GUSTAVO HERINGER

BIOLOGICAL INVASION BY *ACACIA* SPP. IN THE BRAZILIAN ATLANTIC FOREST

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

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APROVADA: 20 de abril de 2018.

João Augusto Alves Meira Neto
(Coorientador)

Ricardo Ribeiro de Castro Solar

Flávia Maria da Silva Carmo

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(Orientadora)

Aos amigos com quem não posso mais conviver; à minha
mãe, ao meu pai e aos meus irmãos que são o maior
presente da minha vida, e aos meus sobrinhos, afilhado e
afilhada que me conectam com o futuro.

(...) “Se vim ao mundo, foi
Só para desflorar florestas virgens,
E desenhar meus próprios pés na areia inexplorada!
O mais que faço não vale nada.” (...)

José Régio (Cântico Negro)

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Agradeço profundamente a todos que contribuíram com esse trabalho, que participaram da minha formação profissional e, especialmente, que fazem parte do meu dia-a-dia e me dão tanta alegria para “seguir em frente”.

SUMÁRIO

ABSTRACT

HERINGER, Gustavo, D.Sc., Universidade Federal de Viçosa, April, 2018. **Biological invasion by Acacia spp. in the Brazilian Atlantic Forest.** Adviser: Andreza Viana Neri. Co-adviser: João Augusto Alves Meira Neto.

Climate change, habitat degradation, and biological invasion are among the most factors threaten biodiversity. These factors, besides affect biodiversity and ecosystem directly, can act synergistically and promote deeper environmental changes. Therefore, in this thesis, we proposed to study the causes and consequences of biological invasion by *Acacia* genus. In the first chapter, we investigate the effects of biological invasion by *Acacia* spp., fire and eucalyptus disturbance, and land-use on a neglected sandy-savanna ecosystem named *Mussununga*; in the second, we tested the effects of landscape functioning and structure in the *Acacia* invasion in *Mussununga* ecosystem; and finally, assessed the potential distribution of *Acacia mangium* and *A. auriculiformis* in five climate scenarios and the potential effects in restoration programs. We found in the first chapter that *Acacia* promoted changes in the structure and phytophysiognomie of the woody layer, but did not affect the herb-shrub layer. On the other hand, anthropogenic factors affected both woody and herb-shrub layer. In the second chapter, we found that in a fragmented landscape with the higher road network, *Mussununga* has a higher chance to be invaded by *Acacia*. Shape index had a negative effect in *Acacia* invasion, while the length of roads, *Mussununga* size, *Mussununga* perimeter, length of highways and landscape conductance had a positive effect. Finally, in the third chapter, we found *A. mangium* has a large suitable area in all scenarios, while *A auriculiformis* is confined to a relatively small region of 13,083 km^2 (± 3.39 SD). In the low greenhouse gas emissions scenario (RCP 2.6), the suitable area for *A. mangium* expanded from the current scenario of 18.4% of the Atlantic Forest to 24.0% in the year 2050, while, achieved around 44,3% of the Atlantic Forest area in the worse scenarios (RCP 8.2, in 2070). Still in the scenarios with higher climatic change, the suitable area for *A. mangium* overlapped around 39.3% of the potential area for restoration programs, in Atlantic Forest.

RESUMO

HERINGER, Gustavo, D.Sc., Universidade Federal de Viçosa, abril de 2018. **Invasão biológica por Acacia spp. na Mata Atlântica brasileira.** Orientadora: Andreza Viana Neri. Coorientador: João Augusto Alves Meira Neto.

Mudanças climáticas, degradação de habitat e invasão biológica estão entre os principais fatores que ameaçam a biodiversidade atualmente. Esses fatores, além de afetarem diretamente a biodiversidade e os ecossistemas, podem atuar de forma sinergética e promover alterações ambientais ainda mais drásticas. Portanto, nesta tese propusemos estudar as causas e efeitos da invasão biológica por espécies do gênero *Acacia*. No primeiro capítulo, nós investigamos os efeitos dos distúrbios antrópicos, mudança no uso da terra e da invasão por *Acacia* na diversidade, estrutura e fitofisionomia do ecossistema de *Mussununga*; no segundo, testamos os efeitos da função e estrutura da paisagem na invasão de ecossistemas de *Mussununga* por espécies de *Acacia*; e finalmente, investigamos a distribuição potencial de *Acacia mangium* e *A. auriculiformis* em cinco cenários climáticos diferentes e os potenciais efeitos dessas mudanças em programas de restauração. No primeiro capítulo nós encontramos que *Acacia* promoveu alterações na estrutura e fitofisionomia da comunidade lenhosa, porém não apresentou relação com as mudanças na comunidade herbáceo-arbustiva. Por outro dado, os fatores antrópicos estudados afetaram tanto a comunidade lenhosa quanto herbáceo-subarbustiva. No segundo capítulo, encontramos que existe maior chance de invasão de *Mussunungas* em paisagens fragmentadas e com maior rede viária. *Shape index* de *Mussununga* tem efeito negativo na invasão por *Acacia*, enquanto condutividade da paisagem, comprimento de estradas e rodovias, e tamanho e perímetro de *Mussununga* apresentam efeito positivo. No terceiro capítulo, finalmente, encontramos uma grande área de disponibilidade climática para *A. mangium* e uma área relativamente pequena para *A. auriculiformis* de 13.083 km^2 (± 3,39 SD). No cenário com menos mudanças climáticas (RCP 2.6), a área de disponibilidade para *A. mangium* aumentou de 18,4% da Mata Atlântica atualmente para 24,0% em 2050, enquanto, no cenário com mais mudanças chegou a 44,3% em 2070 (RCP 8.2). Ainda no pior cenário, a área de disponibilidade climática para *A. mangium* chegou a sobrepor cerca de 39,3% das áreas prioritárias para restauração da Mata Atlântica, indicando que a espécie pode se tornar mais um obstáculo à restauração desse bioma.

INTRODUÇÃO GERAL

Mudanças climáticas, degradação de habitat e invasão biológica estão entre os principais fatores que ameaçam a biodiversidade atualmente (e.g. Vitousek et al. 1997; Sala et al. 2000; Haddad et al. 2015; Pereira et al. 2010; Urban 2015). Esses fatores, além de afetarem diretamente a biodiversidade e os ecossistemas, podem atuar de forma sinergética e promover alterações ambientais ainda mais drásticas (Fridley et al. 2007; Le Maitre et al. 2011; Gaertner et al. 2014). Em ambientes degradados e sob uso antrópico, a perda de habitat afeta diretamente as espécies nativas e, ao mesmo tempo, aumenta as chances de invasão biológica, que por sua vez, pode provocar mais alterações no ecossistema (Didham et al. 2005; Le Maitre et al. 2011).

A Mata Atlântica brasileira é um dos ambientes mais degradados do mundo e possui grande riqueza de espécies e de ecossistemas (Myers et al. 2000; Scarano and Ceotto 2015). A fragmentação da Mata Atlântica promove uma série de alterações que interferem negativamente na diversidade e funcionamento desse ambiente (Magnago et al. 2014, 2015a, 2015b). Além da fragmentação, a Mata Atlântica também sofre os efeitos de outros fatores. Por exemplo, a Mata Atlântica está estre os três *hotspots* que irão sofrer mais alterações devido às mudanças climáticas (Béllard et al. 2014) e também sofre com os efeitos da invasão biológica (Meira-Neto et al. 2017, Lehmann et al. 2017). A convergência de todos esses fatores faz da Mata Atlântica o local adequado para investigar os efeitos da invasão biológica, paisagem e mudanças climáticas na biodiversidade, assim como, para averiguar como esses preditores afetam uns aos outros.

Sendo assim, no primeiro capítulo desse estudo investigamos como a invasão de *Acacia mangium* Willd. and *A. auriculiformis* Cunn. ex Benth. e fatores antrópicos (paisagem e uso da terra) interferem na diversidade, estrutura e fitofisionomia do ecossistema de *Mussununga*. Nesse capítulo encontramos que *Acacia* spp. afeta a comunidade lenhosa, porém não tem efeito sobre as espécies herbáceas, enquanto, paisagem e uso da terra afetam tanto espécies lenhosas quanto herbáceas. Além disso, observamos uma tendência de a *Mussununga* do tipo savana se tornar florestada.

No segundo capítulo, testamos se a fragmentação da paisagem e a rede de estradas no entorno das *Mussunungas* pode aumentar a permeabilidade da matriz e afetar a invasão biológica positivamente. Encontramos que comprimento de estradas, o tamanho da

Mussununga e a condutividade da paisagem afetam positivamente a invasão de *Acacia* spp., enquanto a complexidade da *Mussununga* teve um papel negativo. Além disso, a partir do modelo de condutividade pudemos concluir que florestas tem um papel negativo na invasão biológica, diminuindo a permeabilidade. Esses resultados possibilitam predizer com maior assertividade *Mussunungas* que estão sob alto risco de invasão e pode auxiliar no direcionamento de ações de prevenção à invasão biológica.

Finalmente, em nosso último capítulo exploramos os efeitos do clima presente e futuro na distribuição potencial de *A. mangium* e *A. auriculiformis* para Mata Atlântica. Os modelos mostraram que a Mata Atlântica possui uma grande área de nicho disponível para *A. mangium* e que ocorre uma expansão da área de adequabilidade climática com o passar do tempo e com o aumento de emissão de gases de efeito estufa, podendo chegar a uma área maior que 40% da Mata Atlântica. Ainda, quando fizemos a sobreposição do Mapa de Áreas Potenciais para Restauração da Mata Atlântica (http://www.pactomataatlantica.org.br/) com os mapas de expansão-retração de *Acacia* spp., observamos que pelo menos 22.7% (31,425 km^2) das áreas potenciais para restauração se sobrepõe a áreas de adequabilidade climática para *A. mangium* e, no cenário com maior emissão gases de efeito estufa para 2070, essa sobreposição chega a 39.3% (54,342 km^2).

REFERÊNCIAS BIBLIOGRÁFICAS

Béllard C, Leclerc C, Leroy B, Bakkenes M, Veloz S, Thuiller W, Courchamp F (2014) Vulnerability of biodiversity hotspots to global change. Glob Ecol Biogeogr 23:1376–1386. doi: 10.1111/geb.12228

Didham RK, Tylianakis JM, Hutchison MA, et al (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474. doi: 10.1016/j.tree.2005.07.006

Fridley JD, Stachowicz JJ, Naeem S, et al (2007) The invasion paradox: Reconciling pattern and process in species invasions. Ecology 88:3–17. doi: 10.1890/0012-9658(2007)88[3:Tiprpa]2.0.Co;2

Gaertner M, Biggs R, Te Beest M, et al (2014) Invasive plants as drivers of regime shifts: Identifying high-priority invaders that alter feedback relationships. Divers Distrib 20:733–744. doi: 10.1111/ddi.12182

Haddad NM, Brudvig LA, Clobert J, et al (2015) Habitat fragmentation and its lasting impact on Earth ' s ecosystems. Science 1:1–10. doi: 10.1126/sciadv.1500052

Le Maitre DC, Gaertner M, Marchante E, et al (2011) Impacts of invasive Australian acacias: implications for management and restoration. Divers Distrib 17:1015–1029. doi: 10.1111/j.1472-4642.2011.00816.x

Lehmann JR, Prinz T, Ziller SR, et al (2017) Open-source processing and analysis of aerial imagery acquired with a low-cost Unmanned Aerial System to support invasive plant management. Front Environ Sci. doi: 10.3389/fenvs.2017.00044

Magnago LFS, Edwards DP, Edwards FA, et al (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J Ecol 102:475–485. doi: 10.1111/1365-2745.12206

Magnago LFS, Magrach A, Laurance WF, et al (2015) Would protecting tropical forest fragments provide carbon and biodiversity co-benefits under redd+? Glob Chang Biol 44:n/a–n/a. doi: 10.1111/gcb.12937

Magnago LFS, Rocha MF, Meyer L, et al (2015) Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. Biodivers Conserv 24:2305–2318. doi: 10.1007/s10531-015-0961-1

Meira-Neto JAA, Silva MCNA, Tolentino GS, et al (2017) Early *Acacia* invasion in a sandy ecosystem enables shading mediated by soil, leaf nitrogen, and facilitation. Biol Invasions. doi: 10.1007/s10530-017-1647-2

Myers N, Mittemeier RA, Mittemeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. doi: 10.1038/35002501

Pereira HM, Leadley PW, Proença V, et al (2010) Scenarios for global biodiversity in the 21st century. Science 330:1496–1501. doi: 10.1126/science.1196624

Sala OE., Chapin III FS. S, Armesto JJ., et al (2000) Global Biodiversity Scenarios for the Year 2100. Science 287:1770–1774. doi: 10.1126/science.287.5459.1770

Scarano FR, Ceotto P (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers Conserv 24:2319–2331. doi: 10.1007/s10531-015-0972-y

Urban MC (2015) Accelerating extinction risk from climate change. Science 348:571–573. doi: 10.1126/science.aaa4984

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. Science 277:494–499. doi: 10.1126/science.277.5325.494

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CHAPTER 1 - BIOLOGICAL INVASION, ANTHROPOGENIC DISTURBANCE AND LAND-USE CHANGE THREATEN A NEGLECTED SANDY-SAVANNA ASSOCIATED WITH ATLANTIC FOREST

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ABSTRACT

Invasive species, anthropogenic disturbances, and land-use threaten biodiversity in ecosystems all over the world and may affect species richness and structure as well as the ecosystem functioning. Here we investigated the role of biological invasion by *Acacia* spp., fire and eucalyptus disturbance, and land-use on a neglected sandy-savanna ecosystem named *Mussununga*. *Acacia* invasion, anthropogenic disturbance, and land-use were related to changes in diversity, structure, and physiognomy, suggesting that both are affecting the *Mussununga* ecosystem functioning. We found that in less than 10 years after the invasion, the presence of *Acacia* spp. was correlated negatively with the abundance, basal area, and height of woody species, and correlated positively with the proportion of dead woody plants and with a trend of forestation. However, the basal area of *Acacia* spp. was correlated positively with the abundance and basal area of the woody layer, indicating that other factors are affecting *Mussununga* ecosystem. We hypothesized *Acacia* spp. establishes more easily in treeless *Mussunungas*, probably after disturbance events, and both native and invasive species would (re-)cover the ecosystems in the early stage. The disturbance caused by eucalyptus plantations played a positive role in the woody layer richness, but a negative role in the herb-shrub layer abundance, while, land-use characterized mainly by eucalyptus plantation around the *Mussununga* patches, was associated with increased richness and abundance in the herb-shrub layer. Here we demonstrate biological invasions and anthropogenic activities promote a set of changes in the neglected *Mussununga* ecosystem.

Keywords: *Acacia*, neotropical savanna, alien species, ecosystem changes, disturbance, *Mussununga*

INTRODUCTION

Biological invasions, anthropogenic disturbance, and land-use change are among the most severe drivers on biodiversity and ecosystems services (Vitousek et al. 1997; Steffen et al. 2007; Hautier et al. 2015). These drivers frequently interact with each other promoting feedback loops (Le Maitre et al. 2011; Gaertner et al. 2014). The disturbance has important effect during early *Acacia* invasion in several situations, due to the resulting decrease in the abundance and seed bank of native species, as well as to the fast recovery and seed bank accumulation of *Acacia* spp. (Le Maitre et al. 2011). Further, land-use affects the rates of invasion positively once increase the area of land available for invasion and increase the propagule pressure due exotic species introduction (Donaldson et al. 2014a). Therefore, investigate the effect of biological invasion and anthropogenic factors (disturbances and land-use) together allow the establishment of conceptual models appropriate to each study case and can help managers to implement effective conservation and eradication strategies.

Anthropogenic factors may increase the rate of invasion due to the resulting exclusion of native species (Kennedy et al. 2002), change in disturbance regime (Dillis et al. 2017) or increase in the frequency of introduction events (Donaldson et al. 2014a). At the landscape scale, habitat fragmentation can alter source availability or affect the potential competitiveness of native species, thus facilitating the establishment of invasive species (Raghubanshi and Tripathi 2009). Moreover, highways and roads may either benefit invasive plants due to the increased disturbance intensity (Pollnac et al. 2012) or facilitate seed dispersal of invasive species (Thiele et al. 2008; Delnatte and Meyer 2012). As this complex set of factors can affect ecosystems in many ways depending on the context (Fridley et al. 2007; Gaertner et al. 2014), conducting habitat-specific studies on different landscape types is necessary to understand how invasive species and human factors promote ecosystem changes.

In addition to acting synergistically, anthropogenic factors and biological invasion may affect biodiversity and ecosystem directly in different ways, depending on their context (Vitousek et al. 1997; Miller et al. 2011). For instance, the increase in frequency or intensity of fire due to human activity may contribute to the formation of a treeless savanna (Moreira 2000), mainly through the exclusion of fire-sensitive woody species (Hoffmann 1996). Yet, the decrease of landscape connectivity affects plant dispersal and reduce similarity between fragments (Thiele et al. 2018). Biological invasion, in turn, affects biodiversity by means of competition and replacement of native species (Gaertner et al. 2009; Fischer et al. 2014) or due changes in ecosystem processes (Fridley et al. 2007; Gaertner et al. 2014). Thus, investigating these set of predictive variables allows a better comprehension of how anthropogenic factors and biological invasion interfere in the biodiversity loss and whether they are promoting each other.

The invasive genus *Acacia,* subgenus *Phyllodineae,* originally from Australia and surrounding islands (Murphy 2008), is currently widespread around the world (Richardson and Rejmánek 2011), mainly due to human economic interest on some species aiming their use for different purposes. Individuals of *Acacia* genus growth fast and have good adaptability to soils with low nutrient levels as well as to disturbed areas (National Research Council - US 1983; Griffin et al. 2011). *Acacia* species can be dispersed up to 900 m from the mother plant (Aguiar Jr. et al. 2014) and are able to thrive in several ecosystems, such as dunes, the understory of plantations, savanna vegetation, open forests, forest edges and abandoned lands (Rascher et al. 2011; Delnatte and Meyer 2012; Aguiar Jr. et al. 2014). Species of this genus may also cause changes on the community as well as to the ecosystem functioning, especially regarding light regime and leaf nitrogen contents (Meira-Neto et al. 2017; Große-Stoltenberg et al. 2018).

