

Disturbance-mediated invasions are dependent on community resource abundance

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Abstract

Disturbances can facilitate biological invasions, with the associated increase in resource availability being a proposed cause. Here, we experimentally test the effects of disturbance regime and resource abundance on invasion success. We invaded populations of the bacterium *Pseudomonas fluorescens* with two invader morphotypes in a factorial design containing five disturbance frequencies and three resource levels. As resident populations were altered by the treatments, we additionally tested their effect on invader success. Disturbance frequency and resource abundance interacted to affect the success of both invaders. For one, success was positively affected by disturbance under high resources but negatively under low. For the other, disturbance negatively affected success under high resource abundance but not under low or medium. Resident population changes did not alter invader success beyond direct treatment effects. Overall, how disturbance affects invasion success is dependent on community resource abundance, and this interaction acts differently on invaders with different life-histories.

Introduction

Biological invasions are a global issue with potentially severe consequences for native communities (Davis *et al.* 2000; Fauschet *et al.* 2001; O'Dowd *et al.* 2003; Lake & Leishman 2004). Successful invader colonisations can reduce biodiversity, alter community dynamics and cause large financial costs (Vitousek *et al.* 1997; Sher & Hyatt 1999; Fausch *et al.* 2001; Shea & Chesson 2002; Levine *et al.* 2003; Didham *et al.* 2005; Altman & Whitlatch 2007; Leishman *et al.* 2007). Disturbances - events that, through destroying biomass, change the availability of resources and habitats - often promote invader success (Shumway & Bertness 1994; Roxburgh *et al.* 2004; Altman & Whitlatch 2007; Lear *et al.* 2020). These can be small (e.g. leaves falling) or large (e.g. wildfires) in scale and facilitate invasions in a number of ways, for example by increasing resource availability, which in turn reduces invader-resident competition (Hobbs & Huenneke 1992; Baldwin & Mitchell 2000; Davis *et al.* 2000; Tilman 2004; Lear *et al.* 2020). Disturbances may also remove any priority effects, and cause resident maladaptation (Davis *et al.* 2000; Stachowicz *et al.* 2002; Fargione *et al.* 2003; Altman & Whitlatch 2007; Fukami 2015).

Despite a large body of work showing that disturbance increases invader success (Lake & Leishman 2004; Roxburgh *et al.* 2004; Altman & Whitlatch 2007; Lembrechts *et al.* 2016; Lear *et al.* 2020), some studies show no or even a negative effect (Fausch *et al.* 2001; Narimanov *et al.* 2020). This may be due to disturbance interacting or covarying with other key environmental variables that affect success. Resource abundance is likely to be particularly important in this context (Davis *et al.* 2000; Lear *et al.* 2020). Where resources are abundant but not easily accessible, disturbance is likely to play an important role in promoting invader

establishment. This is because disturbance will lead to an increased availability of resources that would otherwise be stored as biomass and depleted by consumption (Davis *et al.* 2000). In communities with low resources, the amount of resources released by disturbance will necessarily be low (Davis *et al.* 2000).

The effects of disturbance and resource abundance on invasion success are likely to depend on the invader’s life-history traits (Roxburgh *et al.* 2004). Specifically, successful invaders are often fast-growing ‘coloniser’ species (van Kleunen *et al.* 2010) that can quickly convert available resources into biomass (Mächler & Altermatt 2012), and so are expected to excel in high disturbance and resource abundant conditions. However, whether slower-growing ‘competitor’ species invade more successfully at low disturbance and low resource abundance remains unclear.

