


The success of alien plants in an arid ecosystem: Structural equation modeling reveals hidden effects of soil resources

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Abstract. The diversity of a native community is not the sole driving factor determining the success of an invader; abiotic factors can also play a role, making it important to understand their contributions in modifying the expected outcome of biotic and abiotic resistance to invasion. In order to test the contributions of native diversity, relatedness between native and alien plants, and abiotic factors in resisting alien invasion, we used a trait–environment data set of 33 alien- and 130 native plants in 166 invaded plots, covering a gradient of soil resources in Saint-Katherine-Protectorate, an arid-protected area in Egypt. We measured the native diversity components as predictors of native biotic resistance. We quantified the success of alien plants based on their abundance and their performance traits. Additionally, we calculated the mean functional and phylogenetic distance between aliens and natives in each plot. We tested all plausible influences of native diversity components, relatedness, and soil resources on alien abundance and performance first using mixed-effects models and second with a structural equation model (SEM). Mixed-effect models revealed that, in the resource-rich environments, alien abundance increased even though native plants were more productive, but alien performance decreased. SEM direct pathways revealed that native communities with high functional dispersion and richness and high mean-weighted performance traits repelled alien plants by lowering their success. Simultaneously, in line with mixed-effect models results, the effect of soil resources on alien success was found to be indirect, being mediated by the mean functional and phylogenetic distance between aliens and natives: The success of alien plants increased in resource-rich environments when they were dissimilar to the natives, while it decreased for aliens similar to natives in resource-limited environments. Our findings provide new insights on native community resistance to invasion, with resistance being higher in resource-limited environments and when aliens are functionally and phylogenetically similar to resident natives.

Key words: abundance; alien species; biotic and abiotic filters; biotic relatedness; dissimilarity; functional similarity; invasion; performance; resistance; resources availability.

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INTRODUCTION

Ecological resistance to invasion concerns the abiotic conditions and the biotic components of a resident native community that allows it to deter non-native species from invading. Dozens of hypotheses have been put forth to explain what factors enable a native community to be ecologically resistant to invasive species, with each being supported within certain circumstances (Catford et al. 2009, Conti et al. 2018). The main focus of these hypotheses has been on biotic resistance, which involves the diversity of the native community or the competitive ability of native species (Elton 1958, Davis et al. 2000, Fargione et al. 2003), as well as the biotic relatedness (i.e., functional and phylogenetic distances between the invader and native species) (Bennett 2019). The hypothesis of biotic resistance, in particular, predicts that the success of alien plants, in terms of probability of establishment and abundance, is lower in high diverse native communities (Elton 1958, Levine et al. 2004). This hypothesis has been extensively studied (e.g., Gerhardt and Collinge 2007, Saccone et al. 2013, Conti et al. 2018, Sheppard and Schurr 2019) and, most of the plant invasion studies that have investigated it, have found that successful invasions are generally correlated with declines in the biotic resistance of the recipient native assemblages (Levine et al. 2004, Fargione and Tilman 2005, Hooper and Dukes 2010, Vilà et al. 2011, Oakley and Knox 2013).

Although biotic resistance has received much attention in the literature as an essential component of alien species establishment success (El-Barougy et al. 2020), it is not the only component of ecological resistance. Ecological resistance to invasion also includes environmental (abiotic) resistance (Von Holle et al. 2003), which encompasses the disturbance regimes and abiotic conditions of the invaded habitat, for example, resource availability and climate conditions (Levine et al. 2004). Environmental resistance hypotheses propose that alien species are unsuccessful at invasion if they are unable to tolerate the abiotic conditions that encompass the resident native communities (Fox and Fox 1986, Rejmánek 1989). Only alien species with appropriate morphological and physiological traits will be able to invade a particular habitat. This

hypothesis is supported by previous studies, which have shown that alien species richness and abundance are generally low in native communities with high environmental resistance (D'Antonio 1993, King and Grace 2000, Harrison et al. 2001, Burt and Harrison 2002, Seabloom and van der Valk 2003).

Therefore, it is evident that both biotic and abiotic factors play important roles in the ecological resistance of a native community to invasion. For example, if the invader is phylogenetically closely related to native resident species, it will likely share similar traits and occupy a similar niche as the native species due to the strong effect of environmental filtering (pre-adaptation hypothesis, Funk et al. 2016, Cadotte et al. 2018). This filtering restricts the range of trait values of the invader so that it is more similar to that of the native species (Daehler 2001, Duncan and Williams 2002, Kraft et al. 2015). In harsh environments, if the competitive effect is strong, as assumed to be the case among species with similar trait values (Mayfield and Levine 2010), and if resources are limiting, the chances that the invader with lower trait values than natives to establish successfully in the community will greatly decrease. By contrast, if the invader with higher trait values than natives and is distantly related to resident natives, it will occupy a distinct niche and its competitive effect with resident natives is assumed to be low. Additionally, the presence of native species exploiting similar niches as the candidate invader would confer high native biotic resistance due to the lack of an "empty niche" (Levine and D'Antonio 1999, Fargione et al. 2003, Zavaleta and Hulvey 2007), which would decrease the likelihood of establishment success even further.

In addition, functionally and phylogenetically diverse native assemblages have been shown to endure less mortality and procure higher resistance to invasion due to the high complementary utilization of available resources by less competitive species (Strauss et al. 2006, Diez et al. 2008, Gerhold et al. 2011). These findings are in agreement with the resource opportunity hypothesis (Thuiller et al. 2010), which suggests that limiting similarity and niche differentiation among natives plays an important role in resisting alien species, especially in the establishment stage (MacDougall et al. 2009). In this sense, previous

invasion studies have suggested that the biotic resistance needed to repel alien growth was actually lower for alien individuals that shared similar traits with the natives (Hooper and Vitousek 1997, Brown et al. 1998, Young et al. 2009). However, this resistance is determined by the competitive ability of native plants (Gallien et al. 2017, Carboni et al. 2018, Conti et al. 2018), which could change with the availability of resources (environmental resistance).

Complementarity among multiple species (or functional groups) with non-overlapping resource use strategies could lead to a better utilization of available resources, leaving less resources available for a potential invader (Naeem et al. 2000, Byun et al. 2013). Higher native diversity could also provide biotic resistance by increasing the probability to have a more productive species present in a more diverse native community, a mechanism known as the sampling effect (Wardle 2001). This mechanism was largely supported in temperate regions where plant diversity has been experimentally manipulated (Naeem et al. 2000, Hector et al. 2001, Petruzzella et al. 2018). In general, the increased resistance to invader with increasing native species richness could be that communities with higher species richness have higher productivity, and thus provide more resource competition through complementarity and/or sampling effects (Riis et al. 2018).

