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# Early *Acacia* invasion in a sandy ecosystem enables shading mediated by soil, leaf nitrogen and facilitation

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**Abstract** Australian species of the genus *Acacia* are amongst the most invasive trees. As nitrogen fixers, they are able to invade oligotrophic ecosystems and alter ecosystem functioning to their benefit. We aimed to answer three questions: How does early *Acacia* invasion influence nitrogen and light in a sandy savanna? How does early *Acacia* invasion impact biodiversity? Does early invasion alter ecosystem functioning towards the dominance of *Acacia*? We analyzed (using generalized linear mixed models and richness estimators) paired plots focused on plants of *Acacia mangium* (Fabaceae) and plants of *Marcetia taxifolia* (Melastomataceae) by taking hemispherical photos and sampling plants, leaves and soil for measurements of light, richness, leaf nitrogen, leaf δ15N, soil nitrogen and soil coarse sand. The results suggest that early *Acacia* invasion alters the control of soil and of leaf nitrogen and increases shading, enabling a much wider range of light variation. The δ15N results suggest that the nitrogen taken up by *Acacia* is transferred to neighboring plants and influences the light environment, suggesting facilitation. The enrichment of plant species observed during early *Acacia* invasion is consistent with the wider range of light variation, but the forecasted leaf nitrogen conditions during the established phase of *Acacia* invasion might cause loss of light-demanding species because of increased shading. If early *Acacia* invasion turns into an established phase with highly increased shading, *Acacia* seedlings might be favored and ecosystem functioning might change towards its dominance.

**Keywords** Biological invasion · Assembly rules · Ecosystem functioning · Niche theory · Nitrogen fixing · *Acacia* · Plant diversity · δ15N

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## Introduction

Tree species of the genus *Acacia*, subgenus Phyllodineae, native to Australia and Papua New-Guinea (hereafter just *Acacia*), are amongst the most invasive trees in the world (Richardson and Rejmánek 2011).

As nitrogen fixers (Sprent 2009), *Acacia* species are able to invade oligotrophic ecosystems (Rascher et al. 2011b) and alter environmental factors, frequently to their benefit (Peperkorn et al. 2005). Many habitat alterations resulting from the biological invasion of *Acacia* have been reported, mainly nitrogen fixation, shading, seed bank creation, litter accumulation, allelopathy, and water uptake (Le Maitre et al. 2011). Despite the information accumulated from many recent studies, the early phase of plant invasions in general, and of *Acacia* in particular, remain poorly understood (Rouget et al. 2016), including environmental changes in nitrogen and light, the most important factors during the early phases of tree invasion (Siemann and Rogers 2003). As lag phase and early log phase are windows of opportunity for invasion control, so understanding mechanisms underlying early invasion are critical for management of invaded ecosystems (Crooks 2005; Geerts et al. 2013).

There is theoretical and observational evidence that plant invasions mostly impact biodiversity and ecosystem functioning. Comparisons revealed contrasting differences between *Acacia*-invaded plots and non-invaded plots in coastal dunes and in pine forests, with higher values of basal area and canopy cover of trees in invaded plots (Rascher et al. 2011a). Moreover, as *Acacia* uses P more efficiently for biomass production in sandy ecosystems than native flora, native plants in *Acacia*-invaded plots have increased leaf N, and depleted leaf P, altering their N/P balance (Ulm et al. 2017). How increased leaf N, depleted leaf P and changed N/P balance impact invaded ecosystems has remained largely unknown.

Although plant functional traits of invasive species are often related to highly efficient use of resources (Drenovsky et al. 2012), evidence is still lacking with regard to shifts in the environmental determinants of niche (e.g., Hutchinsonian niche dimensions of light and nitrogen) from the initial phase of invasion to environmental conditions realized during the established phase (Guisan et al. 2014). Alterations to the ecological processes of oligotrophic ecosystems caused by tree species invasions has the potential to outfit the native flora (Funk and Vitousek 2007), and is fundamental to understanding the ability of *Acacia* to establish and grow in many low-resource ecosystems around the world. For instance, the soil C:N ratio has been reported to be lower (i.e., higher nutritional status) in soils in invaded plots than in non-invaded

plots, thus depicting high-resource ecosystems for plants, influencing the band composition of soil bacterial communities and, consequently, impacting soil functioning (Lazzaro et al. 2014). The soil of plots invaded by *Acacia* have high rates of nitrification and high nitrogen availability for plants (Marchante et al. 2008). Such increased nitrogen availability has the potential to impact negatively native biodiversity interacting with microclimatic variables (Porter et al. 2012). Therefore, soil nitrogen content, leaf nitrogen, and light are tightly associated in ecosystem processes that support aboveground biodiversity (Clark and Tilman 2008; Hautier et al. 2009; Dickson and Foster 2011).

