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Abiotic heterogeneity underlies trait-based competition and assembly

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Abstract

1. The fitness of individual species depends on their ability to persist and establish at low densities, just as the diversity of ecological communities depends on the establishment and persistence of low-density, "invader" species. Theory predicts that abiotic conditions and the competitive make-up of resident communities jointly shape invader fitness, limiting the phenotypic identity of successful invaders.
2. We use an invasion experiment to ask how competitive traits of 20 introduced plant species alter their absolute fitness in fragments that differ in size, abiotic conditions, and traits of the resident community.
3. We show that abiotic conditions interact with both invader traits and resident functional diversity to determine invader survival. Optimal invader traits depended on the soil characteristics, while greater resident trait diversity lowered invader fitness and had especially strong effects in low-resource environments. Unlike other abiotic conditions, fragment size had consistent effects irrespective of invader identity, decreasing survival in larger fragments.
4. *Synthesis*. Our results illustrate how the abiotic environment mediates the effects of resident and invader traits on establishment, creating fitness landscapes that structure local diversity and the functional identities of successful species.

KEYWORDS

alpha diversity, beta diversity, community assembly, community-weighted mean, functional diversity, leaf dry matter content, plant diversity, specific leaf area

1 | INTRODUCTION

Ecologists aim to understand species diversity and composition, emergent properties of ecological communities, by testing the processes that underlie the accumulation and persistence of different species in a locality. A variety of frameworks have been proposed to formalize these processes, with most focusing on the establishment or persistence of low-density species as a key measure for understanding the maintenance of diversity (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Keddy, 1992; Webb, Ackerly, Mcpeek, & Donoghue, 2002). Despite the promise of these frameworks, they have been difficult to generalize across species, systems, and environments. As a result, researchers have recently combined trait-based community ecology with contemporary coexistence theory to provide new avenues for generalizing community assembly (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; HilleRisLambers et al., 2012).

Under traditional community assembly theory, communities reflect the joint effects of abiotic and biotic filters acting on a regional species pool, with each of these filters expected to select species traits in opposite ways (e.g., Keddy, 1992; Kraft, Adler, et al., 2015; Mittelbach & Schemske, 2015). When physiological traits are adaptive to abiotic conditions, classic theory predicts that these traits will map onto changes in the abiotic environment (Laughlin, Strahan, Adler, & Moore, 2018), resulting in fitness landscapes with a single trait optima in a given locality for both resident and incoming species. In contrast, when trait differences reflect differences in resource uptake or resistance to distinct herbivores, they can reflect niche differences that facilitate coexistence, and traits of successful invaders are predicted to differ from those of residents (HilleRisLambers et al., 2012). These different predictions for the effects of traits on fitness indicate that both the mean and variance of functional traits in a community should influence the success of incoming species.

The effect of trait differences on biotic interactions is also expected to cause diversity to lower invasibility, as richer communities saturate niche axes, causing intensified competition (Levine & D'Antonio, 1999; Lodge, 1993). This, however, will critically depend on whether incoming species differ from residents, increasing trait variation within the community, or overlap with the existing trait distribution of resident species. In simulated communities, for example, altering the mean and variance of traits can both have positive or negative effects on the diversity of a system, depending on the trait of interest (Herben & Goldberg, 2014). An increase in trait variance is equivalent to an increase in functional diversity, linking this theory to trends observed in field studies (Laliberte & Legendre, 2010). Understanding how incoming species are affected by the mean and variation of traits within communities can clarify when these metrics reflect competitive dynamics—a growing body of work shows that the relationships between traits and the biotic and abiotic drivers of assembly must be tested rather than assumed (e.g., Laughlin et al., 2018; Marks & Lechowicz, 2006; Muscarella & Uriarte, 2016).

Recent research that examines the effects of multiple traits on assembly shows that classic predictions of abiotically driven trait optima or increased trait variation due to competitive interactions may be reversed depending on whether biotic or abiotic conditions are ultimately responsible for trait–fitness relationships (Falster, Brännström, Westoby, & Dieckmann, 2017; Kraft, Godoy, & Levine, 2015; Marks & Lechowicz, 2006; Mayfield & Levine, 2010). Indeed, the effects of biotic and abiotic interactions on communities' trait distributions are often interdependent (Loughnan & Gilbert, 2017), meaning that the effect of each factor cannot be examined in isolation. These considerations have led several authors to propose two directions for testing trait-based community assembly. First, biotic and abiotic interactions need to be considered simultaneously, with the goal of understanding how they jointly limit or promote specific species within communities (Cadotte & Tucker, 2017; Thakur & Wright, 2017). Second, the effects of traits on fitness components, such as survival, need to be tested across biotic and abiotic conditions (Laughlin, 2018). Crucially, if biotic and abiotic conditions interact to determine the success of invaders, we cannot view each factor as an independent filter. Rather, multiple factors interact in complex ways to shape the relationship between invader traits and success, creating fitness landscapes akin to those used in evolutionary biology, and increasingly adopted by community ecologists (Laughlin & Messier, 2015). Rather than limiting the study and relevance of biotic and abiotic forces, these recommendations open new avenues for resolving the complexities of community assembly by testing the interactive effects of invader traits, resident traits, and abiotic conditions.