The strength of biotic resistance could also be influenced by positive or negative fluctuations in the interaction between biotic and abiotic conditions of the native community (Byun et al. 2015). For instance, abiotic conditions (e.g., dry soils with limited resources) could directly determine the failure of alien invasiveness, but it could also indirectly affect biotic resistance by influencing the performance of native plants. The importance of this interaction between biotic and abiotic conditions in determining the strength of biotic resistance has been demonstrated already in several ecological studies. For instance, Going et al. (2009) showed the importance of soil nitrogen limitation, in combination with competition from resident species, in repelling invasion by European grasses into a California serpentine plant community, and Prober and Lunt (2008) has demonstrated that the native plant species (*Themeda australis*) is essential for

maintaining the appropriate C/N ratio needed to deter invasion from exotic annuals in Australian woodlands.

In this study, we aimed to determine the biotic and abiotic barriers that prevent alien species establishment in Saint-Katherine-Protectorate (SKP), an arid-protected area in Egypt. First, we estimated the relative contributions of native diversity components (functional and phylogenetic metrics), native productivity (mean-weighted performance traits), and abiotic conditions (soil resources) in determining the ecological resistance to alien invasiveness. We expected that high biotic resistance to alien invasiveness occurs when members of a productive native community are functionally and phylogenetically diverse. This higher diversity will decrease the abundance as well as the growth performance of alien plants (Levine et al. 2004, Vilà et al. 2011) by filling the spatial niche space with diverse and productive native species that efficiently utilized local resources (Case 1990, Kennedy et al. 2002). Second, we assessed whether the biotic relatedness regulates the biotic resistance to alien invasiveness and to what extent the biotic relatedness and abiotic conditions interact to determine the success of alien species. We predicted that high resistance to invasion occurs in limited resource environments when alien species are more similar to natives (El-Barougy et al. 2020a). This might be affected either by the strong competitive effects of resident native species that can repel alien species invasiveness or by the strong effect of the environmental filtering (Fargione and Tilman 2005, Hooper and Dukes 2010, Oakley and Knox 2013).

METHODS

Study area

The study area was conducted in Saint-Katherine-Protectorate (SKP), South Sinai, Egypt (Appendix S1: Fig. S1), from March to July 2018 at the peak of the flowering season (Danin 2006). Saint-Katherine-Protectorate (SKP) was declared in 1996 as full-protected area status was given to approximately 4350 km² of largely mountainous terrain in South Sinai, but the studied area was given to approximately 150 km². The area includes the highest peaks in Egypt and contains

a unique assemblage of natural resources, notably high-altitude ecosystems with surprisingly diverse fauna and flora and with a significant proportion of endemic species. The high mountains (1600–2460 m asl) surrounding the town of St Katherine receive higher levels of precipitation, of up to 100 mm per year (Ayyad et al. 2000).

Saint-Katherine-Protectorate lies in the arid North African belt and is characterized by a Saharan–Mediterranean climate, experiencing extremely dry, hot summers, and cold winters. Average rainfall is 57 mm a year, with maximum temperatures of 35°C and lows of 5°C. The high mountains (1600–2460 m asl) surrounding the town of St Katherine receive higher levels of precipitation, of up to 100 mm per year (Ayyad et al. 2000). Saint-Katherine-Protectorate encompasses approximately 4350 km² of largely mountainous terrain in the South Sinai Governorate, but the study area was approximately 150 km² in size.

Vegetation plots, species abundance, and soil data

Field surveys were carried out in SKP during the spring and summer seasons (March to July) of 2018. Across the entire study area, we sampled 166 plots of 10 m² that were invaded by at least one alien plant species. The maximum number of alien species in a plot was three. We identified all plants to species level (33 aliens and 130 natives), and we measured their abundance as the total number of individuals per species (Appendix S1: Table S2). From this, we calculated the total abundance of alien and of native species in each plot.

The measurements for abiotic environment and resource availability were soil moisture, soil nitrogen, and organic matter content. These measurements were taken for each plot using a hygrometer for soil moisture, by calculating the ratio of total C and CaCO₃% for organic matter (Klute 1986), and with standard methods using a CNH analyzer (EA1108, Carlo Erba Instruments, USA) for soil nitrogen concentration (Allen et al. 1974). A detailed description of the methods can be found in the previously published (El-Barougy et al. 2020). Due to the high correlation between soil resources, a PCA was performed with these three variables (nitrogen, organic matter, moisture). The coordinates of the first axis, which captured 67.3% of the variance, were used

as a composite variable expressing “soil resources” in each plot (Appendix S1: Fig. S3e).

Alien performance data

To estimate the performance traits of alien plant species, we non-destructively measured three traits on all plants in the plots. These traits were plant height from the ground (cm), the number of leaves, and the number of reproductive organs (flowers and fruits). In addition to these three traits, we also determined above-ground biomass (kg) destructively. To obtain measurements for aboveground biomass of alien plants, all aboveground parts (leaves and stems) of all alien plants were dried in a drying oven (VWR International) at 50°C for three days and then weighed using a Mettler Toledo ML Series Precision Balance (ML Analytical balance). Due to the high correlation among the four performance traits, a PCA was performed with these traits. The coordinates of the first axis, which captured 65.1% of the variance, were used as a composite variable expressing the “alien performance” in each plot (Appendix S1: Fig. S3c).

Native community mean-weighted performance traits

As destruction of native biodiversity is strictly forbidden within the SKP, we could not harvest the leaves or any other part of the native species. Therefore, we measured the total leaf area of the plants by first drawing the outlines of their leaves on paper and then measuring the areas of these leaf copies. We then measured the three traits we could only obtain destructively, and aboveground biomass, on individuals of the native species that grew outside their protected range. Then, for each native species, we used multiple regression models to determine allometric equations (Basuki et al. 2009) for aboveground biomass as a function of the non-destructive measurements. We then used these allometric equations, and the non-destructive measurements that we took in the SKP plots to estimate the aboveground biomass of the native plants there. To estimate the productivity of resident native community, we calculated in each plot the performance community-weighted traits including height, biomass, floral production, and leaf production (variables CWM-Height,

CWM-Biomass, CWM-floral production, and CWM-Leaf production, respectively) that are supposed to contribute to the native community productivity (Violle et al. 2007, Petruzzella et al. 2020). We used *cwm* function which is available in the FD package (Laliberté and Legendre 2010) in R version 3.2.5 (R Core Team 2018). Due to the high correlation among these four CWM-traits, PCA was performed with these traits. The coordinates of the first axis, which captured 76.6% of the variance, were used as a composite variable expressing “native CWM-performance trait” in each plot (Appendix S1: Fig. S3a).

Native phylogenetic and functional measures

To quantify phylogenetic diversity and relatedness, we constructed a phylogeny of the 166 species (33 aliens, 130 natives) using four commonly sequenced genes available in GenBank (Benson et al. 2005): *rbcL*, *matK*, *ITS1*, and *5.8s*. Of the 130 native species, 120 species had at least one gene represented in GenBank. For the 10 native species without sequence data, we used the available sequences from congeneric relatives as a proxy (see phylogenetic guidelines by Cadotte and Jin 2014). As an outgroup species, we included the genetic sequence of *Amborella trichopoda* Baill because it diverged early in angiosperm evolution. The methods used to generate the phylogeny are previously described in El-Barougy et al. (2020). Appendix S1: Fig. S2 provides the final ultrametric phylogenetic tree containing all 130 native and 33 alien species found in this study.