The competitiveness of *Acacia* spp. seems to be related to a set of traits that are common to the genus, namely rapid growth, high production of seeds with long viability, high litter deposition, and production of allelopathic compounds (Le Maitre et al. 2011). For instance, *Acacia* spp. can reduce the growth of native seedlings, and thereby negatively affect the regeneration of native vegetation and promote the growth of their own seedlings in pine forests (Rascher et al. 2011). In oligotrophic dune ecosystems, *Acacia* spp. may also increase the contents of macronutrients (N, K, and Mg) and organic matter in the soil (Hellmann et al. 2011), as well as promote litter accumulation (Marchante et al. 2008). Furthermore, *Acacia* spp. may form a plant layer taller than the surrounding native species, thus shading them (Rascher et al. 2011). Alterations in vegetation structure caused by *Acacia* spp., such as increased basal area and plant density and decreased biodiversity (Rascher et al. 2011), could exacerbate the *Acacia* effects on ecosystems formed by species adapted to nutrient-poor soils and high light intensity. Accordingly, *Acacia* spp. have been commonly reported to colonize nutrient-poor, degraded and non-forest ecosystems (e.g. Marchante et al. 2008; Rascher et al. 2011; Delnatte and Meyer 2012; Aguiar Jr. et al. 2014). Nevertheless, *Acacia* spp. are restricted to the edge of closed forests, due to shade intolerance (Osunkoya et al. 2005; Delnatte and Meyer 2012; field observations).

The exotic invasive species *Acacia auriculiformis* Cunn. ex Benth. and *Acacia mangium* Willd. are native to Australia, Papua New Guinea and Indonesia (National Research Council - US 1983), and both are the most widespread *Acacia* species in the world, being used mainly for solid wood, pulpwood and, fuelwood production as well as for recovery of degraded lands (Griffin et al. 2011). In Brazil, these species are reported to occur in several states along the entire coastline (Santa Catarina, Rio de Janeiro, Espírito Santo, Bahia, Pernambuco, Maranhão, Amapá, Amazonas, and Roraima) (I3N Brazil 2017). *Acacia* spp. were introduced in the Lowland Atlantic Forest region at around the 70's, as an alternative for the recovery of degraded lands. Since then, they have spread and invaded not only degraded lands but also pastures, eucalyptus plantations and the *Mussunungas* in the region (Lehmann et al. 2017), having been firstly recorded in the sampling sites less than 10 years ago. Both species are well adapted to regions with a short dry period, high temperatures, mean annual rainfall and nutrient-poor soil conditions (National Research Council - US 1983; Delnatte and Meyer 2012).

In a recent paper, Meira-Neto et al. (2017) showed that early *Acacia* invasion in *Mussunungas* increases shading as well as leaf nitrogen content in the neighborhood plants and concluded the needed to monitor whether *Acacia* invasion could leave to biodiversity loss in the subsequent years. Additionally, is also important to consider the synergetic role of anthropogenic habitat alteration and biological invasion in the biodiversity changes (Gurevitch and Padilla 2004; Didham et al. 2005; Le Maitre et al. 2011). In this paper, we aimed to study the effects of *Acacia* invasion, disturbance and land-use on the species diversity, structure, and physiognomy of the *Mussununga* ecosystem. We investigated three hypotheses: *Acacia* invasion, disturbance, and land-use would (i) cause plant biodiversity loss; (ii) promote changes in the plant community structure; and (iii) *Acacia* invasion would drive *Mussununga* to more closed physiognomies (closed savanna and woodland).

METHODOLOGY

Study site

The study was conducted in eastern Brazil, in the states of Espírito Santo and Bahia. We sampled areas located from Linhares, in northern Espírito Santo (19° 25'S, 40° 04'W), to Caravelas, in southern Bahia (17° 44'S, 39° 15'W) (Fig. 1). The climate in the region ranges from tropical with dry winter to tropical monsoon and tropical with no dry season (respectively, Aw, Am, and Af of Köppen – Alvares et al. 2014). The original vegetation of Atlantic Forest domain is highly fragmented, and the current landscape is dominated by eucalyptus plantations, pastures, crop fields, forest remnants, mangrove, *Restinga* (coastal dunes originated in the Quaternary period and having a wide range of vegetation types, which are composed of herbs, shrubs, and trees) and patches of *Mussununga* savannas.

The *Mussununga* patches vary widely in size and shape and are spread throughout a matrix of Lowland Atlantic Forest (IBGE 2004) and anthropogenic landscape (e.g. eucalyptus plantations, pastures and crop fields). Their heterogeneous vegetation types have different phytophysiognomies, such as grasslands, which are dominated by a few monocot species; the savanna itself, composed of one herb-shrub layer and another layer of scattered woody plants; and woodlands with closed canopies (Saporetti-Junior et al. 2012). The occurrence of *Mussunuga* is strictly associated with acid, nutrient-poor, sandy soils, which are formed by podzolization due to high humidity and by the hydromorphism caused by an impermeable Ortstein layer (Saporetti-Junior et al. 2012; Ferreira et al. 2014). The *Mussununga* ecosystem is still highly neglected in the scientific literature (Eisenlohr et al. 2015), despite the fact that it is already threatened by many factors, such as fire, logging, road construction and biological invasion.

Sampling design

Fieldwork was conducted between September 2015 and March 2016 in 13 *Mussununga* patches (Fig. 1). We sampled each patch by allocating 10 to 15 plots, distributed at least

10 m apart from each other. Due to the characteristic two-layered vegetation of the sandy-savanna *Mussununga*, we used 10 x 10 m plots to survey the woody layer and added one 2 x 2 m subplot within each plot to sample the herb-shrub layer. In the woody layer, we sampled all individuals rooted in the plot and having a diameter at soil height ≥ 3.2 cm, recording for each individual is species name, height, and diameter at soil height. To sample the herb-shrub layer, we added the subplot in the southeast corner of the plot and examined all individuals therein, recording their species name, the cover, and cover-abundance value. We considered the cover-abundance value as a projection of the cover of each species on the ground, in each subplot (Braun-Blanquet 1979).

Selected variables

For the woody layer sampling, we used the presence/absence, basal area, and abundance of *Acacia* spp. as independent variables to test the effects of invasion by these species. Additionally, we included two categorical variables related to anthropogenic activity as independent variables: disturbance and land-use. Disturbance referred to anthropogenic factors that directly affect the *Mussununga* patch. This variable had four levels: no factor, eucalyptus presence, fire, and eucalyptus presence plus fire. The disturbance variable was observed during the fieldwork carried out on forest remnants, and it encompassed factors such as the presence of isolated eucalyptus trees, cut eucalyptus trunks, fire-scorched stems or burned graminoid vegetation. Although no eucalyptus invasion has been seen in the study areas, we considered eucalyptus presence in the patch as a disturbance factor because of the management practices that are necessary during planting and harvesting, such as using a wood harvester and carrying out fertilization. Land-use referred to activities conducted around the *Mussununga* patch. This variable had three levels: forest, eucalyptus plantation, and a mix of forest and eucalyptus plantation. We classified land-use as forest when more than 90% of the vegetation adjacent to the *Mussununga* patch was composed of native forest; as eucalyptus plantation when more than 90% was composed of eucalyptus plantation; and as both when the proportion between forest and eucalyptus plantations was different. Disturbance and land-use were both categorized only based on clear evidence found during fieldwork.

In the woody layer sampling, we investigated the dependent variables species richness, Pielou's evenness, and Shannon's index as diversity predictors; and abundance, proportion of dead individuals, geometric mean of height, basal area, and the first two ordination axes of an NMDS as predictors of native vegetation structure. Moreover, we also tested the basal area and the geometric means of height, including *Acacia* spp. in the sum as dependent variables (henceforth referred to as "total basal area" and "total height", respectively), aiming to evaluate the effect of biological invasion, anthropogenic disturbance and land-use in the phytophysiognomy.

In the case of the herb-shrub layer sampling, we tested the same abovementioned independent variables and added the presence and cover of *Acacia* spp. in the subplots, also as an independent variable, aiming to test the immediate effect of the species. As dependent variables, we used species richness, Pielou's evenness, Shannon's index (diversity variables), cover value, abundance, and the first two ordination axes of an NMDS (structure variables). Neither the cover-abundance value (sensu Braun-Blanquet 1979) nor abundance of *Acacia* spp. in the subplots was used in our model, as they both showed a high Pearson correlation coefficient with *Acacia* spp. cover percentage ($r = 0.99$ and 0.82, respectively), while native cover-abundance value (*sensu* Braun-Blanquet 1979) was not used because showed a high Pearson correlation coefficient with native cover ($r = 0.97$).

Statistical analyses

First, we constructed a matrix with all the above-mentioned variables and then used software R version 3.4.1 (R Development Core Team 2016) to calculate the NMDS axis using the Bray-Curtis distance, species abundance (stress = 0.13 and 0.18 for the woody and herb-shrub layer samplings, respectively) and Shannon's index, with the "vegan" package (Oksanen et al. 2016). Pielou's index was obtained as the ratio between Shannon's index and richness (natural logarithm). Then, we tested Pearson's correlation between variables using the "PerformanceAnalytics" package (Peterson and Carl 2014) and excluded all variables having a Pearson correlation coefficient ≥ 0.80. To choose the best model and proceed with necessary transformations, we tested linearity using the "gof" package (Holst 2014), based on the generalized linear model; and distribution, using the

"MASS" package (Venables and Ripley 2002). We tested the effect of *Acacia* spp. invasion and anthropogenic factors on the diversity, structure and phytophysiognomic variables using generalized linear mixed models in the "lme4" package (Bates et al. 2015) for each plot or subplot (the latter in herb-shrub layer analysis). We added the identity of each *Mussununga* patch as a random effect in our model to account for the nested sampling design. All models were built using transformed data of the basal area and abundance of *Acacia* spp., which were divided by the standard deviation (except for total height, in which case we used square root transformation). For the significant relationships between anthropogenic factors and dependent variables with more than two levels (disturbance and land-use), we conducted a contrast analysis to test the differences between levels.

RESULTS

In this study we found *Acacia* sp. and anthropogenic factors do not promote biodiversity loss, contrarily abundance of *Acacia* spp. affected woody evenness positively and land-use by eucalyptus promoted woody richness. Regarding community structure, *Acacia* spp. presence affected negatively woody plants in abundance, basal area, and height, while anthropogenic factors affect woody community only in the NMDS axis 1 and 2. On the other hand, *Acacia* spp. did not affect herb-shrub sample, while both disturbance and land-use influenced herb-shrub abundance. Finally, *Acacia* spp. invasion induced an increment of height and basal area in the *Mussununga* physiognomy.

Acacia spp. affected the woody layer but not the herb-shrub layer. The presence of *Acacia* spp. tended to be associated with lower values of abundance, basal area, and height of woody plants and with a higher proportion of dead woody individuals (Fig. 2a, b, c; Table 1). The basal area of *Acacia* spp. had no negative effect on the abundance, basal area, or height of woody individuals, in contrast, it had a positive effect on abundance and basal area of woody variables when we did not exclude the outlier from the analysis (Fig. 2d, e; Table 1; Supplementary material, Table S1). The abundance of *Acacia* spp. affected Pielou's evenness and proportion of dead woody individuals positively (Fig. 2f; Table 1). When we tested how *Acacia* spp. variables affected the total basal area and total height, to assess the effects on phytophysiognomy, we found positive effects of the basal area of *Acacia* spp. on both dependent variables (Table 1). *Acacia* spp. had no effect on the herb-shrub layer, even when their presence, percentage cover, and abundance in the subplot were considered (Supplementary material, Table S2).

Additionally, disturbance by eucalyptus was positively associated with woody layer richness and negatively with NMDS axis 1, while forest land-use had a negative effect on NMDS axis 2 (Fig. 3a, b, c; Table 1). The abundance and richness of the herb-shrub layer were affected by anthropogenic factors, yet not by *Acacia* spp. Although the disturbance promoted by eucalyptus was negatively associated with abundance, the eucalyptus plantation land-use had a positive effect on abundance and richness (Fig. 3d, e, f; Table 1). Neither disturbance nor land-use affected total basal area or total height (Supplementary material, Table S2).

During this study, we recorded a total 5539 individuals, 90 species, 74 genera and 40 families, following Brazilian Flora 2020 (2017). In the woody layer, 1361 individuals, 39 species, 35 genera and 23 families were found, while in the herb-shrub layer we sampled 4178 individuals, 79 species, 66 genera and 36 families. In the woody layer plots, the abundance of native species ranged from 0 to 31 individuals (8.7 ± 6.3 SD) and richness from 0 to 8 species (2.6 ± 1.5), while in the herb-shrub subplots the abundance of native species ranged from 4 to 116 individuals (28.9 ± 19.9), richness from 2 to 13 species (6.0 ± 2.1) and cover value from 16 to 221 (104.3 ± 41.7).

DISCUSSION

Here, we found a set of outcomes showing *Acacia* spp. invasion and anthropogenic factors are promoting changes in the *Mussununga* plant community. *Acacia* spp. invasion decreased woody species abundance, basal area and height as well as was associated with increased proportion of dead individuals. Furthermore, basal area of *Acacia* spp. was related with change in the *Mussununga* phytophysiognomy, driving the vegetation from open savanna to closed savanna or woodland. Anthropogenic factors, in turn, affected both woody and herb-shrub *Mussununga* communities, influencing richness, NMDS axis 1, and axis 2 on woody layer and richness and abundance on herb-shrub layer.

The presence of *Acacia* spp. was associated with lower abundance, basal area, and height of native species as well as with increased proportion of dead individuals, which we interpret as a negative impact of *Acacia* spp. on native vegetation, as found by other authors (e.g. Costello et al. 2000; Marchante et al. 2003; Rascher et al. 2011). However, the positive relationship of the basal area of *Acacia* with the abundance and basal area of native woody species challenges this conclusion. In this case, the synergistic effect of disturbance and biological invasion, as found e.g. with *Acacia longifolia* (Andrews) Willd. in the Portuguese dune ecosystem (Le Maitre et al. 2011), seems to be a key explanation. During the post-disturbance recovery stage, both the density of *Acacia longifolia* and richness of native species increase until the advanced invasion stage, from when the ecosystem shows high contents of nitrogen, soil carbon, and increased reinvasion potential, but native species richness decrease (Marchante et al. 2009; Le Maitre et al. 2011). We believe that *Acacia* spp. establish more commonly in less woody *Mussununga*s, probably due to the occurrence of disturbance events such as severe drought, flooding or fire. Subsequently, *Acacia* and native woody species would (re-)grow and (re-)cover the ecosystem without causing negative effects to one another. Nevertheless, at later stages of invasion, which could be seen in some sampled sites, *Acacia* spp. would then become dominant and displace native vegetation by causing ecosystem changes to the soil, seed bank, and by shading the surrounding vegetation (Le Maitre et al. 2011; Gaertner et al. 2014; Meira-Neto et al. 2017) (Fig. 4 summarizes this hypothesis). Therefore, considering abundance and biomass of invasive species in future studies could provide us with more comprehensive information about the dynamics of invasion and provide better understand how invasive species can become dominant.

Although the process observed in the Portuguese dunes fits quite well our case and helps us explain the increased richness in the *Acacia* focal sample found by Meira-Neto et al. (2017), we cannot ignore that *Acacia* spp. could act as a nurse plant for native species during the early invasion stage in the *Mussununga* ecosystem. *Acacia* spp. promotes changes that could ameliorate stress conditions in the *Mussununga* ecosystem, e.g. by providing shade and increasing soil nitrogen and carbon contents (Marchante et al. 2009; Hellmann et al. 2011; Meira-Neto et al. 2017), thereby facilitating the establishment of plants not adapted to stress conditions. For instance, Yang et al. (2009) found better physiological status and lower stress in shaded plants under *Acacia* canopies in China. However, we highlight the positive effect of nitrogen addition and shading in the *Mussununga* should only occur up to a threshold of *Acacia* cover above which light-demanding species would be impaired (Meira-Neto et al. 2017) and *Acacia* seedlings would be favored (Rascher et al. 2011). Yet, the positive effects of the basal area of *Acacia* on the woody community and of the abundance of *Acacia* on the proportion of dead plants found in this study corroborates that *Acacia* spp. act as nurse plants in the early invasion phase (Meira-Neto et al. 2017) but also promote the death of other plants when overabundant (Fig. 2d, e, f).

The positive effect of the basal area of *Acacia* on the total biomass (total basal area and total height) indicates the occurrence of changes to the physiognomic structure of the *Mussununga*. In that sense, after *Acacia* invasion, the sandy-savanna *Mussunungas* may become taller and more closed, which is associated with the expected impact of *Acacia* on light availability and nitrogen content (Le Maitre et al. 2011; Meira-Neto et al. 2017). This trend is clearly related to the *Acacia* capacity to grow faster and taller than native plants from *Mussununga* vegetation, and even in the early invasion can also be detected using aerial images (Lehmann et al. 2017). Under this new environmental condition, the typical *Mussununga* vegetation of shade-intolerant species could be replaced by shade-tolerant ones, most likely by *Acacia* seedlings, saplings and trees (Rascher et al. 2011; Le Maitre et al. 2011; Gaertner et al. 2014; Meira-Neto et al. 2017).