Disturbance and resource abundance may have additional indirect effects on invasion by altering the composition of the resident community. On the one hand, disturbance frequency and resource abundance can help increase community productivity and biodiversity (Agard *et al.* 1996; Worm *et al.* 2002; Kassen *et al.* 2004), which in turn may make the community more resistant to invasion (Levine & D’Antonio 1999; Hodgson *et al.* 2002; Tilman 2004; Brockhurst *et al.* 2006): productive and diverse communities are more likely to contain dominant species (i.e. species that has a disproportionately large influence on invasion resistance) and have priority effects (i.e. situations where the first species to occupy a niche has a fitness advantage over species arriving subsequently) (Hodgson *et al.* 2002; Fargione *et al.* 2003; Fukami 2015). These factors increase invasion resistance mainly by reducing invader access to resources (Naeem *et al.* 2000; Hodgson *et al.* 2002; Seabloom *et al.* 2003; Tilman 2004; Emery & Gross 2007; Fukami 2015). On the other hand, there is growing evidence that diversity may facilitate invasions through increased niche dimensionality (Simberloff & Von Holle 1999; Ricciardi 2001; Green *et al.* 2011), which increases the chance of an invader occupying a niche and leads to a negative relationship between diversity and invasion resistance (Fridley *et al.* 2007). Disturbance may weaken or eliminate these resident effects by decreasing resident population sizes, causing resource influxes and diminishing niche dimensionality.

The complexity of the potential interacting factors means that a simple, one-at-a-time, experimental investigation cannot unravel casual processes. Here, we experimentally investigate the independent and interactive effects of resource abundance and disturbance on invader success. We do this by invading wildtype populations of the bacterium *Pseudomonas fluorescens* SBW25 with genetically marked *P. fluorescens* SBW25 genotypes (Hodgson *et al.* 2002; Zhang & Buckling 2016; Lear *et al.* 2020) at different disturbance frequencies and resource abundances in a fully factorial design. The rapid evolutionary diversification of *P. fluorescens* populations into niche specialists (Rainey & Travisano 1998; Gómez & Buckling 2013) allowed us to determine any additional effects of evolved biodiversity and resident density - caused by disturbance and resource variation - on invasion success (Rainey & Travisano 1998; Kassen *et al.* 2000; Spiers *et al.* 2002; Koza *et al.* 2011; Hall *et al.* 2012). We invaded resident populations with two distinct genotypes: a fast-growing, coloniser morphotype and a slower growing competitor morphotype (Hall *et al.* 2012). This allowed us to determine whether the effects of disturbance and resource abundance on invasion success was contingent on the invader’s life history.

Methods

Resident populations

Ancestral *Pseudomonas fluorescens* SBW25 was grown overnight to carrying capacity in shaken glass vials (microcosms) containing 6mL of King’s medium B (KB) at 28°C. Sixty microliters of this culture was then transferred into static microcosms containing KB of varying concentrations (100% KB, 10% or 1%) to create different resource abundances; KB was diluted with M9 salt solution (3g KH₂PO₄, 6g Na₂HPO₄, 5g NaCl L⁻¹). Microcosms were disturbed every 1, 2, 4, 8 or 16 days (Fig. 1) by transferring 1% of homogenised broth into fresh media (99% mortality) for a total of 16 days. Invaders were inoculated at days 4, 8 and 12 (Fig. 1 and see *Invasions* below). In between transfers and invasions, all microcosms were kept static at 28°C with loose lids to allow oxygen transfer. We used 12 replicates of each resource abundance (3) and disturbance frequency (5) combination, for a total of 180 microcosms. Additional microcosms (n=3 per

resource abundance x disturbance combination) were set up to quantify resident density on day 4 – the first invasion time point. This was necessary as the sampling microcosms required homogenisation of treatments that would otherwise not be disturbed.

