Diversity loss from multiple interacting disturbances is regime-dependent

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Abstract

Anthropogenic activities expose many ecosystems to multiple novel disturbances simultaneously. Despite this, how biodiversity responds to simultaneous disturbances remains unclear, with conflicting empirical results on their interactive effects. Here, we experimentally test how one disturbance (an invasive species) affects the diversity of a community over multiple levels of another disturbance regime (pulse mortality). Specifically, we invade stably coexisting bacterial communities under four different pulse frequencies, and compare their final resident diversity to uninvaded communities under the same pulse mortality regimes. Our experiment shows that the disturbances synergistically interact, such that the invader significantly reduces resident diversity at high pulse frequency, but not at low. This work therefore highlights the need to study simultaneous disturbance effects over multiple disturbance regimes as well as to carefully document unmanipulated disturbances, and may help explain the conflicting results seen in previous multiple-disturbance work.

KEYWORDS
biodiversity, interacting disturbance regimes, invasion, invasion success, multiple disturbances

INTRODUCTION

Disturbances, defined as events that destroy biomass and change species interactions, are ubiquitous and fundamental to structuring natural communities (Buckling et al., 2000; Connell, 1978; Huston, 1979; Kassen et al., 2000; Mackey & Currie, 2001; Wilkinson, 1999). How disturbances structure communities is dependent on their regime, which is characterized by their frequency (number of events over a given time period), severity (proportion of biomass destroyed), extent, timing and duration (Miller et al., 2021). Past studies have shown that a spectrum of disturbance regimes can lead to a wide range of disturbance–diversity relationships (Buckling et al., 2000; Cardinale et al., 2006; Connell, 1978; Mackey & Currie, 2001; Miller et al., 2011; Violle et al., 2010;

Wilkinson, 1999; Wilson & Tilman, 2002). Changes to disturbance regimes can either directly increase or decrease biodiversity in a community, resulting from the complex interactions between the historical and novel disturbance regimes and the life histories of the component species (Lear, Padfield, et al., 2022; Miller et al., 2021). Whilst some changes in disturbance regimes can increase diversity, the global trend suggests that more frequent and intense disturbance regimes are likely to decrease diversity (Seidl et al., 2017). More importantly, disturbances are increasingly occurring simultaneously due to human activities (e.g. extreme fire and drought due to warmer temperatures) (Seidl et al., 2017; Stockwell et al., 2020), and have been shown to have additive, antagonistic or synergistic effects on diversity (Darling & Côté, 2008; Sala & Knowlton, 2006). However, despite

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previous work testing the effect of multiple disturbance (Polazzo et al., 2022; Seidl & Rammer, 2017; Stockwell et al., 2020), whether the interactive effect of multiple disturbances on diversity is the same across different disturbance regimes remains uncertain. Evidence from the multiple stressor (a perturbation that impairs the function of a population) literature suggests that a change in interactive effect is likely, as it shows that the effect of one stressor on the density of a population can vary from antagonistic to synergistic depending on the magnitude of a second stressor (King et al., 2022; Turschwell et al., 2022).

Two common and relatively well studied types of disturbances are pulse mortality events and the introduction of non-native species (invasions) into communities (Didham et al., 2005). Both disturbance types can severely reduce the diversity of the resident community: frequent pulses eliminate organisms before they have a chance to reproduce (Bohn et al., 2014), and aggressive invaders can have a suite of negative impacts (Pyšek et al., 2020) including, for instance, affecting nutrient availability (Mallon et al., 2015; Zhang et al., 2017), introducing novel parasites, pathogens and antimicrobials (Gillor et al., 2008; Prenter et al., 2004), and altering the abiotic environment (Amor et al., 2020).

Importantly, these two different disturbances may interact to affect biodiversity. For example, pulse mortality may temporarily promote invasion by reducing both the competition between the invader and the residents for resources (Altman & Whitlatch, 2007; Davis et al., 2000; Lear et al., 2020), and any priority or dominance effects the residents may have (Fargione et al., 2003; Urban & De Meester, 2009). Invaders, in turn, may aggravate pulse mortality by competing with the residents for resources needed to quickly recover after the event, and thus change the ecological and evolutionary course of the community (Davis et al., 2000) (Faillace et al., 2022). Thus, there may often be strong interactions between these two disturbances, with the specific prediction that frequent pulse mortality and invasion will synergistically interact to decrease resident diversity beyond their additive effects. However, it is also plausible that frequent pulses keep invaders at low density and prevent them from establishing in the resident community (e.g. due to demographic stochasticity; Lear, Padfield, et al., 2022). Therefore, frequent pulses and invasion could instead antagonistically interact to neutralize their additive effects on the resident diversity. Although these two predictions have opposite outcomes, they both lead to the hypothesis that the interactive effects of multiple disturbances on diversity depend on their regimes, such that they may amplify or lessen each other's effect as their magnitude increases.