Understanding how traits and abiotic conditions influence community assembly is increasingly important as global changes alter both the suite of species present in different regions and the environments in which they interact. One of the major consequences of anthropogenic disturbances for natural communities are the fragmentation of natural habitats (Fahrig, 2003). For old-field plant communities in particular, fragmentation is known to be an important determinant of community structure (Cook et al., 2005; Lindborg et al., 2012; Marini et al., 2012; Schweiger, Diffendorfer, Holt, Pierotti, & Michael, 2000), both through modification of biotic interactions and of correlated aspects of the abiotic environment. For example, small communities support fewer predators and thus experience stronger herbivory, which can shape the composition of plant communities through the impacts of herbivores with different feeding preferences (Genua, Start, & Gilbert, 2017). Additionally, changes in fragment size have been shown to favour species with specific dispersal strategies, and may also cause a general increase in the establishment of new species due to higher species turnover in small fragments (Jones et al., 2015; MacArthur & Levins, 1967). Finally, fragments often experience increased edge effects, with more individuals having to withstand harsh edge microclimatic conditions such as increased wind, drought, and light exposure (Fahrig, 2003; Laurance & Yensen, 1991; Murcia, 1995). In general, we can view the negative and uniform effects of fragmentation on all species as decreasing the average height of the absolute fitness landscape, reducing the fitness and invasion probability of all species. Conversely, shifting environmental conditions (e.g., from edge effects) alter the shape of the fitness landscape, shifting the functional traits possessed by successful invaders. Overall, by altering biotic and abiotic conditions, fragmentation may influence the general success of invaders while also determining the identity of successful invaders.

In this study, we use an invasion experiment to understand how biotic and abiotic conditions influence the absolute fitness of 20 functionally diverse plant species, defined as their survival through the first growing season. We introduce individuals of different species into established old-field fragments of varying size, and measure invader traits, resident traits, and abiotic conditions to test three questions: (a) Given an average biotic environment, how do abiotic conditions affect the fitness landscape for species with divergent functional traits? (b) Does the fitness conferred by invader traits depend on resident traits? (c) When do the effects of abiotic and biotic conditions work independently, and when do they interact to alter invader fitness? We test these questions using survival as a key fitness component that is necessary for establishment, and in doing so provide a clear link between demographic rates and traits in different environments, as has been proposed as a standard for trait-based studies (Laughlin, 2018; Laughlin & Messier, 2015).

2 | MATERIALS AND METHODS

2.1 | Study setup

In late fall of 2012, we seeded 168 fragments with a functionally diverse collection of herbaceous species (five species per plot, selected for diverse traits from Reich et al., 2003) at the Koffler Scientific Reserve (KSR), King Township, Ontario, Canada (44°01′48″N, 79°32′01″W). The fragments were divided equally into 14 blocks, where each block consisted of four 0.25 m^2, four 1 m^2, and four 4 m^2 fragments separated by weed blanket (Supporting Information Figure S1). The fragments are kept under natural field conditions and herbaceous species can disperse freely, while woody species are removed annually. In 2016, 71 herbaceous plant species were identified in our annual survey of the communities, with most of these having established from nearby populations independently of our initial seeding. *Solidago canadensis* (Canadian goldenrod) and *Monarda fistulosa* (wild bergamot) were the most abundant species in plots by biomass, and *Festuca rubra* (red fescue) was the most abundant by number of stems (tillers for grasses). Plots of different size showed some variation in the relative abundances of herbaceous species (Supporting Information Table S1), with small but statistically significant differences among plot sizes ($R^2 = 0.02$, $p = 0.003$; Supporting Information Table S2).

