Is biotic resistance to invaders dependent upon local environmental conditions or primary productivity? A meta-analysis

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Abstract

Biotic resistance is an important component to limiting the spread of invasive plants into native communities. However, under certain conditions native plants may also facilitate invasion, a process identified as biotic assistance. Identifying the conditions that associate with resistance and assistance is needed to better understand the factors driving species invasion.

Substantial theory and empirical work suggests net effects of neighbors may be dependent upon habitat productivity and environmental conditions. How that applies to the interaction among the resident community and the invaders is largely untested. Here we compiled data from 23 articles, which had experimentally determined the strength of biotic resistance and/or assistance. We then combined these data with remote-sensing estimates of productivity, precipitation and temperature at each study site. Using standard meta-analytical techniques we determined the overall effect resident communities had on the emergence, growth, reproduction and survival of non-native invaders. Further, we tested whether the interaction between resident communities and invasive species was influenced by primary productivity, temperature and precipitation.

Across all sites, we found broad support for biotic resistance, while evidence for biotic assistance was rare. However, we found the relative magnitude of biotic resistance on invaders increased with temperature or precipitation; a pattern consistent with the stress gradient hypothesis. In contrast we found no evidence that the strength of biotic resistance varied as a function of primary productivity. Further evaluation of the relationship between productivity and environmental conditions on the direction and strength of the effect of resident species on invaders may help predict invasion establishment and success. Understanding or predicting the susceptibility of communities to invasion may help prioritize management efforts.

Zusammenfassung

Biotische Resistenz ist eine wichtige Komponente für die Begrenzung des Eindringens von invasiven Pflanzen in einheimische Gemeinschaften. Indessen können einheimische Pflanzen unter bestimmten Bedingungen die Invasion begünstigen, ein Prozess, der hier als "biotische Assistenz" ("biotic assistance") bezeichnet wird. Die Bedingungen herauszufinden, die mit Resistenz und Assistenz verbunden sind, ist notwendig, um die Faktoren, die die Invasion von Arten steuern, besser zu verstehen. Umfangreiche theoretische und empirische Forschungen legen nahe, dass der Nettoeffekt von Nachbarn von der Produktivität des Lebensraums und den Umweltbedingungen abhängen könnte. Wie dies auf die Interaktion zwischen der vorhandenen Gemeinschaft und den Neuankömmlingen zutrifft, blieb weitgehend ungeprüft. Wir stellten Daten aus 23 Artikeln zusammen, die die Stärke von

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Introduction

Biotic resistance is the ability of a resident community to limit recruitment and growth of invasive species (Levine, Adler, & Yelenik 2004). As such, when looking at biotic resistance we tend to assume that the resident community will have a negative effect on invasive species (i.e. competition) (Levine et al. 2004). However, resident communities may also facilitate invasive species establishment, growth and spread (Badano, Villarroel, Bustamante, Marquet, & Cavieres 2007). The processes where native species facilitate exotic species have been termed biotic assistance (Inderjit & Cahill 2015). Biotic resistance or assistance may result from both direct as well as indirect interactions (Bever 2003; Levine et al. 2004; Inderjit & Cahill 2015). Consequently, the outcome of the interaction between native communities and invasive species may range from biotic resistance to assistance (Fig. 1).

The effectiveness of native communities at limiting invasion varies (Lonsdale 1999), and this variation has been partly explained through changes in species richness and phylogenetic diversity within the native community (Dukes 2001; Kennedy et al. 2002; Strauss, Webb, & Salamin 2006; Gerhold et al. 2011). Absent, however, is a broad analysis across species and systems, investigating how habitat productivity and environmental conditions influence the ability of the resident communities to resist, or potentially facilitate invasion (Fig. 1). This is particularly surprising as substantial theory suggests that the intensity and outcomes of plant–plant interactions are dependent upon primary productivity and environmental stress (Grime 1973; Bertness & Callaway 1994). The same may be true for invasive species’ effect on the resident community with the strength and direction of this effect varying depending on the habitat’s productivity and/or environmental conditions (Fig. 1) (e.g. MacDougall, Boucher, Turkington, & Bradfield 2006).