Invasions

Pseudomonas fluorescens with a *lacZ* marker was used as the invader; the *lacZ* marker makes it visually distinguishable from the wildtype on agar containing X-gal (5-bromo-4-chloro-3-indolyl- β -D-galactopyranoside) due to a blue colour change (Zhang & Rainey 2007). Although originally reported as a neutral marker (Zhang & Rainey 2007), the *lacZ* insert has previously been found to offer a fitness advantage to invaders (Lear *et al.* 2020). The strain was left to diversify for five days in static KB before being plated and a single smooth (SM) and wrinkly spreader (WS) colony was selected, grown and stored in 25% glycerol solution at -80°C. SM morphotypes (our ‘coloniser’ invader) inhabit the broth where they grow rapidly, whereas WS (our ‘competitor’ invader) form biofilms at the air-broth interface: biofilm formation increases competitive ability for oxygen but at a cost to growth rate (Hall *et al.* 2012). Before each invasion, these freezer stocks were used to grow each morphotype overnight in shaken KB as described above; these cultures were diluted to 1% with M9 salt buffer before use. All microcosms were invaded every four days with 60 μ L of either SM or WS invader (total colony forming units (CFU) added over the three events: SM = 8.1×10^6 ; WS = 6.6×10^6). If a microcosm had been disturbed, invasion would occur post-disturbance. This resulted in 6 replicates for each disturbance by resource abundance combination per invader morphotype.

Experiments finished on day 16, when all microcosms were homogenised and a 900 μ L sample was frozen in 25% glycerol at -80°C. After plating on KB agar containing 100 μ g/L of X-gal, wildtype and invader SM, WS and fuzzy spreader (FS; a rarer bottom-dwelling morph (Rainey & Travisano 1998)) colonies were counted.

Statistical Analyses

All counts were first standardised to colony-forming-units (cfu) per mL. Invasion success (relative invader fitness) was calculated as proportional change, v , of the proportion of invader to resident, calculated as: $v = x_2 \cdot (1 - x_1) / x_1 \cdot (1 - x_2)$, where x_1 is the initial invader proportion and x_2 the final (Ross-Gillespie *et al.* 2007). Initial invader proportion (x_1) was calculated as the average frequency of the introduced invader:

$$x_1 = E \left[\frac{I_t}{I_t + R_t} \right] = \frac{1}{3} \sum_{t=\{4, 8, 12\}} \frac{I_t}{I_t + R_t} (1)$$

where I_t is the density of the invader introduced on day t and R_t is the density of the residents getting invaded on day t . We could not measure resident density on days 8 and 12, because it would require destructive sampling of undisturbed treatments. We therefore used the resident density on day 4 and assumed that R_4 , R_8 and R_{12} were equal for 1-, 2-, and 4-days disturbance treatments.

We sampled R_4 for 1-, 2-, and 4-days disturbance treatments during their transfers, but we could not sample R_4 for 8- and 16-days disturbance treatments as it is a destructive process. The disturbance history up to day 4 for 8- and 16-days treatments is identical to that for 4-days treatment. We therefore assumed the resident community dynamics are the same for these three treatments, and used R_4 for 4-days treatment (before the disturbance) to calculate R_4 for 8- and 16-days treatments:

$$R_{4, 8\text{-days}} = R_{4, 16\text{-days}} = \frac{R_{4, 4\text{-days}}}{\text{Disturbance mortality rate}} = \frac{R_{4, 4\text{-days}}}{0.01} (2)$$

where $R_{i,j}$ is the density of the resident on day i under j -days disturbance treatment. Based on this calculation, we further assumed that $R_{8, 16\text{-days}} = R_{12, 16\text{-days}} = R_{4, 16\text{-days}}$ for 16-days disturbance treatment, where $R_{8, 16\text{-days}} = R$ on day 8 in the 16-day disturbance treatment and so forth. For 8-days disturbance treatment, we assumed $R_{12, 8\text{-days}} = R_{4, 8\text{-days}}$ and $R_{8, 8\text{-days}} = 0.01 R_{4, 8\text{-days}}$ to account for the disturbance event on day 8.

In order to eliminate zero inflation, one was added to the final invader density v (post volume standardisation) and was transformed to $\log(v + 1)$ to normalise the residuals. A value greater than 0.69 ($\log(1+1)$) would

indicate that the invader increased in proportion throughout the experiment, whereas a value below this would suggest that invasion was unsuccessful.