Here, we test this hypothesis by leveraging a stably coexisting community of bacteria in which we can manipulate pulse disturbance frequencies, add a defined propagule of an invader and calculate final diversity to tease apart the independent and interactive effects of multiple disturbances on resident diversity. The community used has been shown previously to stably coexist for 10 weeks with weekly transfers: deviations from this passage frequency favours different community members, and consequently alters the stability and the diversity of the community (Castledine et al., 2020), as has been found in other microcosm studies (Buckling et al., 2000; Jiang & Patel, 2008). Specifically, we expose a five-species bacterial community to one of four pulse mortality frequencies, and factorially challenge each with a fast growing 'invasive' species of bacteria. Using this system, we find the greatest loss of resident diversity in the invaded and most frequently disturbed communities, and that interactive effects are weak at low levels of disturbance but strong at high levels. These findings therefore improve our understanding of how multiple disturbances interact, and shed light on why we see a range of interaction outcomes in the current literature.

METHODS

Bacteria strains

Our model synthetic community consists of five bacterial isolates previously cultured and typed (based on 16S rDNA) from potting compost, with the 5 isolates chosen because of their consistent persistence as a community over 6 weeks in multiple replicates in diluted tryptic soy broth (TSB), and the ease with which they can be distinguished morphologically on King's medium B (KB) agar plates (Hesse et al., 2018). The closest sequence matches of the 5 isolates are: *Pseudomonas corrugata*, *Stenotrophomonas rhizophilia*, *Achromobacter agilis*, *Variovorax guangxiensis* and *Ochrobactrum daejonense*. Competition experiments have shown that the interactions among these species range from growth-enhancing asymmetric cross-feeding to competition (Padfield et al., 2020). We have demonstrated stable coexistence of all species combinations (i.e. 2, 3, 4 and 5 species communities) through the ability of each species to establish from rare (a defining condition for a stabilizing mechanism; Chesson, 2000) and to reach and maintain a stable equilibrium density after 14 days that lasted for at least 28 days without pulse disturbance and for at least 10 weeks when pulsed weekly (Castledine et al., 2020; Padfield et al., 2020). Indeed, the species have coexisted, whilst retaining morphological distinctiveness for over the 13 months we have propagated them to date under weekly pulse disturbance (unpublished). For our invader, we used the opportunistic human pathogen *Pseudomonas aeruginosa* PA01 (O'Brien et al., 2018) which also grows well in TSB. *P. aeruginosa* is a fast growing, competitive species capable of invading and surviving in an array of environments including rivers, medical equipment and humans (Chatterjee et al., 2017; Rutherford

et al., 2018). This strain was lacZ-marked, which allows it to be easily identified when plated on agar containing X-gal due to a blue colour change (O'Brien et al., 2018).

Experimental design

Monocultures of the residents (*A. agilis*, *O. daejonense*, *P. corrugata*, *S. rhizophila* and *V. guangxiensis*) were grown statically in glass vials (microcosms) containing 6 mL of 1/64th diluted TSB for 48 h at 28°C. Their densities (number of colony forming units; CFU) were standardized by their optical density measurements and the monocultures were then combined to form an equal mixture of the five species. Sixty microlitres of this mixture was added to each of 48 microcosms containing 6 mL of 1/64th TSB. Monocultures of the invader, *P. aeruginosa*, were also grown statically for 48 h in 1/64th TSB, and then diluted 100-fold in M9 salt buffer in which the bacteria do not grow. Each invader inoculate was plated onto KB agar to confirm its density.

Twelve microcosms received one of four mortality pulse disturbance regimes: every 2, 4 or 8 days, or one disturbance only at initiation ('16 days'). This final treatment served as a control without repeated pulse disturbance; previous work has shown that this community reaches a stable equilibrium by this time (Padfield et al., 2020). Pulse disturbances involved transferring 60 μL (1%) of homogenized community into 6 mL of fresh media, resulting in 99% mortality. For each regime, six microcosms were challenged with 60 μL of the diluted invader culture and six microcosms were used as non-invaded controls; invasions took place post-disturbance on days 4, 8 and 12,

and the invader inoculate was plated to quantify its density (Figure 1). Microcosms were kept static at 28°C with loose lids to allow oxygen transfer.

After 16 days, all microcosms were thoroughly homogenized, mixed with glycerol to a final concentration of 25%, and frozen at -80°C. Thawed samples were plated on KB agar containing X-gal to quantify their CFUs.