Plant ecologists have long focused on the relationship between competition and productivity. It has been proposed that competition becomes stronger and influences community assembly as productivity increases, while stressful conditions are more important for assembly at low productivity (Grime 1973). A slightly different model, the stress gradient hypothesis (Bertness & Callaway 1994) proposes that competition is predominant in environments of intermediate productivity, while facilitation occurs more frequently in both highly stressful and highly productive environments. In contrast, an alternative theory proposes that competition is important across a productivity gradient, with different resources being limiting at both ends of this gradient (Tilman 1988).

Further, two meta-analyses suggest a general decline in competition with increased productivity and decreased stress (Goldberg, Rajaniemi, Gurvitch, & Stewart-Oaten 1999; Maestre, Valladares, & Reynolds 2005). However, these theories have rarely been tested in the context of invasion and biotic resistance (von Holle 2005, 2013; Chambers, Roundy, Blank, Meyer, & Whittaker 2007; Lortie & Cushman 2007; Harrison, Cornell, & Grace 2015; Reisner, Doescher, & Pyke 2015).

Evidence suggests that environmental conditions and productivity may be important in determining invasion success. For example, invasive species are commonly found invading productive environments with greater resource availability (Stohlgren et al. 1999; Foster, Smith, Dickson, & Hildebrand 2002), however, this is not always the case, as invasive species can also be found invading stressful habitats (Badano et al. 2007; Lortie & Cushman 2007). Although invasive species performance tends to increase under benign, fertile conditions (Dukes & Mooney 1999; Chambers et al. 2007; Gerhardt & Collinge 2007; Goldstein & Suding 2014; Harrison et al. 2015), this advantage can be offset or decreased by the presence of a more resistant community in those areas (Chambers et al. 2007; Eskelinen & Harrison 2015).
productivity and/or environmental conditions varied depending on an invaders’ functional group.

Materials and methods

Literature criteria and dataset construction

An ISI Web of Science search was conducted to retrieve relevant publications to include in the meta-analysis. We used – invas* OR exotic* OR alien* OR introd* – as key words, given the number of terms used to define similar concepts (Richardson et al. 2000). We then refined the results to all articles included within the research areas of Ecology, Plant Sciences and Forestry, and to articles published between 1995 and 2015, as environmental data are not available for previous years (Appendix A). This search resulted in 506,678 studies screened. To minimize the likelihood of relevant studies missed in our initial search, we further cross-referenced each of the articles for pertinent articles to potentially include. All resultant publications were screened to meet the following criteria: (1) studies needed to compare the performance of an invasive species in an area with and without the resident community present, (2) studies needed to be under field conditions, (3) the resident community needed to be native to its area and (4) means, standard error and sample sizes for treatments and the control needed to be available. If in graphical form, graphs were digitized and data points were extracted using the software Engauge Digitizer v.2.12 (http://digitizer.sourceforge.net). Including only
experimental tests of biotic resistance (resident community intact vs. removed) limited the number of studies in our dataset, but allowed us to directly calculate the strength of interaction among resident communities and invasive species. We treated publications where investigators subjected different invasive species or the same invader to different communities as separate studies (Gurevitch & Hedges 1993). If a study included various levels of vegetation or neighbor removal, we used data from the most severe treatment.

Response and explanatory variables

From each study, data were collected on invasive species performance with the resident community intact vs. removed. We classified the response variables into 4 categories: emergence, plant size, reproduction and survival. Evaluating different response variables may be important, as some interactions may comprise both competition and facilitation depending on the life stage or the response variable measured in the target species (Callaway & Walker 1997). Further, to look at the direct effect of environmental conditions and productivity on performance, we used data on percent survival and emergence in the absence of competition. Survival and emergence were calculated based on total seeds added or number of initially planted seedlings when metrics were not reported as a percentage. We also extracted information on the exact location of the experiments to obtain data for the following explanatory environmental variables: net primary productivity (NPP), normalized difference vegetation index (NDVI), precipitation and temperature. NPP, NDVI, precipitation and temperature were obtained from the Advances Very High Resolution Radiometer (AVHRR) and the Moderate Resolution Imaging Spectroradiometer (MODIS) remote sensing databases (see Appendix A).

