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Biotic resistance shapes the influence of propagule pressure on invasion success in bacterial communities

Matt L. Jones,[1] Josep Ramoneda, Damian W. Rivett, and Thomas Bell

Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, United Kingdom

Abstract. The number of invaders and the timing of invasion are recognized as key determinants of successful invasions. Despite the recognized importance of "propagule pressure," invasion ecology has largely focused on how characteristics of the native community confer invasion resistance. We simultaneously manipulated community composition and invader propagule pressure in microcosm communities of freshwater bacteria. We show that high propagule pressures can be necessary to establish an invader population, but that the influence of propagule pressure depends on the composition of the resident species. In particular, the number of individuals invading was most important to invasion success when one of the species in a resident community is a strong competitor against other species. By contrast, the timing of invasion was most important when communities had lower growth rates. The results suggest that the importance of propagule pressure varies both between communities and within the same community over time, and therefore have implications for the way we understand the relationship between biotic resistance and invasion success.

Key words: bacteria; biotic resistance; community assembly; invasion; priority effect; propagule pressure; timing.

Introduction

Invasive species have evolved a great variety of specialized ways to outcompete resident species, and there has therefore been much work to characterize the traits of successful invasive species (Davis 2006, van Kleunen et al. 2010). However, invasive species can also be successful irrespective of their traits, simply through the introduction of sufficient numbers of individuals or through repeated introductions (Johnston et al. 2009, Simberloff 2009). "Propagule pressure" in invasion ecology is a measure of the magnitude and pattern of the arrival of invasive individuals (e.g., adults, seeds, spores) (Simberloff 2009). While the traits of an invader are undoubtedly important, recent work has shown that the success of an invader can in some instances depend simply on the propagule pressure of the invasive species.

If it is assumed that a species has the traits that are sufficient for maintaining a population in a new environment, propagule pressure can be important because invasive species that arrive at a high initial abundance are less susceptible to local extinction due to demographic or environmental stochasticity. Similarly, invasive species that arrive frequently, or which time their invasion fortuitously, can increase their likelihood of avoiding environmental perturbations that lead to the local extinction of the newly colonized invasive population. Overall, a large number of individuals introduced at several different points in time will give the highest chance of invasion success (Von Holle and Simberloff 2005, Britton and Gozlan 2013, Yamamichi et al. 2014). For example, some purposeful invasions are unsuccessful for prolonged periods but eventually become successful because of the repeated introduction of large numbers of individuals, as exemplified by the introduction of rabbits to New Zealand (Simberloff 2009). The propagule pressure theory of invasion ecology implies that, while understanding the niche of invasive species is important, there is often a narrow window for successful invasions, resulting in an important role for propagule pressure. In a seminal meta-analysis of 1,000 plant, fish, bird, mammal, invertebrate, and microbial invasions, Colautti et al. (2006) found that the number of individuals introduced was a significant predictor of invasion success in over 85% of documented invasion events, suggesting that propagule pressure could play a pivotal role in understanding the ecology of invasions.

Despite this, much of invasion ecology remains relatively detached from the concept of propagule pressure and focused on niche- or trait-based hypotheses about

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[1] E-mail: mlj13@ic.ac.uk

invasion and the ways in which native species compete with invasive species to limit invasion success (Von Holle and Simberloff 2005). This disproportionate emphasis on "biotic resistance" is also evident in the emerging field of microbial invasion ecology, where most research is focused on the ways in which the richness and diversity of species in the resident community enhances its resistance to invasions (Jousset et al. 2011, Li and Stevens 2012, Liu et al. 2012, van Elsas et al. 2012, De Roy et al. 2013, Eisenhauer et al. 2013, van Nevel et al. 2013, Vivant et al. 2013, Mallon et al. 2015*a,b*, Wei et al. 2015). Some studies have shown that, as long as communities are invasible, increasing invader propagule pressure will increase their establishment (Von Holle and Simberloff 2005, Leung and Mandrak 2007, Houseman et al. 2014). However, these studies are still few and it remains unclear how propagule pressure and biotic resistance interact.