Statistical analysis

Resident biodiversity was calculated using the effective number of species (Jost, 2006) $exp\left(-\sum_{i=1}^{5} p_i \ln p_i\right)$, where p_i is the proportion of the ith species. Diversity was then scaled to the proportion of maximum diversity possible in this experiment (i.e. five species). Previous work in a similar laboratory system has shown that disturbance has quadratic effects on diversity (Buckling et al., 2000). We therefore tested the effect of pulse frequency (quantified as, e.g. 1/16 for every 16 days), its quadratic form, invasion (0 for uninvaded and 1 for invaded) and the interactions between invasion and pulse frequency on resident diversity using a logistic linear regression model:

$$\text{logit(diversity)} \sim \left(\text{pulse} + \text{pulse}^2\right) \times \text{invasion} \quad (1)$$

We performed stepwise model selection on this model. We also performed the same analysis using linear regressions on Gini-Simpson index (Simpson, 1949) for diversity (see Supplemental Information, Figure S1). Additionally, generalized linear models were used to test treatment effects on total resident density and total density (resident + invader).
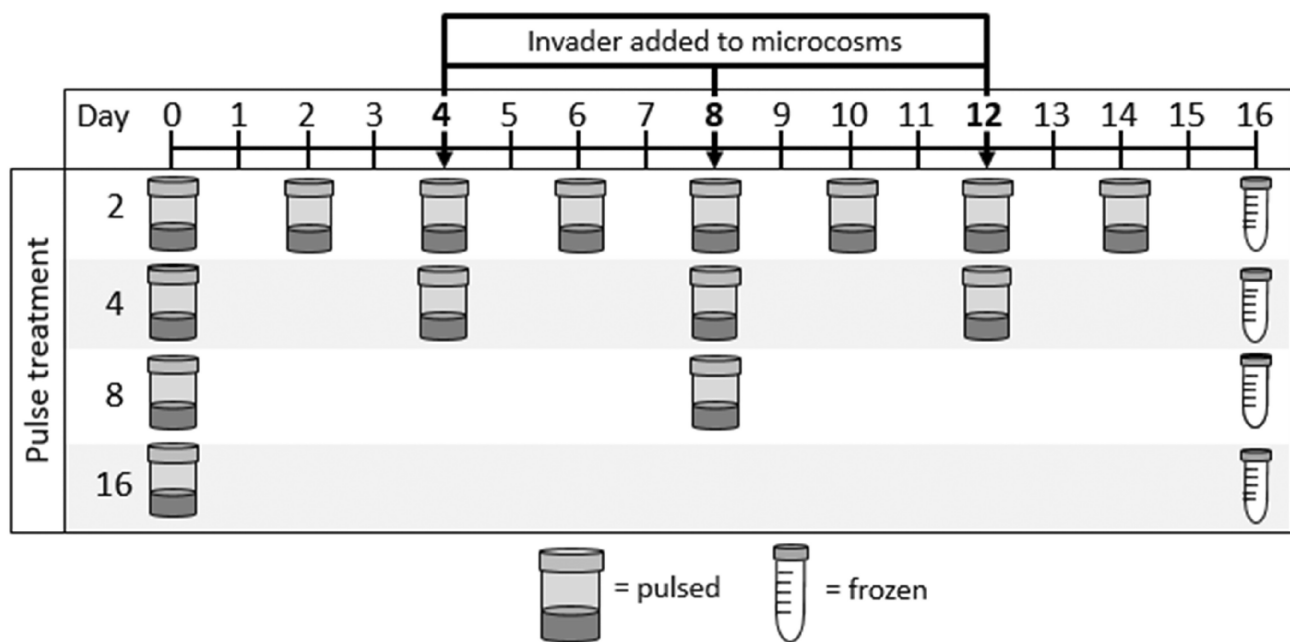

FIGURE 1 Schematic plan of the experimental design used to test the effect of an invader on the diversity of disturbed communities. Microcosms (*n*=48) containing five bacterial species were subject to a pulse disturbance using a 1% transfer either every 2, 4, 8 or 16 days. On days 4, 8 and 12 an invader (*Pseudomonas aeruginosa*) was added to half (*n*=6) of the microcosms in each disturbance regime. On day 16, all microcosms were frozen.

To test the effect of treatments on the density of each of the five resident species, we used a generalized linear latent variable model with the R package 'gllvm' (Niku et al., 2019), as this multivariate approach allows us to separate treatment effects from the latent interactions among the resident species (i.e. it models the species interactions by adding additional parameters as well as treatment effects).

To quantify invader success, we calculated the proportion of the invader in the community (invader CFU / (invader CFU+resident CFU)) at day 16. We then used a binomial regression to test how this responds to pulse frequency.

$$\text{logit(invader proportion)} \sim \left(\text{pulse} + \text{pulse}^2 \right) \quad (2)$$

Additionally, we used a negative binomial regression to test the effects of pulse frequency on the final density of the invader (Ripley et al., 2013).

All statistical tests were carried out in R version 3.4.0 (R Core Team, 2017).

RESULTS

Interaction between disturbance and invasion affected diversity

By factorially invading a community of five bacterial species disturbed at four different frequencies, we tested for interactive effects of pulse frequency and invasion on the diversity of a stably coexisting community. We found that the best fit model is the full model (Equation 1) (see Supplemental Information).