Anthropogenic factors influenced diversity and structure of both woody and herb-shrub layers, but the effect of each type of activity and each category level varied (Fig. 3). This result is not surprising, as a complex set of factors acts on the *Mussununga* ecosystem at the same time. In addition to the variables targeted in our study, flooding and drought regimes could also drastically affect the community, as discussed by Saporetti-Junior (2012). The woody *Mussununga* responded differently to eucalyptus and fire disturbances. While eucalyptus plantation positively affected species richness, fire had no effect on native vegetation. Fire tends to affect woody communities more severely than herb-shrub ones in savanna-type ecosystems (Moreira 2000); however, we did not find such correlation. We also expected that eucalyptus disturbance would negatively affect the whole community due to suppression of native vegetation and movement of machinery during management. Nevertheless, we observed a positive effect on the woody layer richness and a negative one on the herb-shrub layer abundance. As shown by Lannes et al. (2016) in the Brazilian Cerrado, nutrient addition may promote biomass reduction in herbs. Furthermore, nutrient enrichment may alleviate soil conditions in the *Mussununga* and enable the establishment of woody species less adapted to nutrient-poor soils. Therefore, we cannot exclude the possibility of an association, as the negative effect of eucalyptus disturbance on herb-shrub abundance could reduce the dominance of grasses and benefit the establishment and growth of woody species (Pearson's correlation: $r = -0.27$; $p < 0.01$). We highlight that the intensity, frequency and time since the last disturbance event, variables not investigated here, may play an important role in the diversity-disturbance relationship in the sandy-savanna *Mussununga* (Miller et al. 2011). Thus, studies considering disturbance variables in more detail would help us understand how each variable act and how they might promote biological invasion by *Acacia*.

Land-use also had a significant effect on plant communities. *Mussununga* patches surrounded by eucalyptus plantations showed higher richness and abundance in herb-shrub samples (Fig. 3e, f). The sandy-savanna *Mussunungas* are mostly composed of shade-intolerant species, which themselves could not cross the dense forest matrix of Lowland Rainforest. We also speculate that human-aided dispersal plays a role in increasing richness and abundance in the eucalyptus land-use and enhances the dispersal rates of light-demanding species among *Mussununga* patches, as observed with some invasive species (Donaldson et al. 2014a). Furthermore, the set of roads and highways around patches could facilitate dispersal, as observed with invasive species (Thiele et al. 2008; Pollnac et al. 2012). The eucalyptus plantation land-use around patches includes a frequent movement of vehicles that transport timber or manage the plantations, which could help disperse native species, similarly to the observed with *Acacia* spp. (Donaldson et al. 2014b).

Acacia invasion showed a relationship with changes in *Mussununga* ecosystem that in the early stage affect the structure and phytophysiognomie of the woody layer. Yet, the positive effect of the basal area of *Acacia* spp., in contrast with the negative effect of *Acacia* presence, indicates a more complex set of interactions. As we suggested, the (re-)grow of *Acacia* spp. and native plants after a disturbance event could a be possible explanation for this discordant result. Anthropogenic disturbances and land-use also had a relevant role in promoting community changes and should thus be investigated through experimental or dynamic approaches, which might enable us not only to understand how each type of human activity affects the *Mussununga* ecosystem but also to comprehend their effects on invasion over time. Considering the changes promoted by *Acacia* invasion and anthropogenic factors in the sandy-savanna *Mussununga,* we highlight that adopting actions such as discouraging or precluding human disturbances, monitoring recovery after disturbance events and controlling *Acacia* invasion before it crosses the threshold between the early and advanced invasion stages may be the key to preserve the characteristics of this peculiar and neglected ecosystem.

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REFERENCES

Aguiar Jr. A, Barbosa RI, Barbosa JBF, Mourao Jr. M (2014) Invasion of *Acacia mangium* in Amazonian savannas following planting for forestry. Plant Ecol Divers 7:359–369. https://doi.org/10.1080/17550874.2013.771714

Alvares CA, Stape JL, Sentelhas PC, et al (2014) Köppen's climate classification map for Brazil. Meteorol Zeitschrift 22:711–728. https://doi.org/10.1127/0941-2948/2013/0507

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models using lme4. Journal of Statistical Software, 67:1–48. https://doi.org/10.18637/jss.v067.i01

Braun-Blanquet J (1979) Fitosociología: Bases para el estudio de las comunidades vegetales. H. Blume, Madrid

Brazilian Flora 2020 (2017) Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil. Available at: http://floradobrasil.jbrj.gov.br/ (accessed June 29, 2017)

Costello DA, Lunt ID, Williams JE (2000) Effects of invasion by the indigenous shrub *Acacia sophorae* on plant composition of coastal grasslands in south-eastern Australia. Biol Conserv 96:113–121. https://doi.org/10.1016/S0006-3207(00)00058-6

Delnatte C, Meyer J-Y (2012) Plant introduction, naturalization, and invasion in French Guiana (South America). Biol Invasions 14:915–927. https://doi.org/10.1007/s10530-011-0129-1

Didham RK, Tylianakis JM, Hutchison MA, et al (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474. https://doi.org/10.1016/j.tree.2005.07.006

Dillis C, Marshall AJ, Rejmánek M (2017) Change in disturbance regime facilitates invasion by Bellucia pentamera Naudin (Melastomataceae) at Gunung Palung National Park, Indonesia. Biol Invasions 19:1329–1337. https://doi.org/10.1007/s10530-016-1345-5

Donaldson JE, Hui C, Richardson DM, et al (2014a) Invasion trajectory of alien trees: The role of introduction pathway and planting history. Glob Chang Biol 20:1527–1537. https://doi.org/10.1111/gcb.12486

Donaldson JE, Richardson DM, Wilson JRU (2014b) The seed ecology of an ornamental wattle in South Africa - Why has *Acacia elata* not invaded a greater area? South African J Bot 94:40–45. https://doi.org/10.1016/j.sajb.2014.05.004

Eisenlohr PV, Oliveira-Filho AT, Prado J (2015) The Brazilian Atlantic Forest: new findings, challenges and prospects in a shrinking hotspot. Biodivers Conserv 24:2129–2133. https://doi.org/10.1007/s10531-015-0995-4

Ferreira VBR, Nascimento MT, Luis Fernando Tavares de Menezes (2014) Floristic and phytogeographic pattern of native field in southeastern Brazil. Acta Bot Bras 28:465–475. https://doi.org/10.1590/0102-33062014abb3556

Fischer FM, Oliveira JM, Dresseno ALP, Pillar VD (2014) The role of invasive pine on changes of plant composition and functional traits in a coastal dune ecosystem. Nat & Conserv 12:19–23. https://doi.org/10.4322/natcon.2014.004

Fridley JD, Stachowicz JJ, Naeem S, et al (2007) The invasion paradox: Reconciling pattern and process in species invasions. Ecology 88:3–17. https://doi.org/10.1890/0012-9658(2007)88[3:Tiprpa]2.0.Co;2

Gaertner M, Biggs R, Te Beest M, et al (2014) Invasive plants as drivers of regime shifts: Identifying high-priority invaders that alter feedback relationships. Divers Distrib 20:733–744. https://doi.org/10.1111/ddi.12182

Gaertner M, Den Breeyen A, Hui C, et al (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Prog Phys Geogr 33:319–338. https://doi.org/10.1177/0309133309341607

Griffin AR, Midgley SJ, Bush D, et al (2011) Global uses of Australian acacias - recent trends and future prospects. Divers Distrib 17:837–847. https://doi.org/10.1111/j.1472-4642.2011.00814.x

Große-Stoltenberg A, Hellmann C, Thiele J, et al (2018) Invasive acacias differ from native dune species in the hyperspectral/ biochemical trait space. J Veg Sci. https://doi.org/10.1111/jvs.12608

Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? Trends Ecol Evol 19:470–474. https://doi.org/10.1016/j.tree.2004.07.005

Hautier Y, Tilman D, Isbell F, et al (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. Science 348:336–340. https://doi.org/10.1126/science.aaa1788

Hellmann C, Sutter R, Rascher KG, et al (2011) Impact of an exotic N2-fixing *Acacia* on composition and N status of a native Mediterranean community. Acta Oecol 37:43–50. https://doi.org/10.1016/j.actao.2010.11.005

Hoffmann WA (1996) The effects of fire and cover on seedling establishment in a Neotropical Savanna.pdf. J Ecol 84:383–393.

Holst KK (2014) gof: Model-diagnostics based on cumulative residuals. R package version 0.9.1

I3N Brazil – National Database of Invasive Alien Species Brazil (2017) Instituto Hórus de Desenvolvimento e Conservação Ambiental, Florianópolis, Brazil. Available at: http://i3n.institutohorus.org.br/www (accessed June 30, 2017)

IBGE – Instituto Brasileiro de Geografia e Estatística (2004) Mapa da Vegetação do Brasil. Rio de Janeiro, Brasil. Available at: ftp://ftp.ibge.gov.br/Cartas_e_Mapas/Mapas_Murais/ (accessed June 29, 2017)

Kennedy TA, Naeem S, Howe KM, et al (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638. https://doi.org/10.1038/nature00776

Lannes LS, Bustamente MMC, Edwards PJ, Venterink HO (2016) Native and alien herbaceous plants in the Brazilian Cerrado are (co-)limited by different nutrients. Plant Soil 400:231–243. https://doi.org/10.1007/s11104-015-2725-9

Le Maitre DC, Gaertner M, Marchante E, et al (2011) Impacts of invasive Australian acacias: implications for management and restoration. Divers Distrib 17:1015–1029. https://doi.org/10.1111/j.1472-4642.2011.00816.x

Lehmann JR, Prinz T, Ziller SR, et al (2017) Open-source processing and analysis of aerial imagery acquired with a low-cost Unmanned Aerial System to support invasive plant management. Front Environ Sci. https://doi.org/10.3389/fenvs.2017.00044

Marchante E, Kjøller A, Struwe S, Freitas H (2008) Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. Appl Soil Ecol 40:210–217. https://doi.org/10.1016/j.apsoil.2008.04.004

Marchante E, Kjøller A, Struwe S, Freitas H (2009) Soil recovery after removal of the N2-fixing invasive *Acacia longifolia*: consequences for ecosystem restoration. Biol Invasions 11:813–823. https://doi.org/10.1007/s10530-008-9295-1

Marchante H, Marchante E, Freitas H (2003) Invasion of the Portuguese dune ecosystems by the exotic species *Acacia longifolia* (Andrews) Willd.: effects at the community level. In: Child LE, Brock JH, Brundu G et al (eds) Plant invasions: Ecological threats and management solutions. Backhuys, Leiden, pp 75–85

Meira-Neto JAA, Silva MCNA, Tolentino GS, et al (2017) Early *Acacia* invasion in a sandy ecosystem enables shading mediated by soil, leaf nitrogen, and facilitation. Biol Invasions. https://doi.org/10.1007/s10530-017-1647-2

Miller AD, Roxburgh SH, Shea K (2011) How frequency and intensity shape diversity – disturbance relationships. Proc Nat Acad Sci 108:5643–5648. https://doi.org/10.1073/pnas.1018594108

Moreira AG (2000) Effects of fire protection on savanna structure in Central Brazil. J Biogeogr 27:1021–1029. https://doi.org/10.1046/j.1365-2699.2000.00422.x

Murphy DJ (2008) A review of the classification of the *Acacia* (Leguminosae, Mimosoideae). Muelleria 26:10–26.

National Research Council - US (1983) Mangium and other fast-growing Acacias for the humid tropics. National Academy Press, Washington, D.C., National A. Washington DC

Oksanen J, Blanchet FG, Friendly M, et al (2016) vegan: Community ecology package. R package version 2.4-0. https://CRAN.R-project.org/package=vegan

Osunkoya OO, Othman FE, Kahar RS (2005) Growth and competition between seedlings of an invasive plantation tree, *Acacia mangium*, and those of a native Borneo heath-forest species, Melastoma beccarianum. Ecol Res 20:205–214. https://doi.org/10.1007/s11284-004-0027-4

Peterson BG, Carl P (2014) PerformanceAnalytics: Econometric tools for performance and risk analysis. R package version 1.4.3541. https://CRAN.R-project.org/package=PerformanceAnalytics

Pollnac F, Seipel T, Repath C, Rew LJ (2012) Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem. Biol Invasions 14:1753–1763. https://doi.org/10.1007/s10530-012-0188-y

R Development Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: http://www.R-project.org/ (accessed June 29, 2017)

Raghubanshi AS, Tripathi A (2009) Effect of disturbance, habitat fragmentation and alien invasive plants on floral diversity in dry tropical forests of Vindhyan highland: A review. Trop Ecol 50:57–69.

Rascher KG, Große-Stoltenberg A, Maguas C, et al (2011) *Acacia longifolia* invasion impacts vegetation structure and regeneration dynamics in open dunes and pine forests. Biol Invasions 13:1099–1113. https://doi.org/10.1007/s10530-011-9949-2

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species - a global review. Divers Distrib 17:788–809. https://doi.org/10.1111/j.1472-4642.2011.00782.x

Saporetti-Junior AW, Schaefer CEGR, de Souza AL, et al (2012) Influence of soil physical properties on plants of the *Mussununga* ecosystem, Brazil. Folia Geobot 47:29–39. https://doi.org/10.1007/s12224-011-9106-9

Steffen W, Crutzen PJ, McNeill JR (2007) The Anthropocene: Are humans now overwhelming the great forces of nature. AMBIO A J Hum Environ 36:614–621. https://doi.org/10.1579/0044-7447(2007)36[614:TAAHNO]2.0.CO;2

Thiele J, Buchholz S, Schirmel J (2018) Using resistance distance from circuit theory to model dispersal through habitat corridors. J Plant Ecol 11:385–393. https://doi.org/10.1093/jpe/rtx004

Thiele J, Schuckert U, Otte A (2008) Cultural landscapes of Germany are patch-corridor-matrix mosaics for an invasive megaforb. Landsc Ecol 23:453–465. https://doi.org/10.1007/s10980-008-9202-2

Venables WN, Ripley BD (2002) Modern applied statistics with S. Fourth Edition. Springer, New York.

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of earth's ecosystems. Science 277:494–499. https://doi.org/10.1126/science.277.5325.494

Yang L, Liu N, Ren H, Wang J (2009) Facilitation by two exotic *Acacia*: *Acacia auriculiformis* and *Acacia mangium* as nurse plants in South China. For Ecol Manage 257:1786–1793. https://doi.org/10.1016/j.foreco.2009.01.033

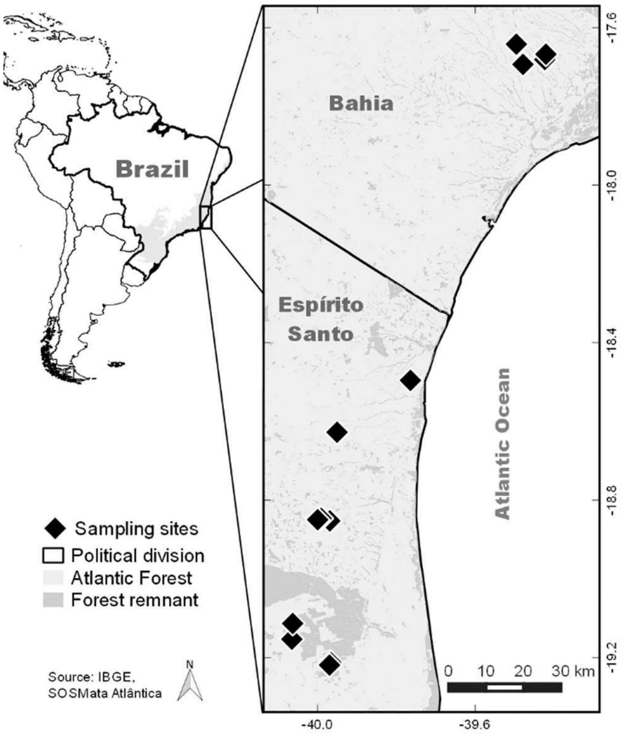

Fig. 1 Study area, forest remnant and sampled sites in the Atlantic Forest domain.

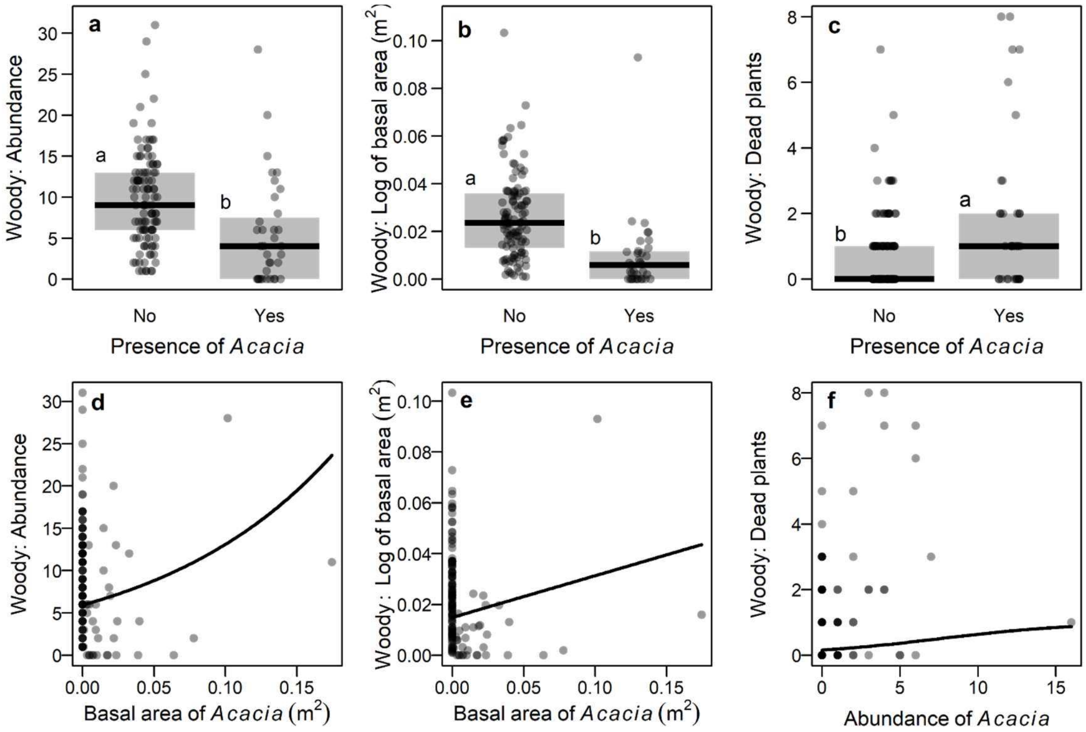

Fig. 2 The relationship between *Acacia* spp. invasion (presence, basal area, and abundance) and woody community variables. Each dot corresponds to the value found in one plot; dots are darker according to the number of plots with the same increase in value. Black bars correspond to the median; grey boxes correspond to the range between the first and third quartiles; and the lower-case letters over the boxes correspond to the significance of $p < 0.05$ in GLMM (a, b and c). Solid curves represent the estimated means (d, e and f).