To analyse the effect of disturbance and resource abundance on invasion success, v , a linear model was used to test effects of disturbance, resource abundance, and invader morphotype, with all two-way and three-way interactions. As the different morphotypes have distinct growth strategies, we expected their invasion success to be markedly different. Given a significant three-way interaction in the most complex model, we did all further analysis on each invader morphotype (SM & WS) separately.

For each invader morph, separate linear models were used to investigate treatment (disturbance frequency and resource abundance) effects on invasion success, evolved biodiversity (calculated using Simpson's index (Simpson 1949)) and total resident density ($\log_{10}(\text{cfu}+1 \text{ mL}^{-1})$). Disturbance frequency was treated as a continuous predictor, whereas resource abundance was treated as categorical due to only having three levels. Model selection was done using likelihood ratio tests.

We then tested whether treatments indirectly affected invasion success through changes in resident populations. To do this we first used a model with resident biodiversity and total resident density, plus their interaction, as predictors of invasion success. We then included treatment (disturbance, resource abundance, and their interaction), alongside resident population effects as predictors of success. The models with both treatment and resident population effects were initially tested using an ANOVA with type III sums of squares, then with type II if no significant interactions were found to account for differences in the ordering of predictors on significance testing.

Post-hoc model comparisons were used to look at significant differences between levels of resource abundances and disturbance. For pairwise comparisons of single treatments (e.g. between high, medium and low resource abundances), model estimates were averaged over other predictors in the model. Where multiple pairwise comparisons were used, p values were adjusted using Bonferroni adjustments. When comparing slopes to 0, confidence intervals overlapping zero indicated no significant effect. All statistical analyses were carried out in R version 4.0.3 (R Core Team).

Results

Invasion success (invader proportional change) differed between invader types

Invader success was significantly affected by a 3-way interaction between disturbance frequency, resource abundance and invader morphotype ($F_{2,163}=10.2$, $p<0.001$; Fig. 2). We therefore analysed treatment effects on each invading morphotype separately. The fast-growing smooth (SM) invaders were significantly affected by an interaction between disturbance frequency and resource abundance ($F_{2,85}=9.7$, $p<0.001$, Fig. 2). Greater disturbance increased invasion success when resources were abundant (slope = 0.12, 95% CI [0.2, 0.050]), but decreased success when they were of low abundance (slope = -0.089, 95% CI [-0.020, -0.16]). Disturbance had no significant effect under medium resource abundance (slope = -0.048, 95% CI [0.021, -0.12]). This meant the highest levels of SM invasion occurred when both disturbance frequency and resource abundance was high.

Wrinkly spreader (WS) success was also affected by an interaction between disturbance frequency and resource abundance ($F_{2,78}=3.31$, $p=0.042$; Fig. 2). Here we found disturbance to be negative for WS success when resources were high (slope = -0.24, 95% CI [-0.11, -0.37]), but to have no effect when they were at medium or low abundance (medium: slope = -0.033, 95% CI [0.069, -0.14]; low: slope = -0.076, 95% CI [0.026, -0.18]).

Resident biodiversity was affected unimodally by disturbance, whereas density linearly

Resident biodiversity (Simpson's index) showed the same unimodal pattern across disturbance frequencies irrespective of invader type (SM invader: $F_{1,86}=10.3$, $p=0.002$, WS: $F_{1,79}=7.87$, $p=0.006$) with the least diverse communities at both high and low disturbance (Fig. 3). Resource abundance also altered resident biodiversity (SM invader: $F_{2,86}=3.84$, $p=0.025$, WS: $F_{2,79}=33.1$, $p<0.001$), with diversity being significantly

lower in the low resource treatment than the medium when invaded by SM ($p=0.025$) and lower than both the medium and high resource treatments when invaded by WS ($p<0.001$ for both).