Over the last few years, the meaning of $\delta 15N$ values as tracers of ecological processes and of different sources of N for plants in natural ecosystems has been increasingly better understood (Craine et al. 2015). $NO^{3-}$ and $NH^{4+}$ uptake have different amplitudes of $\delta 15N$ (Russell et al. 1998; Houlton and Bai 2009), if nitrogen cycling is conservative or not, and depending on the interactions involved in N uptake, such as with nitrogen fixing bacteria and mycorrhizal associations, which are strongly distinguished by $\delta 15N$ (Hobbie and Hobbie 2008; Craine et al. 2015). Therefore, $\delta 15N$ not only allows determine the source of nitrogen used by plants to be determined, but also allows determine if plants have similar nitrogen niches and which ecological processes are involved in nitrogen uptake.

The present work aimed to study plant biodiversity (richness) and soil and leaf variables in order to understand the effects of the early phases of *Acacia* invasion in a sandy oligotrophic ecosystem, and answer the following questions: 1—How does early *Acacia* invasion alter processes and regimes related to soil, nitrogen, and light? 2—How does early *Acacia* invasion impact biodiversity? 3—Do the changes caused by early invasion alter the ecosystem functioning towards the dominance of the invasive *Acacia*?

## Materials and methods

### Study site

The studied invaded ecosystem is the Brazilian Mussununga, a white-sand vegetation that varies from grassland to woodland. It has soils derived from Tertiary sandstones and a patchy physiognomic form

(Meira-Neto et al. 2005; Saporetti et al. 2012). The sampled vegetation is a mosaic of sandy savannas amid a matrix of *Eucalyptus* plantations regenerating after different types of disturbances such as clear-cutting, grazing and fire (Meira-Neto et al. 2005). The climate is tropical, without drought and with a mean annual rainfall of 1400 mm; Af-type according to the Köppen's system.

Sampling design

For comparisons between invaded sites and non-invaded sites, we used *Acacia*-focused plots and native-plant-focused plots (Ulm et al. 2017) in order to determine any differences in vegetation structure as well as in the leaf nitrogen, leaf δ15N and leaf carbon. Fifteen circular invaded plots (3-m radius) focused on *Acacia mangium* Willd. (Fabaceae) plants were plotted and paired (centers 12-m distant) with non-invaded plots (3-m radius) focused on *Marcetia taxifolia* (A. St.-Hil.) DC. (Melastomataceae) plants in the same Mussununga physiognomy, the open savanna, of three different patches (5 pairs per patch) where the invasion was initiating. *Marcetia taxifolia* was chosen as focal native plants because it is a dominant woody species in those comunities. We established 15 pairs of plots distributed among three Mussununga patches, each pair placed at least 30 m distant from any other pair.

Species richness estimation

All of the plants in each plot were sampled and identified to species level. Species richness was computed using EstimateS 9.1.0 and tested by means of sample based rarefaction (Colwell et al. 2012; Colwell 2013).

Soil sampling

Composite soil samples from 0 to 20 cm of depth were taken from each plot for routine chemical analyses of soil, organic matter content and proportions of fine sand, coarse sand, clay and silt (EMBRAPA 1997). We used the Kjeldahl method for measuring total soil nitrogen (Raveh and Avnimelech 1979).

Light

We took digital hemispherical photos during completely overcast days with a Nikon Coolpix 5700 camera with a Nikon Fisheye FC-E9 lens. The photos were taken from the center of the plots at 1.3 m above the ground using a tripod. The camera was pointed to the zenith and oriented to magnetic north, with geographic coordinates and elevation recorded according to the procedures for analysis using GLA software (Frazer et al. 1999). We used total light percentage (the sum of direct and diffuse transmitted light) of each plot as a variable.