Resident diversity (effective number of species) of the uninvaded community increased with pulse frequency (effect size: 14.86, $p < 10^{-4}$) but decreased with pulse^2 (effect size: -23.97, $p < 10^{-3}$), resulting in a hump-shaped relationship with frequency, as found in similar systems (Buckling et al., 2000). There was a small positive main effect of invader addition on resident diversity, as seen in 16-day samples (Figure 2; effect size: 1.54, $p < 0.002$). However, we found the interaction between pulse frequency and invasion to have a very large negative effect on resident diversity (effect size for pulse*invasion: -20.28, $p < 10^{-4}$; effect size for pulse^2*invasion: 22.62, $p < 0.006$; Figure 2). This caused some resident species to become non-detectable (<1 CFU on the agar plate) and presumed extinct at high pulse frequencies in the invaded treatments (Figure 2). We therefore found that the invasion by *P. aeruginosa* reduced diversity at high pulse frequencies but not at low.

Importantly, we note that the invasion qualitatively changes the pulse disturbance–diversity relationship of the resident community in our model (Figure 2). Without invasion, the resident diversity shows the expected unimodal pattern (concave down) with increasing pulse frequency. With invasion, however, the resident diversity shows a slight but statistically significant U-shaped pattern (concave up) with increasing frequency.

Invader success increases with disturbance

To understand the diversity loss at higher pulse frequencies in the invaded treatments, we quantified invader success (proportion and density of invader in the final
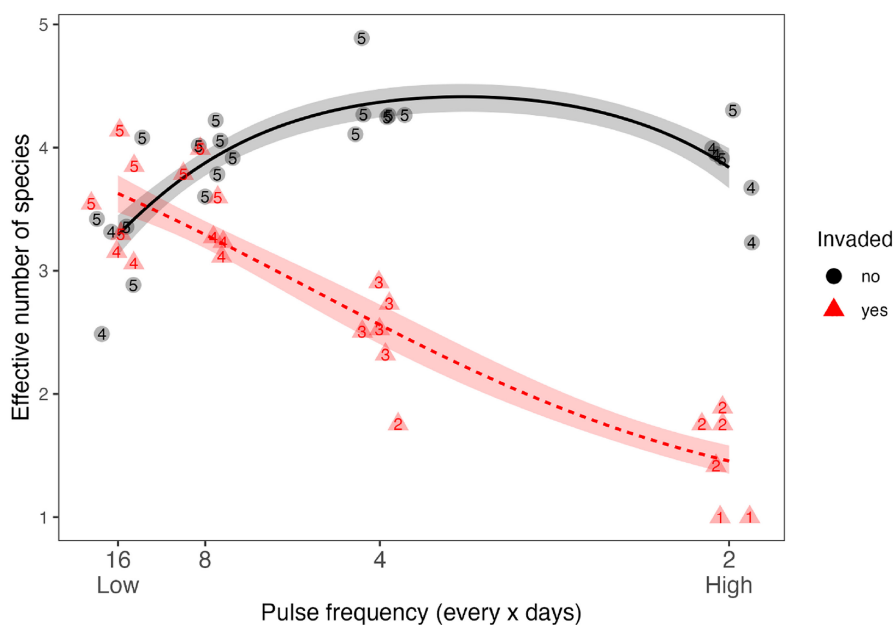

FIGURE 2 Resident diversity (effective number of species) of a five-species community after 16 days in one of four pulse regimes (2, 4, 8 or 16 days), and either invaded by *Pseudomonas aeruginosa* (red dotted line and triangles) or not (black solid line and circles). See Figure S1 for the same analysis using Gini-Simpson's index. The best fit model (Equation 1) and the standard error are shown as the fitted lines and their envelopes. Individual points correspond to each microcosm, and their enclosed number shows the number of resident species present, that is, species richness.

community) and tested whether this differed with pulse frequency. Invader proportion significantly increased with increasing pulse frequency (effect size: 47.87, $p < 0.001$; Figure 3a) and with pulse frequency^2 (effect size: -58.78, $p < 0.001$), as did invader density (effect size of pulse: 37.79, $p < 0.001$; effect size of pulse frequency^2: -53.51, $p < 0.001$; Figure 3b). Overall, these results show invader success is greater at higher pulse frequencies than low.