Here we explore the combined role of the number of individuals invading, invasion timing and resident species on invasion success in experimental microbial communities. Studies of propagule pressure in microbial invasions are limited, but two studies have previously suggested that increasing the number of invader cells will increase invasion success regardless of the composition of the resident community (De Roy et al. 2013, Acosta et al. 2015). Our objective was to determine whether propagule pressure can significantly affect invasion success, and how and why this varies between different communities.

Materials and Methods

Resident communities

We conducted a series of experimental invasions into microcosms containing three-species communities. We manipulated resident species composition by constructing communities containing all three-species combinations drawn from a pool of five environmental bacterial isolates, totaling 10 communities (Appendix S1: Table S1). These species were isolated from water and sediment taken from water-filled beech tree holes and identified using 16S rRNA gene sequencing as described previously (Rivett et al. 2016). Isolates were selected to ensure a diverse mixture of species common in these environments, and thus included species of the genera *Bacillus* (GenBank Accession Number KT248522), *Epilithonimonas* (KT248533), *Flavobacterium* (KT248528), *Pseudomonas* (KT248518), and *Staphylococcus* (KT248530). These genera were abundant and frequently coexisted within tree hole communities, and were frequently isolated from the same tree hole (unpublished culture collection).

Before inoculation, isolates were grown in Luria Bertani (LB) broth for 24 h at 22°C and adjusted in sterile saline solution (0.5% w/v NaCl in water; Sigma-Aldrich, Gillingham, UK) to an optical density at a wavelength of 600 nm (OD_{600}) of 0.1 (100 μL in 96-well clear flat bottom plate, VWR International, Radnor, Pennsylvania, USA) using a spectrophotometer (Synergy II; Biotek, Swindon, UK). Cells were then pelleted by centrifugation (2,375 g for 5 min) and resuspended in sterile saline solution. Resident communities were created by combining equal volumes of each species suspension and adding 600 μL of these mixtures to 1,200 μL of growth medium in replicate microcosms in 2.2 mL deep well plates (STARlab, Milton Keynes, UK). The growth (OD_{600}) of communities prior to invasion was recorded for the first 52 h and at 96 h (Synergy II with BioStack Microplate Stacker; Biotek, Swindon, UK) (Appendix S1: Fig. S1). Microcosms were incubated at 22°C in the dark for the duration of the experiment.

Growth medium

The growth medium was composed of six mono- and disaccharide carbon sources commonly found in soil and leaf litter: glucose, fructose, galactose, sucrose, cellobiose, and xylose (Sigma-Aldrich). Each of the sugars was diluted and combined into a 1X M9 Minimal Salts (Sigma-Aldrich) solution at a concentration of w/v 0.1%, giving a total concentration of 0.6% carbon source. Each of the resident species and the invader strain was assayed for growth on this medium prior to the experiment (Appendix S1: Fig. S2).

Invasions

Communities were invaded with a chromosomally tagged, constitutively expressed, luminescent strain of *Pseudomonas putida* KT2440 (hereafter "invader"). This strain was chosen as a model invader because it possesses metabolic, physiological, and stress-endurance traits that enable it to thrive in many environments, and therefore acts as a useful model invasive species (Nikel et al. 2014). Before each invasion, the invader was grown in LB broth and resuspended in saline following the same procedure as for the community isolates. Three invader inocula of large, medium and small numbers of invaders were produced by diluting the original culture in sterile saline to 100 times the desired cell concentration for each treatment. Each of the inocula was then aliquoted into the microcosms at 1% v/v of the total volume (1.8 mL) of the community. The numbers of invaders applied were as follows: large (10^5 cells/1,800 μL resident community), medium (10^4 cells/1,800 μL resident community), and small (10^3 cells/1,800 μL resident community). For comparison, the starting OD of 0.1 of each of the resident species in the community is equivalent to approximately 10^8 cells/mL and so invaders entered at cell numbers at least three orders of magnitude smaller than the communities. The timing of introduction was manipulated by invading communities at 4, 6, or 8 d after community inoculation. All treatment combinations were replicated eight times, making up a total of 720 microcosms. Sterile controls were included in every plate as well as positive controls in which the invader was grown in monoculture in order to compare their growth alone to that within the communities.

