**Abstract**

Invasive species cause global issues both economically, costing US$314 billion per year in just six countries, and ecologically, reducing species richness by 16.6% with the introduction of just one invasive species. It has long been thought that invasive species are successful due to their lack of specialized niches (i.e. they are generalists). However, it has recently been proposed that invasive species success may also be related to microbial symbiosis. A model system for testing this hypothesis is the Fabaceae family, or legumes, many of whom form mutualistic associations with rhizobia and are prolific invaders world-wide. In a meta-analysis of data collected from 1984-2014, I analyzed 211 experiments spanning 9 continents, 69 countries, and 515 leguminous species to determine if invasive legumes are more commonly generalist or specialist species when it comes to their rhizobial symbionts. Unexpectedly, I found that native legumes on average, actually, associate with more rhizobial species than invasive legumes. Given these data, it is possible that this supports the hypothesis that all microbes exist globally at low levels, providing invasive specialist legumes with their preferred rhizobial symbionts upon arrival to a new ecosystem. However, further data will be analyzed and added to this study to determine the true global patterns.

**Introduction**

There are an estimated 480,000 alien species that have been introduced to ecosystems world-wide (Pimentel et al., 2001). These alien species can be defined as either introduced or invasive, where introduced refers to species not originally from a given area and invasive refers to introduced species that have a negative impact on the natural or cultivated ecosystem (Tobin, 2018). Invasive species have wide-spread negative impacts on both ecosystems and economies. Recognized as one of the greatest threats to biodiversity and general stability of ecosystems world-wide, invasive species threaten native species through competition, predation, or changes to the physical ecosystem (Pimentel et al., 2001) and have been cited as the second greatest cause of extinction of species on the International Union of Conservation of Nature Red List of Threatened Species, second only to exploitation (Bellard, Cassey, & Blackburn, 2016). Ecologically, it has been reported that even just a single invading species in a given environment can cause up to a 16.6% reduction in species richness (Mollot, Pantel, & Romanuk, 2017). Economically, invasive species in just six nations cause more than US$ 314 billion per year in damages (Pimentel et al., 2001).

One main question in the field of invasive species is how they are successful in their non-native environments. Generalist species—characterized by large ecological niches through ecological tolerance, geographic ranges, and higher survival potential—are more successful invaders than specialists species (Stigall, 2012). Although, this alone does not account for all instances of species invasion.

Microbial symbiosis, though, is a leading hypothesis for why invasive species are successful. There is a growing body of literature that supports the principle that microbial symbiosis increases the competitive success of invasive species (Kowalski et al., 2015). The literature supports that the success (e.g. health, productivity, adaptive capacities) of all organisms can be attributed in various ways to microbial communities (Berg, Grube, Schloter, & Smalla, 2014; Bulgarelli, Schlaeppi, Spaepen, van Themaat, & Schulze-Lefert, 2013). Species that have symbiotic relationships with microbial communities, then could have a unique capability to invade, as they can overcome environmental and biotic barriers to invasion.

Most legumes—plants in the Fabaceae (bean and pea) family—have the unique capability to form symbiotic relationships with nitrogen-fixing bacteria called rhizobia. Symbiotic rhizobia are horizontally (infectiously) transferred, therefore transmitted through the soil to their host legumes. These rhizobia infect and form nodules on the plant roots, endo-symbiotically fixing nitrogen from the soil into a usable form for the plant in return for carbon that the plant provides to the rhizobia (Sprent, 2007). In addition to having many species of legumes that are widely cultivated, the Fabaceae family are also prolific invaders world-wide (Yahara et al., 2013). The unique invasive success of the Fabaceae family and the relationship that many legumes form with rhizobia through infection provide us with a model family for invasive species success in relation to microbial symbionts.

In this study, I analyzed 225 studies that assessed non-cultivated legumes world-wide from 1984 – 2014. I addressed one main question: Are invasive legumes generalists or specialists when it comes to their rhizobial symbionts? I hypothesized that invasive legumes would more often be generalists in their invasive ranges.

