Harvey *et al.* 2016) and invasion dynamics (Mächler & Altermatt 2012). Detailed microcosm description and set-up are presented in Appendix S4. In short, we performed a factorial experiment in which we varied disturbance frequency and intensity, resulting in a total of 20 different disturbance regimes. Disturbance was achieved by boiling a subsampled fraction of the well-mixed community in a microwave so that all species experience the same level of density reduction. All protists were killed by the microwaving process. We let the medium cool down before putting it back into the microcosm. We disturbed microcosms at five intensities: 10, 30, 50, 70 and 90 % and at four frequencies: $f = 0.08, 0.11, 0.16$ and 0.33 , corresponding to a disturbance every 12, 9, 6 and 3 days respectively. The experiment lasted for 21 days, or about 10–50 generations depending on species. Each disturbance regime was replicated six times. To control for the intrinsic variability of community size structure, we cultured eight undisturbed microcosms under the same conditions. We sampled 0.2 ml of each microcosm daily to quantify individual body-sizes (i.e. cell area in μm^2), protist abundances (individuals/ μl) and total community biomass (i.e. total bioarea in $\mu\text{m}^2/\mu\text{l}$) using a standardised video procedure (Altermatt *et al.* 2015; Pennekamp *et al.* 2017). We binned the observed individuals into 12 size classes ranging from 0 to $1.6 \times 10^5 \mu\text{m}^2$ in order to get statistically comparable community size structures. Mean protist abundance and its standard deviation in each size class were calculated over 21 time points and six replicates (total of 126 observations) for each treatment communities and over 21 time points and eight replicates (total of 168 observations) for the control communities. We performed Welch two sample *t*-tests of mean comparison (treatment versus control) to determine which disturbance regime had a significant effect on community size structure and total community biomass (Table S2).

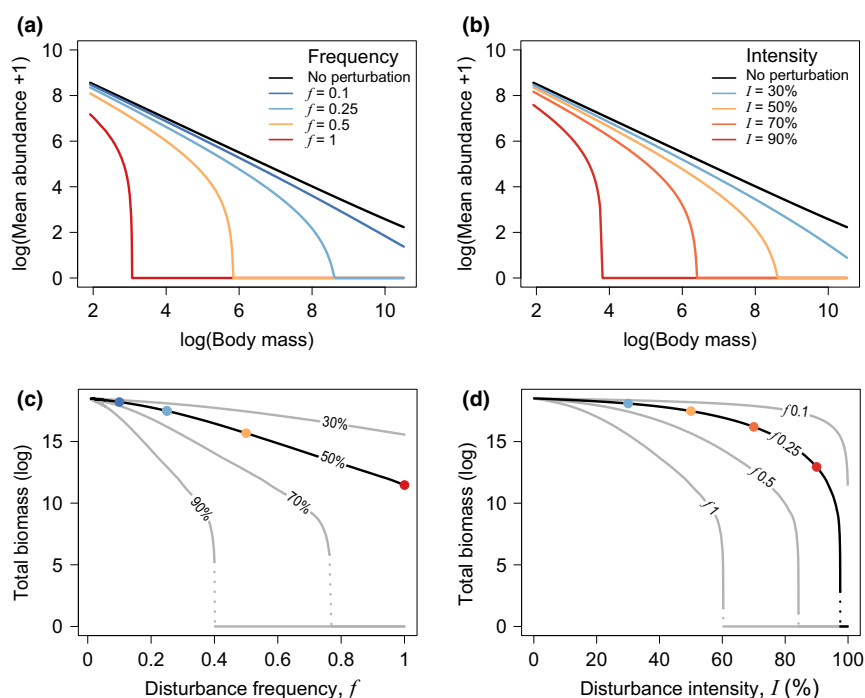


Figure 3 Effects of disturbance frequency and intensity on community size structure and average total biomass at dynamical steady state. Analytical results derived from eqn (5). (a) Effect of disturbance frequency (disturbance intensity is fixed to 50% abundance reduction) and (b) disturbance intensity (disturbance frequency is fixed to 0.25) on community size structure. (c) Effect of disturbance frequency and (d) intensity on average total biomass (in log), for different intensities (c) and frequencies (d) respectively. Points on the black lines in (c) and (d) show the disturbance regimes corresponding to community size structures of the respective colours displayed in panels (a) and (b).