We chose 20 herbaceous species that are native to Southern Ontario as our invading species (Supporting Information Table S3). We used a total of 840 transplants, 42 individuals of each species. For all species, we assigned one individual per fragment size per block (three individuals per block), and transplants were randomly assigned to fragments within this block-wide constraint. To avoid crowding of transplants and to ensure they mainly interacted with the resident community rather than other transplants, we transplanted five randomly selected individuals of different species into each fragment, with four fragments of each size making up each block (Figure 1).

Prior to planting, we grew the transplants in a greenhouse for 8 weeks, fertilizing twice (15-30-15 NPK) and watering daily. All (840) individuals were transplanted into the field on 28–29 June 2016. Each plant was 10 cm from the fragment edge and separated from the next transplant by 10 cm, with all transplants in the southwest corner of fragments (Figure 1). This planting standardizes distance to the nearest edge, but we note that plants likely still experienced different conditions due to fragment size (farthest distance to an edge was 40 cm in small fragments vs. 190 cm in large fragments). For every transplant, we dug a hole 12 cm deep in the planned transplant location, removing any resident plant that might be present at that spot, removed the transplant from greenhouse cone-tainers and placed it in the soil. Remaining soil from the greenhouse was not washed off the transplants' roots, yet the soil surrounding roots was mainly from the plots themselves given the small size of the cone-tainers used. Transplant mortality within the first 48 hr was attributed to transplant shock, and failed transplants were then replaced by individuals of the same species. The experiment was conducted in an unusually dry year with little natural recruitment of plants. To avoid complete drought-induced mortality, transplants were watered every other day for the extent of the experiment with approximately 0.6 L of water per individual. The water was applied directly above the transplants with a watering can, likely not favouring the resident vegetation. Final mortality was assessed 8 weeks after planting, at the end of the 2016 growing season. Previous research has shown that seedling mortality is often greatest in summer months when plants are active and potentially competing (Gibson, Urban, & Baer, 2011), suggesting that the most important influences of competition and environmental conditions on seedling fitness were likely captured in our study.

To measure transplant traits, individuals used for trait measurements were kept separately in pots in an outdoor greenhouse. This approach was used to standardize the age and size of individuals from which trait estimates were taken. Our greenhouse measurements showed clear effects of transplant size on traits, and we opted to eliminate intraspecific trait variation that would arise from differences in size, as this type of intraspecific variation is distinct from

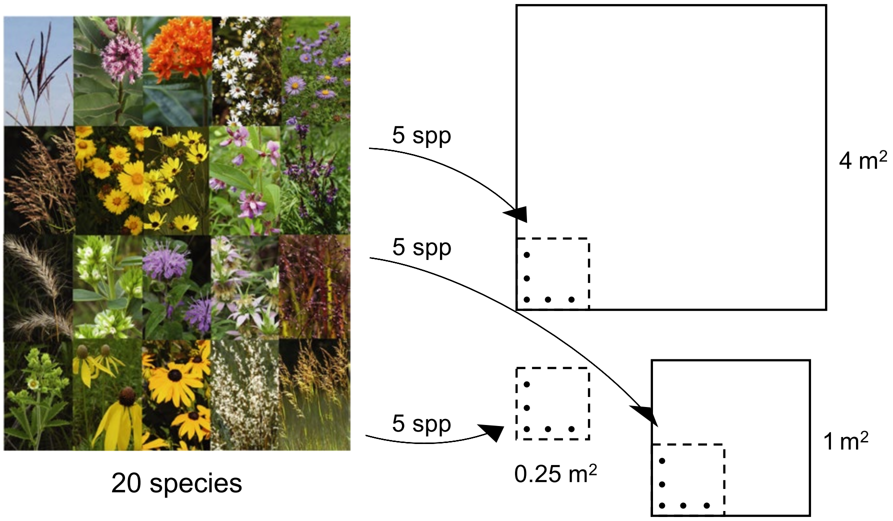

FIGURE 1 Diagram of experimental design. Squares represent plots of different size, dots represent placement of transplants within each plot, and dashed lines represent the area that was surveyed to determine community-level traits (CWM and FDis). Every block was made up of 12 plots used in the experiment, four of each size. Twenty species were used in total, with every species represented once per plot size per block. Within those constraints, a set of five species was randomly selected for placement in each plot [Colour figure can be viewed at wileyonlinelibrary.com]

adaptive trait variation and can confound causes and effects of trait differences among individuals.