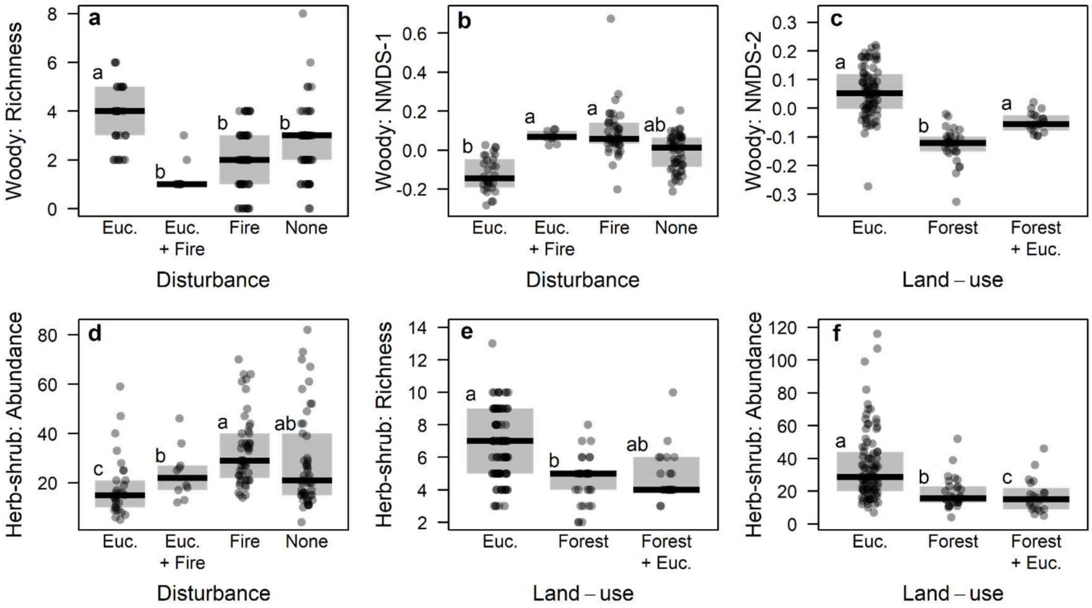

Fig. 3 The relationship of human factors (disturbance and land-use) with woody community variables (a, b and c) and herb-shrub sampling variables (d, e and f). Each dot corresponds to the value found in one plot; dots are darker according to the number of plots with the same increase in value. Black bars correspond to the median; grey boxes correspond to the range between the first and third quartiles; and the lower-case letters over the boxes correspond to the significance of $p < 0.05$ in contrast analysis, when different. Euc. = Eucalyptus.

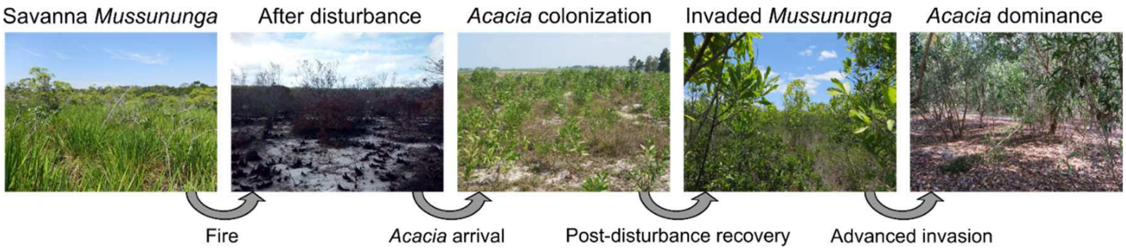

Fig. 4 Hypothetical process of change in a *Mussununga* ecosystem due to *Acacia* invasion and human factors.

Table 1 Results of all models with significant relationship of *Acacia* spp. invasion and human factors with community variables ($p \leq 0.05$). The distribution used in each model is shown in parenthesis after the respective dependent variable.

Native vegetation ~ *Acacia* + anthropogenic factors	**Estimate**	**df**	**X^2**	**p**
Woody sample				
Richness (Poisson)				
Disturbance		3	9.440	0.024
Pielou's evenness (Binomial)				
Acacia abundance	0.733	1	8.310	0.004
Abundance (Negative binomial)				
Acacia presence	-0.605	1	6.116	0.013
Acacia basal area	0.155	1	3.949	0.047
Proportion of dead individuals (Binomial)				
Acacia presence	0.980	1	6.899	0.009
Acacia abundance	0.430	1	6.733	0.009
Basal area (Gaussian)				
Acacia presence	-0.012	1	5.539	0.019
Acacia basal area	0.003	1	3.853	0.050
Height (Gaussian)				
Acacia presence	-0.757	1	12.449	<0.001
NMDS axis 1 (Gaussian)				
Disturbance		3	13.004	0.005
NMDS axis 2 (Gaussian)				
Land-use		2	13.167	0.001
Total basal area (Gamma)				
Acacia basal area	0.329	1	17.824	<0.001
Total height (Gaussian)				
Acacia basal area	4.772	1	10.084	0.001
Herb-shrub sample				
Richness (Poisson)				
Land-use		2	10.837	0.004
Abundance (Negative binomial)				
Land-use		2	23.567	<0.001
Disturbance		3	16.453	<0.001

SUPPLEMENTARY MATERIAL

Table S1 Results of the models testing the relationship of *Acacia* spp. invasion and anthropogenic factors with abundance and basal area of woody species (outlier values of dependent variable were excluded). The distribution used in each model is shown in parenthesis after the respective dependent variable.

Native vegetation ~ *Acacia* + anthropogenic factors	**Estimate**	**df**	**X^2**	**p**
Woody sample				
Abundance (Negative binomial)				
Acacia presence	0.653	1	7.264	0.007
Acacia abundance	-0.050	1	0.241	0.623
Acacia basal area	0.066	1	0.692	0.405
Land-use		2	2.168	0.338

Disturbance		3	2.367	0.500
Basal area (Gaussian)				
Acacia presence	-0.014	1	8.630	0.003
Acacia abundance	-0.001	1	0.397	0.529
Acacia basal area	0.000	1	0.000	0.997
Land-use		2	2.147	0.342
Disturbance		3	0.870	0.833

Table S2 Results of all models testing the relationship of *Acacia* spp. invasion and anthropogenic factors with community variables. The distribution used in each model is shown in parenthesis after the respective dependent variable.

Native vegetation ~ *Acacia* + anthropogenic factors	**Estimate**	**df**	**X^2**	**p**
Woody sample				
Richness (Poisson)				
Acacia presence	-0.4192	1	3.0843	0.0791
Acacia abundance	-0.0211	1	0.0603	0.8061
Acacia basal area	0.0640	1	0.9352	0.3335
Land-use		2	3.1807	0.2039
Disturbance		3	9.4404	0.0240
Pielou's evenness (Binomial)				
Acacia presence	-0.5264	1	0.9153	0.3387
Acacia abundance	0.7334	1	8.3104	0.0039
Acacia basal area	-0.1738	1	1.7570	0.1850
Land-use		2	5.0166	0.0814
Disturbance		3	4.8567	0.1826
Shannon's index (Gaussian)				
Acacia presence	-0.1319	1	0.9700	0.3247
Acacia abundance	0.0278	1	0.3586	0.5493
Acacia basal area	0.0285	1	0.4566	0.4992
Land-use		2	1.9426	0.3786
Disturbance		3	7.0158	0.0714
Abundance (Negative binomial)				
Acacia presence	-0.6054	1	6.1163	0.0134
Acacia abundance	-0.1142	1	1.4178	0.2338
Acacia basal area	0.1554	1	3.9493	0.0469
Land-use		2	2.0988	0.3502
Disturbance		3	2.2575	0.5207
Proportion of dead individuals (Binomial)				
Acacia presence	0.9796	1	6.8987	0.0086
Acacia abundance	0.4304	1	6.7328	0.0095
Acacia basal area	-0.7259	1	3.5556	0.0593
Land-use		2	1.2347	0.5394
Disturbance		3	1.2962	0.7300
Basal area (Gaussian)				
Acacia presence	-0.0120	1	5.5385	0.0186
Acacia abundance	-0.0033	1	3.4481	0.0633
Acacia basal area	0.0032	1	3.8527	0.0497

Land-use		2	2.1412	0.3428
Disturbance		3	0.8532	0.8367
Height (Gaussian)				
Acacia presence	-0.7567	1	12.4492	0.0004
Acacia abundance	-0.0164	1	0.0485	0.8256
Acacia basal area	0.0522	1	0.5621	0.4534
Land-use		2	0.1827	0.9127
Disturbance		3	1.5238	0.6768
NMDS axis 1 (Gaussian)				
Acacia presence	0.0256	1	0.6043	0.4369
Acacia abundance	-0.0101	1	0.7776	0.3779
Acacia basal area	0.0095	1	0.8398	0.3595
Land-use		2	0.1938	0.9077
Disturbance		3	13.0038	0.0046
NMDS axis 2 (Gaussian)				
Acacia presence	0.0232	1	1.1605	0.2814
Acacia abundance	0.0090	1	1.6940	0.1931
Acacia basal area	-0.0023	1	0.1229	0.7259
Land-use		2	13.1665	0.0014
Disturbance		3	1.7420	0.6276
Total basal area (Gamma)				
Acacia presence	-0.3142	1	1.9148	0.1664
Acacia abundance	0.0974	1	1.3326	0.2483
Acacia basal area	0.3288	1	17.8236	<0.0001
Land-use		2	2.7748	0.2497
Disturbance		3	2.7151	0.4377
Total height (Gaussian)				
Acacia presence	0.1875	1	0.3386	0.5606
Acacia abundance	-0.1730	1	1.0658	0.3019
Acacia basal area	4.7720	1	10.0836	0.0015
Land-use		2	0.4568	0.7958
Disturbance		3	2.8337	0.4180
Herb-shrub sample				
Richness (Poisson)				
Acacia presence	-0.0047	1	0.0013	0.9714
Acacia abundance	-0.0090	1	0.0402	0.8411
Acacia basal area	0.0031	1	0.0063	0.9369
Acacia presence (subplot)	0.0322	1	0.0331	0.8557
Acacia cover (subplot)	-0.0258	1	0.3120	0.5764
Land-use		2	10.8373	0.0044
Disturbance		3	4.0537	0.2557
Pielou's evenness (Binomial)				
Acacia presence	0.2379	1	1.1389	0.2859
Acacia abundance	-0.0166	1	0.0361	0.8494
Acacia basal area	0.0406	1	0.2853	0.5932
Acacia presence (subplot)	0.2947	1	0.5116	0.4744
Acacia cover (subplot)	-0.0070	1	0.0064	0.9362
Land-use		2	3.0342	0.2193
Disturbance		3	1.4891	0.6848

Shannon's index (Gaussian)				
Acacia presence	-0.0930	1	0.7404	0.3895
Acacia abundance	-0.0068	1	0.0330	0.8559
Acacia basal area	0.0044	1	0.0163	0.8985
Acacia presence (subplot)	0.0859	1	0.2278	0.6332
Acacia cover (subplot)	-0.0145	1	0.1439	0.7044
Land-use		2	2.6598	0.2645
Disturbance		3	1.6844	0.6404
Abundance (Negative binomial)				
Acacia presence	-0.1509	1	0.9967	0.3181
Acacia abundance	0.0208	1	0.1527	0.6959
Acacia basal area	0.0026	1	0.0028	0.9578
Acacia presence (subplot)	-0.1670	1	0.4039	0.5251
Acacia cover (subplot)	-0.0538	1	0.8854	0.3467
Land-use		2	23.5665	<0.0001
Disturbance		3	16.4525	0.0009
Cover (Gaussian)				
Acacia presence	-2.4300	1	0.0354	0.8508
Acacia abundance	-4.9850	1	1.1223	0.2894
Acacia basal area	6.2500	1	2.1294	0.1445
Acacia presence (subplot)	7.1620	1	0.1020	0.7494
Acacia cover (subplot)	-3.7910	1	0.6289	0.4278
Land-use		2	0.3117	0.8557
Disturbance		3	1.4795	0.6870
NMDS axis 1 (Gaussian)				
Acacia presence	0.0255	1	0.4306	0.5117
Acacia abundance	0.0020	1	0.0238	0.8773
Acacia basal area	0.0009	1	0.0048	0.9447
Acacia presence (subplot)	0.0393	1	0.3810	0.5371
Acacia cover (subplot)	-0.0009	1	0.0047	0.9452
Land-use		2	4.2407	0.1200
Disturbance		3	2.8487	0.4155
NMDS axis 2 (Gaussian)				
Acacia presence	-0.0488	1	1.6318	0.2015
Acacia abundance	-0.0023	1	0.0315	0.8591
Acacia basal area	0.0069	1	0.3186	0.5725
Acacia presence (subplot)	-0.0176	1	0.0787	0.7791
Acacia cover (subplot)	-0.0141	1	1.1325	0.2872
Land-use		2	4.1015	0.1286
Disturbance		3	2.0572	0.5606

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CHAPTER 2 - FRAGMENTATION AND ROAD NETWORK INCREASE THE LANDSCAPE PERMEABILITY TO *ACACIA* SPP. INVASION

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ABSTRACT

Context. Land degradation and biological invasion are among the most important causes of biodiversity crisis and may promote changes in diversity and ecosystems in a synergetic way. Additionally, landscape fragmentation and the net of roads and highways has been reported as drivers of biological invasion.

Objectives. Our aim was to assess the effect of fragmentation and road network in the *Acacia* spp. invasion. We investigated whether 1) forest fragments are a barrier to invasions; 2) roads and highways are working as corridors for its spread; and 3) *Mussununga* size and patches complexity, measured by shape index, increase the chance of invasion by *Acacia*.

Methods. Acacia invasion was recorded in 32 *Mussununga* sites within Atlantic Forest domain. We tested the effect of landscape conductance based in circuit theory and other nine landscape structure metrics in *Acacia* occurrence using three buffer zones sizes (0.5, 1.0, and 2.0 km).

Results. Landscape conductance (1.0 km buffer) was significantly related with *Acacia* invasion. The best landscape conductance selected was calculated using the following values of cell-level conductance in the input: highways = 90, roads = 80, forests = 30, water = 0, and 50 for the other land-cover classes. Furthermore, our model selection (ΔAICc < 2) shown that shape index had negative effect in *Acacia* invasion, while length of roads, *Mussununga* size, *Mussununga* perimeter, length of highways and landscape conductance had positive effect.

Conclusions. The landscape in the Atlantic Forest affects the biological invasion in the peculiar *Mussununga* ecosystem. Therefore, restoration of degraded areas and eradicate *Acacia* trees in the roadside could reduce the landscape permeability for biological invasion.

Keywords: biological invasion, landscape conductance, resistance distance, circuit theory, land-use, *Mussununga*

INTRODUCTION

Land degradation and biological invasion are listed among the main threats to biodiversity (Vitousek et al. 1997; Sala et al. 2000; Haddad et al. 2015). In fragmented landscapes, the remaining patches of habitats become susceptible to a set of environmental changes that affect communities for a long time (Haddad et al. 2015). Habitat degradation (e.g. land-use change, mining, and deforestation) affects directly the species-area relationship (MacArthur and Wilson 1967) and, therefore, threaten the biodiversity and ecosystems services (Haddad et al. 2015). Further, land degradation exposes the remnant fragments to a set of changes that can expose the habitat to a continuous chain of changes, such as connectivity reduction, increase in the disturbance regimen and shifts in the microclimatic conditions (Haddad et al. 2015; Magnago et al. 2015). Understand how these set of ecological process resulting from landscape degradation interact with other types of drivers, such as biological invasion, is still needed (Haddad et al. 2015; Wilson et al. 2016).

Habitat fragmentation and human made roads and highways affect directly the occurrence of invasive species (Parendes and Jones 2000; Dawson et al. 2015), favoring landscape degradation and biological invasion, may interact and promote deeper changes in biodiversity and ecosystems functioning (Didham et al. 2005). Fragmented landscapes under human-use have elements that work as barriers and, at the same time, others that will aid the invasive species spread. New elements in the landscape, such as roads and highways, that work as corridors for invasive plants (Parendes and Jones 2000; Hansen and Clevenger 2005; Thiele et al. 2008) increase the landscape permeability for invasive species owing to increase of suitable habitat (Parendes and Jones 2000; Raghubanshi and Tripathi 2009), shifting the dynamic of disturbance events (Hansen and Clevenger 2005; Pollnac et al. 2012) and increasing propagule pressure (Donaldson et al. 2014). The impacts of fragmentation and road network may increase opportunities for the establishment of invasive species and, both, may additively impact the native ecosystem (Didham et al. 2005; Le Maitre et al. 2011).

Plant invasion may generate a set of changes in the ecosystem, such as increase nitrogen fixation, organic matter deposition, and biodiversity loss (Fridley et al. 2007;

Gaertner et al. 2009; Hellmann et al. 2011; Fischer et al. 2014; Gaertner et al. 2014). The genus *Acacia* is a widely known invasive plant of many ecosystems worldwide, also promoting several ecosystems changes (Le Maitre et al. 2011; Richardson and Rejmánek 2011). *Acacia* is a nitrogen fixing genus with high rate of growing, seed and litter production (Le Maitre et al. 2011). In oligotrophic ecosystems, characterized by few biomass production, poor-nutrient soil conditions and light demanding species, *Acacia* has caused soil enrichment, litter accumulation and shading (Marchante et al. 2008; Hellmann et al. 2011; Rascher et al. 2011; Meira-Neto et al. 2017). Consequently, these changes could to harm species adapted to oligotrophic conditions and still benefit the establishment of *Acacia* seedlings (Le Maitre et al. 2011; Rascher et al. 2011). Thus, understanding the role of degraded landscapes in the process of biological invasion is crucial to guide monitoring actions and could help to detect specific sites that are prone to invasions, preventing the consequences of biological invasion in the environment.