**Methods**

Two hundred and twenty-five experiments conducted and published between 1984 – 2014 were compiled via Web of Science and Google Scholar using 92 search terms. Experiments were removed from the analysis if they did not contain enough data to extract, leaving a total of 211 experiments used in analyses. Once compiled, data regarding which Fabaceae species were studied and the country where study took place were extracted from experiments manually. Species were identified as native, introduced, or invasive based on the Plants of the World database (<http://www.plantsoftheworldonline.org/>?).

**Results**

Of the 211 total experiments assessed, 515 different leguminous species were found from 9 continents and 69 countries, with the top 50% of data collected from China, Australia, Senegal, Belgium, the United States, and South Africa (Figure 1).

With a combination of 211 experiments, 515 leguminous species, from 69 countries, 724 total plants were studied as some species were studied across multiple experiments. Of the 724 total plants, 2 were classified as introduced, 131 were classified as invasive, and 591 were classified as native in the country they were studied in (Figure 2). Although significance has not yet been tested for, visually it appears that the experiments tested significantly more native legumes than invasive or introduced legumes.

On average, native species found in their native range associated with approximately three rhizobial species, introduced species found in their introduced range associated with five rhizobial species, and invasive species found in their invasive range associated with approximately two rhizobial species (Figure 3). Again, although significance has not yet been assessed, it appears that invasive legumes associate with significantly fewer rhizobial symbionts than native legumes.

**Discussion**

Contrary to expectations, I show here that native legumes are more commonly generalists than invasive legumes (Figure 3). While introduced species associated with the most rhizobia on average, these data consist of only two introduced legumes, whereas invasive and native legumes account for 131 and 591 of the 724 total legumes assessed, respectively. Therefore, introduced species do not visually associate with significantly more rhizobia than invasive or native species. Although it was unexpected that native legumes were more commonly generalists than invasive legumes based on general theory that in order to have success, invasive species would more often be generalists than native species (Mcginn et al., 2016), little data has actually been published assessing this question on a global scale.

In addition to the lack of data published at a global level on how invasive legumes are successful, this study also had limitations. Although a large sample size of 211 total experiments were assessed, data regarding an additional 120 experiments will be added in before publication but has not yet been extracted. Moreover, the vast majority of studies between 1984 and 2014 identified here analyzed native legumounous species and were conducted in China which has the ability to skew the data. In the future, an additional 120 experiments will be used to extract data and analyses will be re-run. After which, it is expected that invasive species will in fact more often be generalists than natural species. However, if this is not the case, this data will be used as a starting point to determine how invasive species are successful in relation to microbial symbionts.

If the patterns found in these data stay consistent as additional data is added in, it will be an unexpected finding that invasive legumes are not necessarily generalists when it comes to their rhizobial symbionts. This will lead to many questions, including how these legumes are successful invaders. One hypothesis for this question going forward is that leguminous species bring their rhizobial symbionts with them through seed coatings when they invade new areas. This mechanism would provide the legume the opportunity to be an invasive species while still being a specialist when associating with rhizobia. Secondarily, it is possible that this trend will support the *‘everything is everywhere but the environment selects’* hypothesis set forth by Martinus Wilhelm Beijerinck in the early twentieth century (discussed in O’Malley, 2008). Per this hypothesis, all microbial species are be present at low levels in all environments. Therefore, if a specialist legume occurs in a non-native area for first time, it’s rhizobial symbionts may already be present in the soil community, even if at low levels. This could explain why legumes are highly prolific invaders, because their rhizobial symbionts may be present world-wide.

**Conclusion**

This meta-analysis is incomplete, although it provides us with exciting preliminary data. Going forward, this analysis will provide us with a general idea of how invasion works in relationship to microbial symbionts and will give us a starting point for future studies regarding similar questions.

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Literature used in analyses but not cited in paper text can be found after figures.

**Figures**

**A picture containing tree

Description automatically generated**

Figure 1. Map of the world with countries found in 211 experiments colored in blue. The number of studies from the top 50% of data collected are identified: China (170), Australia (70), Senegal (61), United States (41), Belgium (38), South Africa (37).

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Figure 2. Out of 725 total legumes studied, 2 were classified as introduced, 131 were classified as invasive, and 591 were classified as native in the country they were studied in.

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Figure 3. Species classified as introduced (and found in their introduced ranges) and invasive (and found in their invasive ranges) associated with five and two rhizobial species on average, respectively. Species found in their native ranges associated with three rhizobial species on.

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