Leaf nitrogen, leaf δ15N and leaf carbon

Every plant inside plots with at least three adult leaves was sampled (three leaves each) for measuring carbon, nitrogen and δ15N.

To determine δ15N, the sampled leaves were dried at 65 °C to constant weight and ground to a powder using a ball mill (Retsch, Haan, Germany). Nitrogen and carbon concentration and δ15N were analyzed using an elemental analyzer (HEKAtech, Weinberg, Germany) with a continuous-flow stable isotope ratio mass spectrometer (ISOPRIME, GV, Manchester, UK), and measured against an ammonium sulphate standard (IAEA.N2). N isotope ratios are presented in δ notation:

$$\delta15N\,sample = (Rsample - Rstandard)/Rstandard$$

where Rstandard is the 15N/14N ratio of atmospheric $N_2$ and Rsample is the 15N/14N ratio of the sampled leaves. The repeated measurement precision was $0.2^o/_{oo}$.

Statistical analyses

To test the relationships between vegetation, soil properties, leaf properties and light, we performed generalized linear mixed models (Glmm) using the lmer function of the lme4 package (Bates et al. 2014) testing differences of leaf δ15N, leaf nitrogen content, and light between invaded plots and non-invaded plots.

A global model of Glmm was tested with the following formula: light ∼ coarse sand * focal species + leaf nitrogen * focal species. That model was chosen among others as explained below, and depicts

light as response variable of interacting coarse sand, focal species of plots (i.e., *Acacia* and *Marcetia*), and leaf nitrogen.

Patches were the random effects for Glmms. For global model selection we used an information theoretical approach based on the Akaike Information Criterion of the Second Order (AICc). We used the dredge function from the MuMIn package to test all combinations of variables included in the models. The lowest AICc value indicated the best model, if delta < 2 (Burnham et al. 2010). We performed analyses using R version 2.15.1 (R Development Core Team 2012).

Bidimensional environmental forecast

Based on known values of leaf nitrogen in established phases of *Acacia* invasion in sandy ecosystems (Rascher et al. 2012), we used the leaf N × light equation found by the global model of Glmm to predict the bidimensional environment of leaf N and light in the future established phase of *Acacia* invasion in Mussununga.

## Results

Among 15 focal *Marcetia* plants of non-invaded plots, five exhibited values of δ15N between 0 and − 5, two exhibited δ15N higher than 0, and eight exhibited δ15N lower than − 5. In contrast, of the 15 focal *Acacia* plants of the invaded plots, 14 exhibited values of δ15N between 0 and − 5, and only one with δ15N lower than − 5 (data not shown). Therefore, the invaded plots had more plants within the δ15N class of values of 0 to − 5 than the non-invaded plots, whereas there were no significant differences in the number of plants within the δ15N classes of lower than − 5 or higher than 0 (Fig. 1, Table 1). Figure 1 suggests that *Acacia*-focused plots have more plants within the δ15N class of values of 0 to − 5 because *Acacia* focal plants have their δ15N in this class and transfer nitrogen to neighbor plants.

Leaf nitrogen content did not differ between invaded and non-invaded plots. However, invaded plots had a lower light percentage than non-invaded plots (Fig. 2, Table 1).

The selected global Glmm 'light ∼ coarse sand * focal species + leaf nitrogen * focal species' had

delta = 0 (i.e., significant, Table 1), with light as a response variable of coarse sand and leaf nitrogen in invaded and in non-invaded plots. The selected global model suggests that light responds widely to variation in coarse sand and leaf nitrogen in invaded plots, whereas in non-invaded plots its response to variation in these variables is negligible (Fig. 3). In invaded plots, light increases as coarse sand (%) increases (Fig. 3a), whereas light decreases as leaf nitrogen increases (Fig. 3b). Therefore, the results suggest that *Acacia* invasion relates the light environment with coarse sand and leaf nitrogen.