2.2 | Data collection

For the transplanted species, we measured functional traits on eight individuals per species. We also measured the traits of up to seven individuals for all 71 species present in the fragments at the time of the experiment. For all invader and resident species, we measured specific leaf area (SLA) and leaf dry matter content (LDMC). SLA is measured as leaf area divided by leaf dry mass (measured in cm^2/g), and LDMC as leaf dry mass divided by leaf wet mass (g/g; Pérez-Harguindeguy et al., 2013). Dry weights were measured after samples were dried for a minimum of 48 hr at 60°C, and all leaf measurements included petioles for species that possessed them.

Biologically, SLA is correlated with parameters related to gas exchange and photosynthesis, as well as leaf longevity and investment in secondary compounds, while LDMC is also correlated with leaf longevity and resistance to herbivory (Pérez-Harguindeguy et al., 2013). SLA has been shown to be mathematically related to the inverse of LDMC, with leaf lamina thickness and density modifying the exact relationship (Vile et al., 2005), such that lamina thickness in particular often modulates the differences in the ecological significance of SLA and LDMC (Shipley et al., 2017). We used both metrics because SLA can vary strongly with leaf thickness, causing it to be variable among replicates, but nonetheless influence fitness (e.g., Harrison, Gornish, & Copeland, 2015). LDMC is largely independent of leaf thickness and shows lower variability (Wilson, Thompson, & Hodgson, 1999). We note that other traits, such as reproductive traits, seed mass, and so on, were not included because we used transplants in our experiment.

To quantify abiotic conditions, we measured soil macronutrients and salient chemical properties, which were analysed using PCA (Supporting Information Table S4), along with soil moisture in all fragments in 2017. We measured soil moisture with a TDR soil moisture probe at 14 cm from the southwest corner towards the fragment centre once in July 2017. We collected soil samples at the same location, and chemical analysis was performed at Brookside Laboratories. The analysis generated data on the concentration of various soil macronutrients (see Supporting Information Table S4), as well as cation exchange capacity (CEC), pH, percent organic matter, and nitrogen release.

2.3 | Statistical analyses

In our analyses, we tested the effects of transplant traits, the distance of those traits from traits of the resident community, and the variation in resident community traits on transplant survival, all within the context of plot abiotic conditions. Below, we first outline how these measures were quantified and then describe our statistical tests.

To quantify the mean and variance of the resident community leaf functional traits, we calculated the community-weighted mean (CWM) and functional dispersion (FDis). The CWM is the average value of a trait (SLA or LDMC) for all species, weighted by each species' abundance (number of individuals) within a community. The FDis is the weighted mean distance of all species to the multivariate trait CWM within each community, a measure of multivariate variation that is frequently used to characterize functional diversity (Laliberte & Legendre, 2010). We included SLA and LDMC to calculate FDis ("FD" package in R; Laliberte & Legendre, 2010). Since transplants were in the southwest corner of each plot, we used a 0.25 m^2 nested fragment in this southwest corner of 1 and 4 m^2 plots to estimate species abundances; this nested plot was the same size as our smallest fragment treatment (Figure 1). Standardizing the resident community by area avoided confounding fragment size with FDis (due to richness-FDis relationships, L. Forsyth, unpublished; Laliberte & Legendre, 2010) and ensured that we captured only species that were likely to interact with the transplants.

To calculate the difference of transplant traits from those of the resident community, we first contrasted transplant trait values from fragment CWMs. We used the mean SLA and LDMC of the eight individuals measured for each transplant species. Trait distance was the absolute difference between the average transplant trait value and the resident CWM value for each community. Transplant traits (SLA and LDMC) were not correlated ($r = 0.02$, $p = 0.9$; Supporting Information Figure S2), suggesting that leaf lamina thickness is negatively correlated with LDMC in these species (Vile et al., 2005). Despite this relationship amongst transplants, distances of these traits from the resident community were highly correlated due to the correlation between resident CWMs for SLA and LDMC (Supporting Information Figure S2). We scaled these trait distances by their standard deviations (using the "scale" function) to put them on a common scale. We then conducted a principal components analysis (PCA) of all SLA and LDMC distances. The first PC axis explained 76% of the variation in SLA and LDMC distances and was positively correlated to both, whereas the second PC axis was positively correlated to LDMC distances and negatively correlated to SLA distances. Distributions of predictor variables, including transplant traits, the first PC axis of SLA and LDMC distances, and FDis is provided in Supporting Information Figure S3, and biplots of predictors are provided in Supporting Information Figure S4.

We statistically tested for the effects of trait differences, resident trait variance, or the transplant trait values themselves on transplant survival. To aid in model convergence, we used standardized predictor variables (except fragment size, which we log transformed) for all subsequent analyses. We used a generalized linear mixed model with a binomial distribution for each test described below ("glmmADMB" package in R3.2.2; R Core Team, 2015). For all tests, we included plot nested within block, and species as random effects. The inclusion of species as a random effect accounts for a lack of independence in our transplant trait measurements (each species was planted in 42 fragments but does not represent 42 independent assessments of each trait).

