Matheus Batista dos Santos Pepe

Help or Harm: a meta-analytic synthesis about the effect of nitrogen fixing plants on non-fixing plants

Ajuda ou Problema: uma síntese meta-analítica dos efeitos de plantas fixadoras de nitrogênio sobre plantas não-fixadoras

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Abstract

Plants can have positive and negative interaction between each other. In the last three decades, the positive interactions (i.e., facilitation) have been recognized as an important ecological interaction, shaping communities' and ecosystems' structure and the dynamics. Amongst the many mechanisms by which facilitation occurs, there is the addition of soil nutrients through plants which can establish symbiotic relationships with nitrogen fixing bacteria. Despite the relevant volume of papers on facilitation through nitrogen addition, there is still no clear idea of which environmental conditions and plant characteristics may favour the occurrence and magnitude of this facilitation mechanism. Thus, in this study we ~~utilize~~ used meta-analysis techniques in order to understand if the following factors affect facilitation intensity between nitrogen fixing and non-fixing plants: i) inorganic nitrogen quantity available in the soil; ii) hydric severity in the environment; iii) fixing and target plant lifeform; iv) fixing and target plant lifestage and v) plant performance estimator used in the observation. Out of 2145 papers, we included in our meta-analysis 30 papers with 238 observations. Nitrogen fixers offer clear positive effects to their targets, though the effect is less clear when taking into account only the N addition mechanism through nitrogen fixation. When considering all the facilitation mechanisms provided by nitrogen fixers, most environmental conditions and plant~~a~~ characteristics do not have a clear effect on the interaction between neighbours and targets. However, there is an indication that non-seedling target plants may have a higher chance of being positively affected when compared to seedling targets. When considering only N addition through nitrogen fixation, there was a clear indication that increasing levels of monthly precipitation resulted in more facilitative interactions when evaluating individual performance observations. However, no effect was found on community-level observations. Our dataset also indicates current knowledge gaps. Tropical and subtropical regions are underrepresented when taking into consideration that many N-fixing species exist in these specific regions. In the same vein, many papers lack information on plant characteristics, methodology, nitrogen content in the soil and even result reports. These gaps and problems have to be tackled if we are to fully comprehend the factors that shape the effects that nitrogen fixing plant species have in their natural environments and what exactly are the consequences of these presence of these fixers in the natural communities they are part of.

Keywords: environmental stress, facilitation mechanisms, negative interactions, plant competition, plant facilitation, positive interactions, quantitative synthesis.

Resumo

Plantas podem ter interações positivas ou negativas entre si. Nas últimas três décadas, interações positivas (i.e., facilitação) têm sido reconhecidas como uma interação ecológica importante, capaz de moldar estruturas e dinâmicas de comunidades e ecossistemas. Dentre os vários mecanismos pelos quais a facilitação ocorre, existe a adição de nutrientes no solo por plantas que conseguem estabelecer relações simbióticas com bactérias fixadoras de nitrogênio. Apesar da grande quantidade de estudos de facilitação por meio da fixação de nitrogênio, ainda não há consenso sobre quais condições ambientais e características vegetais podem favorecer a ocorrência e magnitude desse mecanismo de facilitação. Dessa forma, nesse estudo utilizamos técnicas meta-analíticas para entender se os seguintes fatores afetam a intensidade de facilitação entre plantas fixadoras e não-fixadoras: i) quantidade de nitrogênio inorgânico presente no solo; ii) severidade hídrica do ambiente; iii) forma de vida das plantas fixadora e alvo; iv) estágio de vida das plantas fixadora e alvo e v) indicador de performance da planta alvo. De 2145 estudos inicialmente identificados, 30 artigos com 238 observações atenderam os critérios de inclusão. Os resultados indicam que plantas fixadoras de nitrogênio claramente provêm efeitos positivos para seus alvos, apesar de que esse efeito é menos claro quando levamos em conta somente o mecanismo de adição de N por meio da fixação de nitrogênio. Quando consideramos todos os mecanismos de facilitação oferecidos por plantas fixadoras, a maioria das condições ambientais e características das plantas não tem um efeito claro sobre a interação entre vizinhos e alvos. Apesar disso, há uma indicação de que planta alvo que não são plântulas tem uma maior chance de serem positivamente afetadas quando comparadas a alvos plântula. Quando consideramos somente a adição de N por meio da fixação de nitrogênio, há uma indicação clara que quantidades crescentes de precipitação mensal resultam em interações com facilitação mais forte quando avaliamos observações de performance individual. Contudo, nenhum efeito é visto em observações de nível de comunidade. Nosso trabalho também indica atuais lacunas no conhecimento. Regiões tropicais e subtropicais são sub-representadas quando levamos em consideração que muitas espécies fixadoras de nitrogênio existem nessas regiões específicas. Da mesma forma, muitos estudos não contêm informação sobre as características das plantas, metodologia, conteúdo de nitrogênio no solo ou das estatísticas necessárias para integrar uma meta-análise. Essas lacunas e problemas precisam ser reconhecidas e resolvidas para que possamos compreender de forma completa os fatores que moldam os efeitos que plantas fixadoras de nitrogênio têm nos seus ambientes naturais e quais exatamente são as consequências da presença desses fixadores nas comunidades das quais eles fazem parte.