Invasion success

Luminescence of lux-tagged bacterial strains is directly related to the density of metabolically active cells (Close et al. 2012). Therefore, luminescence values of each microcosm were used to calculate the number of metabolically active invader cells produced from the original invader inoculum. We calibrated the luminescence values by performing growth assays of the invader in the six-carbon medium prior to the experiment, measuring luminescence and plating cultures onto LB agar to obtain cell numbers. There was a strong relationship between $\log_e$ luminescence and $\log_e$ plate counts ($R^2 = 0.97$), so we used the calibration curve to convert luminescence values into invader cell densities (Appendix S1: Fig. S3).

Microcosms were sampled by transferring 100 μL from the deep-well plates into 96-well opaque flat bottom half-area white plates (Greiner Bio-One, Gloucestershire, UK). Luminescence was measured every 3 h for 45 h after the final invasion in each treatment using a spectrophotometer fitted with an automated plate handler (Appendix S1: Fig. S4, Synergy 2 Multi-Mode Reader & BioStack Microplate Stacker; BioTek, Swindon, UK). This time was sufficient to allow the invader to reach the stationary phase in monoculture. The initial density of metabolically active invader cells in each microcosm at 0 h was then subtracted from the maximum density reached in the 45 h period. Invasion success was thus defined as the maximum change in the density of metabolically active invader cells/mL in the resident communities.

Resource-use assays

In order to provide a potential explanation for the patterns of invasion success observed across our communities, we estimated the resource use patterns of the invader and each of the resident species. According to previous studies, invaders that use different resources to those used by resident species should be more successful (Eisenhauer et al. 2013, Mallon et al. 2015*b*). Data were collected on each species' (including the invader) usage of each of the six carbon sources in the experimental medium. Prior to the experiment, each isolate was grown in Luria Bertani (LB) broth for 24 h at 22°C, before being diluted to 10^4 cells/mL in sterile saline solution and 20 μL inoculated in 180 μL of a each of the sugars in 1× M9 Minimal Salts (Sigma-Aldrich) solution at a concentration of w/v 0.1%. Growth (OD_{600}) after 45 h was used to approximate each strain's usage of each substrate (Appendix S1: Fig. S5). We used this information to understand how the preferred resources of all the resident species overlapped with those of the invader.

Statistical analysis

All statistical analyses were conducted in R (R Core Team 2016). The effect of community composition on invasion success in our system could be explained by the presence of *Pseudomonas* sp. in the communities. Our final linear model therefore included the $\log_{10}$ number of individuals invading, timing of introduction and the presence/absence of the *Pseudomonas* sp. as interaction terms affecting invasion success ($\log_{10}$ maximum density change in *P. putida* invader, cells/mL). We used the linear model coefficients to describe how each treatment impacted invasion success, and report means with standard errors. Normality of the data and error homogeneity were checked visually. Resource-use data were qualitatively used to provide an ecological explanation for modelling results.

Results

In this study, the presence of a resident *Pseudomonas* sp. strain, invasion timing and the interaction between the presence of a resident *Pseudomonas* sp. and the number of individuals introduced had significant effects on invasion success (maximum change in the density of metabolically active invader cells/mL) (Table 1).

The largest effects were related to the presence of the *Pseudomonas* sp. in a community. *Pseudomonas* sp. presence dramatically reduced the success of the invader

Table 1. Influence of timing and propagule size in presence and absence of resident *Pseudomonas* sp.