The role of the landscape connectivity in the species distribution also depends of the biological traits of the species (Minor and Gardner 2011; Thiele et al. 2018). For instance, short-dispersed species tend to be negatively affected by fragmentation (Magnago et al. 2014; Thiele et al. 2018). On the other hand, invasive species, that are commonly reported invading ruderal habitats (Parendes and Jones 2000; Vilà et al. 2007; Le Maitre et al. 2011), would be favored by fragmentation (Dawson et al. 2015). In this sense, new elements in the landscape, such as roads and highways, would work as corridors for invasive plants (Parendes and Jones 2000; Hansen and Clevenger 2005; Thiele et al. 2008). *Acacia*, specifically, is a light-demanding genus that can invade non-forest and degraded ecosystems and, in turn, is highly limited by closed canopy of forests (Delnatte and Meyer 2012; field observations). Hence, in addition to fragmentation, the enlargement of the road network may facilitate *Acacia* dispersion and establishment in consequence to the increase of human transportation and plantation (Griffin et al. 2011; Aguiar Jr. et al. 2014; Donaldson et al. 2014).

Investigate how landscape and its elements are affecting biological invasion by *Acacia* in *Mussununga* ecosystem is a necessary step to establishment monitoring and eradication efforts (Lehmann et al. 2017). Because the landscape presents an important role in the invasive plants dispersion and establishment (Thiele et al. 2008; Minor et al.

2009; Resasco et al. 2014; Dawson et al. 2015), we hypothesized that in a fragmented landscape with larger road network the *Mussununga* ecosystem would suffer higher risk of biological invasion by *Acacia* species. Therefore, the present study aimed to test whether 1) forest fragments is a barrier to *Acacia*; 2) roads and highways are working as corridors to invasion by *Acacia*; and 3) *Mussununga* size and patches complexity, measured by shape index, increase the chance of invasion by *Acacia*.

METHODOLOGY

Study area

This study was conducted in eastern Brazil, in the states of Espírito Santo and Bahia. We sampled areas ranging from municipalities of Linhares in central Espírito Santo (19° 25'S, 40° 04'W) to Caravelas in the extreme south of Bahia (17° 44'S, 39° 15'W) (Fig. 1). The climate in this region was classified as tropical and varies from between Aw, Am, and Af of Köppen (Alvares et al. 2014). The original vegetation of Atlantic Forest was highly fragmented and currently is composed of eucalyptus plantations, pastures, crop fields, remnant forests, mangrove, *Restinga* and *Mussununga*. The *Mussununga* patches have a wide variation in size and shapes (from circular to amoeboid) and are spread around the matrix of remnant forests and anthropogenic land cover. *Mussununga* is a Tertiary vegetation, delimitated by Spodosols that were originated through podsolization, and composed by a specialized flora with less diversity and less biomass than Atlantic Forest (Saporetti-Junior et al. 2012). *Mussununga* physiognomy is heterogeneous and has range of types, from grassland, open savanna vegetation, closed savanna, and woodland (Saporetti-Junior et al. 2012). Woodland *Mussununga* can be distinguished from Atlantic Forest by Spodosols and low-growing.

Mussununga ecosystem, especially the non-woodland physiognomies, has been invaded by *Acacia auriculiformis* Cunn. ex Benth. and *Acacia mangium* Willd. These species were introduced to the Lowland Atlantic Forest region as an alternative for land reclamation around the 70's and since then has been spreading and invading degraded areas, pastures, and eucalyptus plantations in the region (Lehmann et al. 2017). Even in *Mussununga* patches invaded recently (less than ten years ago), several ecosystem changes were related recently (Meira-Neto et al. 2017; Heringer et al. unpublished). For more detail about the study region and *Acacia* invasion see Heringer et al. (unpublished).

***Acacia* invasion sampling**

In this study, *Acacia* occurrence was used as a metric of invasion (response variable). The occurrence data were taken from the field between September 2015 and March 2016 when we travelled across the Lowland Atlantic Forest looking for *Mussununga* patches. During this time, we visited several *Mussununga* patches to select our study sites, that should be *Mussununga* patches with or without *Acacia* invasion. However, some of the visited sites were logged, burned or had recently suffered management for eucalyptus plantation recently and, therefore, was impossible to detect the occurrence of *Acacia* for sure. Thirty-two patches were assessed regarding biological invasion, when we walked through all patches looking for *Acacia* trees and considered the presence of *Acacia* individuals in different stages of life (such as seedling, adult, and fertile adult) as an indicator to the invasion process. Since *Acacia* occur largely roadsides, we only considered as invaded those *Mussunungas* where *Acacia* were observed within the patch (at least 2 meters from roadside).

Landscape classification

The landscape classification was conducted from six Sentinel-2 scenes of February 2016 (ESA 2010). In the preprocessing, all bands from the six scenes were resampled to 10 meters in Sentinel Application Platform – SNAP 5.0 before layer stacking. Afterwards, atmospheric corrections were proceeded by using Quick Atmospheric Correction algorithm (QUAC ®). To avoid waste of computational time, we create a mosaic with all scenes and then we masked it by using a smaller region of interest (ROIs) using ENVI 5.3 software (Exelis Visual Information Solutions, Inc. – Boulder, CO, USA). Still in ENVI 5.3, we conducted the classification process with two algorithms, maximum likelihood and neural network classification, using 1663 ROIs as training samples. The ROIs were created using the geographic coordinates from all target classes collected during the fieldwork. The target classes are: water, new eucalyptus plantation, old eucalyptus plantation, native forest, *Mussununga*, bare soil and grassland/pasture. After the classifications we select the best result based on the confusion matrices using other 1280

ROIs as validation samples. Maximum likelihood algorithm presented better land cover classification than neural network (Kappa = 0.92 and Overall accuracy = 93.5% vs. Kappa = 0.41 and Overall accuracy = 48.7%, respectively; Supplementary material, Table S1). As a post-classification process, we applied a median filter testing three different kernel sizes (3 x 3, 5 x 5 and 7 x 7 pixels) and assessed the results from the confusion matrix using the validation ROIs above mentioned. The results increased progressively with the increase of kernel size. Therefore, the 7 x 7 window that presented the best result, while preserving the features' borders, was selected (Kappa = 0.94 and Overall accuracy = 94.88%, Supplementary material, Table S1; Table S2). Additionally, to exclude the misclassification due to small elements in the landscape that could not fill the entire pixel, especially roads and highways, we conducted manual corrections inside the buffer zones of 2.0 km in each site sample. To do this, we compared the final classification output with the original Sentinel-2 images and high-resolution Google images using QGIS 2.18.12 (Quantum GIS Development Team 2017). Whenever necessary, we edited the thematic raster in the Semi-automatic Classification Plugin - SCP (Congedo 2016) to correct those erroneously classified pixels. Simultaneously, we added a new class called "*Mussununga* core", that are sandy-savanna *Mussununga* patches where the sample site was allocated and added the roads and highways in the previous classification (classification #2). Both classifications were used posteriorly to proceed the landscape conductance calculation, considering here as a functional metric, and to get the landscape structure metrics (see below).

Landscape conductance calculation

Based in the reviewed landscape classifications, we created a set of exploratory conductance surface maps, where we attributed values of cell-level conductance from 0 to 100 (minimum to maximum conductance) for each class of the classified map using SCP (Congedo 2016). Conductance surfaces were created based in our hypothesis, where as a general rule roads, highways and non-forest elements would work as corridors, while forest and water would work as barriers to *Acacia* invasion (Fig. 2; Supplementary material, Table S3). We named each conductance surface using codes, where "L" means variations in the cell-level conductance for land-cover elements and "R" means variations in the cell-level conductance for road network elements (see Supplementary material,

Table S3). We also created rasters comprising the centroid of the each *Mussununga* sampled and buffer rings with radius of 0.5 km, 1.0 km, and 2.0 km around the centroids. We consider the area between the buffer ring and the central point as the ground where *Acacia* must cross to invade the *Mussununga* (our sample sites). Afterwards, we used each conductance surface and the buffer nodes as input file in the Circuitscape 4.0.5 (www.circuitscape.org, ©Brad McRae, Viral B. Shah and Tanmay K. Mohapatra) and applied the pairwise mode. Subsequently, we transformed the effective resistance output in effective conductance using the equation $\hat{G} = 1 / \hat{R}$, where $\hat{G}$ = effective conductance and $\hat{R}$ = effective resistance. The effective conductance (hereafter, landscape conductance) can be interpreted as a measure of connectivity and increases with the increase of suitable pathways (Mcrae et al. 2008), therefore, similarly was considered here as permeability of the ground to the *Acacia*. At the end, we got the landscape conductance of the 32 sample sites for each of the 16 conductance surfaces in the input and for each of three buffer sizes. The landscape conductance outputs were used as exploratory metrics to test the effect of landscape functioning in biological invasion and in a global model together with landscape structure metrics (see Statistical analyses).

Landscape structure metrics

To test the role of the landscape structure in the *Acacia* invasion we used metrics that could be a surrogate of corridors or barriers and then affect the permeability of the landscape. Among the elements that could work as corridors, we used length of roads and highways in the buffer zone, distance from the nearest road, and distance from the nearest highway (even if outside of the buffer zone). As a barrier element we used total area of native forest area inside the buffer zone. Additionally, we tested whether *Mussununga* could affect *Acacia* occurrence using *Mussununga* area inside the buffer zone and *Mussununga* size, *Mussununga* perimeter, and shape index (SI) of the *Mussununga* patch considering whole *Mussununga* extension (even if outside of the buffer zone). The landscape metrics were calculated using field calculator in QGIS software (Quantum GIS Development Team 2017), and shape index was calculated using the equation SI = *Mussununga* perimeter / 2 x √ (π x *Mussununga* size), where *Mussununga* perimeter and *Mussununga* size are in meters (McGarigal et al. 2012). Shape index is a measure independent of area that increases with the patch shape complexity, where a higher shape index value indicates that the patch is more irregular and has less core area and larger edge.

Statistical analyses

To test if the landscape permeability affects the *Acacia* invasion, we firstly created one GLM model with binomial distribution for each of the 16 conductance surfaces with the three buffer sizes (“stats” package, R Development Core Team 2017). After, we used the “dredge” function (“MuMIn” package, Barton 2016) for each model to select the best buffer size based in Akaike information criterion of second order (AICc) due our small sample number (Burnham and Anderson 2002). Then, we used the best buffer size of each conductance surface (with the smaller AICc value) and built another model with them. Again, we applied “dredge” function to select the best conductance surface within those with better buffer size. We divided the analysis into two steps due to the high number of exploratory predictive variables that extrapolate the number allowed by the function. Finally, we considered only the models with single conductance surface (or one predictive variable), since all them were derived from the same landscape

In order to test the effect of whole landscape metrics on *Acacia* invasion, we firstly created four GLM models with binomial distribution to select the best buffer size for each of the following predictive metrics: forest area, *Mussununga* area, length of roads and highways. To do this, we applied “dredge” function and select the models with minor ΔAICc. After, we created a global model with the landscape structure metrics and the best landscape conductance selected before, and used “dredge” function to select the best predictors. We selected among the models with $\Delta\text{AICc} < 2$ and performed the calculation of the relative weights for each predictive variable in the selected models (Burnham and Anderson 2002; Carrara et al. 2015). The relative weights were calculated using “importance” function (“MuMIn” package, Barton 2016). To avoid correlations between predictive variables we calculated the Pearson correlation for all variables using “cor.test” function (“stats” package, R Development Core Team 2017) and variables with $r \geq 0.7$ were not included in the same model (Dormann et al. 2013). Therefore, during the model selection we applied the “subset” function (“base” package, R Development Core Team 2017) to create models without correlated variables together.

RESULTS

Here we found that landscape permeability, where roads and highways were tested as corridor and forest as barrier, had positive effect in *Acacia* invasion, as well as road network and *Mussununga* size. On the other hand, *Mussununga* shape index affected biological invasion negatively. Yet, our model selection shown models where *Mussununga* perimeter, effective conductance and length of highways also presented positive effect in *Acacia* invasion (Table 2).

In all models used to select among the best buffer size, the 1.0 km is the best buffer size, except for the L1R1 that was used as a null model with 50 % of conductance for all classes (Table 1; Supplementary material, Table S3; S4). Landscape conductance used as a measure of permeability presented a significant role in the occurrence of *Acacia.* Among the exploratory conductance surfaces used, L11R3 presented the best results (ΔAICc = 0; GLM: $X^2 = 3.999$; df = 1; $p = 0.045$; Table 1). The conductance values used in the input data L11R3 was 90 for highways, 80 for roads, 30 for forests, 0 for water and 50 for the other classes (Fig. 2; Supplementary material, Table S3). The landscape conductance values to L11R3 varied from 171.4 to 255.2 (235.0 ± 18.7). According to our model selection the worse conductance surface was the L2R4, when we did not use the classes roads and highways (Table 1; Supplementary material, Table S3).

The models used to select best buffer size among the landscape structure presented the buffers of 1.0 km presented the best ΔAICc values for forest area and length of highways, while buffers of 2.0 km presented the best ΔAICc value for length of roads and the second-best for *Mussunuga* area (after the null model; Supplementary material, Table S5). In all models selected, landscape structure affected the occurrence of *Acacia* spp. The best model selected, has shape index with negative effect in *Acacia* presence (GLM: $X^2 = 8.263$; df = 1; $p = 0.004$; Fig 3), while length of roads and *Mussununga* size presented positive role in the *Acacia* invasion (respectively, GLM: $X^2 = 7.554$; df = 1; $p = 0.006$; GLM: $X^2 = 5.851$; df = 1; $p = 0.016$; Fig 3).

Additionally, other three models presented ΔAICc ≤ 2. In the second-best model shown, shape index had negative effect in *Acacia* invasion, while length of roads and *Mussununga* perimeter had positive relationship (Table 2). In the third-best model, shape index had negative effect in *Acacia* while length of roads and *Mussununga* size had positive effect (Table 2). Although selected in this model, forest area had no significative effect in *Acacia* occurrence ($p = 0.234$). Finally, the fourth-model had the landscape conductance L11R3 and length of highways affecting positively the *Acacia* presence (Table 2). The relative Akaike weight of the variables selected in the models with ΔAICc < 2 were: shape index = 0.83, length of road = 0.83, *Mussununga* size = 0.62, *Mussununga* perimeter = 0.22, forest area = 0.21, landscape conductance L11R3 = 0.17, and highways length = 0.17.

We also tested the effect of *Mussununga* size without one outlier site (the biggest *Mussununga* patch) and, in this case, *Mussununga* size appeared only in the fourth-best model without significant effect in the *Acacia* occurrence (GLM: $X^2 = 0.7334$; df = 1; $p = 0.392$; Supplementary material, Fig S1; Table S6). Length of roads and shape index were selected in all models with ΔAICc ≤ 2, where length of roads presented positive effect in *Acacia* invasion and shape index presented negative effect. Length of roads and shape index were selected individually in the best model, while forest area was selected with them in the second-best model; distance from nearest road was selected in the third-best model; and *Mussununga* size was selected in the fourth-best model. None variable, except length of roads and shape index, affected *Acacia* invasion (Supplementary material, Table S6).

DISCUSSION

Here we found that fragmentation and increase of road network increase the landscape permeability for biological invasion by *Acacia* in the *Mussununga* ecosystem. Furthermore, *Mussununga* patch complexity and size were also important predictor to model *Acacia* invasion. Our model selection presented that *Mussununga* complexity affected negatively *Acacia* invasion, while length of roads, length of highways, *Mussununga* size, and *Mussununga* perimeter has a positive effect. Further, landscape conductance, built using forest as a barrier and road network as corridor for *Acacia*, presented a positive effect in biological invasion can provide an additional approach to understand biological invasion in the heterogeneous landscape of Atlantic Forest. Despite the direct effects of human activities in the Mussununga ecosystem, the increase biological invasion may lead to additional changes in the ecosystem functioning and community of *Mussununga* (Lehmann et al. 2017; Meira-Neto et al. 2017; Heringer et al. unpublished).

The increase of road network in the landscape can contribute to *Acacia* invasion by many ways. Roads and highways are often associated with deforestation, modification of plant structure roadside and shifts in disturbance regimen (Hansen and Clevenger 2005; Pollnac et al. 2012). Additionally, vehicles can carry non-native seeds for hundreds of kilometers and can active vector for long-distance dispersal of invasive species (Von Der Lippe and Kowarik 2007; Taylor et al. 2012). For instance, in our study site eucalyptus plantation is the most important economic activity and the high traffic of trucks during the planting or logging phases may disperse seeds from an *Acacia*'s plantation to other areas. Furthermore, as we could observe during the fieldwork, roadsides are largely occupied by *Acacia* and the high number of *Acacia* tree may increase the propagule pressure expanding the chance of successful dispersal (Donaldson et al. 2014). Although *A. mangium and A. auriculiformis* are dispersed by wind, birds and humans (Kull and Rangan 2008; Griffin et al. 2011), our results shown *Acacia* occurrence was highly impacted by landscape permeability. This scenario would be expected mainly for short-distance dispersed species (Minor and Gardner 2011; Thiele et al. 2018) and with large seed production with regional spread, once more than 80 % of the offspring are spread until 0.5 km from the *Acacia*'s plantation source (Aguiar Jr. et al. 2014).