The relationship between leaf nitrogen content and light percentage delimits different environmental conditions in invaded plots versus non-invaded plots because of the non-overlapping range of variation in light. As a result, there was greater bidimensional environment in invaded plots than in non-invaded plots (Figs. 3, 4). Congruently, invaded plots had higher species richness than non-invaded plots (Fig. 5), suggesting niche diversification.

## Discussion

*Acacia* invasion enables the ecosystem to respond with a significantly wider range of shading due to soil variation (i.e., drought stress amelioration caused by the decreasing percentage coarse sand, Saporetti et al. 2012), and to increasing leaf nitrogen. This represents quite a different functioning of the invaded ecosystems, considering that the non-invaded ecosystems do not respond with shading to decreasing proportion of coarse sand and increasing leaf nitrogen content, even within the same range of variation. This change in functioning potentially threatens light-demanding species of the native flora due to increased shading.

The δ15N values of almost all *Acacia* plants were in the class of − 5 to 0. Furthermore, there were more plants with leaf δ15N values in this class in invaded plots than in non-invaded plots, suggesting that the nitrogen from *Acacia* plants spread to other plants in invaded plots, just as has been observed in other invasions of *Acacia* in sandy oligotrophic ecosystems (Rascher et al. 2012). Therefore, the more *Acacia* plants in the sandy savanna, the more nitrogen taken up by *Acacia*, the more N transference to other plants, and the more shading in that ecosystem. Thus, the δ15N results suggest positive interactions between
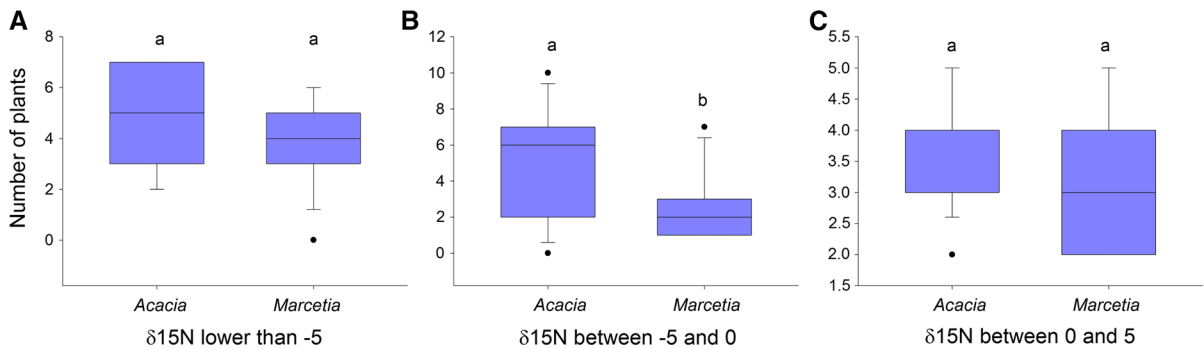
**Fig. 1** Box-plots of number of plants per invaded plot focused on *A. mangium* (*Acacia*) plants and non-invaded plots focused on *Marcetia taxifolia* (*Marcetia*) plants. Glmms for three classes of $\delta 15N$: **a–c** Poisson distribution, $p = 0.0023$; model selection in Table 1. Different lower case letters indicate significant differences

*Acacia* and other plants in invaded plots; in short, it suggests plant–plant facilitation.

The light attenuation, increased leaf nitrogen, and increased richness caused by the *Acacia* trees reinforce the suggestion of facilitation. Moreover, light attenuation with higher leaf nitrogen content in invaded plots may cause positive feedback between nitrogen and shade (Siemann and Rogers 2003) as well as plant growth and shade (Egerton et al. 2000). These positive feedbacks are similar to results found in patchy savanna of Mussununga vegetation (Meira-Neto et al. 2017 unpublished). Therefore, *Acacia* invaders may have nursing plants of other species in the highly illuminated sandy savanna.

Since early invasion enables the ecosystem to respond to variation in soil and leaf nitrogen with more shading, the $\delta 15N$ results suggest the hypotheses that the increased leaf nitrogen in plants of invaded plots is an effect of nitrogen uptake mediated by interactions such as *Acacia* roots with nitrogen fixing bacteria (Sprent 2009), as is seen with plant roots with mycorrhiza (Rodríguez-Echeverría et al. 2013), or soil microorganisms (Lorenzo et al. 2010). The results also suggest that soil nitrogen does not influence canopy openness and aboveground biomass in neither the early-invaded plots nor the non-invaded plots. Since soil C:N ratio has been reported to be lower (i.e., higher nutritional status) in soils of invaded plots than in non-invaded plots (Lazzaro et al. 2014), the early *Acacia* invasion may not have yet changed the C:N ratio of the soil, although there is already change in soil functioning, at least at the level of interactions between plants.