P. Aeruginosa displaced the resident community

To determine how *P. aeruginosa* affected resident populations, we first tested invasion and pulse effects on resident density (Figure 4). Resident density was significantly affected by the main effect of pulse and by invasion (pulse frequency: likelihood ratio $\chi^2 = 364.1$, d.f. $= 3$, $p < 10^{-4}$; invasion likelihood ratio $\chi^2 = 57.5$, d.f. $= 1$, $p < 10^{-4}$). Furthermore, the negative effect of pulse on resident density was significantly greater in the invaded treatments compared to the non-invaded treatments (interaction between pulse and invasion: likelihood ratio $\chi^2 = 62.1$, d.f. $= 3$, $p < 10^{-4}$; Figure 4a). In contrast, although the total density (resident + invader CFU) decreased with pulse frequency (likelihood ratio $\chi^2 = 242.3$, d.f. $= 3$, $p < 10^{-4}$), invasion only had a marginal, non-significant, effect on density (likelihood ratio $\chi^2 = 2.9$, d.f. $= 1$, $p = 0.09$). Crucially, we did not find a statistically
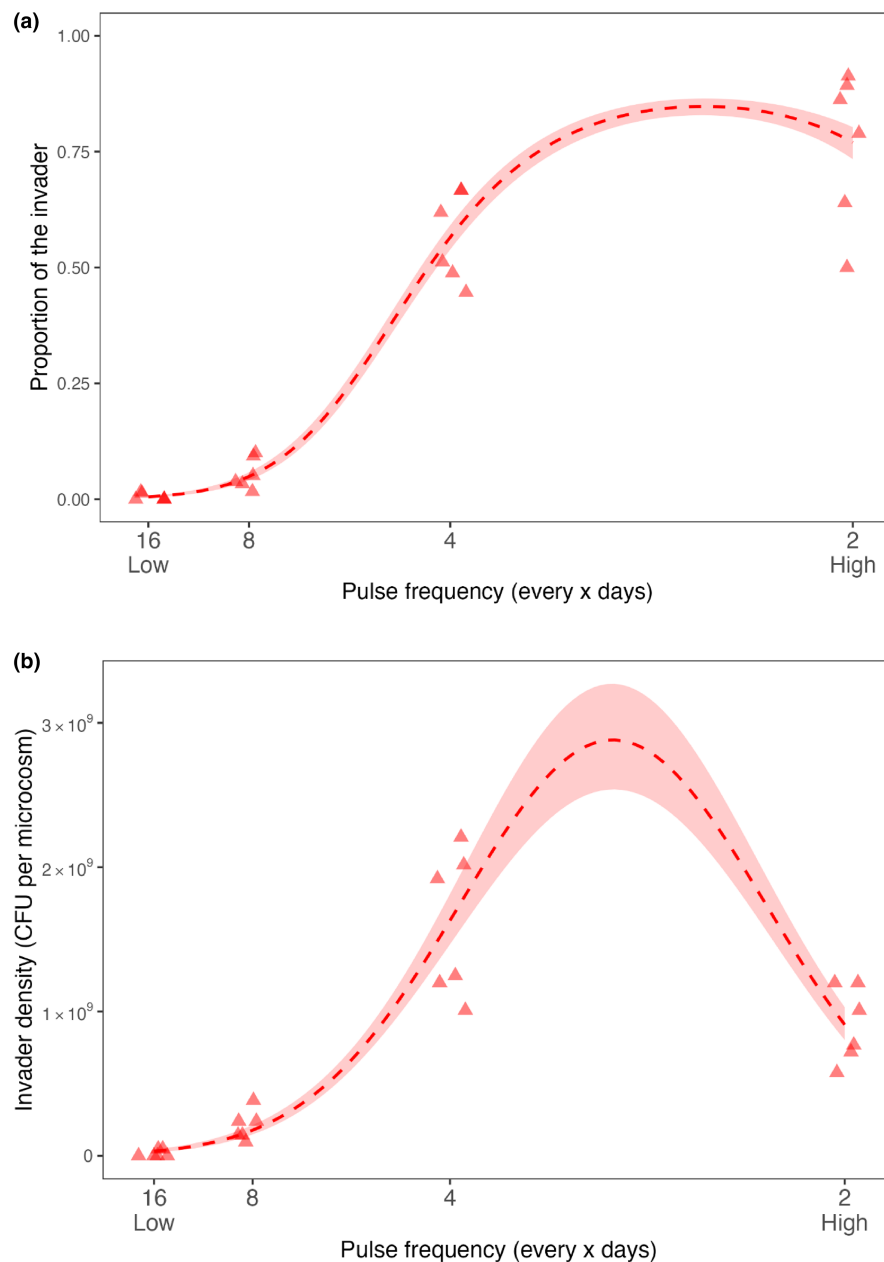