Palavras-chave: competição, estresse ambiental, facilitação, interações negativas, interações positivas, mecanismos de facilitação, síntese quantitativa.

Introduction and justification

Plants interact between each other in various ways. They can compete for nutrients, water or sunlight (Gillet 2008) or improve conditions in their proximate vicinity and/or raise resources availability and thus enhance neighbour plants performance (Hunter & Aarssen 1988; Callaway 1995; Brooker *et al.* 2008). Given that positive and negative effects may occur simultaneously in space and time, what matters to define the effect of a plant on another is the final balance between these positive and negative interactions (Maestre *et al.* 2003). When the balance between these interactions is negative, there is competition. On the other hand, when the balance is positive, there is facilitation. Therefore, facilitation is an interaction in which an individual (usually called facilitator or neighbour) exerts a measure positive effect on the performance of another individual in the same trophic level (usually called facilitated or target) (Pakeman *et al.* 2009).

The mechanisms through which facilitation is mediated are very distinct. Plants are capable of directly improving the biotic and abiotic conditions or resources in the environment (Koffel *et al.* 2018), allowing improvement of soil characteristics (e.g., moisture, nutrients and oxygenation), aboveground abiotic conditions (e.g., temperature, humidity) and even eliminate potential competitors or providing protection from herbivores (Callaway 1995). An important widespread facilitation mechanism is the addition of soil nutrients (Callaway 2007; Bonanomi *et al.* 2011). Plants in many different communities have their niches limited by nutrient restrictions. The addition of nutrients may potentially increase their realized niche, decreasing interspecific competition for soil nutrients and improving plants' competitive ability to obtain other important nutrients such as sunlight and water (Hunter & Aarssen 1988; Bruno *et al.* 2003). Nitrogen, regarded as an important nutrient for plant growth and survival, can be biologically fixated by some plants (*Fabaceae*, Lindl*; Alnus*, Mill; *Myrica*, L; *Rosaceae*, Juss; among others) through symbiosis with different nitrogen fixing bacteria, especially in the families *Rhizobiaceae*, *Brukholdericeae* and *Nostocaceae* and the genus *Frankia* (Mylona *et al.* 1995; Tamme *et al.* 2021). As a result of this nitrogen fixation, the soil surrounding fixer plants is enriched with nitrogen as the nutrient is released via root exudates and nitrogen-rich tissue decomposition originated from these plants (Hunter & Aarssen 1988; Mulder *et al.* 2002; Marty *et al.* 2009). The increased fertility in the proximate region of the fixing plant has the potential to improve non-fixer neighbour plants' performance, improving the concentration of nitrogen in leaves (Siddique *et al.* 2008), photosynthesis rates (Lee *et al.* 2003), seedlings' performance (Maestre *et al.* 2003) and biomass (Pugnaire *et al.* 2004). The effect of soil enrichment can even be found after the death of a fixer plant, as the decomposition of the nitrogen fixing plant may result in a sunlight and nitrogen-rich, competitor-free area (Maron & Connors 1996).