We constructed separate tests for the effects of transplant traits and the resident community traits. For the former, the fixed effects included were transplant trait values and their interactions with environmental variables—soil moisture, PC 1–3 of soil macronutrients (47% total variance explained, Supporting Information Table S4) and fragment size. Because transplant LDMC and SLA values were not correlated, transplant traits were considered independent in our tests. To test the effects of resident community traits, we tested both trait differences (transplant vs. resident, described above) and FDis, and their interactions with environmental gradients and fragment size as fixed effects (Supporting Information Table S5). We tested each model independently (each transplant trait and each metric of resident traits), starting with the most complex models (up to two-way interactions). We reduced these models by sequentially eliminating non-significant terms, starting with higher order terms (using Wald *Z* scores, Bolker et al., 2009). Once all models were reduced to include only significant terms, we combined the significant terms from all models into a single model to confirm that they independently explained survival (Supporting Information Table S6). We note that problems with model convergence and convergence times prevented us from beginning with a single model that included all independent variables at the outset and also necessitated removing non-significant fixed effects to allow a single model to be analysed. We also acknowledge that there is likely a phylogenetic signal with respect to species traits, and therefore their response to the biotic and abiotic environment. The issue of shared evolutionary history is only a problem insofar as it increases the likelihood that other correlated traits are driving observed patterns. However, this is an issue with all trait-based studies in ecology and evolution, and in our case, there are relatively well-established links between the traits we measured and plant performance, reducing the likelihood of correlated trait effects.

3 | RESULTS

Overall, our results show that traits of the invader and the resident community influence invader survival, and that both are contingent on the abiotic environment. Shifts in biotic and abiotic conditions create gradients that, in some cases, favour species with specific traits, whereas in other cases, they uniformly alter survival for all invaders and thus appear to promote or limit accumulation of additional diversity. Below, we outline the specific results that lead to these conclusions and present full results in Supporting Information Tables S5 and S6.

Invader SLA predicted survival across the main gradient of soil macronutrients (PC1), with high SLA species experiencing higher survival in conditions with high pH, calcium and cation exchange capacity (CEC), and low amounts of organic material (Figure 2a; SLA × soil PC axis 1, $p = 0.039$). However, neither of these predictors (invader SLA or soil PC axis 1) were significant in the absence of the interaction (both $p > 0.1$). Invader LDMC did not influence survival alone or in conjunction with abiotic conditions (all $p > 0.25$). Fragment size had a direct effect on survival, with all species more likely to survive in smaller fragments (Figure 2b; $p = 0.026$), but the impact of fragmentation was not influenced by invader traits (both traits × fragment size $p > 0.6$).