The best conductance surface selected indicated that forest is working as a barrier to *Acacia* invasion (Table 1). *Acacia* species occurring in the study area are light-demanding and unable to cross the original matrix of dense forest (Delnatte and Meyer 2012; field observations). Hence, the Atlantic Forest fragmentation associated with a high concentration of urban areas (Scarano and Ceotto 2015) increase the availability of habitat and allow the dispersal of *Acacia*. Although, the role of landscape conductance in the *Acacia* invasion indicated that deforestation is an important element to increase the landscape permeability, forest area was selected only in the third-best model and without significance (Tables 1; 2). In our point of view this inconsistence could be explained because, even in buffers with large forest area, if there is a large road network or if the forest area is formed by many small fragments *Acacia* may disperse across the roadside or forest borders. In general, the good fits of landscape conductance in our results and the consistence of the results, when compared with structure metrics, allow us to consider circuit analyses as a powerful tool to assess areas at high risk of invasion and could be used in larger scales to predict regions with higher permeability to *Acacia*, as used recently for establish corridors between protected areas (Dickson et al. 2017). This approach would allow detect areas under high-risk of *Acacia* invasion (as suggested by Minor and Gardner 2011) and consider them as target for monitoring and eradication efforts (Lehmann et al. 2017).

The occurrence of *Acacia* was consistently related with the decrease of *Mussunuga* shape index, as shown by all models selected (except the model 41, Table 2). Contrary to the expectations, *Acacia* can invade easier *Mussununga* patches with proportionally less border. Previous studies and the theory suggest that patches with proportionally more border would be achieved by a propagule with greater probability (Collinge and Palmer 2002; Petrášová-Šibíková et al. 2017; see discussion in Ewers and Didham 2006). Nevertheless, our findings and some reports that also shown the opposite relationship between invasion and shape index (Moser et al. 2002; Yates et al. 2004; Tanentzap et al. 2010), may indicate the effect of shape index in biological invasion can be jumbled by other factors, such as propagule pressure, distance from forest fragments, land-use around the patch and human disturbance (Tanentzap et al. 2010; González-Moreno et al. 2013). Further, some studies reporting an increase of invasion in more complex patches were conducted in forest ecosystems where is difficult discern between shape index effect or edge effect, since the proportional increase of border will be strongly related with the increase edge effect. Edge effects comprises several ecosystems changes in the abiotic and biotic structure of the forest (Haddad et al. 2015; Magnago et al. 2015) and these changes may favor biological invasion (Dawson et al. 2015). Nevertheless, in our case the patches studied are composed by savanna-type *Mussunungas* where there is no edge effect and native vegetation do not exert an effective shading to *Acacia* (see an example in Lehmann et al. 2017). Yet, border of *Mussununga* patches is not always a disturbed area, in many cases most of the *Mussununga* perimeter is bordered by forest and, therefore, would not be an expected path to *Acacia* dispersal (sample site 28 is a good example; Fig. 1). Ecosystems formed by patches like *Mussununga* could be interesting to conduct studies that are looking for understand the role of shape index in natural community when edge effect is not occurring.

Regarding the role of *Mussununga* patches, we supposed *Mussununga* ecosystem would not be a barrier to *Acacia*, once species invading this region are light-demanding and able to grow in the poor-nutrient soils (Rascher et al. 2011; Meira-Neto et al. 2017). Although our findings corroborate this assumption, we cannot give a solid conclusion because there is a strong effect of one outlier (site sample 8). When we excluded this outlier, *Mussununga* perimeter did not appeared in any model with ΔAICc < 2, while *Mussununga* size only appeared in the fourth-best model and with no significance (Supplementary Material, Fig S1; Table S6).

Deforestation and human development in Atlantic Forest generated a highly fragmented landscape (Scarano and Ceotto 2015), which in turn increase the permeability to *Acacia* dispersal and favors the invasion in the *Mussununga* ecosystem. Our results shown roads and highways are acting as a corridor to the dispersal of *Acacia* over the landscape. Landscape conductance results also corroborates that forest fragments are landscape elements that can act as a barrier to *Acacia*. These results corroborate other studies where high degraded landscape are more susceptible to biological invasion (Vilà et al. 2007; Thiele et al. 2008; Dawson et al. 2015). Yet, our results highlight the chain of events that threat *Mussunuga* ecosystem, since the biological invasion by *Acacia* is promoting several changes in *Mussununga* ecosystem (Lehmann et al. 2017; Meira-Neto et al. 2017; Heringer et al. unpublished).

CONCLUSION

As expected, we present here our findings that roads and highways are working as pathways for *Acacia* species, while forest fragments around *Mussununga* patches are barriers for biological invasion in this savanna-type ecosystem. Nevertheless, the *Mussununga* patch complexity decrease the chance of biological invasion. Regarding conservation actions, conductance surface could be used to detect areas of high risk of invasion in regional scales benefiting the decision making. In addition to it, local actions focusing on hampering dispersal and establishment of *Acacia* are required. For instance, promote fast restoration of degraded areas, discourage *Acacia*'s plantations and replace

Acacia's trees roadside per native trees will help to reduce the factor that may promote biological invasion, such habitat availability and propagule pressure. Hence, the biological invasion in the peculiar *Mussununga* ecosystem is extended by fragmentation and road network, and the actions above mentioned could reduce the landscape permeability to *Acacia* and, synergistically, increase the connectivity for native species.

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REFERENCES

Aguiar Jr. A, Barbosa RI, Barbosa JBF, Mourão M (2014) Invasion of Acacia mangium in Amazonian savannas following planting for forestry. Plant Ecol Divers 7:359–369. doi: 10.1080/17550874.2013.771714

Alvares CA, Stape JL, Sentelhas PC, et al (2014) Köppen's climate classification map for Brazil. Meteorol Zeitschrift 22:711–728. doi: 10.1127/0941-2948/2013/0507

Barton K (2016). MuMIn: Multi-Model Inference. R package version 1.15.6. https://CRAN.R-project.org/package=MuMIn

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: a practical information-theoretic approach (2nd ed). Springer, New York

Carrara E, Arroyo-Rodríguez V, Vega-Rivera JH, et al (2015) Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biol Conserv 184:117–126. doi: 10.1016/j.biocon.2015.01.014

Collinge SK, Palmer TM (2002) The influences of patch shape and boundary contrast on insect response to fragmentation in California grasslands. Landsc Ecol 17:647–656.

Congedo, L. (2016). Semi-Automatic Classification Plugin Documentation. doi: 10.13140/RG.2.2.29474.02242/1

Dawson W, Burslem DFRP, Hulme PE (2015) Consistent effects of disturbance and forest edges on the invasion of a continental rain forest by alien plants. Biotropica 47:27–37. doi: 10.1111/btp.12183

Delnatte C, Meyer J-Y (2012) Plant introduction, naturalization, and invasion in French Guiana (South America). Biol Invasions 14:915–927. doi: 10.1007/s10530-011-0129-1

Dickson BG, Albano CM, McRae BH, et al (2017) Informing strategic efforts to expand and connect protected areas using a model of ecological flow, with application to the western United States. Conserv Lett 10:564–571. doi: 10.1111/conl.12322

Didham RK, Tylianakis JM, Hutchison MA, et al (2005) Are invasive species the drivers of ecological change? Trends Ecol Evol 20:470–474. doi: 10.1016/j.tree.2005.07.006

Dormann CF, Elith J, Bacher S, et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27-46. doi: 10.1111/j.1600-0587.2012.07348.x

Donaldson JE, Hui C, Richardson DM, et al (2014) Invasion trajectory of alien trees: the role of introduction pathway and planting history. Glob Chang Biol 20:1527–1537. doi: 10.1111/gcb.12486

ESA – European Space Agence (2010) GMES Sentinel-2 mission requirements document, issue 2 revision 1, 08/03/2010, EOP-SM/1163/Mr-dr

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev Camb Philos Soc 81:117–142. doi: 10.1017/S1464793105006949

Fischer FM, Oliveira JM, Dresseno ALP, Pillar VD (2014) The role of invasive pine on changes of plant composition and functional traits in a coastal dune ecosystem. Nat Conserv 12:19–23. doi: 10.4322/natcon.2014.004

Fridley JD, Stachowicz JJ, Naeem S, et al (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17. doi: 10.1890/0012-9658(2007)88[3:Tiprpa]2.0.Co;2

Gaertner M, Biggs R, Te Beest M, et al (2014) Invasive plants as drivers of regime shifts: Identifying high-priority invaders that alter feedback relationships. Divers Distrib 20:733–744. doi: 10.1111/ddi.12182

Gaertner M, Den Breeyen A, Hui C, et al (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Prog Phys Geogr 33:319–338. doi: 10.1177/0309133309341607

González-Moreno P et al (2013) Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats. Landsc Ecol 28:891–903. doi: 10.1007/s10980-013-9857-1

Griffin AR, Midgley SJ, Bush D, et al (2011) Global uses of Australian acacias - recent trends and future prospects. Divers Distrib 17:837–847. doi: 10.1111/j.1472-4642.2011.00814.x

Haddad NM, Brudvig LA, Clobert J, et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Science 1:1–10. doi: 10.1126/sciadv.1500052

Hansen MJ, Clevenger AP (2005) The influence of disturbance and habitat on the presence of non-native plant species along transport corridors. Biol Conserv 125:249–259. doi: 10.1016/j.biocon.2005.03.024

Hellmann C, Sutter R, Rascher KG, et al (2011) Impact of an exotic N2-fixing Acacia on composition and N status of a native Mediterranean community. Acta Oecologica 37:43–50. doi: 10.1016/j.actao.2010.11.005

Kull CA, Rangan H (2008) Acacia exchanges: wattles, thorn trees, and the study of plant movements. Geoforum 39:1258–1272. doi: 10.1016/j.geoforum.2007.09.009

Le Maitre DC, Gaertner M, Marchante E, et al (2011) Impacts of invasive Australian acacias: implications for management and restoration. Divers Distrib 17:1015–1029. doi: 10.1111/j.1472-4642.2011.00816.x

Lehmann JR, Prinz T, Ziller SR, et al (2017) Open-Source processing and analysis of aerial imagery acquired with a low-cost Unmanned Aerial System to support invasive plant management. Front Environ Sci. doi: 10.3389/fenvs.2017.00044

MacArthur RH, Wilson EO (1967) The Theory of Island Biogeography. Princeton University Press, Princeton, N.J.

Magnago LFS, Edwards DP, Edwards FA, et al (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J Ecol 102:475–485. doi: 10.1111/1365-2745.12206

Magnago LFS, Rocha MF, Meyer L, et al (2015) Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. Biodivers Conserv 24:2305–2318. doi: 10.1007/s10531-015-0961-1

Marchante E, Kjoller A, Struwe S, Freitas H (2008) Short- and long-term impacts of Acacia longifolia invasion on the belowground processes of a Mediterranean coastal dune ecosystem. Appl Soil Ecol 40:210–217. doi: 10.1016/j.apsoil.2008.04.004

McGarigal, K., Cushman, S.A. & Ene, E. (2012) FRAGSTATS v4: Spatial pattern analysis program for categorical and continuous maps. University of Massachusetts, Amherst, USA. Available at: http://goo.gl/aAEbMk.

Mcrae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89:2712–2724. doi: 10.1890/07-1861.1

Meira-Neto JAA, da Silva MCNA, Tolentino GS, et al (2017) Early Acacia invasion in a sandy ecosystem enables shading mediated by soil, leaf nitrogen and facilitation. Biol Invasions 1–9. doi: 10.1007/s10530-017-1647-2

Minor E, Tessel S, Engelhardt K, Lookingbill T (2009) The role of landscape connetivity in assembling exotic plant communities: a network analysis. Ecology 90:1802–1809. doi: 10.1890/08-1015.1

Minor ES, Gardner RH (2011) Landscape connectivity and seed dispersal characteristics inform the best management strategy for exotic plants. Ecol Appl 21:739–749. doi: 10.1890/10-0321.1

Moser D, Zechmeister HG, Plutzar C, et al (2002) Landscape patch shape complexity as an effective measure for plant species richness in rural landscapes. Landsc Ecol 17:657–669. doi: 10.1023/A:1021513729205

Parendes LA, Jones JA (2000) Role of light availability and dispersal in exotic plant invasion along roads and streams in the H. J. Andrews Experimental Forest, Oregon. Conserv Biol 14:64–75. doi: 10.1046/j.1523-1739.2000.99089.x

Petrášová-Šibíková M, Bacigál T, Jarolímek I (2017) Fragmentation of hardwood floodplain forests — how does it affect species composition? Community Ecol 18:97–108. doi: 10.1556/168.2017.18.1.11

Pollnac F, Seipel T, Repath C, Rew LJ (2012) Plant invasion at landscape and local scales along roadways in the mountainous region of the Greater Yellowstone Ecosystem. Biol Invasions 14:1753–1763. doi: 10.1007/s10530-012-0188-y

Quantum GIS Development Team (2017) Quantum GIS geographic information system. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: http://www.R-project.org/

Raghubanshi AS, Tripathi A (2009) Effect of disturbance, habitat fragmentation and alien invasive plants on floral diversity in dry tropical forests of Vindhyan highland: a review. Trop Ecol 50:57–69.

Rascher KG, Große-Stoltenberg A, Maguas C, et al (2011) Acacia longifolia invasion impacts vegetation structure and regeneration dynamics in open dunes and pine forests. Biol Invasions 13:1099–1113. doi: 10.1007/s10530-011-9949-2

Resasco J, Haddad NM, Orrock JL, et al (2014) Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. Ecology 95:2033–2039. doi: 10.1890/14-0169.1

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species - a global review. Divers Distrib 17:788–809. doi: 10.1111/j.1472-4642.2011.00782.x

Saporetti-Junior AW, Schaefer CEGR, de Souza AL, et al (2012) Influence of soil physical properties on plants of the *Mussununga* ecosystem, Brazil. Folia Geobot 47:29–39. doi: 10.1007/s12224-011-9106-9

Sala OE., Chapin III FS. S, Armesto JJ., et al (2000) Global Biodiversity Scenarios for the Year 2100. Science 287:1770–1774. doi: 10.1126/science.287.5459.1770

Scarano FR, Ceotto P (2015) Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers Conserv 24:2319–2331. doi: 10.1007/s10531-015-0972-y

Tanentzap AJ, Bazely DR, Lafortezza R (2010) Diversity-invasibility relationships across multiple scales in disturbed forest understoreys. Biol Invasions 12:2105–2116. doi: 10.1007/s10530-009-9612-3

Taylor K, Brummer T, Taper ML, et al (2012) Human-mediated long-distance dispersal: an empirical evaluation of seed dispersal by vehicles. Divers Distrib 18:942–951. doi: 10.1111/j.1472-4642.2012.00926.x

Thiele J, Kellner S, Buchholz S, Schirmel J (2018) Connectivity or area: what drives plant species richness in habitat corridors? Landsc Ecol 1–9. doi: 10.1007/s10980-017-0606-8

Thiele J, Schuckert U, Otte A (2008) Cultural landscapes of Germany are patch-corridor-matrix mosaics for an invasive megaforb. Landsc Ecol 23:453–465. doi: 10.1007/s10980-008-9202-2

Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. J Veg Sci 18:35–42. doi: 10.1111/j.1654-1103.2007.tb02513.x

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human Domination of Earth' s Ecosystems. Science 277:494–499. doi: 10.1126/science.277.5325.494

Von Der Lippe M, Kowarik I (2007) Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv Biol 21:986–996. doi: 10.1111/j.1523-1739.2007.00722.x

Wilson MC, Chen X, Corlett TR, et al (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landsc Ecol 31:219–227. doi: 10.1007/s10980-015-0312-3

Yates ED, Levia DF, Williams CL (2004) Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. For Ecol Manage 190:119–130. doi: 10.1016/j.foreco.2003.11.008

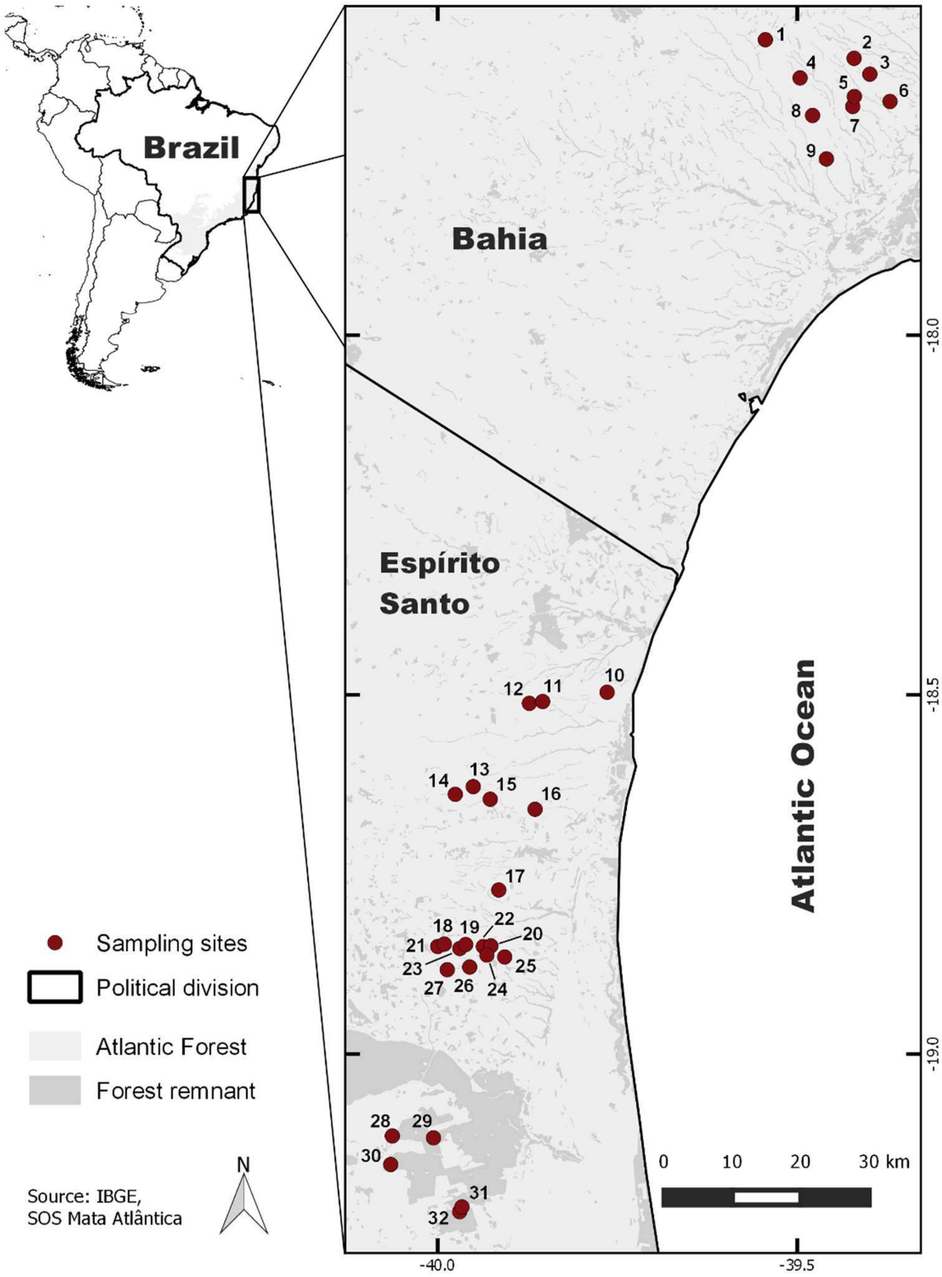

Fig. 1 Study region, forest remnant and *Mussununga* sampled sites in Atlantic Forest domain.