Data analysis

We calculated Hedge’s effect size \( d \) (Gurevitch & Hedges 1993), which is the standardized mean difference between the control group (neighbor intact) \( \bar{X}_C \) and the experiment group (neighbor removal) \( \bar{X}_E \) for plant size, emergence, reproduction and survival, separately using the following equation:

\[
d = \frac{\bar{X}_E - \bar{X}_C}{SD_{\text{pooled}}}
\]

A positive effect size \( d \) indicates a negative effect of neighbors on invasive species performance (competition) while a negative effect size \( d \) indicates a positive effect of neighbors on invasive species performance (facilitation). \( J \) was calculated to correct for small sample bias (Borenstein, Hedges, Higgins, & Rothstein 2009) using the following equation:

\[
J = 1 - \frac{3}{4(n_C + n_E - 2) - 1}
\]

We conducted a random-effects meta-analysis, which is a meta-analysis model (different from a random effect linear model) that allows for variation between study effects in contrast to a fixed-effect model that assumes variance among study effects is known. Between study heterogeneity was assessed by calculating and testing for the significance of \( Q \) (see Appendix B for more details). Analyses were done using weighted linear models, where the models were weighted by the study’s precision \( (W^*) \) using the function \( rma \), from the \textit{metafor} package (Viechtbauer 2010) in R (v.2.15.3, R Core Team, 2013). \( W^* \) was calculated for each study as the inverse of the variance,

\[
W^*_i = \frac{1}{V^*_{si}}
\]

where \( V^*_{si} \) is the within-study variance plus the between-studies variance. Methods for meta-analysis followed those presented in Borenstein et al. (2009). Publication bias, before the inclusion of moderator variables, was assessed through a funnel plot and the trim and fill method (Appendix B for more details).

Linear models were performed to test for the direct effects of environmental conditions on invasive species performance using percent emergence and survival in the absence of neighbors as response variables. Linear mixed effect models were used when testing for the effect of NPP and NDVI, where data source (MODIS or AVHRR) was added as a random effect to control for differences between the two sensors (see Appendix A). Effects of environmental variables and productivity on the neighbor effects on invasive species performance were tested for using meta-regressions. A meta-regression is a meta-analysis that includes, in this case, a continuous variable to describe variation among study effects (moderator) (Borenstein et al. 2009). Each explanatory variable or moderator was tested for individually, in separate models, due to small sample size. In models including NPP and NDVI, data source (MODIS or AVHRR) was added as a random effect; however no random effect was added when evaluating the effect of temperature or precipitation. All meta-regressions were run using the \textit{lm} function (for linear model) in the \textit{stats} package and \textit{lme} function (for linear mixed models) in the \textit{lme4} package in R, with effect size \( d \) as the response variable and weighted by \( W^* \) (Koricheva, Gurevitch, & Mengersen 2013). To test for the robustness of our results (Koricheva & Gurevitch 2014) and because of the significant heterogeneity between studies (see Appendix B) we ran separate models for different invasive functional groups (i.e. forb, shrub, grass and tree). Appendix C when the number of replicates per functional group allowed for it (minimum of 6 replicates). Among all sites included in this study, there was no correlation between precipitation and temperature \((r^2 = -0.07, P = 0.69)\). Neither temperature nor precipitation correlated with NPP \((r^2 = -0.12, P = 0.544; r^2 = -0.1, P = 0.615, \text{respectively})\) or NDVI \((r^2 = -0.06, P = 0.74; r^2 = -0.03, P = 0.873, \text{respectively})\). NPP and NDVI were strongly correlated \((r^2 = 0.87,\)
Results

We found a total of 23 publications that met our criteria (see Appendix C), of which most included more than one invasive species or multiple study sites (treated as different studies). In total, emergence of invasive species was evaluated in 21 studies, plant size in 27, reproduction in 11 and survival in 21. Further, 26 studies included a measure of invasive species survival and 21 studies of emergence reported (or could be calculated) as a percentage. Sites included in our analyses range in temperature and precipitation covering drier areas with high and low temperatures, as well as wetter ones with low temperatures (Fig. 2). Wetter sites with low temperatures are under-represented in most of our analyses, except when looking at the impact of the resident community on invader’s size (Fig. 2B). Thus, our results are applicable to systems with those climatic conditions.