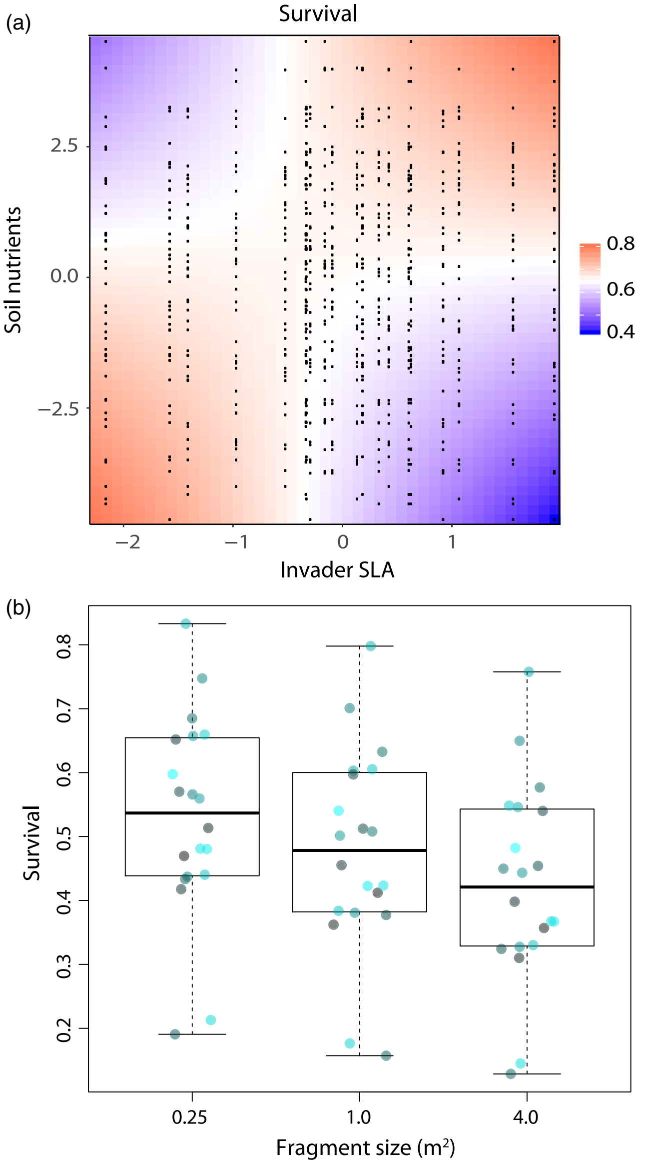

FIGURE 2 The effect of invader traits and abiotic conditions on survival. (a) The "Soil Nutrients" axis represents PC1 of soil properties, with higher values representing richer soils. Survival was greatest for low SLA species in low nutrient fragments (low CEC and pH; Supporting Information Table S4) and for high SLA species in high nutrient fragments. Points show data coverage, with each vertical line of points corresponding to a single species. (b) Survival was universally higher in smaller fragments, and invader LDMC (coded by color) did not influence survival. Each point in the boxplot represents 1 of 20 native species used as invaders, with LDMC increasing from grey (low LDMC) to blue (high LDMC) [Colour figure can be viewed at wileyonlinelibrary.com]

Traits of the resident community also determined invader survival, with the strength of this effect depending on the abiotic environment. Higher functional diversity in the resident community (higher FDis) led to lower survival of all invaders, and these effects were strongest in soils with low nutrient availability (low CEC, low pH, and high organic

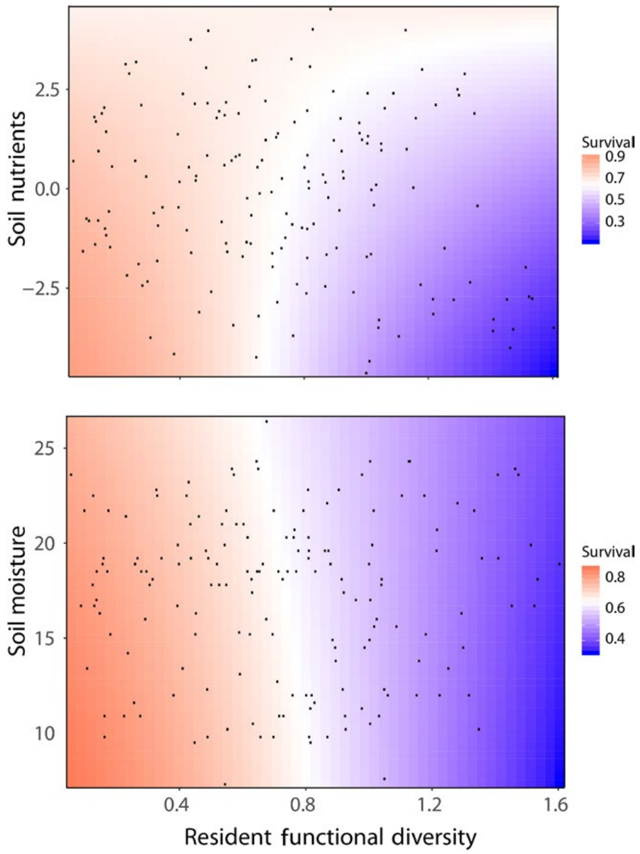

FIGURE 3 The interactive effects of resident functional diversity (trait variation) and fragment environmental conditions on invader survival. Functional diversity decreased survival, with this effect being strongest in (a) low nutrient fragments (Soil PC Axis 1; Supporting Information Table S4) and (b) fragments with low soil moisture. Points show data coverage across the response surfaces [Colour figure can be viewed at wileyonlinelibrary.com]

content—Figure 3a; FDis × soil PC axis 1, $p = 0.014$) and in fragments with low soil moisture (Figure 3b; FDis × soil moisture, $p = 0.048$). Despite their interactive effects, resident trait variation (FDis), and soil nutrients were not significant on their own (all $p > 0.05$), but soil moisture was once its interactive effect with FDis was accounted for ($p = 0.019$). Resident trait variation influenced survival of all invader species regardless of their traits, and the difference between invader traits and mean resident traits had no effect on survival, regardless of abiotic conditions (all $p > 0.1$).