As the facilitation effects derived from the nitrogen fixation are so intertwined with the different aspects of the environment, it is not surprising that the environmental conditions in which fixing and non-fixing plants exist can affect the magnitude of interaction. Likewise, nitrogen fixation through the plant-bacteria symbiosis does not occur evenly in all environments. Factors such as light availability (Dovrat *et al.* 2018; Taylor & Menge 2018; Zheng *et al.* 2019), herbivory intensity (Vitousek & Howarth 1991) and nodule size (Tajima *et al.* 2007) may affect nitrogen fixation rates. It has also been observed that when inorganic N is abundant in the soil, there is a subsequent inhibition of nitrogenase synthesis (Zheng *et al.* 2019), resulting in a reduction of biological nitrogen fixation. As fixing nitrogen turns into a smaller competitive advantage, the fixing plant allocates resources away from nitrogen fixation mechanisms (Kiers *et al.* 2003; Zheng *et al.* 2019).

Furthermore, water availability can affect both nitrogen fixation itself and the ability of facilitated plants to obtain soil nitrogen. It has been shown that it might reduce plants' N caption ability even more than would be expected if only considering a reduction of biological N fixation (He & Dijkstra 2014). Lower soil humidity also causes a reduction in the diffusion of nutrients in the soil, decreasing nutrient supply available to plants (Schimel *et al.* 2007; Rouphael *et al.* 2012) and causes negative effects on leaf litter decomposition in terrestrial ecosystems (Sanaullah *et al.* 2012). Water availability also affects biological N fixation (Marino *et al.* 2007). Nitrogen fixation and growth of N-fixing plants decreases with increasing hydric stress (Engin & Sprent 1972; Gerosa Ramos *et al.* 2003) and it has been recorded that nitrogenase activity is extremely sensible to the reduction of water attainability (Rao & Venkateswarlu 1987; Guerin *et al.* 1990; Gerosa Ramos *et al.* 2003). As one of the mechanisms of soil nitrogen enrichment occurs through organic matter decomposition originated from the N fixers, nitrogen availability for facilitated plants may be negatively affected even further by water restrictions. Conversely, water excess can result in nutrient leaching, therefore nullifying any fertility benefit originated from N fixing plants. Therefore, the facilitation effect provided by N-fixing plants may be stronger when an adequate amount of water is present.

Beyond the conditions and resources of the environment, the magnitude of facilitative effect can also be affected by the habit and ontogenetic stage of the fixing and target plants. While graminoids are good competitors because of their efficient radicular system, trees and shrubs may have a bigger potential to aid less-resistant plants. These bigger trees and shrubs can offer various positive effects while having smaller probability of competing for nutrients with smaller or younger target plants, as their roots are likely present in more superficial soil strata (Gómez-Aparicio 2009; Bonanomi *et al.* 2011). Neighbour trees and shrubs also have higher leaf litter production and present larger canopies and root area, resulting in a higher area of effect for the addition of nitrogen through the decomposition of leaf litter and root exudates. The lifestage of facilitated plants may also affect facilitation magnitude. When these target plants are fragile, improving of local conditions (e.g., nitrogen addition to the soil) has a higher probability and potency of causing beneficial effects. However, once established, they can grow and eventually start to compete against the plant which offered the facilitative effects (Callaway & Walker 1997; Miriti 2006). On the other hand, the neighbour ontogenetic stage can also be important to determine the magnitude and direction of the interaction. When neighbours are young, they can compete with another young target species. However, after growing up to be well established adults, they eventually turn to contribute positively to the development of other their targets (Allegrezza *et al.* 2016).