Native community’s impact on invasive species performance

On average, native communities reduced invasive species emergence, size, reproduction and survival, indicating biotic resistance was common (Fig. 3).
Biotic assistance was rare with only one case of net facilitative effects found when looking at the effect on size and one when looking at survival (see Appendix D: Fig. 1). The lack of evidence for biotic assistance is not an artifact of publication bias since the assessment of publication bias through funnel plots revealed that the overall effect size did not change after controlling for it. The trim and fill method revealed three studies missing from the right hand side of the funnel (i.e. those reporting biotic resistance) when evaluating survival (see Appendix B: Fig. 1). We also found significant heterogeneity between studies for three of the four response variables analyzed (size, reproduction and survival) (Appendix B). Significant heterogeneity was expected and further justifies the need to explore other moderator variables to explain the variance between studies.

The effect of productivity, precipitation and temperature on invasive species performance

We found no direct effect of habitat productivity or environmental conditions on invasive species survival and germination in the absence of the resident community (Table 1).

<table>
<thead>
<tr>
<th></th>
<th>Emergence (n = 21)</th>
<th>Survival (n = 26)</th>
</tr>
</thead>
<tbody>
<tr>
<td>NPP Estimate</td>
<td>-0.006</td>
<td>0.033</td>
</tr>
<tr>
<td>F-value</td>
<td>0.833</td>
<td>0.833</td>
</tr>
<tr>
<td>p-Value</td>
<td>0.374</td>
<td>0.374</td>
</tr>
<tr>
<td>Temperature Estimate</td>
<td>-0.003</td>
<td>-1.911</td>
</tr>
<tr>
<td>F-value</td>
<td>3.487</td>
<td>2.128</td>
</tr>
<tr>
<td>p-Value</td>
<td>0.08</td>
<td>0.158</td>
</tr>
<tr>
<td>Precipitation Estimate</td>
<td>-0.074</td>
<td>0.118</td>
</tr>
<tr>
<td>F-value</td>
<td>0.026</td>
<td>3.099</td>
</tr>
<tr>
<td>p-Value</td>
<td>0.872</td>
<td>0.091</td>
</tr>
</tbody>
</table>

and strength (Fig. 4F and I, Appendix E). Temperature was positively associated with the neighbor effect on invasive species size, indicating more biotic resistance in warmer locations. However temperature did not affect biotic resistance for emergence, reproduction or survival (Fig. 4E–H, Appendix E). Precipitation was positively associated with the neighbor effect on invasive species emergence and size, indicating more biotic resistance in wetter locations, but had no effect on the invader reproduction or survival (Fig. 4I–L, Appendix E). Although the addition of moderator variables reduced the heterogeneity between the studies looking at the effect of neighbors on invasive species’ size, the remaining heterogeneity was still significant (Appendix B). This indicates that although moderators were significant, much of the variation remains unexplained, which may be due to the scale at which moderator variables were measured (Appendix A).
Fig. 4. Effect of productivity, temperature and precipitation on the net neighbor effect (effect size \(d\)) on invasive species emergence (A, E, I), plant size (B, F, J), reproduction (C, G, K) and survival (D, H, L). Positive effect size \(d\) indicates negative effect of neighbors on invasive species performance (competition) while a negative effect size \(d\) indicates a positive effect of neighbors on invasive species performance. NPP, temperature and precipitation were averaged for the growing season or duration of the experiment.