Model parameterisation

We parameterised the model using the experimental data in order to test the capacity of the model to predict the effect of a given disturbance regime on the size structure of real communities. The model required the following input parameters: the carrying capacities of each size class as well as the slope and the intercept of the allometric relationship between growth rate and body-size. We took the average abundances of the undisturbed communities (eight controls) to estimate carrying capacities in each size class. We fitted a logistic growth model to the recovery dynamics of each size class after one disturbance ($I = 90\%$) to obtain growth rate estimations. Specifically, we used the data from the treatment $\{I = 90\%, f = 0.08\}$ (i.e. highest intensity, lowest frequency) to estimate the parameters of a logistic growth model over 12 time points using the function *nls()* of the *stats* package in R (R Core Team 2019). We determined the relationship between growth rate and body-size in our experimental communities using the 13 time-series (covering six size classes) that displayed a logistic growth. We obtained the following allometric relationship: $\ln(r) = -0.37 \times \ln(M) + 3.75$ (P -value = 0.005, $R^2 = 0.47$). Using this parameterisation, we produced theoretical predictions on the size-abundance pyramids expected in the experimental disturbance regimes. We then quantitatively compared these predictions with the size-abundance pyramids observed in the experimental communities. We performed ordinary least-squares regressions to characterise the relationship between observed and predicted log-transformed mean abundances among size classes for all the disturbance regimes.

RESULTS

Model predictions

We first explore the effects of increasing disturbance frequency (Fig. 3a and c). Infrequent disturbances do not

strongly affect community size structure and only decrease the mean abundance of the largest size classes (Fig. 3a, $f = 0.1$ in dark blue). Maximum body-size gradually decreases as disturbance frequency increases, corresponding to the extinction of large, slow-growing species (Fig. 3a, $f = 0.25$ in light blue). Disturbance frequency also affects the community size structure through its effect on mean abundance. For frequent disturbance events, the mean abundance of all size class decreases (Fig. 3a, $f = 0.5$ and 1 in orange and red respectively). The effect of disturbance frequency on community size structure have direct consequences for community-level properties: we indeed observe an approximately linear decrease in total community biomass (log) along a gradient of disturbance frequency, followed by an abrupt collapse of the community for extreme disturbance regimes (Fig. 3c).

We then investigate the effect of increasing disturbance intensity (Fig. 3b and d). Similarly, low-intensity disturbances marginally affect community size structure (Fig. 3c, $I = 30\%$ in blue) and increasing disturbance intensity decreases maximum body-size and population mean abundance. (Fig. 3b). Interestingly, the effect of disturbance intensity on community total biomass is clearly nonlinear (Fig. 3d). Low to intermediate disturbance intensities do not affect total biomass when disturbance frequency is low (e.g. $f = 0.1$ or 0.25 in Fig. 3d). However, strong intensities affect all population abundances and trigger a sharp decrease in total biomass, culminating in a crash of the system (e.g. $\{I > 90\%, f = 0.25\}$ in Fig. 3d).

Experimental results

We experimentally investigated the effect of disturbance frequency and intensity on the size structure of microbial communities. For a fixed intensity (set to $I = 90\%$ in Fig. 4a, see Fig. S2 for other intensities), infrequent disturbances (i.e. $f = 0.08$ and $f = 0.11$) had a significant negative impact only