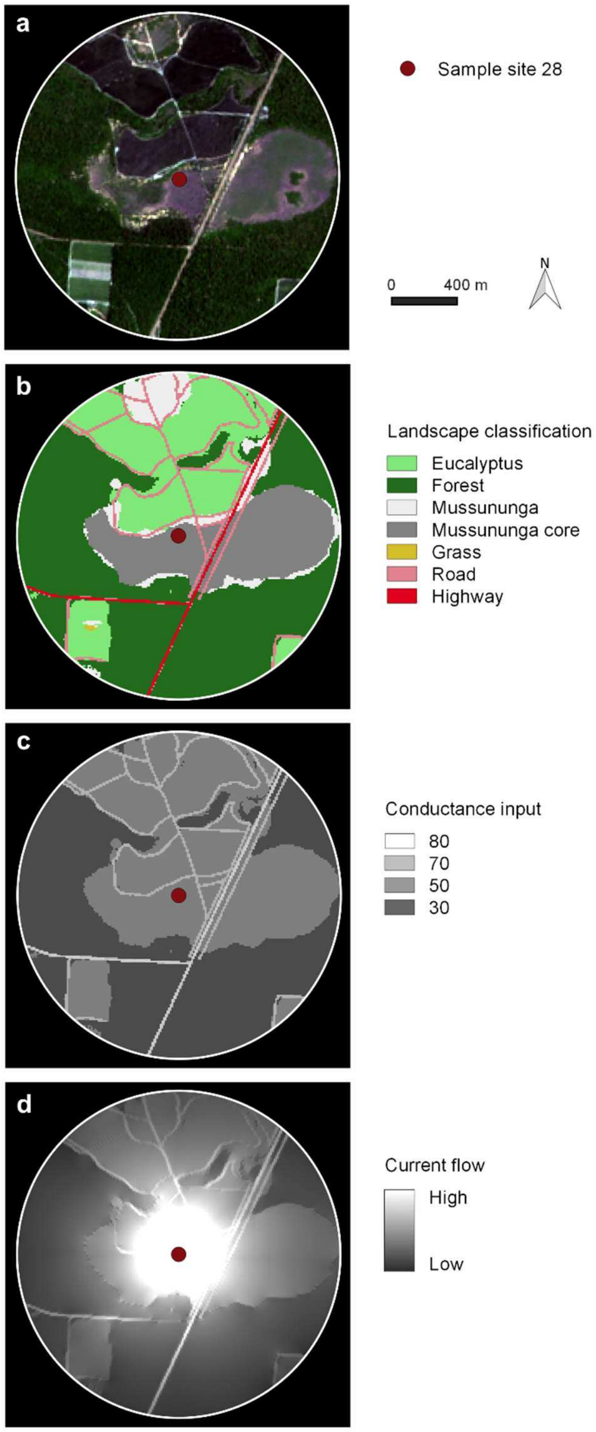

Fig. 2 Map of the study area 28 with a buffer zone of 1.0 km. **a** Show the Sentinel-2 image used to landscape classification. **b** Landscape classification output. **c** Input conductance values attributed to each landscape element in the landscape. The landscape ranges from corridors (80 and 70 values) to neutral (50) and barrier (30). **d** Map of current flow showing the permeability between the buffer ring and central plot.

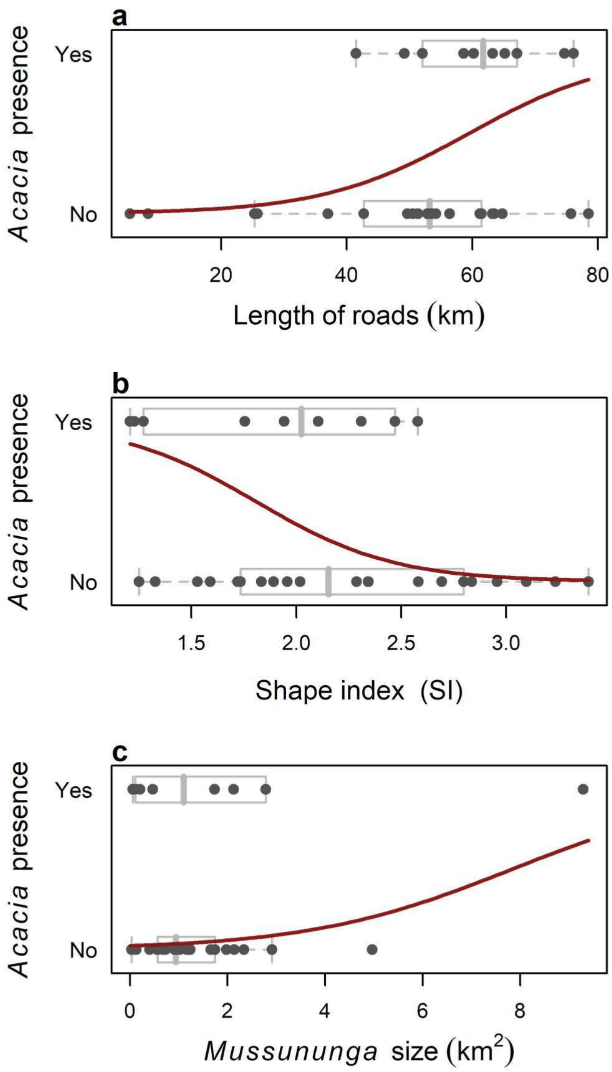

Fig. 3 GLM Logistic regression showing the relationship between **a** Length of roads and *Acacia* occurrence; **b** Shape index and *Acacia* occurrence; and **c** Mussununga size and *Acacia* occurrence. Dots corresponds to the value found in one *Mussununga* sample site; the grey box corresponds to the range between the first and the third quartile, the thick line inside the box refers to the median; and the solid red curve represents the estimated mean.

Table 1 Results for model selection based in Akaike information criterion and GLM logistic regression statistical results for the effect of conductance surface in the *Acacia* invasion (models with single predictive variable). The models were named according to the conductance surface, where “L” means the exploratory cell-level conductance for land-cover and “R” the exploratory cell-level conductance for road network. Only models with ΔAICc ≤ 2 are presented.

Model	Intercept	Estimate	AICc	ΔAICc	AICc weight	X^2	p value
L11R3_1km	-17.922	0.072	40.164	0	0.106	3.999	**0.045**
L10R3_1km	-9.875	0.039	40.530	0.366	0.088	3.633	0.057
L2R3_1km	-2.738	0.011	41.173	1.009	0.064	2.990	0.084
L2R2_1km	-2.700	0.011	41.217	1.053	0.063	2.946	0.086
L8R9_1km	-2.702	0.009	41.246	1.082	0.062	2.917	0.088
L4R2_1km	-2.716	0.014	41.247	1.083	0.062	2.917	0.088
L8R8_1km	-2.696	0.009	41.258	1.094	0.061	2.906	0.088
L8R3_1km	-2.671	0.009	41.283	1.119	0.061	2.880	0.090
L2R1_1km	-2.651	0.011	41.284	1.120	0.061	2.880	0.090
L9R9_1km	-2.640	0.008	41.345	1.181	0.059	2.819	0.093
L9R8_1km	-2.634	0.008	41.355	1.191	0.058	2.808	0.094
L9R3_1km	-2.611	0.008	41.381	1.217	0.058	2.783	0.095
L3R2_1km	-2.618	0.011	41.394	1.230	0.057	2.769	0.096
L5R3_1km	-2.457	0.009	41.701	1.537	0.049	2.462	0.117
L2R4_1km	-2.364	0.010	41.792	1.628	0.047	2.371	0.124
Null	-0.788	0	41.883	1.719	0.045	0	0

Table 2 Results of model selection based in Akaike information criterion and GLM logistic regression statistical results for the effect of landscape structure and the landscape conductance L11R3 in *Acacia* invasion. L11R3 corresponds to best landscape conductance selected. Only models with ΔAICc ≤ 2 are presented.

Model	Intercept	Estimate	df	AICc	ΔAICc	AICc weight	X^2	p
645	-1.4934		4	36.4345	0.00	0.4146		
Mussununga shape index		-1.9438					8.2626	**0.0040**
Length of road (2.0 km)		1.8372					7.5541	**0.0060**
Mussununga size		1.3199					5.8508	**0.0156**
643	-1.4463		4	37.7454	1.31	0.2152		
Mussununga shape index		-2.4910					8.0890	**0.0045**
Length of road (2.0 km)		1.6005					6.6285	**0.0100**
Mussununga perimeter		1.5877					4.5400	**0.0331**
646	-2.0138		5	37.8429	1.41	0.2050		
Mussununga shape index		-2.2568					9.0697	**0.0026**
Length of road (2.0 km)		2.0177					4.7158	**0.0299**
Mussununga size		1.1971					4.0562	**0.0440**
Forest area (1.0 km)		-1.3110					1.4178	0.2338
41	-1.3573		3	38.2749	1.84	0.1652		
L11R3 (1.0 km)		1.8814					4.6221	**0.0316**
Length of highway (1.0 km)		0.8810					4.3324	**0.0374**

SUPPLEMENTARY MATERIAL

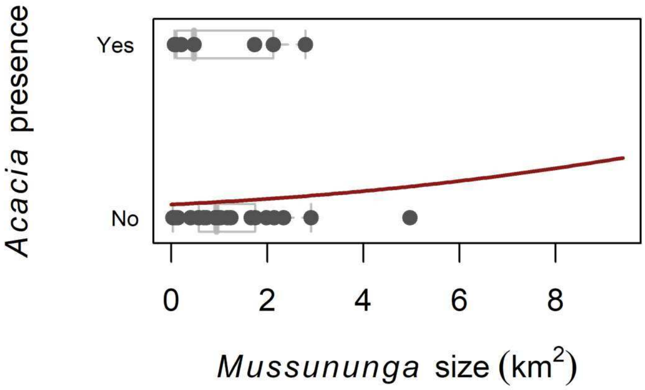

Fig S1 GLM Logistic regression showing the absence of relationship between *Mussununga* size and *Acacia* occurrence (without outlier site 8). Each dot corresponds to the value found in one *Mussununga* sample site; the grey box corresponds to the range between the first and the third quartile; the thick line inside the box refers to the median; and the solid red curve represents the estimated mean.

Table S1 Classification assessment of neural network and maximum likelihood classification, with all tested kernel size of filtering.

	Neural	Maximum Likelihood			
	No filter	No filter	Kernel size =	Kernel size =	Kernel size =
Overall	48.6752%	93.4811%	94.5900%	94.8149%	94.8795%
Kappa	0.4144	0.9235	0.9365	0.9392	0.9399

Table S2 Confusion matrix output for maximum likelihood classification (kernel size = 7 x 7). Eucal_new = new eucalyptus plantations; Eucal_old = old eucalyptus plantations; Mussun = *Mussununga*; Grass = grassland or pasture.

Overall Accuracy = (157350/165842) 94.8795%

Kappa Coefficient = 0.9399

	Ground Truth (Pixels)							
Class	Water	Eucal_new	Eucal_old	Forest	Mussun	Bare_soil	Grass	Total
Unclassified	0	0	0	0	0	0	0	0
Water	22033	0	0	0	0	0	0	22033
Eucal_new	235	13575	388	7	742	0	1377	16324
Eucal_old	39	571	28193	293	263	0	5	29364
Forest	23	6	0	28779	173	0	0	28981
Mussun	20	1880	12	0	23210	0	694	25816
Bare_soil	727	1	0	0	0	24175	1	24904
Grass	0	1035	0	0	0	0	17385	18420
Total	23077	17068	28593	29079	24388	24175	19462	165842

	Ground Truth (Percent)							
Class	Water	Eucal_new	Eucal_old	Forest	Mussun	Bare_soil	Grass	Total
Unclassified	0	0	0	0	0	0	0	0
Water	95.48	0	0	0	0	0	0	13.29
Eucal_new	1.02	79.53	1.36	0.02	3.04	0	7.08	9.84
Eucal_old	0.17	3.35	98.6	1.01	1.08	0	0.03	17.71
Forest	0.1	0.04	0	98.97	0.71	0	0	17.48
Mussun	0.09	11.01	0.04	0	95.17	0	3.57	15.57
Bare_soil	3.15	0.01	0	0	0	100	0.01	15.02
Grass	0	6.06	0	0	0	0	89.33	11.11
Total	100	100	100	100	100	100	100	100

Class	Comm. (Percent)	Omis. (Percent)	Comm. (Pixels)	Omis. (Pixels)	Prod. Acc. (Percent)	User Acc. (Percent)	Prod. Acc. (Pixels)	User Acc. (Pixels)
Water	0	4.52	0/22033	1044/23077	95.48	100	22033/23077	22033/22033
Eucal_new	16.84	20.47	2749/16324	3493/17068	79.53	83.16	13575/17068	13575/16324
Eucal_old	3.99	1.4	1171/29364	400/28593	98.6	96.01	28193/28593	28193/29364
Forest	0.7	1.03	202/28981	300/29079	98.97	99.3	28779/29079	28779/28981
Mussun	10.09	4.83	2606/25816	1178/24388	95.17	89.91	23210/24388	23210/25816
Bare_soil	2.93	0	729/24904	0/24175	100	97.07	24175/24175	24175/24904
Grass	5.62	10.67	1035/18420	2077/19462	89.33	94.38	17385/19462	17385/18420

Table S3 Codes and values of cell-level conductance used for each element in the landscape to create the 16 input conductance surfaces. The codes were named according to the conductance surface, where "L" means the exploratory cell-level conductance for land-cover and "R" the exploratory cell-level conductance for road network.

Code	Conductance surface value							
	Road	Highway	Water	Eucalyptus	Forest	Grass	*Mussununga*	*Mussununga* core
L1R1	50	50	50	50	50	50	50	50
L2R1	50	50	0	50	0	50	50	50
L2R2	60	70	0	50	0	50	50	50
L2R3	70	80	0	50	0	50	50	50
L2R4	none	none	0	50	0	50	50	50
L3R2	60	70	0	50	0	30	50	50
L4R2	60	70	0	40	0	30	40	40
L5R3	70	80	0	50	0	50	60	60
L8R3	70	80	0	60	0	50	60	60
L8R8	80	80	0	60	0	50	60	60
L8R9	80	90	0	60	0	50	60	60
L9R3	70	80	0	70	0	50	70	70
L9R8	80	80	0	70	0	50	70	70
L9R9	80	90	0	70	0	50	70	70
L10R3	70	80	0	50	20	50	50	50
L11R3	70	80	0	50	30	50	50	50

Table S4 Results for model selection applied to choose the best buffer size among landscape conductance outputs. The models were named according to the conductance surface, where "L" means the exploratory cell-level conductance for land-cover and "R" the exploratory cell-level conductance for road network. Only the minor ΔAICc per model are presented.

Model	Best buffer size	AICc	ΔAICc	AICc weight
L1R1	Null	41.9	0.00	0.226
L2R1	1.0 km	41.3	0.00	0.224
L2R2	1.0 km	41.2	0.00	0.223
L2R3	1.0 km	41.2	0.00	0.220
L2R4	1.0 km	41.8	0.00	0.221
L3R2	1.0 km	41.4	0.00	0.217
L4R2	1.0 km	41.2	0.00	0.216
L5R3	1.0 km	41.7	0.00	0.223
L8R3	1.0 km	41.3	0.00	0.221
L8R8	1.0 km	41.3	0.00	0.219
L8R9	1.0 km	41.2	0.00	0.219
L9R3	1.0 km	41.4	0.00	0.221
L9R8	1.0 km	41.4	0.00	0.219
L9R9	1.0 km	41.3	0.00	0.219
L10R3	1.0 km	40.5	0.00	0.283
L11R3	1.0 km	40.2	0.00	0.300

Table S5 Results for the model selection applied to choose the best buffer size among landscape structure metrics. Only the minor ΔAICc per model are presented.

Predictive strusture metric	Best buffer size	AICc	ΔAICc	AICc weight
Forest area	1.0 km	40.7	0.00	0.315
Mussununga area	2.0 km	42.8	0.92	0.244
Length of highway	1.0 km	40.5	0.00	0.388
Length of road	2.0 km	40.8	0.00	0.403

Table S6 Results of model selection based in Akaike information criterion and GLM logistic regression statistical results for the effect of landscape structure and the landscape conductance L11R3 in *Acacia* invasion (without outlier area 8). Only models with ΔAICc ≤ 2 are presented.