Like biodiversity, resident density showed the same patterns irrespective of invader type (Fig. 4), with an interaction between disturbance frequency and resource abundance significantly affecting density (SM invader: $F_{2,85}=49.4$, $p<0.001$, WS: $F_{1,79}=47.0$, $p<0.001$; Fig. 4). Resident density increased with disturbance under high resources, but disturbance negatively impacted density at low and medium resources (Fig. 4).

Resident population changes did not alter success above the direct effects of treatments

To test if these changes to the resident populations impacted invasion success, we first analysed a model with resident biodiversity and total resident density, plus their interaction, as sole predictors of invasion success. Once again this was done separately for each invader morph. SM invaders were significantly affected by resident density ($F_{1,88}=5.03$, $p=0.028$), but not by biodiversity ($F_{1,88}=2.64$, $p=0.11$) or an interaction between density and diversity ($F_{1,87}=3.06$, $p=0.084$). Conversely, the WS invader was only significantly affected by biodiversity ($F_{1,81}=7.07$, $p=0.010$), with density having no significant effect either as a main effect ($F_{1,81}=0.67$, $p=0.42$) or as through an interaction with biodiversity ($F_{1,80}=1.25$, $p=0.27$). This demonstrates treatments may have indirectly affected the success of both invaders by manipulating resident populations. We therefore tested whether the direct effect of treatments on success remained when these manipulations were considered. SM invaders were still significantly affected by the interaction between disturbance and resources ($F_{2,82}=9.27$, $p<0.001$). However, we find the effect of both biodiversity and total resident density to not be significant (biodiversity: $F_{1,82}=2.49$, $p=0.12$; Fig. 5A; density: $F_{1,82}=0.24$, $p=0.63$; Fig. 5B). When testing resident population effects alongside treatments on the success of the WS invader, we no longer found any significant interactions. Disturbance and resource abundance both significantly affected WS success ($F_{1,75}=8.27$, $p=0.005$ and $F_{2,75}=27.8$, $p<0.001$, respectively). However, resident population effects did not have a significant effect (biodiversity: $F_{1,75}=2.88$, $p=0.094$, total resident density: $F_{1,75}=0.006$, $p=0.94$). We therefore show that, although treatments had a significant effect on resident populations, this did not have an effect on success above the direct effects of disturbance and resource abundance.

Discussion

Here, we used a microbial system to experimentally test how disturbance frequency and resource abundance interact to affect the success of two ecologically different invaders. Both invaders were affected by an interaction between disturbance and resources, however this acted differently on each type of invader. The success of the fast-growing smooth (SM) invader increased with increasing disturbance frequency when resources were abundant, but decreased when resources were low. Conversely, the slower growing wrinkly spreader (WS) suffered decreasing success with increasing disturbance frequency under high resource abundance, but was not affected by disturbance in medium or low resource conditions.

Disturbances are commonly linked with invasion success (Shumway & Bertness 1994; Roxburgh *et al.* 2004; Altman & Whitlatch 2007; Lear *et al.* 2020), and the positive relationship between disturbance frequency and SM invasion success in the resource rich treatment supports this view. Disturbances open up resources for the fast growing invaders and reduce biotic resistance (Hodgson *et al.* 2002; Fargione *et al.* 2003; Fukami 2015; Lear *et al.* 2020). Moreover, high resource availability allows rapid population growth between disturbances, reducing the chance of small invader populations being stochastically removed by disturbance. That SM invaders had reduced fitness at low disturbance frequency-high resource abundance was likely a consequence of escalating broth toxicity and oxygen depletion. Moreover, surviving residents may have reduced invader access to resources through priority and dominance effects (Hodgson *et al.* 2002; Zee & Fukami 2018). These factors (broth toxicity, oxygen depletion and resident effects) will likely be weaker when resources are less abundant as growth will be slower, potentially explaining why success was higher at low disturbance when resource abundance was less. The inability of disturbances to facilitate invasion under lower resources can be explained by disturbances not providing sufficient additional resources to benefit the invader (14). At the lowest resource levels, the inhibitory effect of disturbance on invasion is presumably because invader populations could not grow fast enough between disturbances to recover. These results

may offer an explanation as to why disturbance may not always facilitate invasion by fast-growing coloniser species.