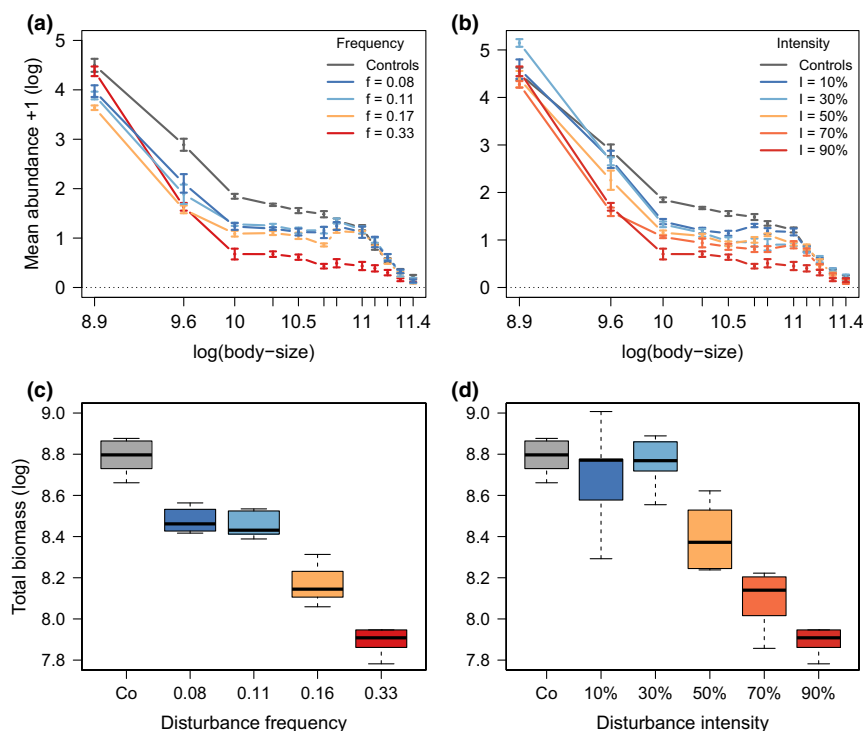


Figure 4 Experimental results. (a) Effect of disturbance frequency on community size structure. Vertical bars illustrate mean abundance (individuals/ μm^2) and its standard deviation over 21 time points and six replicates for each size class (μm^2). Disturbance intensity is fixed to $I = 90\%$; other intensities are shown in Fig. S2 and statistics in Table S2. (b) Effect of disturbance intensity on community size structure. Disturbance frequency is fixed to $f = 0.33$, other frequencies are shown in Fig. S3 and statistics in Table S2. Controls are in grey (undisturbed environment) and axes are on a logarithmic scale. (c) Effect of disturbance frequency on total community biomass (temporal mean, $n = 6$ for treatments, $n = 8$ for controls, in $\mu\text{m}^2/\mu\text{l}$). Disturbance intensity is fixed to $I = 90\%$ as in panel (a); other intensities are shown in Fig. S2. All frequencies have a significant negative effect on total biomass compared to controls: Welch two sample t -tests: $f_{0.08}$: $t = 8$, P -value < 0.001 , $f_{0.11}$: $t = 8.5$, P -value < 0.001 , $f_{0.16}$: $t = 13.2$, P -value < 0.001 , $f_{0.33}$: $t = 14.2$, P -value < 0.001 . (d) Effect of disturbance intensity on total community biomass (temporal mean, $n = 6$ for treatments, $n = 8$ for controls, in $\mu\text{m}^2/\mu\text{l}$). Disturbance frequency is fixed to $f = 0.33$ as in panel (b); other frequencies are shown in Fig. S3. All intensities except $I = 10\%$ and 30% have a significant negative effect on total biomass compared to controls: $I_{10\%}$: $t = 0.75$, P -value $= 0.48$, $I_{30\%}$: $t = 0.5$, P -value $= 0.63$, $I_{50\%}$: $t = 6.1$, P -value < 0.001 , $I_{70\%}$: $t = 12.7$, P -value < 0.001 , $I_{90\%}$: $t = 14.2$, P -value < 0.001 .

on the mean abundance of intermediate size classes (between $\exp(9.6)$ and $\exp(10.5)$ μm^2 , Welch two sample t -tests: $t \geq 2.6$, P -values ≤ 0.02 , Table S2). When disturbance frequency increased to $f = 0.16$, the mean abundance of the smallest size class also decreased ($t = 3.6$, P -value $= 0.01$, Table S2). Finally, at even more frequent disturbances ($f = 0.33$), all size classes were negatively impacted, except the smallest one (Fig. 5a and Table S3). Overall, increasing disturbance frequency led to an abundance depletion at intermediate sizes compared to undisturbed control communities.