When analyzing different invader functional groups separately our results remain quite consistent with our previous results (Fig. 4, Appendix E). NPP was not a significant predictor of neighbor effects on emergence, size or survival of invasive forbs, emergence of invasive shrubs or size of invasive grasses (Appendix F). Temperature was positively associated with neighbor effect on the size of invasive forbs, but not the size of invasive grasses (Appendix F). This indicates that the relationship we observed between temperature and neighbor effect on size is mainly driven by invasive forbs. Consistent with Fig. 4, temperature was not related to emergence or survival, independent of functional group. Precipitation was positively associated with neighbor effect on invasive forb and shrub emergence as well as on the effect on the size of invasive forbs (Appendix F). Interestingly, when looking at different functional groups, precipitation was negatively associated with neighbor effect on invasive forb survival (Appendix F). The relationship between productivity and environmental conditions on invader’s reproduction could not be assessed by functional group due to small sample size.

Discussion

We found a consistent pattern of change in net neighbor effect along precipitation and temperature gradients. This is in spite of having found a limited number of case studies that experimentally manipulated the presence of neighbors
to evaluate their effects on invasive species (Appendix C), which reflects an important hole in our knowledge about invasive species and their interaction with native species. Overall, we found that native communities have a negative impact on invasive species at all measured life stages, indicating biotic resistance (Fig. 3), while examples of biotic assistance were uncommon (Appendix D: Fig. 1). However, we found significant heterogeneity between studies (Appendix B) which highlights the limitations of comparing the effect of different community types on invaders and further stresses the need to explain the variation between studies by including, for example, environmental variables. We found that the strength of the interaction was partly explained by the habitat’s temperature and precipitation, but not by productivity (Fig. 4). Our results support the stress gradient hypothesis (Bertness & Callaway 1994; Maestre, Callaway, Valladares, & Lortie 2009) indicating that net neighbor effects are dependent on abiotic conditions (Fig. 1): stronger suppression of invasive species under warmer and wetter conditions and neutral to facilitative interactions under more stressful conditions. We found no support for a relationship between the strength and/or direction of the interaction and productivity as proposed by Grime (1973) (Fig. 1).

Facilitation seems to be a common outcome of plant–plant interactions among native plants (Brooker et al. 2008; Venail et al. 2014). Venail et al. (2014) found, when reviewing mostly observational – studies testing Darwin’s naturalization hypothesis, that facilitative interactions were almost as common as competitive interactions. However, this does not seem to be the case for the interaction between native communities and invasive species. Further, when evaluating the effect of neighbors on species survival, studies have found that neighbors tend to have neutral to positive effects, while negative effects are commonly found on plant growth (Howard & Goldberg 2001; Maestre et al. 2009). In our meta-analysis, this was not found when looking at the interaction between native communities and invasive species. Although the overall negative effect on survival was not as strong as on the other response variables (Fig. 3), facilitation was rare (Appendix D: Fig. 1). Invasive species facilitation may be uncommon because of their strong competitive ability (Levine et al. 2003; Vila & Weiner 2004), or potentially because they invade areas close to their ecological optimum (Reisser et al. 2015); both being good predictors of facilitation (Brooker & Callaghan 1998; Liancourt, Callaway, & Michalet 2005). Although negative impacts on facilitator species are known to occur even within native species (Schöb et al. 2014) they are thought to destabilize or select against facilitation (Bronstein 2009). The lack of evidence for facilitation may also be a result of the experimental designs included in our analyses. Venail et al. (2014) reviewed mostly observational studies, in contrast to the experimental studies included in our meta-analysis. Both observational and experimental studies have been commonly used to measure facilitation, but greater evidence for facilitation comes from observational studies (Maestre et al. 2005).