It is likely that low disturbance-high resource facilitated WS invasion because of its ecological niche: WS forms a mat at the air-broth interface that provides access to both nutrients and oxygen. Mat formation requires a threshold density to be reached, and low disturbance and high resource abundance will make this more likely (Buckling *et al.* 2000; Brockhurst *et al.* 2006; Hallet *et al.* 2012). At higher disturbances and lower resources, the slower growth rate of WS relative to SM (Haddad *et al.* 2008) also likely increases the importance of stochastic removal of WS invaders, which would have happened less under high resources due to faster growth rates. We therefore demonstrate high resource abundance can reduce the negative effects of disturbance on slower-growing species. That the WS invader had much greater success than the faster growing SM under high resources-low disturbance shows the classical view that invaders are fast growing coloniser species (van Kleunen *et al.* 2010; Mächler & Altermatt 2012) depends strongly on the new disturbance regime. This suggests the balance between disturbance-induced mortality and growth rate is an important factor deciding invader success, with resource abundance dictating growth rate and disturbance affecting mortality.

As well as invader success, treatments affected resident populations, with disturbance and resources affecting resident biodiversity and total density. That diversity peaked at medium disturbance frequency in our treatments is in line with previous work in this system and supports the Intermediate Disturbance Hypothesis (Connell 1978; Wilkinson 1999; Buckling *et al.* 2000; Cardinale *et al.* 2006; Benmayoret *et al.* 2008; Violle *et al.* 2010). This proposes that diversity is lost at high disturbance due to species being unable to recover between events, lost at low through competitive exclusion and highest when disturbance facilitates a balance between tolerant and competitive species (Huston 1979). In our system we found this pattern to remain the same across resource treatments, but diversity to be lower under the lowest resource abundance. This pattern is consistent with previous findings in this system (Kassen *et al.* 2004). Our prior work (Miller *et al.* 2011; Hall *et al.* 2012) also shows that this result depends on the other disturbance aspects, such as disturbance intensity. Resident density decreasing with increasing disturbance in low and medium (but not high) resource abundances is most likely explained by resource-limited growth causing slow population recovery between disturbances. Changes to resident populations were, however, found to have little indirect effect on invasion resistance, with their explanatory power non-significant when direct treatment effects were included in the model. This does not rule out a role for resident species, but shows that they were relatively unimportant compared with the direct effects of treatments. Further, we show factors that cause differences in biodiversity (for example disturbance frequency and resource abundance) need to be controlled for when studying the effect of diversity on invasion resistance, as the direct effect of these may be causing the differences in success rather than biodiversity *per se* (as is the case of the SM invader here).

In conclusion, we find disturbance frequency and resource abundance to both affect the success of two different invaders. Further, we find both invaders to be differently affected by an interaction between these factors: the fast growing SM success is positively associated with disturbance frequency when resources are readily available, but negatively when they are limited whereas the slower-growing WS is only affected by disturbance when resource abundance is high. As this interaction between disturbance and resources acts on two ecologically fundamental processes – growth and mortality – we suggest it is applicable to species outside of this microbial system. Additionally, and contrary to classical theory stating invaders are generally fast growing species, the slower growing WS invader had very high success when disturbance was infrequent and resource abundance high. We therefore demonstrate that when studying invasion ecology multiple factors need to be considered to create an accurate predictive theory of invasibility, with the same disturbance frequency having both positive and negative effects depending on resource abundance and invader life-history. Finally, we show that, by understanding these interactions, it may be possible through ecological manipulations of resource abundance to reduce the effect that disturbances have on invasion resistance.