Similarly, for a fixed frequency (set to $f = 0.33$ in Fig. 4b, see Fig. S3 for other frequencies), a low disturbance intensity $I = 10\%$ (Fig. 4b) only affected intermediate size classes (between $\exp(10)$ and $\exp(10.5)$ μm^2 , $t \geq 4.5$, P -values ≤ 0.001 , Table S2). Disturbance intensities $I = 30\%$ and 50% had a negative effect on the mean abundance of larger size classes (between $\exp(10)$ and $\exp(11)$ μm^2 , $t \geq 2.8$, P -values ≤ 0.03 , Table S2). Finally, intensities $I = 70\%$ and $I = 90\%$ had an impact on all size classes, except the smallest size class that were not negatively impacted by change in disturbance intensity (Fig. 4b, Table S2). Interestingly, the following disturbance regimes had a positive effect on the mean abundance of the smallest size class: $\{I = 30\%, f = 0.33\}$, $t = -6.1$,

P -value < 0.001 , (Fig. 4b), as well as $\{I = 50\%, f = 0.16\}$ and $\{I = 70\%, f = 0.11\}$ (Table S2, Fig. S2 and S3).

At the community-level, total biomass gradually decreased with disturbance frequency as expected by theory (Fig. 4c). All frequencies had a significant negative effect on total biomass compared to controls ($t \geq 8$, P -value < 0.001 , Fig. 4c). Disturbance intensities $I = 10\%$ and 30% had no significant effects on total community biomass ($I_{10\%}$: $t = 0.75$, P -value $= 0.48$, $I_{30\%}$: $t = 0.5$, P -value $= 0.63$), while total biomass strongly decreased for intensities above $I = 50\%$ ($I_{50\%}$: $t = 6.1$, P -value < 0.001 , $I_{70\%}$: $t = 12.7$, P -value < 0.001 , $I_{90\%}$: $t = 14.2$, P -value < 0.001 , Fig. 4d).

Observed versus predicted effect of disturbances on size-abundance pyramids

We then compared our experimental results with the predictions of the model parameterised for our freshwater microbial communities (Fig. 5). The model predicted well the observed mean abundances relative to carrying capacity for all the disturbance regimes in most of the size classes. The slope of the linear regression between observed and predicted log mean abundances, including all size classes in all disturbance

regimes (240 points), was very close to the 1:1 line, which indicates a very good fit (Fig. 5a, linear regression: $y = -0.012 + 1.01x$, $R^2 = 0.96$, $P\text{-value} < 0.001$). Additionally, the intercept of the linear regression was not significantly different from zero ($t = 0.95$, $P\text{-value} = 0.34$). We illustrate in Fig. 5b–d the similarities as well as the differences between the predicted and observed community size structures for varying disturbance frequencies with a disturbance intensity fixed to $I = 90\%$ (other disturbance regimes are shown in Figs S4 and S5). Overall, the predicted community structures were very similar to the observed ones. The model, however, often underestimated the mean abundance in the smallest size class (Fig. 5d). Furthermore, as mentioned in the previous section, some disturbance regimes had a positive effect on the mean abundance of the smallest size class, which cannot, by construction, be predicted by our model. We discuss below how this pattern can be explained by a disruption of biotic interactions following a disturbance and present further analyses using a predator–prey model to support this possible explanation (Fig. 6c, Appendix S3).

DISCUSSION

Most theories in community ecology have been developed under the assumption of steady-state conditions (Hastings

2010). Yet, most of the world's ecosystems – specifically $\geq 75\%$ of land/freshwater and 50% of marine systems – have been altered by human activities and are facing disturbances that put them clearly outside such a steady state (IPBES 2018). Thus, to meet the societal demand for an ecological science able to predict how ecosystems will respond to global change (Petchey *et al.* 2015; Urban *et al.* 2016), this assumption needs to be relaxed. The challenge is to develop models that make quantitative predictions regarding the impact of fluctuating environmental conditions on the structural and functional characteristics of biological systems.