4 | DISCUSSION

Community assembly is influenced by the complex interplay of traits of establishing species, traits of the resident community, and how these traits alter invader fitness in a given abiotic milieu. We studied 20 transplant species representing a broad range of leaf strategy traits, and resident communities that differ in trait means and functional diversity even in similar abiotic conditions. In this diverse system, the influence of both invader and resident traits on invader fitness depended on the abiotic environment, whereas the abiotic environment sometimes acted independently (Figures 2 and 3). The overarching effect of these influences was twofold. First, some fragments supported more invaders, either because of the direct effect of abiotic characteristics (fragment size) or because functionally impoverished resident communities increased invader survival in specific abiotic conditions. Second, invaders with specific traits had an advantage in specific environments (Figure 2a). These effects correspond to abiotic and biotic conditions limiting diversity in general (sinking the fitness landscape), and those that limit the establishment of species with specific traits (shaping the fitness landscape). By understanding these overarching effects, we are able to map the effects of traits and abiotic conditions onto their influences on species diversity and composition, allowing a deeper understanding of the factors and processes shaping ecological communities.

Abiotic conditions were pervasive drivers of invasion, either tempering survival rates for all species or allowing the invasion of species with particular traits. Fragment size had a direct effect on survival by sinking the fitness landscape, allowing more individuals to survive in small fragments regardless of their trait values. Although this finding is broadly consistent with classic and current theory, our results do not appear to support the hypothesized mechanisms of those theories. For example, island biogeography theory posits that small fragments have higher turnover, and thus require higher rates of colonization for a given diversity (MacArthur & Levins, 1967). Similarly, recent work on ecological drift has shown that species composition of environmentally identical small fragments varies greatly (Gilbert & Levine, 2017), suggesting that small fragments could contribute disproportionately to invader success through nonlinear survival effects of the resident community. However, both of these proposed mechanisms act through their impacts on resident species, which in turn are predicted to impact invaders. Subsequent analyses of our data do not find support for this indirect effect of fragment size through the resident community, as the effect of fragment size remained unchanged when resident community traits were included in the statistical model. These results suggest instead that unmeasured aspects of the environment associated with fragment size are likely responsible for changes in survival. As a result, we can view fragment size as a filter that uniformly shifts the fitness surface (i.e., changes mean fitness regardless of trait values), reducing survival of transplants in larger fragments.

Beyond the universal effect of fragment size in augmenting or preventing invasion, other abiotic conditions shaped the functional identity of successful invaders. In our study, soils with low macronutrient concentrations facilitated the invasion of species with low SLA, to the relative disadvantage of high SLA species (Figure 2a). This finding is concordant with past work showing that resource acquisitive (“fast”) species tend to have high SLA and be associated with rich soils (Grime, Cornelissen, Thompson, & Hodgson, 1996; Pérez-Harguindeguy et al., 2013; Westoby, 1998; Wilson et al., 1999). This positive relationship between SLA values and soil nutrients can be altered at different levels of light intensity (Meziane & Shipley, 1999), and the trait is known to reflect both abiotic conditions in tandem (Hodgson et al., 2011). In our experiment, however, all fragments were exposed to fairly uniform light conditions in an open field and the distance of transplants to fragment edges was standardized within and across treatments (Figure 1), suggesting that the SLA effect observed reflected the impact of nutrients in fairly homogeneous, high light conditions. The fact that we saw no significant effect of LDMC on survival across this study, and the general lack of correlation between SLA and LDMC in our invader species (Supporting Information Figure S2) suggests that species differences in leaf lamina thickness and density distinguish the functional importance of these traits for survival in different soil conditions (Shipley et al., 2017; Vile et al., 2005). More generally, these results highlight how different aspects of the abiotic environment (fragment size and soil abiotic conditions) may differentially influence how invaders alter alpha and beta diversity by creating trait-independent and trait-dependent effects, respectively.