FIGURE 3 The (a) proportion and (b) the density of *P. aeruginosa* in a stable community of five species of bacteria exposed to different disturbance frequencies from every 16 days (low) to every 2 days (high) for 16 days. *P. aeruginosa* was added on days 4, 8 and 12. Triangles show individual microcosms, the dashed line the model fit and its envelope the standard error.
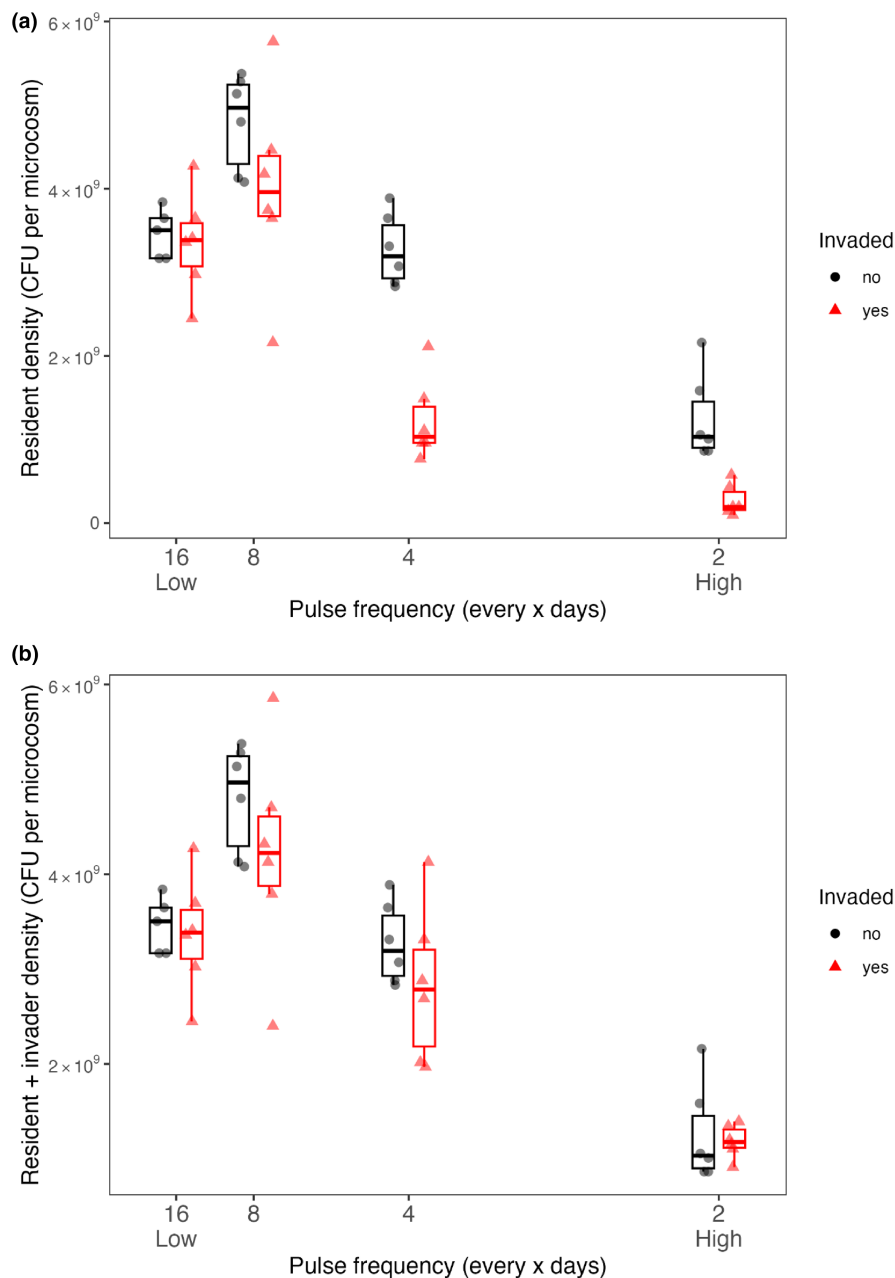
FIGURE 4 Effects of disturbance frequency and invasion on (a) resident density and (b) total density (resident + invader) of a five-species community either invaded by *P. aeruginosa* (red triangles) or not (black circles). Triangles and circles show individual microcosms.

significant interaction between pulse frequency and invasion on total density (i.e. resident plus invader; likelihood ratio $\chi^2 = 0.75$, d.f. $= 3$, $p = 0.86$). Taken together, these results imply that the pulse frequency determines the density of the total community but that some of the residents are displaced by the invader (Figure 4b).

To determine if *P. aeruginosa* displaced each resident species equally, we used a multivariate approach to test how the densities of each of the five resident species were affected by pulse frequency, invasion or their interaction (Figure 5, Figure S2). The density of *A. agilis* was not affected by the invasion ($p \geq 0.12$ for all covariates). The densities of *P. corrugata*, *S. rhizophila* and *V. guangxiensis*, however, were greatly reduced by invasion at high