We calculated Faith’s phylogenetic diversity (PD), which quantifies the total independent evolutionary history of a subset of taxa (Villéger et al. 2008, Veron et al. 2017) of all native species in each of the 166 plots. We also calculated the mean pairwise phylogenetic distance (NMPD) within each plot (Swenson 2014) to represent the phylogenetic relatedness among natives, as well as between aliens and natives (ANMPD) (Webb et al. 2002). These phylogenetic metrics were calculated using the functions PD and MPD in the R package picante (1.8 version (Kembel et al. 2010)). Due to the high correlation between native richness (TSR) and the phylogenetic diversity (PD), a PCA was performed with those two variables. The coordinates of the first axis, which captured 96.3% of the variance, were used as a composite

variable expressing “native richness” in each plot (Appendix S1: Fig. S3d).

To quantify the functional diversity in each plot, we measured three functional traits for native plants. These traits were plant height from the ground (cm), SLA (specific leaf area [cm^2/g]), and seed mass (g). Specific leaf area was estimated using allometric equations (see details on native aboveground biomass). We scanned the leaves of native species outside their protected range and measured the total leaf area using the IMAGEJ software, version 1.49. Then, we dried the leaves and determined the leaf dry weight and calculated the SLA (cm^2/g) as the leaf area divided by the leaf weight (Basuki et al. 2009). These three traits were used to calculate multi-trait functional richness (FRic) and functional dispersion (FDis). FRic is the amount of functional space filled by the community, an analogue of trait range in a multidimensional space (Villéger et al. 2008). FRic is calculated as the pairwise functional dissimilarity across species, using the Euclidean distance in multi-trait space after standardizing each trait to a mean of zero and a standard deviation of one. FDis is the multidimensional trait space or mean distance of each species, weighted by its relative abundance, to the centroid of all species in a community (Laliberté and Legendre 2010, Spasojevic and Suding 2012). FDis for each plot was calculated using function dbFD, which is available in the FD package (Laliberté and Legendre 2010) in R version 3.2.5 (R Core Team 2018). Due to the high correlation between FDis and FRic, PCA was performed with those two metrics. The coordinates of the first axis, which captured 65.6% of the variance, were used as a composite variable expressing “native functional diversity” in each plot (Appendix S1: Fig. S3b).

In addition to the functional diversity of the native communities, we also quantified the mean functional distance (ANMFD) of the alien species to the native species as well as the mean functional distance within natives (NMFD), using the same set of traits as used for the calculation of FRic and FDis. ANMFD was calculated as the mean-weighted (by abundance) pairwise Euclidean distance of each alien species to the native community; NMFD was calculated as the mean-weighted pairwise Euclidean distance among natives within each plot (Gallien and Carboni

2017, Carboni et al. 2018), using the “dist” function in R (package “stats” version 3.7.0).

Mixed-effects models

We constructed a series of mixed linear effect models including alien performance and abundance as response variables. First, in univariate models, the fixed effects were native richness, phylogenetic diversity (PD), and biotic relatedness, including mean pairwise phylogenetic distance among native species (NMPD), mean pairwise functional distance among native species (NMFD), functional and phylogenetic distances between alien and native species (ANMPD, ANMFD), native CWM-traits (height, biomass, leaf production, floral production), native functional dispersion (FDis) and functional richness (FRic), and soil resources (nitrogen, organic matter, water content) (Table 1). Second, in multivariate models, the fixed effects

were two-way interactions between soil resources (PCA axis), native components (CWM-height, CWM-biomass, CWM-floral production, CWM-leaf production, richness, PD, FDis, FRic), and the biotic distances between aliens and natives (Table 2). We included plot identity as a random effect since the measurements for the different alien plant species are more likely to be similar within than between plots. All analyses were conducted in R v.3.3.1 (R Core Team 2018) using the package “lme4” (version 1.1-20; Bates et al. 2015). The residuals were plotted against the fitted values to detect potential outliers and to determine any violation of homogeneity. Soil resources and functional and phylogenetic distances between aliens and natives were log-transformed to acquire a normal distribution, which was necessary after an initial inspection of the QQ plot and was verified with a Shapiro-Wilks test (Shapiro and Wilk 1965).

Table 1. Results of univariate linear mixed-models testing the significance of the explanatory variables on alien performance and abundance. Significant values are in bold.

Explanatory variable	Estimate	SE	<i>t</i>	Pr(> <i>t</i>)	R_m^2	R_c^2
Alien performance						
Log (Soil Nitrogen) (mg/L)	0.26	0.12	2.24	0.05	0.02	0.03
Log (Soil Organic Matter) (%)	0.24	0.12	2.06	0.05	0.02	0.05
Log (Soil Moisture) (%)	0.26	0.12	2.08	0.04	0.02	0.11
Soil Resources (PCA)	0.036	0.078	0.46	0.65	0.001	0.079
Richness	-0.23	0.07	-3.38	0.01	0.05	0.05
PD	-0.18	0.07	-2.64	0.09	0.02	0.032
FDis	-0.44	0.11	-3.91	<0.001	0.07	0.07
CWM-Height	-0.49	0.11	-4.45	<0.001	0.09	0.09
CWM-Floral Production	-0.46	0.11	-4.19	<0.001	0.08	0.08
Log (ANMFD)	0.27	0.08	3.40	<0.001	0.07	0.36
Log (ANMPD)	0.06	0.07	0.79	0.43	0.00	0.09
Alien abundance						
Log (Soil Nitrogen) (mg/L)	0.29	0.08	3.46	0.01	0.08	0.29
Log (Soil Organic Matter) (%)	0.30	0.08	3.85	0.01	0.09	0.34
Log (Soil Moisture) (%)	0.25	0.09	2.81	0.01	0.06	0.41
Soil Resources (PCA)	0.13	0.073	1.73	0.093	0.02	0.041
Richness	-0.14	0.07	-1.95	0.05	0.02	0.06
PD	-0.14	0.07	-1.95	0.054	0.02	0.07
FDis	-0.33	0.13	-2.56	0.01	0.06	0.95
CWM-Height	-0.22	0.08	-2.72	0.01	0.05	0.38
CWM-Floral Production	-0.27	0.08	-3.35	<0.001	0.07	0.37
Log (ANMFD)	0.31	0.07	4.32	<0.001	0.09	0.18
Log (ANMPD)	1.41	0.75	1.88	0.06	0.02	0.41

Notes: Plot identity was used as a random effect. The first four variables express soil resources. The next five variables represent native diversity components (richness, phylogenetic diversity (PD); functional dispersion (FDis); functional richness (FRic); CWM-height). The last two variables represent the mean functional (ANMFD) and phylogenetic (ANMPD) distances between alien and native species. Only the significant relationships are shown in the table. R_m^2 and R_c^2 are the marginal and conditional coefficients of determination, respectively. The former expresses the proportion of variance explained by the fixed effect only, the latter by the fixed and the random effects combined.