The leaf nitrogen that influences the light environment seems not to be related to soil nitrogen content during early *Acacia* invasion. Thus, these results suggest that most of the nitrogen taken up by plants in invaded plots is not from the soil stock, but from the atmosphere and precipitation, mediated by interactions with nitrogen fixing bacteria, mycorrhiza and other plants, including non-leguminous plants (Sprent 2007; Santi et al. 2013); this may be the main cause of the negative $\delta 15N$ in most of the plants, since nitrogen uptake via mycorrhizal associations might deplete 15N. One possible cause is that fungi have quite selective enzymes acting on organic nitrogen that largely prefer 14N, thereby decreasing 15N in plants (Zabinski et al. 2002; Wilson et al. 2006; Hobbie and Hobbie 2008). Additionally, negative $\delta 15N$ values are expected in ecosystems with open N cycling, especially in ecosystems with low nutrient stock, and in unpolluted regions (Garten 1992; Austin and Vitousek 1998).

The relationship between leaf nitrogen and light in the invaded plots of this oligotrophic ecosystem allows the prediction of environmental shifting of niche determinants if the current invasion trend is maintained up to the established phase. The shifting indicated by the blue arrow of Fig. 4, obtained from leaf nitrogen values of established phases of *Acacia* invasions in other sandy ecosystems, might cause an increase in leaf nitrogen as well as increased shading, narrowing the environmental condition determined by light and leaf nitrogen, with a possible impoverishment of niche diversity (i.e., decreased species richness). In this case, leaf nitrogen content might be around 2.5% with low variation in light and leaf

**Table 1** AICc values corresponding to Fig. 4 of the global Generalized Linear Mixed Models for plants with values of δ15N between − 5 and 0 with focal species (dN); for plots with light (LI) with focal species; for plots with coarse sand (CS) and leaf nitrogen (LN) with light (LI) interacting with focal species; focal species *Acacia mangium* and *Marcetia taxifolia* (SP)

| Model | SP | dN ~ SP | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|
| 2 | 1.503 | + | 3 | − 18.219 | 43.4 | 0.00 | 0.994 |
| 1 | 1.216 | | 2 | − 24.505 | 53.5 | 10.09 | 0.006 |

| Model | SP | LI ~ SP | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|
| 2 | 69.69 | + | 4 | − 115.491 | 240.6 | 0.00 | 1 |
| 1 | 82.44 | | 3 | − 127.794 | 262.5 | 21.93 | 0 |

| Global model | CS | LN | LI ~ SP | LI ~ CS*SP | LI ~ LN*SP | df | logLik | AICc | Delta | Weight |
|---|---|---|---|---|---|---|---|---|---|---|
| 24 | 0.9079 | − 71.13 | + | | + | 7 | − 103.057 | 225.2 | 0 | 0.539 |
| 23 | | − 83.72 | + | | + | 6 | − 105.457 | 226.6 | 1.36 | 0.273 |
| 32 | 1.265 | − 66.17 | + | + | + | 8 | − 102.615 | 228.1 | 2.88 | 0.128 |
| 8 | 1.146 | − 36.19 | + | | | 6 | − 107.841 | 231.3 | 6.13 | 0.025 |
| 16 | 1.806 | − 32.65 | + | + | | 7 | − 106.43 | 232 | 6.75 | 0.018 |
| 7 | | − 47.09 | + | | | 5 | − 110.67 | 233.8 | 8.64 | 0.007 |
| 14 | 2.332 | | + | + | | 6 | − 109.4 | 234.5 | 9.25 | 0.005 |
| 6 | 1.564 | | + | | | 5 | − 111.206 | 234.9 | 9.71 | 0.004 |
| 5 | | | + | | | 4 | − 115.491 | 240.6 | 15.38 | 0 |
| 3 | | − 71.33 | | | | 4 | − 122.011 | 253.6 | 28.42 | 0 |
| 4 | 1.114 | − 60.84 | | | | 5 | − 120.822 | 254.1 | 28.94 | 0 |
| 2 | 1.874 | | | | | 4 | − 125.063 | 259.7 | 34.52 | 0 |
| 1 | | | | | | 3 | − 127.794 | 262.5 | 37.31 | 0 |