Data accessibility

The full dataset used is accessible from the Zenodo Digital Repository: 10.5281/zenodo.5057319

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Figures

Fig. 1

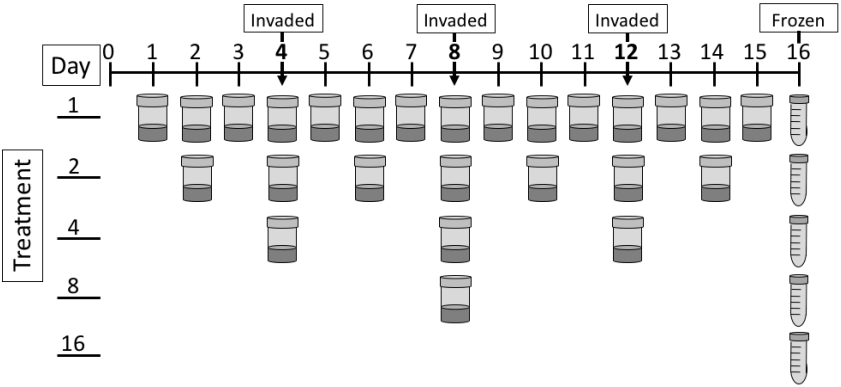


Fig. 2

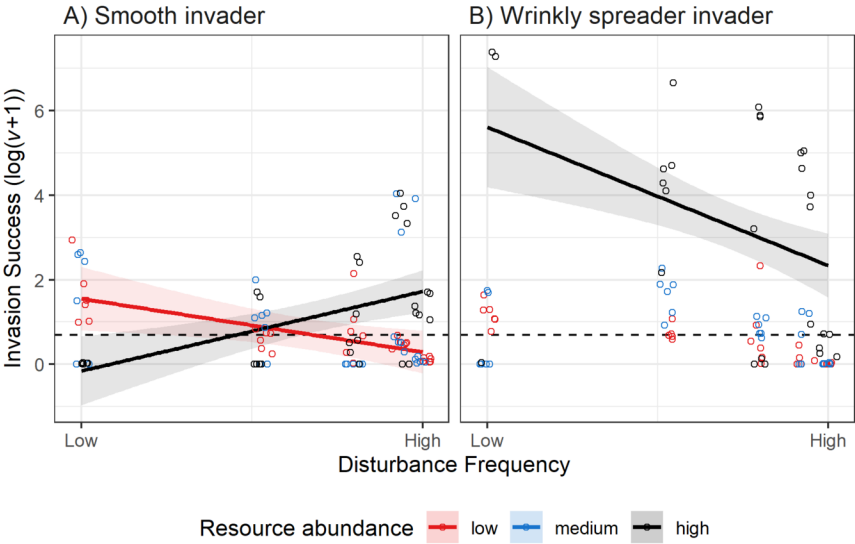


Fig. 3

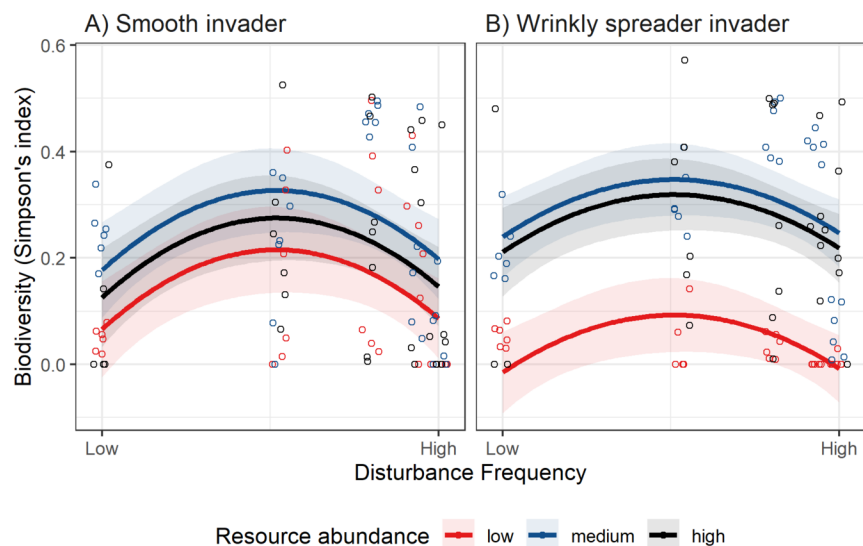


Fig. 4

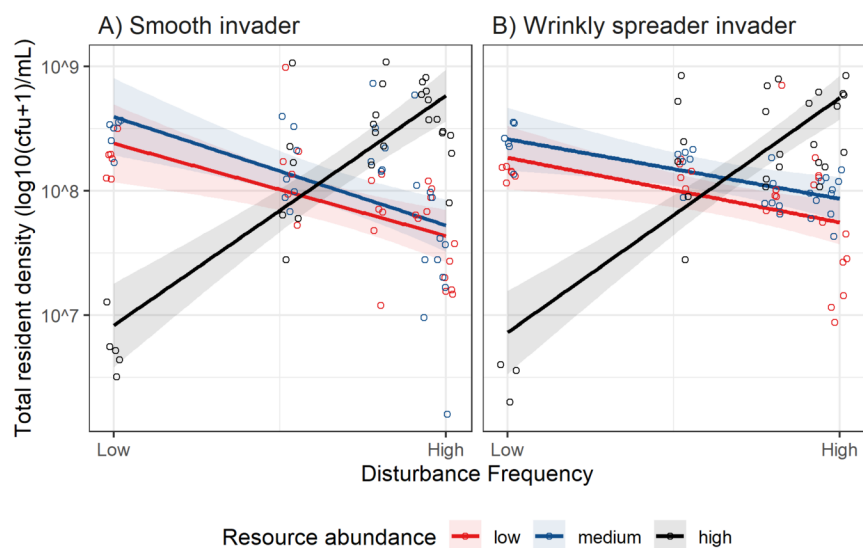


Figure legends

Figure 1 Schematic of the experimental design. Microcosms of either 100%, 10% or 1% resource concentration were disturbed every 1, 2, 4, 8 or 16 days (denoted by an icon of a microcosm) to test for the effects of both disturbance frequency and resource abundance on invader success. Disturbances involved 1% transfer of homogenised broth into fresh media. All microcosms were invaded every four days (immediately post-disturbance) with either a smooth (SM) or wrinkly spreader (WS) invader. Six replicates per treatment were used.

Figure 2 Invasion success, $\log(v + 1)$, of (A) the smooth (SM) invader and (B) the wrinkly Spreader (WS), in response to different disturbance frequencies and resource abundances (low resources = red circles and

lines, medium = blue, high = black). v is the proportional change in invader density compared to the residents; the dashed line shows the value of equal population growth rate between residents and invaders, where invaders would have the same proportion in the community at the beginning and the end of the experiment. Jittered points represent individual replicates. Lines show the best model fits and shaded areas show the 95% confidence interval.

Figure 3 Evolved resident *P. fluorescens* biodiversity (Simpson’s index) in treatments of different disturbance frequencies (increasing from left to right within panels) and resource abundances (low resources = red circles and lines, medium = blue, high = black) when invaded by (A) a smooth (SM) invader and (B) a wrinkly spreader (WS). Diversity was significantly lower in the low resource treatment for both invaders. Resource abundance and invader type affected diversity through an interaction. Jittered points represent individual replicates. Lines show the best model fits and shaded areas show the 95% confidence interval.

Figure 4 Final resident density ($\log_{10}(\text{cfu}+1)/\text{mL}$) after sixteen days in treatments of different resource abundances (low resources = red circles and lines, medium = blue, high = black and disturbance frequencies). Panel A shows treatments invaded with a smooth (SM) morphotype, panel B by a wrinkly spreader (WS). Jittered points represent individual replicates. Lines show the best model fits and shaded areas show the 95% confidence interval.