Table 2. Results of multivariate linear mixed models showing the effects of the significant interactions between soil resources as a PCA axis, native components, and the mean functional distance between aliens and natives (ANMFD) on alien performance and abundance. Significant values are in bold.

Explanatory variable	Estimate	SE	<i>t</i>	Pr(> <i>t</i>)	R_m^2	R_c^2
Alien performance						
Richness	-0.127	0.032	-3.970	<0.001		
Soil Resources	0.474	0.171	2.780	0.006		
Soil Resources: richness	-0.068	0.021	-3.357	<0.001	0.107	0.17
PD	-0.141	0.043	-3.327	<0.001		
Soil Resources	0.496	0.173	2.857	0.005		
Soil Resources: PD	-0.084	-0.026	-3.259	0.001	0.08	0.18
CWM-Height	-0.003	0.0716	-4.219	<0.001		
Soil Resources	0.119	0.104	1.189	0.235		
Soil Resources: CWM-Height	-0.002	0.0085	-2.211	0.03	0.105	0.15
log (ANMFD)	0.27	0.08	3.40	<0.001		
Soil Resources	-0.71	0.211	-3.317	0.001		
Soil Resources: log. ANMFD	0.109	0.033	3.345	<0.001	0.08	0.34
Alien abundance						
Richness	-0.093	0.031	-3.084	0.005		
Soil Resources	-0.531	0.152	-3.485	0.0014		
Soil Resources: richness	-0.064	0.019	-3.373	0.002	0.12	0.31
PD	-0.071	0.043	-1.662	0.004		
Soil Resources	-0.481	0.168	-2.865	0.006		
Soil Resources: PD	-0.064	0.026	-2.490	0.002	0.067	0.35
CWM-Height	-0.002	0.007	-2.551	0.0142		
Soil Resources	0.112	-0.188	-1.910	0.061		
Soil Resources: CWM-Height	-0.0013	0.0009	-1.547	0.013	0.068	0.38
log (ANMFD)	0.31	0.07	4.32	<0.001		
Soil Resources	-0.61	0.191	-3.173	<0.001		
Soil Resources: log. ANMFD	0.069	0.0263	2.622	0.009	0.06	0.51

Notes: Plot identity was used as a random effect. See Table 1 for abbreviations.

Structural equation model (SEM)

To estimate the plausible influences of biotic components (native diversity and relatedness) and abiotic components (soil resources) on performance and abundance of alien plants, we used a structural equation model (Grace and Pugsek 1997, Grace 2006) starting with the most complex one (Appendix S1: Section S3), from which we selected simpler plausible models. The explanatory variables were native diversity components (richness, functional diversity, NMPD, NMFD, CWM-performance traits), biotic relatedness (ANMPD, ANMFD), and soil resources which were linked to two response variables (alien performance and abundance). We included the relationships among native components as underlying structures in the model. Additionally, we included the effect of soil resources on the relatedness component and on the native diversity component. This a priori full model was then subjected to backward elimination using AICc as

a criterion. As a first stage of analysis, distributional assumptions were examined for all variables to determine whether transformations were necessary. Additionally, relationships between variables were examined for indications of nonlinearities before inclusion in the SEM. Model adequacy was evaluated based on model chi-square values and associated *P* values. Note that model adequacy is indicated by *P* values >0.05, since it is a goodness-of-fit test. The SEM model was calculated using the “psem” function in R (package “piecewise,” version 2.1.0, Lefcheck 2016).

RESULTS

Influences of biotic components, resources availability, and their interactions on alien abundance and performance

First, univariate mixed-effect models revealed almost exclusively negative relationships between

the performance of alien plants and resident native diversity measures. Alien performance declined significantly in species-rich and functionally diverse native assemblages (high FDis), which had high values of community-weighted mean (CWM) leaf production, biomass, height, and floral production (Table 1). However, mixed-effect models revealed non-significant effects of native phylogenetic diversity (PD), of the functional richness (FRic), and of the mean phylogenetic and functional distances among natives (NMPD, NMFD). The results for alien abundance were similar to those for alien performance, except for CWM for biomass and leaf production that were not statistically significant.

Second, the univariate mixed-effects models indicated highly significant positive effects of the functional biotic distance (ANMFD, mean functional distances between aliens and natives) on both alien performance and abundance (Table 1). The biotic distance based on phylogeny (ANMPD, mean phylogenetic distances between aliens and natives) was only marginally significant for alien abundances. In addition, univariate models exhibited non-significant positive relationships between the performance and abundance of alien plants and the availability of soil nitrogen content, of organic matter, and of soil water content in all plots ($P = 0.65, 0.93$; $R_c^2 = 0.041, 0.08$ for alien abundance and performance, respectively).

We found that the importance of soil resources to invasion was impossible to discern in univariate models because of significant interactions of soil resources with native components and biotic distances, so that we set up the importance of these interaction effects using multivariate mixed-effects models. These models unraveled significant interaction between soil resources (PCA) and the mean functional distance between aliens and natives (ANMFD), which had a significant positive effect on alien performance ($P = 0.009, R_c^2 = 0.34$) and on alien abundance ($P = 0.001, R_c^2 = 0.51$). Alien performance and abundance increased with increasing mean functional distance between aliens and natives in high resources plots. Accounting for significant interactions between soil resources and native diversity components revealed that abiotic factors affected alien performance and abundance, but that the strength and direction of abiotic

effects depend strongly on native richness, phylogenetic diversity, and CWM-height. These native components were significantly interacting with soil resources, and such interactions had negative significant effects on both alien performance ($P = 0.001, P = 0.001, P = 0.03, R_c^2 = 0.17, 0.18, 0.15$, respectively) and abundance ($P = 0.002, P = 0.002, P = 0.01, R_c^2 = 0.31, 0.35, 0.38$, respectively) (Table 2 and Fig. 1). In addition, we found evidence that, in the resource-rich environments, alien abundance increased while alien performance decreased with increasing height of native plants (Fig. 1a, d).

Structural equation model (SEM) for alien performance and abundance

Firstly, the best SEM model revealed a strong significant effect of CWM-performance traits and native richness on native functional diversity (Table 3, Fig. 2). Secondly, there was a strong significant negative effect of CWM-performance traits of native community on both alien abundance and performance and of native functional diversity on alien abundance. However, the SEM model also revealed non-significant negative effects of native richness, phylogenetic measures (PD, NMPD), and mean biotic distances among natives (NMPD, NMFD) on alien abundance and growth performance. Thirdly, the SEM model unraveled a strong significant positive direct effect of mean functional distance between aliens and natives (ANMFD) on alien abundance and performance, and of mean phylogenetic distance between aliens and natives (ANMPD) on alien abundance in all invaded plots (Table 2, Fig. 2). In other words, higher values of alien performance and abundance were significantly explained by high functional distance between aliens and natives. Interestingly, there was no direct significant pathway from soil resources to alien performance and abundance; however, there was an indirect significant positive pathway from soil resources to the mean functional distance between aliens and natives (ANMFD), which is in accordance with the results of the multivariate mixed-effects models (Fig. 2c, f).