Factor	Linear model coefficient	df	*P*
Intercept	5.72	7,712	$<2.2^{-16}$ *
Number of individuals introduced	−0.15	7,712	0.17
Timing of introduction	−0.63	7,712	1^{-15} *
Pseudomonas sp. presence	−6.08	7,712	$<2.2^{-16}$ *
Number of individuals introduced × timing of introduction	0.07	7,712	3.7^{-5} *
Number of individuals introduced × *Pseudomonas* sp. presence	0.56	7,712	2.1^{-4} *
Timing of introduction × *Pseudomonas* sp. presence	0.70	7,712	3^{-12} *
Number of individuals introduced × timing of introduction × *Pseudomonas* sp. presence	−0.11	7,712	1.5^{-6}*

Notes: Effects of number of individuals introduced, timing of introduction, and *Pseudomonas* sp. presence in the resident communities on the $\log_{10}$ maximum density change (cells/mL) attained by the model invader *P. putida* 45 h after inoculation. The magnitude of the linear model coefficient indicates its importance in impacting invasion resistance, while the sign of the coefficient indicates whether it helped (positive) or hindered (negative) the ability of the invader to grow. Significant terms and interactions ($P < 0.05$) are denoted with asterisks.

compared to communities in which there was no *Pseudomonas* sp. (Table 1); the mean maximum change in the invader density in these communities was over two orders of magnitude lower (6.04 ± 0.26 cells/mL) than that in communities without the *Pseudomonas* sp. (4,763.81 ± 333.22 cells/mL). We tested whether species composition had an effect on invasion resistance while controlling for the presence of *Pseudomonas* sp. There was no difference in invasion success among communities that did not contain *Pseudomonas* sp. ($F_{3,272} = 2.13$, $P = 0.09$), while in communities that did contain this strain there were some significant differences ($F_{5,408} = 3.33$, $P = 0.005$). However, post-hoc Tukey tests indicated this overall significant effect was due to 1 significant pairwise difference ($P = 0.006$) of a total of 15 pairwise comparisons between communities. The remaining 14 pairwise tests were non-significant. Furthermore, linear model interactions between community identity, the timing of introduction and the number of individuals invading could be simplified to the interaction between *Pseudomonas* sp. presence, the timing of introduction and the number of individuals invading.

The timing of introduction had a moderate effect on invasion success (linear model coefficient −0.63, $P < 0.05$). Overall, the earlier the timing of introduction the more successful invasion was, with invaders achieving higher increases in density when invaded at 4 d since community establishment (4,579 ± 408.82 cells/mL) compared to invasions at 6 (769 ± 110.69 cells/mL) and 8 d (378.76 ± 61.27 cells/mL; Fig. 1). This negative effect of the timing of introduction on invasion success was weaker in communities containing the *Pseudomonas* sp. (coefficient = 0.70, $P < 0.05$).

The number of individuals introduced had no overall effect on invasion success (coefficient = −0.15, $P = 0.17$), but rather its effect depended upon the composition of the resident communities (Table 1). In particular, increasing the number of individuals introduced had a significantly more positive effect on invasion success in communities containing the *Pseudomonas* sp. (Fig. 1, coefficient = 0.56, $P < 0.01$). In addition, the effect of the number of individuals introduced decreased slightly more strongly with time in communities containing the *Pseudomonas* sp., having no effect upon invasion success at 8 d (Fig. 1).

Community-invader resource-use dissimilarity patterns qualitatively confirmed that communities with the resident *Pseudomonas* sp. were more similar to the *Pseudomonas putida* invader in their resource use than other communities. The resident *Pseudomonas* sp. had a similar pattern of resource use to the invader, characterized especially by high growth yields on galactose, glucose, and xylose (Appendix S1: Fig. S5).