Significance if delta < 2.00, and best model is always the one with the lowest delta
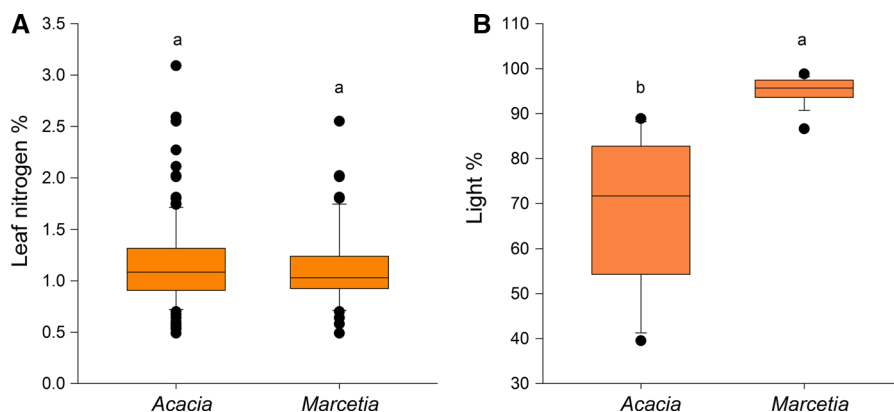
*Means interaction, + means significance



**Fig. 2** Box-plots of leaf nitrogen percentage per plot. **a** Glmms (Poisson distribution family) of leaf nitrogen in plants of invaded plots focused on *A. mangium* (*Acacia*) plants and non-invaded plots focused on *Marcetia taxifolia* (*Marcetia*) plants, $p < 0.4$. **b** Glmm (Gaussian distribution family), with a significant difference in light between invaded plots and non-invaded plots; Poisson distribution, $p < 0.0001$; details in Table 1. Different lower case letters indicate significant differences

**Fig. 3** Glmm of the significant selected global model of coarse sand % and leaf nitrogen content with light % (Table 1). **a**, **b** are from the same global model. Green circles and solid lines are of invaded plots focused on *Acacia mangium*, and red circles, and dashed lines are of non-invaded plots focused on *Marcetia taxifolia*; details of the global models in Table 1
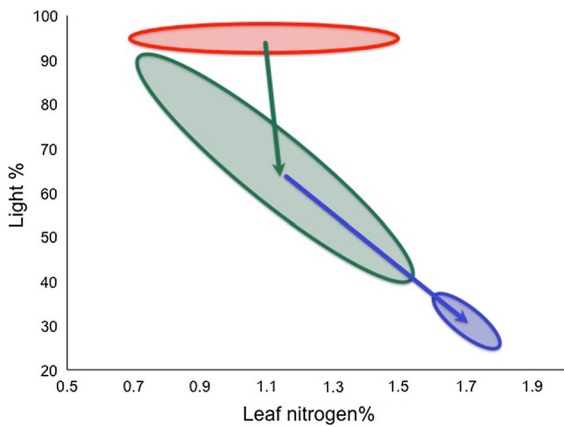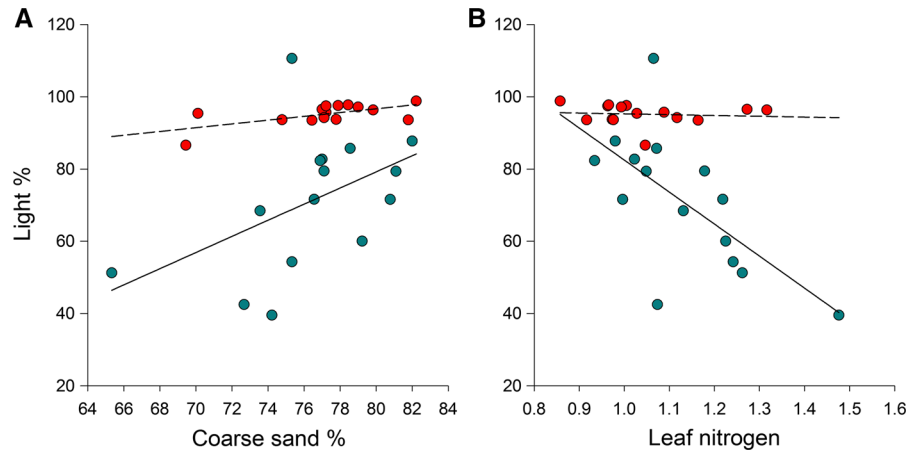