DISCUSSION

Our study investigated the likely biotic and abiotic factors that are important for preventing the

invasion of alien plant species in an arid ecosystem. We emphasized a framework that linked native diversity components, phylogenetic and functional similarity to natives, and harshness of the abiotic environment to alien invasiveness. We highlighted two intriguing results. First, soil resources had no significant direct effect on alien success but had a strong influence in interaction with other variables. When resources were limited, native productivity (high CWM-traits values) and functional diversity reduced significantly the growth performance and abundance of alien plants that were functionally and phylogenetically similar to natives. Second, we found evidence in resource-rich environments that alien species were in higher abundance even when native plants were competitive (i.e., taller), but their performance remained low (Fig. 1a, d). This could occur if empty niches facilitate the establishment of alien plants, while high productivity of native plants negatively impact alien performance.

The relative contribution of both the biotic and abiotic components of ecological resistance was highly important in predicting the success of alien invasiveness in this arid ecosystem. Alien plants performance and abundance increased when they were functionally and phylogenetically distantly related to natives and when soil resources were high (Fig. 2). In this sense, environmental conditions in terms of resource availability are partially able to prevent alien species establishment, especially in species-diverse communities. This is possible because diverse native communities are more likely to contain species that utilize their resources more efficiently, making it difficult for less abundant invaders that compete for the same resources to establish. These results fit well with the idea of assembly theory, which predicts that a successful invasive species must be able to pass through all potential biotic and abiotic filters (Booth et al. 2003, Von Holle 2005). A main finding in this study was that alien species that were functionally closely related to the natives performed poorly and had low abundance and performance when native functional diversity was high. This finding suggested that the interaction of biotic filtering (competitive exclusion) and abiotic conditions might be the main driver of resisting potential invaders (Gallien et al. 2017, Bennett 2019). Indeed, competition from the resident native community in

stressful conditions (Bertness and Callaway 1994) can eliminate alien taxa that are similar to natives and that have a very narrow range of traits (e.g., short with small leaves, see Mayfield and Levine 2010).

Although competitive interactions are often considered less important in harsh or stressful ecosystems (Grime 1977), native species competition can determine whether the establishment of potential invader is possible or not (Chesson and Huntly 1997). In harsh environments, resource scarcity may limit the competitive advantage conferred to fast-growing potential invaders, and biotic resistance may additionally prevent their invasion. For example, competitive native species may outcompete stress-intolerant invaders to different stressors, including extreme resource scarcity (e.g., low nutrients, water, light) that slow or halt invaders metabolism and therefore decline their growth (Alpert et al. 2000, Shea and Chesson 2002). Additionally, if stress-adapted natives are more efficient at assimilating limited resources, they may drive resources down to levels that are inappropriate for potential invaders to survive.

The productivity of the native communities also played a role in determining the invasion success of the alien species. According to the productivity hypothesis (Petruzzella et al. 2020), more productive communities are better able to repel invasion simply because there is less space available for the invaders to occupy. However, this was not the case in our study. Instead, in high-resource environments, we found that highly productive native communities included a high abundance of alien species, yet the performance of these invaders remained low. There were still empty niches that could be filled by alien plants; however, their performance declined likely due to the competitive effects of the native species. For example, the competitive advantage of being taller for resident natives has been considered to be a potentially strong biotic filter and are thus better competitors (Mayfield and Levine 2010, Kraft et al. 2015) to resist alien plants in rich-resources environments (Fried et al. 2018). This competition will hinder alien species establishment success because they will be less capable of competing for light and water when in low numbers (Angadi and Entz 2002). Furthermore, native individuals with higher leaf and biomass production have high relative

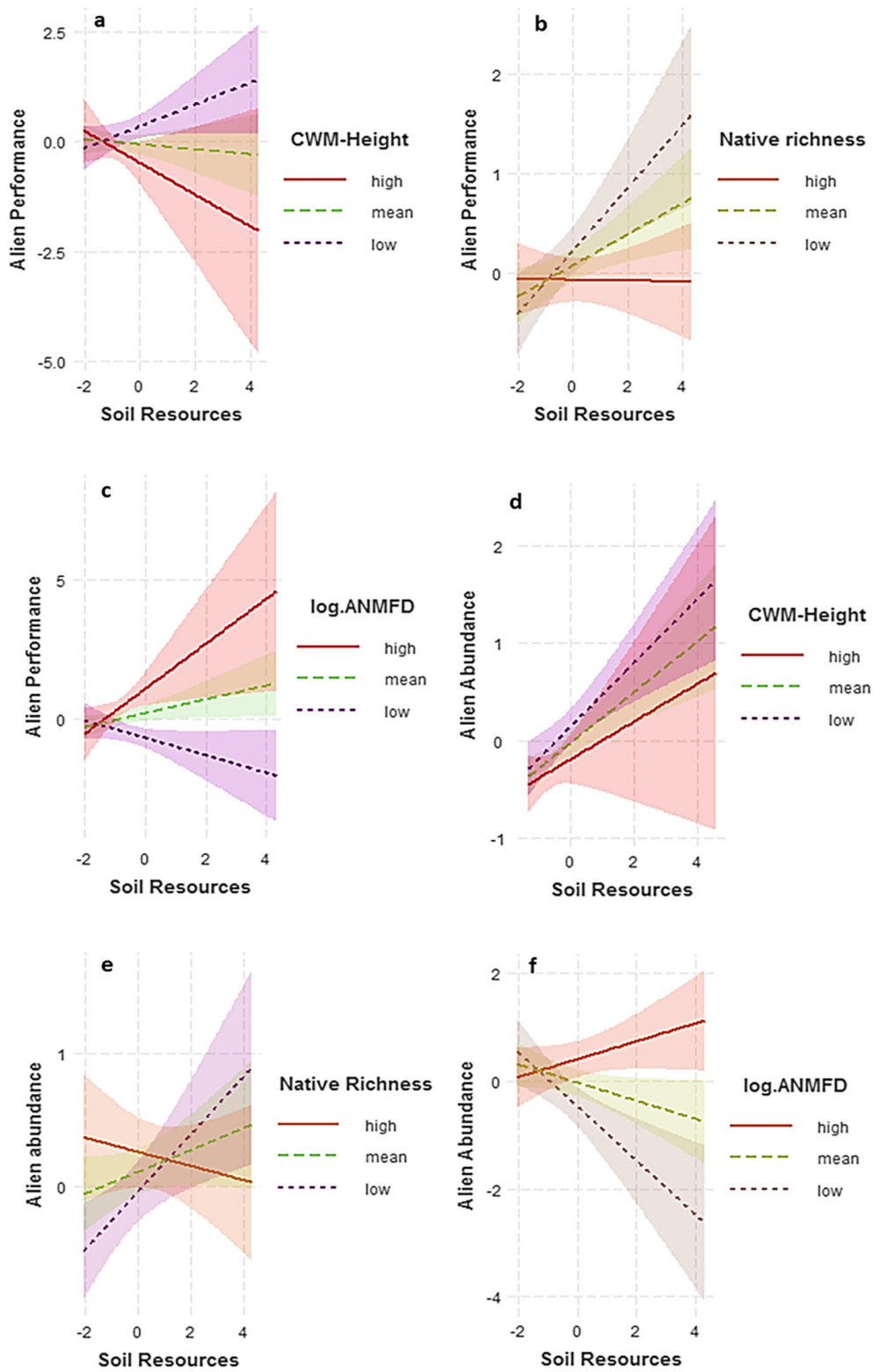


Fig. 1. Significant positive responses of alien performance (panel c) and alien abundance (panel f) to the