Consequences of the growth–size relationship for communities exposed to disturbances

Here, we provide a robust and simple approach for predicting the size structure of communities exposed to any combination of disturbance frequency and intensity affecting all species in a similar way, regardless of their body-size. We combine theory on disturbances with the metabolic theory of ecology and assume that the scaling of population growth rate with body-size is the leading mechanism determining the response of size-abundance pyramids to disturbances. The model makes an important advance over the steady-state predictions of the metabolic theory of ecology as it links quantitatively the

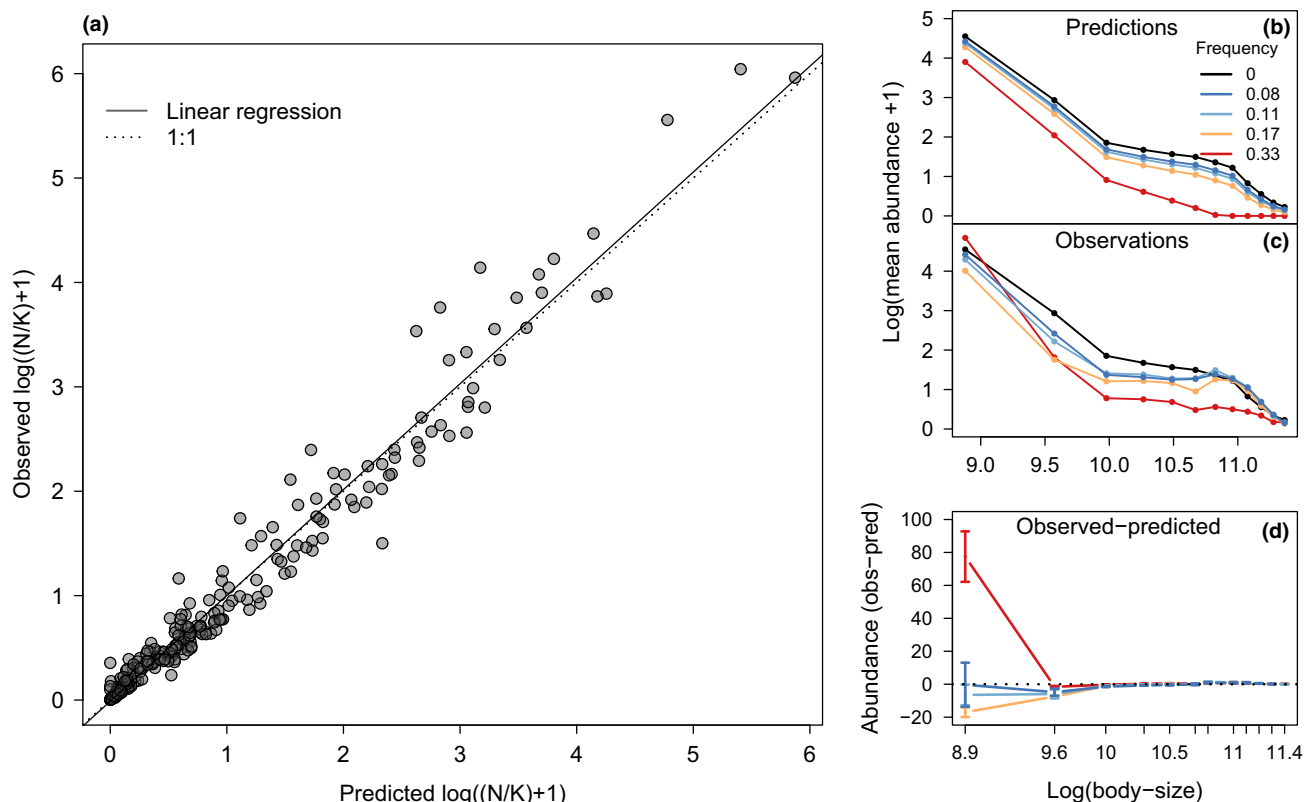


Figure 5 Comparison between experimental results and model predictions. (a) Predicted vs. observed mean abundance N relative to carrying capacity K in the 12 size classes for all the disturbance regimes ($n = 240$). Solid line: linear regression [$y = -0.012 + 1.01x$, $R^2 = 0.96$, $P\text{-value} < 0.001$. Standard error for slope: 0.01, intercept: 0.02]. Dashed line indicates a 1:1 relationship. (b) Predicted effect of disturbance frequency on the community size structure of experimental communities. Disturbance intensity is fixed to $I = 90\%$; other disturbance regimes are shown in Figs S4 and S5. Controls are in black (undisturbed environment) and axes are on a logarithmic scale. (c) Observed effect of disturbance frequency on the community size structure of experimental communities (similar to Fig. 4a). (d) Difference between observed and predicted mean abundance for each size class.