As fixer plants can increase the quantity of nitrate and ammonium around them (Ritchie & Tilman 1995; Ritchie *et al.* 1998), facilitation via this mechanism can act on many different ecological levels. N-fixing plants can alter the growth (Gosling 2005; Hall Cushman *et al.* 2010) and abundance of non-fixing plants (Walker *et al.* 2003; Marty *et al.* 2009), species richness and the composition of neighbouring species (Thomas & Bowman 1998; Rodríguez-Echeverría & Pérez-Fernández 2003), improve primary productivity (Maron & Connors 1996; Rodríguez-Echeverría & Pérez-Fernández 2003; Hughes & Denslow 2005; Hall Cushman *et al.* 2010) and accelerate ecological succession (Bormann & Sidle 1990; Maron & Connors 1996; Kamijo *et al.* 2002; Arfin Khan *et al.* 2014).

Despite the great accumulation of evidence on the effects of N-fixing plants on the plant community and the fact that facilitation has been the focus of many studies in the last three decades (Brooker *et al.* 2008), as far as we know no revision has quantitatively evaluated the occurrence and intensity of facilitation mediated by fixation of nitrogen in natural environments. Hence, there is still no consensus on which of the environment and plant characteristics affect the frequency and magnitude of this facilitation mechanism. Given that facilitation via N addition has great potential to influence populations, communities and ecosystems, the different factors which module its occurrence must be better comprehended in order to understand the inner workings of natural environments. As there is a considerable number of papers on the facilitation through N fixation in natural environments, a synthesis can be a very productive way of understanding and quantifying how the conditions and characteristics previously discussed here can modulate the magnitude of this interaction.

Conclusion

Interactions between nitrogen fixing plants and their non-fixing targets are predominantly positive. Though most of the biotic and abiotic factors investigated in this study do not have a clear effect on the interaction between these two types of plants, there is some weak indication that some biotic factors, such as the target lifestage, may affect the interaction magnitude and direction. Considering only the nitrogen fixation as a facilitation mechanism, the overall effect is less clear but still is, on average, more positive than negative. Just like before, most of the biotic and abiotic factors suggested do not have a clear effect on the interaction regarding this specific mechanism. There is a clear indication that the local precipitation has an effect on the individual performance of plants, but this effect is not present when analysing the performance of the whole community.

Though a lot of progress has been made, there are still some knowledge gaps that need to be more thoroughly researched. Less environmentally stressed regions such as tropical and subtropical regions are underrepresented. There is no uniformity on the description of plant characteristics, soil nitrogen, methodology or sample sizes and some papers did not present all of their results. This can make gathering all the information challenging. These issues have to be addressed if we are to correctly infer how the different biotic and abiotic factors may change N-fixing plant-plant interactions throughout the planet. As efforts to standardize and systematize searches for meta-analyses have been made in the latest years, we conclude that, when applicable, the same should be done for primary research. This will help us to increase the quality, robustness and accessibility of research synthesis in future research.

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Appendix

S1. Search terms for primary study collection.

Web of Science: ((((“facilitat*” OR “positive interaction*” OR “positive effect” OR “nurs* plant*” OR “compet*” OR “negat* interaction*” OR “negative effect*”) NEAR/15 (plant* OR tree* OR wood* OR bush* OR brush* OR shrub* OR herb* OR weed* OR seed* OR sprout*)) AND (“nitrogen fixer*” OR “nitrogen fixation” OR “biological nitrogen fixation” AND “symb*”)) NOT (“crop*” OR “agriculture*” OR “farm*”)).

Scopus: ((((“facilitat*” OR “positive interaction*” OR “positive effect” OR “nurs* plant*” OR “compet*” OR “negat* interaction*” OR “negative effect*”) W/15 (plant* OR tree* OR wood* OR bush* OR brush* OR shrub* OR herb* OR weed* OR seed* OR sprout*)) AND (“nitrogen fixer*” OR “nitrogen fixation” OR “biological nitrogenfixation AND symb*”)) AND NOT (“crop*” OR “agriculture*” OR “farm*”)).