pulse frequencies (*P. corrugata* in the 2 and 4-day treatments, *V. guangxiensis* in the 2, 4 and 8-day treatments and *S. rhizophila* in the 2-day treatment only), to the point where they were undetected in 2-day disturbance frequency samples (Figure 5). *O. daejonense* followed a similar, but less severe, trend. This demonstrates that *P. aeruginosa* reduces the relative proportions of some species rather than reducing the density of each species equally (Figure 5; Figure S2). We see that *S. rhizophila* is resistant to displacement by the invader in all but the highest disturbance treatment, showing that this effect differs among residents. We therefore demonstrate that high pulse frequency facilitates the establishment of *P. aeruginosa*, which negatively affects resident *P.*
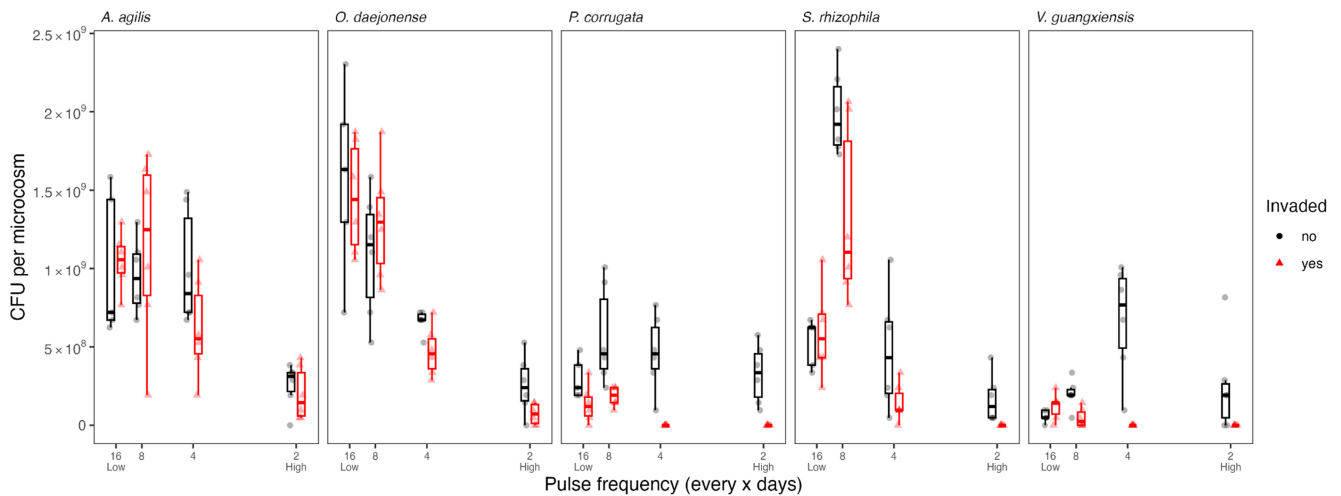
FIGURE 5 Density (CFU per microcosm) of five bacterial species after 16 days in one of four pulse disturbance regimes (every 2, 4, 8 or 16 days), and either invaded by *Pseudomonas aeruginosa* (red triangles) or not (black circles).

corrugata, *S. rhizophila* and *V. guangxiensis* densities to the point of local extinction, and this results in reduced diversity.

DISCUSSION

Here, we experimentally test the interactive effects of multiple disturbances on resident diversity, by exposing a bacterial community to different regimes of pulse mortality and invader disturbances. A challenge in understanding the effects of multiple disturbances is the potential for different interactive mechanisms to operate at different levels of disturbance (Foster et al., 2016). We found a significant interaction between the disturbance types, such that at low pulse disturbance frequencies invasion had a positive effect on total resident diversity, whereas at high pulse disturbance invasion had a negative effect. Consequently, our results demonstrate that, depending on the disturbance regime, multiple disturbances can act both antagonistically (have reduced combined effects on diversity) or synergistically (have greater combined effects on diversity).

It is commonly hypothesised that co-occurring disturbances have synergistic effects on diversity because communities that are disrupted by one disturbance may be less stable, and therefore less resilient to a second disturbance (Burton et al., 2020; Christensen et al., 2006; Crain et al., 2008). However, evidence for such synergism between disturbances is mixed, with previous work frequently finding no or even antagonistic interactions between multiple disturbances (Darling & Côté, 2008). Here, we show a possible reason for such mixed empirical results: the direction of the interaction can depend on the regimes of the disturbances involved, and synergistic interactions may only be apparent in highly disturbed systems.

The dependence of the direction of the interactive effect on the disturbance regime strongly suggests that the negative effects of invasion on resident diversity might be missed at some disturbance frequencies. This may result in an invader erroneously being categorized as beneficial based on its positive effects at other disturbance frequencies. That the effect of the invader is highly contingent on the pulse disturbance regime may be particularly important for the passenger, driver and back seat driver hypothesis, which categorizes an invader based on its effect on resident diversity (Bauer, 2012; Didham et al., 2005; Fenesi et al., 2015; MacDougall & Turkington, 2005; Wilson & Pinno, 2013). A 'driver' invader changes ecosystem properties and causes a decline in resident diversity independently from other factors of change going on in that environment (MacDougall & Turkington, 2005; Wilson & Pinno, 2013). In contrast, a 'passenger' invader takes advantage of available resources created by other causes of change, such as disturbance, but does not cause biodiversity or functionality loss themselves (Bauer, 2012; MacDougall & Turkington, 2005). Lastly, 'back seat drivers' act synergistically with other factors of change—they require ecosystem change to establish, like a passenger, but once established will themselves cause change, like a driver (Berman et al., 2013; Fenesi et al., 2015). In our experiment, the invaders acted as a back seat driver: they benefitted from higher disturbance frequency (as this lowered resident densities and offered more periods of reduced priority and dominance effects, and hence reduced invasion resistance), and subsequently affected the resident community. However, at low disturbance this may be missed, and the invader erroneously categorized as a passenger due to having no negative effect on the resident community. Similar phenomena may be observed with other pulse disturbance types. This shift in apparent invader effect at different levels of disturbance highlights the need to consider the

characteristics of the disturbance regime when drawing inference, and raises concerns that invaders previously considered harmless (passengers) may shift to being detrimental for resident diversity (back seat drivers) as other disturbances increase.