Stressful habitats are generally assumed to be less susceptible to invasion, although in our meta-analysis we found no direct effect (in the absence of the native community) of environmental conditions on invasive species performance. This is potentially driven by the fact that we are evaluating different species, each potentially invading areas with climatic conditions to which they are adapted. In fact, modeling invasive species climatic niches has been one of the tools used for predicting invasions (Thuiller et al. 2005; Nuñez & Medley 2011). However, when looking at individual species responses, they have been shown to respond to abiotic and biotic gradients (Chambers et al. 2007; Gerhardt & Collinge 2007; Harrison et al. 2015). Environmental conditions did nonetheless affect the interaction between native communities and invasive species. The relationship between temperature and precipitation and the effect of neighbors on invasive species performance is consistent with the stress gradient hypothesis (Bertness & Callaway 1994; Maestre et al. 2009). Under more stressful conditions (lower average temperature and precipitation) the effects of the resident communities on the invaders were found to be weaker or slightly positive (though not significant) (Fig. 4, Appendix D). Although stressful conditions may be a relative term (Körner 2003), we found temperatures of around 9–15°C or precipitation of 0–50 mm per month to result in weaker effects of the resident community on the emergence and size of invaders (Fig. 4). Abiotic conditions seem therefore to at least partially determine whether the effect of resident communities on invasive species results in biotic resistance or assistance, and the strength of the positive or negative effect (Fig. 1). However, significant variation remained across studies (Appendix B). Measuring environmental variables at more local scales and accounting for other potentially important abiotic factors (e.g. nutrients) may help better explain the variation in the effect of neighbors on invasive species (Fig. 1). Similar results were found at a within-community scale by von Holle (2005, 2013), where the native community had a negative effect on invasive species under more favorable conditions, but not under stressful conditions.

In general, when separating invasive species by their functional groups, we find similar results to those in Fig. 4, supporting the stress gradient hypothesis (Appendix F). The one exception to the stress gradient hypothesis in our results was observed in the lack of a negative effect on invasive forbs survival in the more moist environments (Appendix F), however, this was only observed for invasive forbs, but not shrubs (Appendix F). Overall, invasive forbs were more responsive to the effect of neighbors along precipitation and temperature gradients, while the contrary seems to be true for invasive grasses (Appendix F). This may be explained by a higher root to shoot ratio in invasive grasses which may make them stronger competitors and less susceptible to environmental stressors (Caldwell & Richards 1986; Gordon, Menke, & Rice 1989; Pywell et al. 2003; Hoekstra, Suter, Finn, Husse, & Luescher 2015).
Productivity, as measured here at broad scales, seems to have no impact on species interactions. Although the inclusion of more studies, across a broader range of productivity values is needed to assess the role of productivity on plant–plant interactions, our results are consistent with the growing body of evidence suggesting that productivity is not a strong proxy for competition strength (Fig. 1, Goldberg et al. 1999; Maestre et al. 2005; Bennett & Cahill 2012). The way productivity is measured may be inadequate as we tend to ignore belowground biomass which may represent up to 80% of the total biomass of a community (Lamb & Cahill 2006). Alternatively, competition may not depend on community attributes, such as productivity, but rather on the balance of resource supply and demand (Davis, Wrage, & Reich 1998; Davis, Grime, & Thompson 2000). Our results also show that temperature and precipitation, within the ranges of included studies (Fig. 2), are better predictors of competition, however, the mechanisms behind their impact on species interactions need to be further explored. Maestre et al. (2009) suggested that facilitation is more probable when stress is caused by a non-resource-related environmental factor such as salinity or pH, while competition is more probable under resource-related stress. However, temperature and precipitation can have mixed effects. They are not only a measure of non-resource stress, but also are related to resource availability. Both precipitation and temperature are related to water availability and can alter microbial activity and nutrient cycling in the soil affecting the amount of resources available to plants (Brady & Weil 2007). Further research is needed to disentangle the mechanisms behind the effects of environmental conditions on plant–plant interactions.

**Conclusion and synthesis**

Combining meta-analysis and remote sensing data enabled us to test hypotheses among, instead of just within, sites allowing for broader generalizations; however, the use of remote sensing data measured at broad scale is not without limitations. Moreover, we wish to use this article to emphasize the necessity of more experimental studies to be performed in different geographic locations and community types to better understand the interaction among native communities and invasive species. We found that native plant communities resisted invasion, which limited the emergence, growth, reproduction and survival of invasive species. Although there is variation in the effect on invasive species, facilitation was not found to be a common outcome. The variation in the strength of the interaction could not be explained by the habitat productivity, but in part, by temperature and precipitation. Understanding why some communities are more susceptible to invasion than others is important not only to target invasive species management strategies, but also to understand the mechanisms behind invasion, species interactions and overall community assembly.

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**Appendix A. Supplementary data**

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1111/j.1365-2745.2016.04.001.

**References**