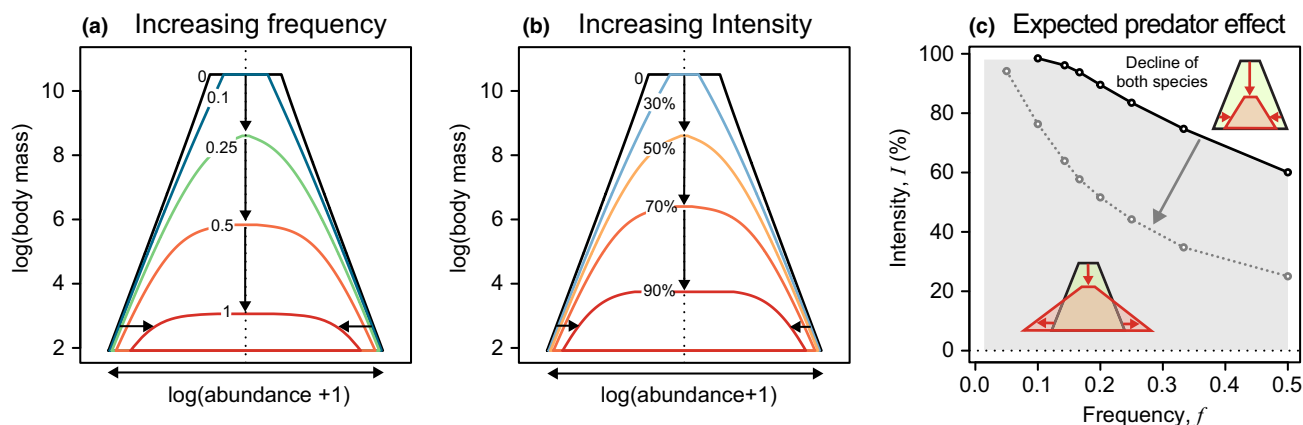


Figure 6 Graphical summary of the effects of disturbances on the shape of size-abundance pyramids. Panels (a) and (b) show size-abundance pyramids for increasing disturbance frequency and intensity respectively (same analytical results as in Fig. 3a and b). Panel (c) illustrates the expected change in the shape of size-abundance pyramids resulting from a predator–prey dynamic. Lines and points in panel (c) represent the isoclines of disturbance regimes $\{I, T\}$ under which we can expect a predation–release effect leading to wider bases of size-abundance pyramids. Points represent the disturbance intensity for which prey species switch from higher to lower mean abundances at dynamical equilibrium in presence compared to in absence of disturbances, for a given disturbance frequency and a set of predator parameters. Black points are estimated for a smaller prey, that is with higher growth rate, than grey points (see detailed method in Appendix S3 and Table S4 for parameter values).

shape of a size-abundance pyramid to the disturbance regime experienced by the community (Fig. 6a–b). Overall, increasing disturbance frequency or intensity narrows the bases of size-abundance pyramids and lowers their height. This corresponds to the extinction of the largest species and a general reduction of population mean abundances in all size classes. Hence, we demonstrate that disturbances that are not size-selective and do not target large species have nonetheless a higher impact on large species than on smaller ones.

The model is applicable across all biological and temporal scales as population growth rate and disturbance frequency are expressed with the same time units. Eqn (2) can also apply to populations that do not show a scaling relationship between growth rate and body-size and predicts which disturbance regimes a species can sustain, or not, based on its generation time (Fig. 2 and Fig. S1). Importantly, our results are not specific to repeated pulse disturbances but also hold for press disturbances, which will affect the shape of size-abundance pyramids in an equivalent way (see Appendix S1 for a mathematical demonstration).