Our finding of the pulse-invader interaction shifting from antagonistic at low levels of pulse disturbance to synergistic at high levels highlights the importance of looking at multiple disturbances over different regimes. A recurrent theme in understanding the effects of disturbances on diversity is that different disturbance aspects can interact in a complex way to shape communities, and that our interpretations of the disturbance–diversity relationships depend crucially on the extent and resolution of the observations. Even under a single disturbance type, a gradient of aspects of disturbances (e.g. frequency and severity) interact to produce various disturbance–diversity relationships. This may help to resolve previously reported conflicting patterns on disturbance–diversity relationships (Hall et al., 2012; Miller et al., 2011). Similarly, previous analyses of the interactive effects of multiple disturbances (Darling & Côté, 2008) have shown that the empirical patterns generated by interactions are mixed. Here, we use multiple disturbance regimes to show that, as in previous disturbance–diversity studies, a gradient of disturbance is crucial to fully understanding the effect of simultaneously co-occurring disturbances.

That the invader shifts to having severe negative consequences for diversity at high mortality pulse disturbance, and even qualitatively changes the pulse disturbance–diversity relationship, raises applied concerns as the number, frequency and intensity of disturbances is increasing with climate change (Essl et al., 2020). In our experiment, one mechanism underlying the synergistic effect of high disturbance in the invaded treatments is that the invader could have been interacting similarly with each member of the resident community (i.e. reducing each resident species' population equally). We observed, however, that this is not the case; the invader only negatively affects some species. This highlights that conservation efforts need to consider a species' vulnerability to invasion under different disturbances and disturbance regimes, as well as that of the entire community. For example, if just pulse mortality is considered in our system, *A. agilis* would require greater resources to conserve than *P. corrugata* as it is more vulnerable under a changing disturbance regime. However, if we then additionally consider vulnerability to exclusion by an invader in a situation with high pulse mortality, *P. corrugata* would be regarded as more at risk than *A. agilis* and therefore should receive more resources. One reason for this interaction being particularly present in *P. corrugata* is that it is closely related to our invader, *P. aeruginosa*, and so is more likely to compete for the same niche. We find that at low pulse frequencies, *P. corrugata* benefits

from a priority effect and excludes *P. aeruginosa*. High frequencies, however, can reduce this priority effect and consequently, *P. aeruginosa* (a better competitor) can outcompete *P. corrugata*. This suggests that the finding that invaders that are more related to residents have less of an impact (Cox & Lima, 2006; Ricciardi & Atkinson, 2004; Saul & Jeschke, 2015) may be in part due to priority effects, and may therefore not hold when disturbance regimes change. We note, however, that the role of post-invasion co-evolution between the resident species and the invaders in further shaping the community is unclear. These findings further suggest that increasing disturbance may cause previously latent invaders to start competitively driving diversity loss. Moreover, this in itself may act as a disturbance, creating a positive feedback loop that facilitates further invasion (Wonham et al., 2005).

The differences in vulnerability to invasions among the resident species and the resulting changes in diversity imply that community robustness against invasion may significantly change over different disturbance regimes. This could be because frequent disturbances open up resources and niches and therefore reduce the competitive advantage of some resident species over the invader (i.e. eliminate any priority or dominance effects they have). It is also important to note that in a stably coexisting community, such as the one studied here, an invader may indirectly reduce a resident species' fitness by outcompeting a different species on which the resident relies.

Importantly, our findings can be applied to other natural microbial communities. For example, frequent disturbances by antibiotics have been shown to not only facilitate the invasion of clinically relevant opportunistic pathogens, such as *Clostridium difficile*, into a host microbiome, but also to have catastrophic effects for the diversity of the resident community (Shah et al., 2021). The antibiotic and pathogen may then interact synergistically and feedback to one another to reduce microbiome diversity, and consequently may further increase the risk of dysbiosis and infection (Blaser, 2016; Ribeiro et al., 2020), including from pathobionts (Ribeiro et al., 2020). Our results suggest that this interaction may reduce diversity principally by eliminating specific species—this could have particularly severe consequences in the microbiome, where species can play specific roles in host health and defence (Lange et al., 2016).

In conclusion, we provide experimental evidence that the interactive effect of two disturbances on resident diversity is dependent on their regime. Specifically, we find higher frequencies of pulse disturbance to increase the success of an invader, and to lead to multiple extinctions and a collapse in diversity, whereas at low pulse disturbance the invader had a positive effect on resident diversity. These findings help to create a predictive framework to understand

how multiple disturbances interact to affect diversity—a pressing issue under climate change. Moreover, they demonstrate the importance of recording or deliberately using different disturbance regimes when testing for the interactive effects of multiple disturbances on diversity. Furthermore, we show that invaders can aggravate the negative effect of high pulse frequency on diversity. This raises serious concerns for global biodiversity, as the global trend towards increasing disturbance frequency may amplify negative effects of invasion worldwide, and the increasing number of invasions may amplify the negative effect of frequent pulse disturbances worldwide.

AUTHOR CONTRIBUTIONS

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and R code used to analyse it are deposited on Zenodo (Lear, Inamine, et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.