(Fig. 1. *Continued*)

interaction between soil resources and the mean functional distance ANMFD, and significant negative responses of alien performance and abundance to the interaction between soil resources and CWM-height (panels a, d), native richness (panels b, e). Continuous and dashed lines represent three levels (high mean-low) of the explanatory variables (CWM-height-richness-ANMFD) mediated by soil resources and expected by the model with 95% confidence intervals (shaded areas). All *x*-axes and *y*-axes were scaled.

Table 3. Results of the best piecewise structural equation model (SEM) explaining the performance and abundance of alien plant species as response variables of interest. Significant values are in bold.

Response variable	Explanatory variable	Estimate	SE	df	<i>t</i>	<i>P</i>
Alien performance	ANMPD	0.028	0.0612	93	0.455	0.65
	ANMFD	0.503	0.0569	110	8.847	0.0001
	NMPD	-0.013	0.0599	110	-0.216	0.829
	NMFD	-0.045	0.0604	110	-0.752	0.454
	Native richness	-0.11	0.0731	110	-1.504	0.135
	Native functional diversity	-0.046	0.072	110	-0.634	0.527
	Native CWM-performance traits	-0.29	0.0818	93	-3.544	0.0006
log. alien abundance	Soil resources	0.0204	0.0612	93	0.333	0.739
	ANMPD	0.194	0.0651	93	2.972	0.0038
	ANMFD	0.402	0.06	111	6.7076	0.0001
	NMPD	-0.022	0.0637	110	-0.3479	0.7286
	NMFD	-0.0499	0.0642	110	-0.7769	0.4389
	Native richness	-0.023	0.0777	110	-0.301	0.764
	Native functional diversity	-0.121	0.0765	110	-1.5764	0.0011
ANMPD	Native CWM-performance traits	-0.262	0.087	93	-3.0089	0.0034
	Soil resources	0.0039	0.065	93	0.06	0.95
	Soil resources	0.022	0.0444	95	0.2688	0.079
	Soil resources	0.083	0.0973	95	0.8533	0.0040
	Native CWM-performance traits	0.613	0.069	209	8.826	0.0001
	Native richness	0.226	0.069	209	3.245	0.0014

Notes: The explanatory variables are composed of three components: (1) biotic distances between alien and native species (see Table 1 for abbreviations); (2) native diversity components ("Native functional diversity" is the first PCA axis of FRic and FDis; "Native CWM-performance traits" is the first PCA axis of the four CWM variables); (3) resources availability ("Soil resources" is the first PCA axis of the three soil variables in Table 1). Note that the full a priori model included the effect of soil resources on the native diversity components (see Appendix S1), but these relationships were not retained in the best model.

growth rates and are more exploitative in their resources utilization (Westoby 1998). These features could generally allow natives to better endure high competition effects on the potential invaders (Goldberg and Landa 1991, Kraft et al. 2014). Thus, alien individuals growing in such competitive native communities may respond by shifting to lower trait values (Tecco et al. 2010) that potentially explained the observed pattern of lower performance of alien plants in rich-resource environments.

STUDY CONSTRAINTS

This study demonstrates how biotic and abiotic components interact to shape the ecological

resistance to plant invasion in an arid ecosystem. However, we acknowledge some limitations associated with our study, necessitated by constraints working in the SKP. First, a pairwise design was practically not implementable because we generally could not find non-invaded plots in similar environmental conditions. This is due to the sparse vegetation under the arid conditions that prevail in SKP. Second, in such mountainous arid ecosystems with rocky hard soil, a bias toward sites with higher species diversity (selective sampling) may be unavoidable (Lepš and Hadincová 1992), as randomly selecting 10 by 10 m surfaces in our study site would most of the time yield plots with no or very low vegetation cover.

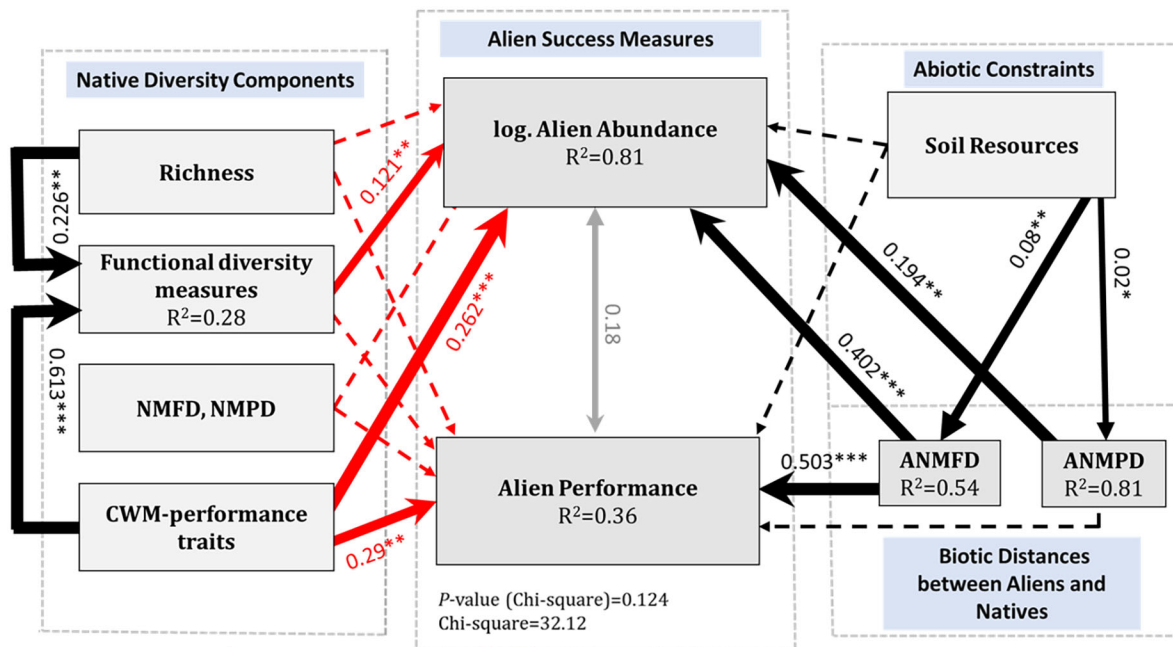


Fig. 2. Result of the best fitted piecewise structural equation model showing the pathways explaining the negative (red arrows) and positive (black arrows) effects of specific native diversity components, of the biotic distances between aliens and natives, and of soil resources on alien success measures. Boxes represent measured variables and arrows unidirectional relationship among variables. Arrow thickness is proportional to their standardized regression coefficient (given in number with their significance). Non-significant effects are represented by dashed arrows. The gray arrow between alien abundance and performance is Pearson correlation ($P = 0.18$). The P value and chi-square are the results of the goodness-of-fit test of the model. Full results and abbreviations are in Table 3.