Our model offers a new perspective on community responses to disturbances by exploring the effect of repeated pulse disturbances of varying frequency and intensity on community size structure. The majority of theoretical studies on community stability have focused on local stability, which examine community's response to small pulse disturbances around one single equilibrium (Donohue *et al.* 2016), reflecting the great interest for the so-called diversity–stability debate (May 1972; McCann 2000; Allesina & Tang 2012; Jacquet *et al.* 2016). Our approach goes beyond local stability measures at the vicinity of one single attractor and is applicable to any combination of disturbance frequency or intensity. It predicts which species, based on its growth rate, can persist and how the abundances of the remaining species will be affected by a whole gradient of disturbances.

Note that the model depends on a number of technical assumptions. First, we restricted our theoretical approach to

disturbance regimes where pulse disturbances are applied at fixed intervals with a fixed intensity. This choice, though relatively simplistic, allowed us to mirror the disturbance regimes applied to the experimental communities. To generalise, we also performed simulations where we added stochasticity in the frequency and intensity of the disturbance regime to test the sensitivity of the theoretical results to variability in the periodicity and intensity of disturbances (Appendix S2). Our results were qualitatively robust to the addition of noise around average values of disturbance frequency and intensity, which simply increased the negative effect of one given disturbance regime on the largest size classes (Fig. S6). Second, we consider that the allometric parameters of the relationships between population growth rate, carrying capacity and body-size are the same for all species (i.e. same slopes and intercepts). We therefore performed sensitivity analyses of Eqn (5) and demonstrate that our results are robust to variation in these allometric parameters (Appendix S2, Figs S7 and S8).

Experimental test of the theory

The disturbance experiment on microbial communities showed some similarities but also some departures from the theoretical predictions (Fig. 5b–d). As expected from the analytical model, total community biomass gradually decreased with disturbance frequency and in a more nonlinear way with disturbance intensity (Fig. 4c–d, and Fig. 3c–d for the theoretical predictions). Interestingly, it was the intermediate and not the largest size classes that were the most sensitive to disturbances in the microbial community. We provide below two possible explanations for this observation. Most likely, the abundances of the largest size class might be already too low, and therefore too close to the methodologically defined detection threshold, in the control communities to observe a significant effect of the disturbances of these size classes. Second, this might be explained by the duration of the experiment (21 days), which was not long enough to capture the

extinction of the largest species. We estimated the time to reach the dynamical equilibrium in the experiment with the model parameterised with experimental data (see Table S3). The model predicted that equilibrium is reached by the end of the experiment (21 days) for the size classes considered in all disturbance regimes but the strongest. With the highest frequency and intensity $\{I = 90\%; f = 0.33\}$ the equilibrium is reached by the three smallest size classes (in 12, 18 and 21 days respectively).

Additionally, some combinations of disturbance frequency and intensity had a positive effect on the smallest size class of microbes compared to controls, which corresponded to the main departure from the theoretical predictions (Fig. 4a and b and Fig. 5d). This could be explained by a disruption of biotic interactions (predation or competition) following a disturbance, allowing the remaining small species to grow in higher densities in the absence of other species (Cox & Ricklefs 1977; Ritchie & Johnson 2009; Bolnick *et al.* 2010). Such 'interaction-release' mechanism could not be captured by our model of co-occurring species. We discuss below how interspecific interactions, such as competition, predation or parasitism, could modulate the shape of size-abundance pyramids exposed to disturbances.

Extending the model to communities of interacting species

To observe an 'interaction-release' effect that will widen the pyramid's base, two conditions are required (but not sufficient): (1) the existence of a significant mismatch between the growth rates of the two interacting species, leading to differential response to disturbances; and (2) the species with the slowest growth rate has a negative effect on the other species (i.e. predator, competitor or parasite). The latter condition seems unlikely for parasitism. For competitive interactions, a 'competition-release' effect can potentially increase the abundance of small, fast-growing species that will recover faster from a disturbance event compared to larger competitors (e.g. Xi *et al.* (2019)). Finally, the existence of a 'predation-release' effect is very likely as predators are generally larger than their prey and have slower growth rates (Brose *et al.* 2006, 2016; Barnes *et al.* 2010). In an additional analysis, we performed simulations using a predator-prey model to explore in which conditions a 'predation-release' effect could increase the abundance of small prey species (see Appendix S3 for detailed methods). We found that small to intermediate disturbance regimes can increase average prey abundance through a 'predation-release' effect, which should generate size-abundance pyramids with a wider base (Fig. 6c). This effect vanishes above some disturbance thresholds, where prey species are also negatively impacted by disturbances (Fig. 6c and Figs S9–S11).