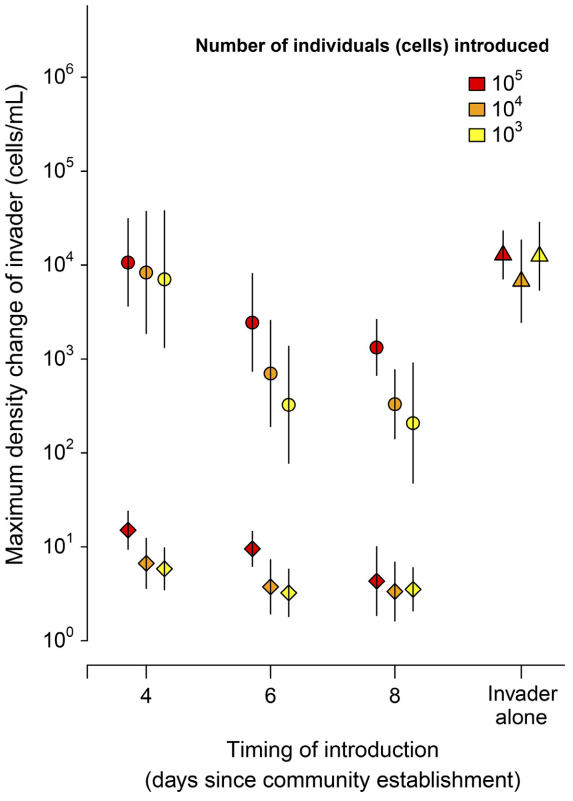

FIG. 1. Impact of the number of individuals introduced and timing of introduction on mean invasion success (maximum density change in *P. putida* invader, $\log_{10}$ scale) in communities with (diamonds) and without (circles) a native *Pseudomonas* sp. Number of individuals introduced treatments represent the number of *P. putida* invader cells entering 1.8-mL microcosms containing approximately 10^8 live resident community cells. Effects of large (10^5 invader cells, in red), medium (10^4 cells, in orange) and small (10^3 cells, in yellow) numbers of individuals introduced are shown. Timing of introduction is represented as days since the resident community was established. A positive control (triangles) containing the invader in monoculture is shown. Error bars represent standard deviation of the mean.

DISCUSSION

Our results show that the effect of propagule pressure on invasion success strongly depends on the resident community being invaded. The main determinant of *Pseudomonas putida* invasion success in our system was the presence of a congeneric strain in the resident communities. We interpret this result as a strong selection effect, whereby the presence of one species with a disproportionate influence on functioning (here invasion resistance) drives functional differences between communities. Such effects are particularly likely to occur where a small species pool is used to assemble experimental communities. Selection effects are regarded as major drivers of biodiversity–functioning relationships in plant (Forgone et al. 2003, De Schryver and Vadstein 2014, Handa et al. 2014, Jing et al. 2015) and animal (Duffy et al. 2007, Carey and Wahl 2011, Aguirre and Marshall 2012) communities, and have been identified as important in shaping invasion resistance in microbial and non-microbial communities alike (Hector et al. 2001, Hodgson et al.

2002, Avolio et al. 2015). These studies have indicated that selection effects often arise because communities become dominated by the species that achieves the highest biomass when grown alone, though it has been pointed out that this is not always necessarily the case (Loreau and Hector 2001, Jiang et al. 2008). In our experiment, the resident *Pseudomonas* sp. achieved the lowest biomass (OD_{600}) in monoculture, but when resident species were mixed, communities containing the *Pseudomonas* sp. retained similar levels of growth to the *Pseudomonas* sp. monocultures, while those without it experienced lower levels of growth than any of their constituent species in monoculture (Appendix S1: Figs. S1, S2). This suggests a trade-off in our system between species growth in mixture vs. monoculture. *Pseudomonas* has previously been characterized as a particularly stress-tolerant genus, that modifies its resource metabolism in the presence of other species (Nikel et al. 2014). Such traits could explain why *Pseudomonas* sp. was apparently able be relatively unaffected by competitors by avoiding resource competition and tolerating the toxic by-products of its own and other species' metabolism. Alongside using similar resources to the invader (Appendix S1: Fig. S5), communities containing *Pseudomonas* sp. presented the strongest biotic resistance to the invading *Pseudomonas putida*.