CONCLUSION

Overall, our results provide evidence that functional native diversity and similarity to natives, linked indirectly with low resources availability, increases ecological resistance to potential invaders. Most importantly, these results emphasize the interaction between biotic and abiotic constraints to the potential invaders. We found an evidence that alien plants that are most dissimilar to natives can overcome biotic resistance in resource-rich environments, thereby possibly having a better chance to succeed in the invasion process. We suggest that the biotic resistance to potential invaders is shaped by the competitive ability of native species that is regulated by native diversity and productivity. Therefore, future experimental and field studies aimed at unraveling the mechanisms

of biotic resistance across an environmental gradient should not neglect the relatedness of the invader species to native species, nor the changes in the competitive outcomes among species under different stress levels.

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LITERATURE CITED

- Allen, S. E., H. M. Grimshaw, J. A. Parkinson, and C. Quarmby. 1974. Chemical analysis of ecological materials. Blackwell Scientific Publications, Hoboken, New Jersey, USA.
- Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3:52–66.
- Angadi, S., and M. Entz. 2002. Root system and water use patterns of different height sunflower cultivars. *Agronomy Journal* 94:136–145.
- Ayyad, M. A., A. M. Fakhry, and A.-R.-A. Moustafa. 2000. Plant biodiversity in the Saint Catherine area of the Sinai peninsula, Egypt 17.
- Basuki, T. M., P. E. Van Laake, A. K. Skidmore, and Y. A. Hussin. 2009. Allometric equations for estimating the above-ground biomass in tropical lowland Dipterocarp forests. *Forest Ecology and Management* 257:1684–1694.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67:1–48.
- Bennett, J. A. 2019. Similarities between invaders and native species: moving past Darwin's naturalization conundrum. *Journal of Vegetation Science* 30:1027–1034.
- Benson, D. A., I. Karsch-Mizrachi, D. J. Lipman, J. Ostell, and D. L. Wheeler. 2005. GenBank. *Nucleic Acids Research* 33:D34–D38.
- Bertness, M. D., and R. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9:191–193.
- Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invasibility and vegetation dynamics. *Journal of Ecology* 91:36–48.
- Brown, C. S., K. J. Rice, and V. P. Claassen. 1998. Competitive growth characteristics of native and exotic grasses.
- Burt, J., and S. Harrison. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications* 12:40–51.
- Byun, C., S. De Blois, and J. Brisson. 2013. Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology* 101:128–139.
- Byun, C., S. de Blois, and J. Brisson. 2015. Interactions between abiotic constraint, propagule pressure, and biotic resistance regulate plant invasion. *Oecologia* 178:285–296.
- Cadotte, M. W., S. E. Campbell, S.-P. Li, D. S. Sodhi, and N. E. Mandrak. 2018. Preadaptation and naturalization of non-native species: Darwin's two fundamental insights into species invasion. *Annual Review of Plant Biology* 69:661–684.
- Cadotte, M. W., and L. S. Jin. 2014. All in the family: relatedness and the success of introduced species. Pages 147–162 in R. P. Keller, M. W. Cadotte, and G. Sandiford, editors. *Invasive species in a globalized world*. University of Chicago Press, Chicago, Illinois, USA.
- Carboni, M., I. Calderon-Sanou, L. Pollock, C. Violle, DivGrass Consortium, and W. Thuiller. 2018. Functional traits modulate the response of alien plants along abiotic and biotic gradients. *Global Ecology and Biogeography* 27:1173–1185.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences of the United States of America* 87:9610–9614.
- Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15:22–40.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* 150:519–553.
- Conti, L., et al. 2018. Functional trait differences and trait plasticity mediate biotic resistance to potential plant invaders. *Journal of Ecology* 106:1607–1620.
- Daehler, C. C. 2001. Darwin's naturalization hypothesis revisited. *American Naturalist* 158:324–330.
- Danin, A., editor. 2006. *Flora of Israel Online*. The Hebrew University of Jerusalem, Jerusalem, Israel.
- D'Antonio, C. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. *Ecology* 74:83–95.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528–534.
- Diez, J. M., J. J. Sullivan, P. E. Hulme, G. Edwards, and R. P. Duncan. 2008. Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. *Ecology Letters* 11:674–681.
- Duncan, R. P., and P. A. Williams. 2002. Ecology: Darwin's naturalization hypothesis challenged. *Nature* 417:608.
- El-Barougy, R. F., I. Elgamal, R. P. Rohr, A. F. Probert, A. A. Khedr, and S. Bacher. 2020a. Functional similarity and dissimilarity facilitate alien plant invasiveness along biotic and abiotic gradients in an arid protected area. *Biological Invasions* 22:1997–2016.