Our model cannot capture cascading effects triggered by complex interactions networks in its current form. A promising future direction is the extension of the model to multi-trophic communities, which will allow further explorations of the potential of interspecific interactions to modulate the impact of disturbances on size-abundance pyramids and community biomass. Indeed, it is likely that predator species will also be impacted indirectly through a bottom-up transmission of the disturbances (i.e. decrease in prey availability).

Additional mechanisms shaping size-abundance pyramids exposed to disturbances

Here, we propose a systematic approach, based on the metabolic theory of ecology, to predict the response of size-abundance pyramids to persistent disturbances. Our results are specific to a class of persistent disturbances (i.e. pulse or press) that affect the abundance of all species in a similar way, regardless of their specific body-size or growth rate. We also assume that the leading mechanism that determines the response of size-abundance pyramids to this type of disturbances is the allometric relationship between species growth rate and body-size. However, additional mechanisms can generate size-dependent abundances or size-dependent responses to disturbances in real-world ecosystems. First, species sensitivity to disturbances that are not size-selective can be nonetheless unequal among size classes, with particular size classes being more resistant to a given disturbance intensity. For example, strong windstorms or droughts generally cause greater mortality among larger or taller trees (Woods 2004; Hurst *et al.* 2011; Bennett *et al.* 2015). Second, from a spatial perspective, size-specific mobility and immigration-extinction dynamics could largely affect the relationship between species recovery dynamics and their size (McCann *et al.* 2005; Jacquet *et al.* 2017). It would be interesting to extend our approach to metacommunities, where the depletion of large species in a disturbed habitat patch could be balanced by immigration from undisturbed neighbouring patches (Pawar 2015).

Finally, some disturbances can be size-selective, as illustrated by studies on abundance size spectra that specifically addressed the effect of a press, size-selective disturbance, often reflecting disturbances expected under commercial fishing (Shin *et al.* 2005; Sprules & Barth 2016). Our model can easily be refined to more specific cases, in which disturbances have unequal effects on species, by adding size-specific disturbance intensities to the model. The abundance size spectra of harvested fish communities are generally characterised by steeper slopes than unfished communities, and are used as a size-based indicator of fisheries exploitation (Shin *et al.* 2005; Petchey & Belgrano 2010; Sprules & Barth 2016). We demonstrate that size-abundance pyramids are also predictably affected by more general pulse disturbances that are not size-selective such as floods or wildfires. Hence, when compared to a reference state, size-abundance pyramids provide information on the level of disturbances an ecosystem is facing and could be used as 'universal indicators of ecological status', as advocated in Petchey & Belgrano (2010).

CONCLUSION

Our findings have direct implications regarding the effects of disturbances on ecosystem functioning. Indeed, the model makes predictions on total biomass and demographic traits correlated with productivity rate and energy flows, which are among the most relevant metrics to quantify ecosystem functioning (Oliver *et al.* 2015; Schramski *et al.* 2015; Brose *et al.* 2016; Barnes *et al.* 2018). In the current context of global change, we demonstrate that the expected increase in disturbance frequency and intensity should accelerate the extinction

of the largest species, leading to an increasing proportion of communities dominated by small, fast-growing species and lower levels of standing biomass. Importantly, the effect of increasing disturbance regimes will be nonlinear and abrupt changes in community structure and functioning are expected once a disturbance threshold affecting the equilibrium abundances of smaller species is reached.

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AUTHORSHIP

CJ and FA designed research, CJ conducted the experimental research, CJ and IG designed the theoretical research and IG did the mathematics and simulations to produce the theoretical figures. CJ wrote the first draft of the manuscript and all authors critically contributed to the edition of the paper.

DATA AVAILABILITY STATEMENT

The data supporting the experimental results as well as a Rmarkdown document, which explains in detail the theoretical approach and produces the figures, are archived in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.95x69p8g7>.

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