Our results show how biotic resistance can have important implications for the way propagule pressure affects invasion success. Communities containing the resident *Pseudomonas* sp. were more strongly affected by the number of individuals introduced than those lacking it (Fig. 1). This appears to be because resident *Pseudomonas* sp. growth causes resource limitation, so high propagule pressure was required for even low numbers of the *P. putida* invader to establish. This effect was diminished over time, presumably as resource depletion continued resulting in a corresponding decline in the establishment of the invader. Conversely, communities lacking *Pseudomonas* sp. were more strongly affected by the timing of introduction. This appears to be because the *P. putida* invader possessed similar stress and community tolerance traits to the resident *Pseudomonas* sp., enabling it to easily dominate in the absence of another *Pseudomonas* strain regardless of the original number of individuals invading. Invasion success decreased more steeply with time due to a gradual build-up of biotic resistance as the resident community grew and used up more of the available resources. As invasion became more difficult over time in this way, there also appeared to be a gradual increase in the influence on invasion success of the number of individuals introduced (Fig. 1).

Our results agree with computer simulations suggesting that priority effects emerging from resident species interactions determine the threshold for invasion, thus shaping the relative effects of timing and the number of individuals introduced on invasion success (Case 1990, Yamamichi et al. 2014). The presence of a congeneric species with similar stress-tolerance traits to the invader was the single most important determinant of invasion success in our system because it was apparently the only species able to tolerate strong negative interactions with other species. Consequently, its rapid growth in the communities relative to other species meant a strong priority effect was achieved by the time the earliest invasion took place. Similarly critical roles for resident species that are congeneric to the invader have also been demonstrated in plant and animal systems, being implicated for example in limiting the invasion success of the quagga mussel in the Black Sea basin (Orlova et al. 2005).

The second most important factor in our system, the timing of introduction, also demonstrated the importance of priority effects emerging from species interactions. Although timing mattered little in the presence of the rapidly growing congeneric species, communities not containing the congeneric species were limited in their growth rate by interspecific competition, and were thus unable to develop a strong priority effect. Invasion success thus decreased with later timings of introduction due to the temporal build up of biotic resistance. The Broadbalk experiment, a long-term (>150 yr) experiment tracking plant communities in agro-ecosystems, similarly demonstrated that invasions are most successful when their timing is synchronized with periods of reduced resident community growth (Crawley 1989). In this case, the invasion success of two of the most important weeds in the wheat field system was not correlated with their contrasting seed bank sizes but instead resulted from one species, black grass, being naturally introduced into the system during a fallow period in which resident crop growth was limited by the wheat bulb fly *Leptohylemyia coarctata* (Crawley 1989).

We found that the number of individuals introduced had the weakest effect on invasion success of all of the treatments in our experiment. Nonetheless, a high number of introduced individuals overcame the strong priority effects noted above, enabling a small population of invader to become established, which can be crucial to invasion success in more natural systems. The result is comparable to experimental studies of propagule pressure in tropical woody plant communities, which found that the number of individuals introduced was the single most important determinant of invasion success and had the biggest effect when invading high-diversity polycultures (Brooks and Jordan 2013).

There remains a limited mechanistic understanding of the interaction between biotic resistance and propagule pressure, but our results are encouraging in that they suggest their may be some general mechanisms linking these two major hypotheses in invasion ecology. For example, our results suggest that communities that have been established for a very short or very long time will be unaffected by the number of individuals introduced, because of the extreme ease or difficulty of invasion at these times, respectively (Fig. 1). The complexities of natural communities are likely to complicate this relationship. However, propagule pressure is still likely to be

key to invasion success since most introductions are iterative, which would maximize both the chance of invading at an opportune moment and cumulatively increase the number of individuals introduced (see preliminary results, Appendix S1: Fig. S6). Clarifying whether our results can be generalized beyond a simple microcosm system requires integrating propagule pressure into studies of biotic resistance more widely. While substantial differences within and between microbial, plant and animal systems no doubt exist, we believe that establishing a more general theory of invasion ecology is an overdue and necessary goal for improving informed action on invasive species of all types (Catford et al. 2009).

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1852/suppinfo