**Fig. 4** Bidimensional environment (i.e., leaf nitrogen and light percentage) amplified in invaded plots focused on *Acacia mangium* (green) compared to non-invaded plots focused on *Marcetia taxifolia* (red); based on values shown in Figs. 2 and 3b; a future hypothetical environmental condition (blue ellipsis) based on a global model of Fig. 3b; green arrow indicates the changing limits of the environmental condition of observed values for nitrogen and light on non-invaded plots to invaded plots; blue arrow indicates hypothetical change of environmental condition to the established phase of *Acacia mangium* invasion, with a reduction of environmental variation

**Fig. 5** Rarefactions of species richness per invaded plots (green, dashed lines CI = 95%) and non-invaded plots (red, dashed lines CI = 95%)

nitrogen in the invaded plots (blue ellipsis), which is a common leaf nitrogen level in environments in the late phases of *Acacia* invasion (Rascher et al. 2011b).

The shading caused by canopies in invaded plots seems to be mediated by abiotic factors, and by positive biotic interactions between *Acacia* and, at least, other plants of the invaded ecosystem. Therefore, these results suggest that ecological interactions (Soberón 2007) have been added to the abiotic variables of niches (Winemiller et al. 2015) as
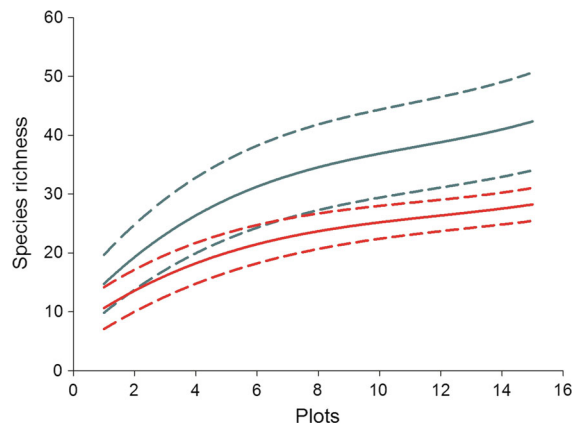
assembly rules of *Acacia*-invaded ecosystems, resulting in a mix of Hutchinsonian and Eltonian niches.

Concerning the questions raised at the beginning of this study, the results revealed that early *Acacia* invasion alters the control of soil and of leaf nitrogen, enabling variation in the light environment and enhancing remarkably shading. As a result, the changed control of the light environment in invaded ecosystems causes much more shading than in the non-invaded ecosystems. The δ15N results suggest nitrogen transference by *Acacia* to neighboring plants, and that the altered controls of the light environment became enabled, at least partially, by ecological interactions during early *Acacia* invasion, including facilitation. The enrichment of plant species observed during early *Acacia* invasion reinforces the suggestion

of facilitation, which is consistent with the wider range of the light environment, and suggests niche diversification. However, the leaf nitrogen conditions forecasted by the models found for the established phase of *Acacia* invasion might cause loss of light-demanding native species because of increased shading. Additionally, studies indicate that *Acacia* seedlings may be favored by shading in the established phase (Rascher et al. 2011a, b). Monitoring should be done to see if changes to the ecosystem during early invasion alter ecosystem functioning towards the dominance of the invasive *Acacia* during the established phase, and whether this leads to loss of native species, and destruction of the Mussununga ecosystem. Future studies are needed to confirm the results found here, and raise additional hypotheses for *Acacia*-invaded ecosystems, especially sandy ecosystems.

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