- El-Barougy, R., J. S. MacIvor, C. A. Arnillas, R. M. Nada, A.-H.-A. Khedr, and M. W. Cadotte. 2020b. Richness, phylogenetic diversity, and abundance all have positive effects on invader performance in an arid ecosystem. *Ecosphere* 11:e03045.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America* 100:8916–8920.
- Fargione, J. E., and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters* 8:604–611.
- Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pages 57–66 in R. H. Groves and J. J. Burdon, editors. *Ecology of biological invasions: an Australian perspective*. Australian Academy of Science, Canberra, ACT, Australia.
- Fried, G., L. Mahaut, A. Pinston, and M. Carboni. 2018. Abiotic constraints and biotic resistance control the establishment success and abundance of invasive *Humulus japonicus* in riparian habitats. *Biological Invasions* 20:315–331.
- Funk, J. L., R. J. Standish, W. D. Stock, and F. Valadares. 2016. Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology* 97:75–83.
- Gallien, L., and M. Carboni. 2017. The community ecology of invasive species: Where are we and what's next? *Ecography* 40:335–352.
- Gallien, L., N. E. Zimmermann, J. M. Levine, and P. B. Adler. 2017. The effects of intransitive competition on coexistence. *Ecology Letters* 20:791–800.
- Gerhardt, F., and S. K. Collinge. 2007. Abiotic constraints eclipse biotic resistance in determining invasibility along experimental vernal pool gradients. *Ecological Applications* 17:922–933.
- Gerhold, P., M. Pärtel, O. Tackenberg, S. M. Hennekens, I. Bartish, J. H. Schaminée, A. J. Fergus, W. A. Ozinga, and A. Prinzing. 2011. Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *American Naturalist* 177:668–680.
- Going, B. M., J. Hillerislambers, and J. M. Levine. 2009. Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia* 159:839–847.
- Goldberg, D. E., and K. Landa. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79:1013–1030.
- Grace, J. 2006. References. Pages 350–360 in *Structural equation modeling and natural systems*. Cambridge University Press, Cambridge, UK. <http://dx.doi.org/10.1017/CBO9780511617799.016>
- Grace, J. B., and B. H. Pugsek. 1997. A structural equation model of plant species richness and its application to a coastal wetland. *American Naturalist* 149:436–460.
- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Harrison, S., K. Rice, and J. Maron. 2001. Habitat patchiness promotes invasion by alien grasses on serpentine soil. *Biological Conservation* 100:45–53.
- Hector, A., K. Dobson, A. Minns, E. Bazeley-White, and J. Hartley Lawton. 2001. Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecological Research* 16:819–831.
- Hooper, D. U., and J. S. Dukes. 2010. Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology* 98:764–777.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- Kemmel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417:636.
- King, S., and J. Grace. 2000. The effects of soil flooding on the establishment of cogongrass (*Imperata cylindrica*), a nonindigenous invader of the Southeastern United States. *Wetlands* 20:300–306.
- Klute, A. 1986. Water retention: laboratory methods. Pages 635–662 in A. Klute, editor. *Methods of soil analysis: part 1—physical and mineralogical methods*. Soil Science Society of America, American Society of Agronomy, Madison, Wisconsin, USA.
- Kraft, N. J. B., G. M. Crutsinger, E. J. Forrester, and N. C. Emery. 2014. Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. *Oikos* 123:1391–1399.
- Kraft, N. J. B., O. Godoy, and J. M. Levine. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences of the United States of America* 112:797–802.

- Labrière, E., and P. Legendre. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305.
- Lefcheck, J. S. 2016. piecewiseSEM: piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution* 7:573–579.
- Lepš, J., and V. Hadincová. 1992. How reliable are our vegetation analyses? *Journal of Vegetation Science* 3:119–124.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7:975–989.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26.
- MacDougall, A. S., B. Gilbert, and J. M. Levine. 2009. Plant invasions and the niche. *Journal of Ecology* 97:609–615.
- Mayfield, M. M., and J. M. Levine. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities: phylogeny and coexistence. *Ecology Letters* 13:1085–1093.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* 91:97–108.
- Oakley, C. A., and J. S. Knox. 2013. Plant species richness increases resistance to invasion by non-resident plant species during grassland restoration. *Applied Vegetation Science* 16:21–28.
- Petruzzella, A., J. Manschot, C. H. A. van Leeuwen, B. M. C. Grutters, and E. S. Bakker. 2018. Mechanisms of invasion resistance of aquatic plant communities. *Frontiers in Plant Science* 9:134.
- Petruzzella, A., T. A. D. S. S. R. Rodrigues, C. H. A. van Leeuwen, F. de Assis Esteves, M. P. Figueiredo-Barros, and E. S. Bakker. 2020. Species identity and diversity effects on invasion resistance of tropical freshwater plant communities. *Scientific Reports* 10:5626.
- Prober, S., and I. Lunt. 2008. Restoration of *Themeda australis* swards suppresses soil nitrate and enhances ecological resistance to invasion by exotic annuals. *Biological Invasions* 11:171–181.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rejmánek, M. 1989. Invasibility of plant communities. Pages 369–383 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley & Sons, Chichester, UK.
- Riis, T., A. Olesen, S. M. Jensen, A. B. Alnoee, A. Baattrup-Pedersen, T. L. Lauridsen, and B. K. Sorrell. 2018. Submerged freshwater plant communities do not show species complementarity effect in wetland mesocosms. *Biology Letters* 14:20180635.
- Saccone, P., J. Girel, J.-P. Pages, J.-J. Brun, and R. Michalet. 2013. Ecological resistance to *Acer negundo* invasion in a European riparian forest: relative importance of environmental and biotic drivers. *Applied Vegetation Science* 16:184–192.
- Seabloom, E., and A. van der Valk. 2003. Plant diversity, composition, and invasion of restored and natural prairie pothole wetlands: implications for restoration. *Wetlands* 23:1–12.
- Shapiro, S. S., and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52:591–611.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution* 17:170–176.
- Sheppard, C. S., and F. M. Schurr. 2019. Biotic resistance or introduction bias? Immigrant plant performance decreases with residence times over millennia. *Global Ecology and Biogeography* 28:222–237.
- Spasojevic, M. J., and K. N. Suding. 2012. Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *Journal of Ecology* 100:652–661.
- Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America* 103:5841–5845.
- Swenson, N. 2014. *Functional and phylogenetic ecology* in R. Springer-Verlag, New York, New York, USA.
- Tecco, P. A., S. Dazíaz, M. Cabido, and C. Urcelay. 2010. Functional traits of alien plants across contrasting climatic and land-use regimes: Do aliens join the locals or try harder than them? Alien traits across climates and land uses. *Journal of Ecology* 98:17–27.
- Thuiller, W., L. Gallien, I. Boulangeat, F. D. Bello, T. Münkemüller, C. Roquet, and S. Lavergne. 2010. Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions* 16:461–475.
- Veron, S., T. J. Davies, M. W. Cadotte, P. Clergeau, and S. Pavoine. 2017. Predicting loss of evolutionary history: Where are we? *Biological Reviews* 92:271–291.
- Vilà, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive

- alien plants: a meta-analysis of their effects on species, communities and ecosystems: ecological impacts of invasive alien plants. *Ecology Letters* 14:702–708.
- Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301.
- Violle, C., M.-L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Von Holle, B. V. 2005. Biotic resistance to invader establishment of a southern Appalachian plant community is determined by environmental conditions. *Journal of Ecology* 93:16–26.
- Von Holle, B., H. R. Delcourt, and D. Simberloff. 2003. The importance of biological inertia in plant community resistance to invasion. *Journal of Vegetation Science* 14:425–432.
- Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility - evidence of a biological mechanism or a consequence of sampling effect? *Oikos* 95:161–170.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475–505.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Young, S. L., J. N. Barney, G. B. Kyser, T. S. Jones, and J. M. DiTomaso. 2009. Functionally similar species confer greater resistance to invasion: implications for grassland restoration. *Restoration Ecology* 17:884–892.
- Zavaleta, E. S., and K. B. Hulvey. 2007. Realistic variation in species composition affects grassland production, resource use and invasion resistance. *Plant Ecology* 188:39–51.

DATA AVAILABILITY

Data are available from Zenodo: <https://doi.org/10.5281/zenodo.5628255>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3893/full>