Abiotic conditions directly influenced invasion by sinking and shaping the fitness landscape, and by modifying the effects of biotic interactions on survival. In our study, communities with high functional diversity conferred low invasion success, but this effect was more pronounced when abiotic conditions were harsh (low macronutrient availability and low soil moisture). This result contradicts many classic models that posit that competition is reduced in stressful environments, but is consistent with recent theory and experiments (e.g., Hart & Marshall, 2013; Napier, Mordecai, & Heckman, 2016). Intuitively, although species may be able to survive harsh environmental conditions or high competition, the combination of these stressors can lead to disproportionately high mortality. As a result, communities that are functionally diverse and yet abiotically harsh prevent invasion, creating a stronger limit to alpha diversity. Abiotic conditions can then limit invasion by modifying the importance of biotic interactions. Importantly, the idea of sequential filters shaping the identity of successful invaders breaks down in our study—putative filters are not independent, but rather are contingent on one another. As a result, we can better understand the processes shaping invader success and ultimately the patterns of diversity by considering the simultaneous effects of many factors on the key demographic rates of species (i.e., fitness landscapes). The interaction we found between the environment and functional diversity not only supports findings from simpler, low-diversity experiments (Hart & Marshall, 2013; Loughnan & Gilbert, 2017; Napier et al., 2016), it emphasizes the need for joint and simultaneous consideration of biotic and abiotic drivers of community assembly.

Functional diversity reduced invasion success for all species, suggesting that functional diversity may be a general predictor of limits to alpha diversity. Negative diversity-invasibility relationships are thought to be common (Levine & D'Antonio, 1999; Lodge, 1993) following historical ideas of higher niche occupancy and resource monopolization in richer communities (MacArthur & Levins, 1967; May & MacArthur, 1972). Empirical studies, however, often fail to uncover such relationships, or even find the opposite pattern when considering species richness (Fridley et al., 2007; Levine & D'Antonio, 1999). This disconnect may arise because classic theory is contingent on increased species richness reducing open niche space, but greater richness need not imply higher functional diversity (Cadotte, Carscadden, & Mirotchnick, 2011). Given that functional traits can be used to describe resource use and occupied niche space of communities (Cadotte et al., 2011; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007), they more directly test for the niche processes assumed to cause biotic resistance.

While functional diversity reduced invasion success, differences between invading trait values and community-weighted mean traits (CWM) had no effect on invader survival. This result is surprising given the large body of literature linking community-level trait values to abiotic conditions (e.g., McGill et al., 2006), but our result may nevertheless arise for several reasons. First, as with most trait-based studies, it is possible that unmeasured traits ultimately drive patterns of invasion, which in our study could be correlated to functional diversity rather than community-level trait values. Second, it could be that the moments of the trait distributions that are commonly tested (weighted mean and weighted variance) are not always the most appropriate for determining how community traits influence invasion. For example, rare species are poorly represented by abundance-weighted mean trait values, but may nevertheless have disproportionate effects on invader survival (Leitão et al., 2016; Lyons & Schwartz, 2001; but see Gilbert, Turkington, & Srivastava, 2009). Community trait variation metrics, like FDis, may better capture some of the influence of these species (Laliberte & Legendre, 2010). Finally, and most intriguingly, abundance might be a poor indicator of adaptive trait–environment matching. A common interpretation of community mean trait values is that they represent some trait optimum set by the environment (Ackerly, 2003; Laughlin et al., 2018). However, recent work has shown that this may not be the case; dispersal limitation, disturbance, or temporally fluctuating environmental conditions can cause abundances and thus community-level traits to vary, straying from the true adaptive trait optimum (Laughlin et al., 2018). Moreover, there may be multiple optima for a given trait that depends on the combination of other traits (Laughlin et al., 2015). Although we cannot distinguish among these hypotheses, our work indicates that using functional diversity, rather than an abundance-based mean, appears to be more biologically relevant to invading species.

Ecologists are increasingly examining invader traits, resident traits and the abiotic environment to understand both the basic processes shaping community assembly, and applied aspects of species' responses to global changes. Our study provides evidence that these three axes of communities independently and interactively determine the establishment of species. Abiotic conditions can limit the ability of all species to invade by reducing fitness for all species and thus limiting local diversity. However, abiotic conditions can also shape fitness landscapes, favouring species with particular trait values and setting the conditions necessary for maintaining beta diversity in spatially heterogeneous landscapes. Finally, abiotic conditions can influence patterns of invasion by modifying the importance of biotic interactions, with harsh environmental conditions and high functional diversity interactively shaping invader success. The impact of resident functional diversity on invasibility further suggests that local variation in traits rather than community mean trait values per se captures biotic interactions and thus serves as a more useful predictor of invasion success. These results challenge the classic separation of abiotic and biotic filters, requiring a consideration of the interactive effects of both on fitness landscapes to understand community assembly.

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AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed methodology, I.L.B. and L.Z.F. collected the data, I.L.B., B.G., and L.Z.F. analysed the data. All authors contributed to the writing and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.gq156st (Borges, Forsyth, Start, & Gilbert, 2018).

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