Model	Intercept	Estimate	df	AICc	ΔAICc	AICc weight	X^2	p
321	-1.4282		3	34.1	0.00	0.389		
Length of road (2.0 km)		1.8154					7.8152	**0.0052**
Mussununga shape index		-1.2680					5.3373	**0.0209**
322	-2.0370		4	34.8	0.68	0.277		
Mussununga shape index		-1.6636					6.8988	**0.0086**
Length of road (2.0 km)		2.0118					4.8261	**0.0280**
Forest area (1.0 km)		-1.5175					1.9725	0.1601
449	-1.6083		4	35.6	1.49	0.185		
Length of road (2.0 km)		2.1188					8.9543	**0.0028**
Mussununga shape index		-1.5582					6.3983	**0.0114**
Distance from road		0.5269					1.1632	0.2808
353	-1.5694		4	36.0	1.92	0.149		
Length of road (2.0 km)		1.8973					7.8245	**0.0051**
Mussununga shape index		-1.7453					5.4741	**0.0193**
Mussununga size		0.5438					0.7334	0.3918

To be submit to Biodiversity and Conservation

CHAPTER 3 - BIOLOGICAL INVASION CAN HINDER RESTORATION PROJECTS IN THE BRAZILIAN ATLANTIC FOREST

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ABSTRACT

Climatic change and biological invasion are two of the most cited factors that can affect biodiversity in the coming decades. Here we used five climate scenarios to investigate the potential distribution of two invasive tree species, *Acacia mangium* and *A. auriculiformis*, in the Atlantic Forest hotspot based in five climate scenarios. Additionally, we used the expansion-retraction maps and the map of potential areas for forest restoration to investigate whether biological invasion could affect restoration projects. We found *A. mangium* has a large suitable area in all scenarios, while *A auriculiformis* is confined to a relatively small region of 13,083 km^2 (± 3.391 SD). In the low greenhouse gas emissions scenario (RCP 2.6), the suitable area for *A. mangium* expanded from the current scenario of 18.4% of the Atlantic Forest to 24.0% and 24.5% in the years 2050 and 2070, respectively. When we considered the high greenhouse gas emission scenario (RCP 8.5), the expansion increased for 37.3% and 44.3% in 2050 and 2070, respectively. Approximately 22.7% of the potential area for restoration are overlapped with the suitable area for *A. mangium* currently and this overlap can reach 39.3% of the potential area for restoration in the worse climate scenario (RCP 8.5 in 2070). *A. mangium* can invade a large area in the Atlantic Forest and, further, could become a barrier for restoration projects in the next decades. The expansion-retraction map should be used to establish environmental policies promoting both forest restoration and biological invasion prevention in suitable areas.

Keywords: *Acacia mangium*, *Acacia auriculiformis*, species distribution model, climate change, invasion risk

INTRODUCTION

Global warming will affect biodiversity and species distributions in the next decades (e.g. Sala et al. 2000; Pereira et al. 2010; Urban 2015). Climate is an important filtering factor that determine species distribution in regional scales (Bradley et al. 2009), therefore, climate conditions is one of the most important barriers that invasive species need to overcome to invade different regions. Additionally, the increase of invasive species worldwide due climatic change (Bradley et al. 2010), biodiversity loss (Kennedy et al. 2002), anthropogenic factors, such as commercial trades, propagule pressure, and disturbance (Meyerson and Mooney 2007; van Kleunen et al. 2015), suggest an increase of biological invasion success with global changes in the next decades. Hence, several studies highlight the need to concern about global change and need of rise the practical actions to reduce its effects (e.g. Hulme 2009; Richardson and Rejmánek 2011; Lehmann et al. 2017; Meira-Neto et al. 2017).

Species distribution models (SDM) allow the prediction of the potential distribution of species and can be applied to assess the effectivity of Protect Areas (Ferro et al. 2014; Lemes et al. 2014), estimating extent of occurrence and search for new populations of threatened species (Kamino et al. 2012; Pena et al. 2014), or to investigate the role of climate change and soil in the biomes distribution (Bueno et al. 2016; Arruda et al. 2017). Yet, SDM are largely applied in the detection of invasive species (e.g. Bradley et al. 2009; Bradley et al. 2010; Wei et al. 2017) and may be a powerful tool to the management. Based in the area suitability, land managers and policy maker may stablish policy to discourage or avoid invasive species plantation, and create areas of high risk of invasion, where detection and monitoring of invasive species populations should be applied (Lehmann et al. 2017) and strategy of population control could be applied, such as biological control (Marchante et al. 2011). Furthermore, SDM can also be applied to the future climatic conditions, and favor initiatives to control biological invasion earlier. The earlier invasive species are detected, greater are the probabilities of control, greater the cost-efficient of the management (Lehmann et al. 2017), and less the impact of invasion in the ecosystem.

The effects of biological invasion in ecosystem functioning and community are widely reported in the literature (e.g. Hellmann et al. 2011; Rascher et al. 2011; Meira-Neto et al. 2017). The genus *Acacia* are largely spread and has been invading several ecosystems worldwide (Griffin et al. 2011; Richardson and Rejmánek 2011) and may generate a set of ecosystem changes, such as change disturbance regime and increase soil nutrient content (Fridley et al. 2007; Le Maitre et al. 2011; Gaertner et al. 2014). In Brazilian Atlantic Forest, *Acacia* spp. are invading *Mussununga*, dunes, roadsides, and deforested areas (Lehmann et al. 2017; Meira-Neto et al. 2017). These species may disperse throughout the fragmented matrix and quickly colonize open areas, promoting soil nutrient increase, shading, plant richness decrease, and changes in ecosystem physiognomies (Lehmann et al. 2017; Heringer et al. unpublished; Meira-Neto et al. 2017). Because *A. mangium* Willd. and *A. auriculiformis* Cunn. ex Benth. easily invade and became mono-dominant in abandoned deforested areas, these species may become a barrier to restoration programs in Atlantic Forest. Furthermore, several restoration practitioners introduce *Acacia* spp. as an alternative to restore degraded areas, increasing the possibilities of invasion mainly in the Atlantic Forest.

Both species are native to Australia, Papua New Guinea and Indonesia (National Research Council - US 1983) and were introduced in Atlantic Forest around the 70's and have invaded degraded areas, pasture, eucalyptus plantations, and *Mussununga* ecosystem into the hotspot (Lehmann et al. 2017; field observations). Brazilian Atlantic Forest is amongst the major threatened ecosystems in the word due the high diversity, endemism, fragmentation, and land-use (Myers et al. 2000; Ribeiro et al. 2009). The high level of fragmentation, and its consequence in biodiversity and ecosystem services loss (Magnago et al. 2014; Magnago et al. 2015; Matos et al. 2016), make necessary the adoption of policies to rise the restoration in Atlantic Forest. However, restoration is money- and time-demanding process that include the participation of several stakeholders (Rodrigues et al. 2011; Brancalion et al. 2016b). Additionally, many factors may difficult the success of restoration projects, such as seed dispersal, seed and saplings bank, landscape connectivity, socioeconomic limitations, and biological invasion (Martnez-Ramos 2016, Melo 2013, de Souza Leite et al. 2013). Therefore, an alternative to achieve better results can be the adoption of the win-win strategy (Rey Benayas 2009; Brancalion 2017), prioritizing actions that affects more than one factor. For instance, promote restoration in areas of high risk of invasion will reduce the habitat availability for invasion and, at the same time, will decrease the possibility of invasive species difficult the succession in restoration areas.

Based in the effects of *A. mangium* and *A. aurculiformis* in the local communities as well as the high capability that these species shown to invade open and degraded ecosystems (Lehmann et al. 2017; Meira-Neto et al. 2017; Heringer et al. unpublished), our aim was to investigate whether *A. mangium* and *A. auriculiformis* could expand their distribution and, consequently hinder restoration programs in Atlantic Forest. To do this we, firstly investigated the climatic suitable area of *A. mangium* and *A. auriculiformes* in current and future climatic conditions; and second, we overlapped the expansion and retraction maps of both species with potential areas for forest restoration.

MATERIALS AND METHODS

Occurrence data

Distribution data for *A. auriculiformis* and *A. mangium* were taken from fieldwork and from online databases: Atlas of Living Australia – ALA (ala.org.au – accessed November 2017), Global Biodiversity Biodiversity Facility – GBIF (gbif.org – accessed November 2017), Instituto Hórus (i3n.institutohorus.org.br/www/) and Species Link (splink.cria.org.br – accessed November 2017). Data collection in the field were taken besides the adult plant, in areas where we recognize individuals in different stages of life characterizing an invasion process. The occurrence database was clipped using the Atlantic Forest shape as a mask in software ArcGis (ESRI). We choose to use the occurrence data from Atlantic forest 1) because many invasive species present differences when compared native with invaded niches (Broennimann et al. 2007; Wei et al. 2017), 2) *Acacia auriculiformis* and *A. mangium* are planted worldwide and were selected genetically (Griffin et al. 2011), and 3) these species have been introduced since 70's due the good performance and has been invading several places in the study area, showing that these species are well adapted to the Atlantic Forest. After that, the duplicates are excluded, once many of the online databases are overlapped, and got 117 points of *A. auriculiformis* and 119 points of *A. mangium* (Fig. 1).

Climatic variables

Climatic variables used to create the current climatic suitable area were download from WorldClim database, version 1.4 with spatial resolution of 30 seconds (~1 km^2) (Hijmans et al. 2005; http://www.worldclim.org/). To avoid correlated predictive variables, we proceeded a Pearson test using compute covariance and correlation tool in software ArcGis (ESRI 2012). Correlated variables ($r \geq 0.9$) were removed, using as criteria exclude variables that shown higher number of correlations. Thirteen remained variables were Annual Mean Temperature (BIO1), Mean Diurnal Range (Mean of monthly (max temp - min temp)) (BIO2), Isothermality (BIO2/BIO7) (*100) (BIO3), Temperature Seasonality (standard deviation *100) (BIO4), Max Temperature of Warmest Month (BIO5), Temperature Annual Range (BIO7), Mean Temperature of Wettest Quarter (BIO8), Mean Temperature of Driest Quarter (BIO9), Annual Precipitation (BIO12), Precipitation of Wettest Month (BIO13), Precipitation of Driest Month (BIO14), Precipitation of Warmest Quarter (BIO18), and Precipitation of Coldest Quarter (BIO19).

To predict the future climatic suitable area of *A. mangium* and *A. auriculiformis* in Atlantic Forest we used the climatic global models for two representative concentration pathways (RPC 2.6 and RPC 8.5, respectively) for the year of 2050 and 2070. The RCPs represents the low (RPC 2.6) and high (RPC 8.5) possible greenhouse gas emissions scenarios, that can be interpreted as best and worst future scenarios. Therefore, we got for combinations of future scenario: RPC 2.6 in 2050 (average from the years 2041 to 2060), RPC 2.6 in 2070 (average from the years 2061 to 2080), hereafter, current-2.6/50, current-2.6/70, current-8.5/50, and current-8.5/70, respectively. Future climatic data were downloaded from WorldClim database with spatial resolution of 30 seconds (~1 km^2) (http://www.worldclim.org/) and the same thirteen predictable variables used to build the current climatic suitable area, described above, were used here.

Modelling approach

The suitable area for current and future climate scenarios was modeled using the occurrence data and the thirteen climatic variables in the input of MaxEnt software (versão 3.3.3k; Phillips et al. 2006). MaxEnt is used to estimate the propability distribution based in maximum-entropy principal (Phillips et al. 2006) and widely applied approach. In this study, MaxEnt was chosed especially because presents good performance in comparasons with different models (Elith et al. 2006; Phillips et al. 2006). Moreover, MaxEnt allows to use presence-only data and also presents good performance even with low number of presence data (Phillips et al. 2006; Wisz et al. 2008). We setup the MaxEnt analysis to use jacknife test to get the degree ofimportance of each variable, 10,000 max number of background points, 5,000 maximum interactions, and 10^{-5} convergence threshold. The threshold value provided in the output of MaxEnt analysis was used to convert the continuous maps of probability of occurrence into a binary map, with areas of suitability and non-suitability of area. Later, these set of maps were used to estimate expansion and retraction (hereafter, expansion-retraction) of *A. mangium* and *A. auriculiformis*, where the current maps were overlaped with the future maps intependently. Therefore, we got the the expansion-retraction areas for the combinations curret-8.5/70, curret-8.5/50, curret-2.6/70, and curret-2.6/50 for both species.

Model evaluation

The SDM performance was tested using the area under the curve (AUC) and true skill statistics (TSS). The AUC was calculated as an average of 10 runs, using 25% of random test, therefore, 25% of our occurrence data were selected randomically to test the model results that was conducted with the others 75%. The AUC values range from 0 to 1 and give an estimate about the performance of the model to predict the species occurrence in random places (Elith 2002), where values ≥ 0.75 indicate the model is potentially useful (Elith 2002; Peterson et al. 2011). The AUC values can be obtained as an output of the niche modeling in the software MaxEnt (versão 3.3.3k; Phillips et al. 2006). The TSS analyses were proceeded through the comparison between *Acacia's* niche model and *Eugenia uruguayensis* Cambess. niche model. The TSS analysis allow to evaluate the modeling accuracy through the threshold-dependent measure (Allouche et al. 2006). The values in TSS analysis range -1 to +1, where results ≥ 0.6 are good, between 0.2 and 0.6 moderate, and < 0.2 are bad (Jones et al. 2010).

Restoration data

To assess the potential impact of *A. mangium* and *A. auriculiformis* in the restoration programs we used the map of potential areas for forest restoration of Atlantic Forest (hereafter, potential areas for restoration) developed by the Atlantic Forest Restoration Pact, a group of stakeholders from large spectrum of the society with an aim to restore the Atlantic Forest (AFRP; http://www.pactomataatlantica.org.br/). In order to estimate the potential areas for restoration could be invaded by *A. mangium* and *A. auriculiformis* we used the map of potential area for restoration as mask to clip the rasters of expansion-retraction in different scenarios (curret-8.5/70, curret-8.5/50, curret-2.6/70, and curret-2.6/50), using pixel size of ~0.01 km^2. Then we used the field calculator tool in QGis 2.18.12 (Quantum GIS Development Team 2017) to calculate the remnant of non-suitable area, suitable area, expansion-retraction of all scenarios. Although, the rasterization involves loss of information due the high number of small potential areas for restoration, the pattern of overlapping is the same and so we avoided waste computational time.

The aim of the potential areas for forest restoration was to target restoration actions to areas close to Protected Areas, with occurrence of endemic or threatened species, that promote connectivity between native fragments, areas of permanent preservation (beside rivers, on top of hill, and with greater slope greater than 45 degrees), degraded areas with low value for agriculture and with potential for regeneration, with good conditions for environmental services payment, and areas where restoration projects are ahead occurring (more information at http://www.pactomataatlantica.org.br/). Currently, the potential areas for restoration is a tool of governance and planning and has been used to plan several projects in Atlantic Forest (Melo et al. 2013; Brancalion et al. 2016b), therefore, this map will give us a good measure of how biological invasion could impact restauration actions in the next decades.

RESULTS

Model performance

The model performance was much better than random for both species. For *A. auriculifomis*, average training AUC was 0.991 (ranging from 0.988 to 0.993) and average test AUC was 0.974 (from 0.955 to 0.995), while for *A. mangium* average training AUC was 0.953 (ranging from 0.943 to 0.965) and average test AUC was 0.896 (ranging from 0.843 to 0.963) (Supplementary material, Fig. S1, S2, S3). The TSS test also presented the good accuracy of the models, being 0.971 for *A. auriculifomis* (1.00 of sensitivity and 0.97 specificity) and 0.866 for *A. mangium* (0.91 of sensitivity and 0.95 specificity) (Supplementary material, Table S2, S3). Temperature variables had better predictive value for both species. Around 79% of the model for *A. mangium* was explained by six variables, Annual Mean Temperature (18%), Temperature Annual Range (15.4%), Mean Diurnal Range (13.1%), Temperature Seasonality (11.4%), Mean Temperature of Wettest Quarter (11.3%), and Isothermality (9.4%). The full list of relative contributions for both models is presented in the Supplementary material (Table S1). On the other hand, 76% of the model for *A. auriculiformis* was explained by four predictive variables, Temperature Annual Range (28.5%), Mean Temperature of Wettest Quarter (21.7%), Temperature Seasonality (14.7%), and Precipitation of Driest Month (11.1%). The threshold values were obtained from the 10th percentile training presence in the output of MaxEnt analysis and was 0.047 for *A. mangium* and 0.270 for *A. auriculifomis.*

Current invasion pattern

The current climatic suitable area, determined by the binary map, for *A. mangium* was much larger and spread through Atlantic Forest than for *A. auriculiformis*. *Acacia mangium* presented a large suitable area extending from north to south of eastern Atlantic Forest, and occupying almost all coastal area of Sergipe, Bahia, Espírito Santo, and Rio de Janeiro states (Fig. 1, 2, Table 1). Yet, *A. mangium* had some suitable areas in the continental regions, mainly in Minas Gerais, Goiás, Mato Grosso do Sul, and São Paulo states. Contrarily, *A. auriculiformis* map shown a potential distribution in the central-east of Atlantic forest, between Espírito Santo and south Bahia states (Fig. 1, 2, Table 1). The climatic suitable area for *A. auriculiformis* and *A. mangium* occupy around 1.0% and 18.4% of the Atlantic Forest, respectively (Table 1).

Changes in the invasion pattern

The change in future climatic suitable areas, considering in the expansion-retraction maps, for *A. mangium* presented much more variation among the different scenarios than for *A. auriculiformis* (Fig. 2; Table 1). *Acacia mangium* suitable area in RCP 2.6 gas emission in the year 2050 (current-2.6/50 scenario) shown expansion in several directions, expanding the climatic area to the north (in Pernambuco and Alagoas states) and to the south of Atlantic Forest (mainly in São Paulo, Santa Catarina, and Rio Grande do Sul) (Fig. 2a). Additionally, two large expansion areas appeared in the continental Atlantic Forest; one in the boundary with Cerrado domain (in Minas Gerais, Goiás, and São Paulo states) and other in Mato Grosso do Sul state. The retraction region was concentrated in the non-coastal central Atlantic Forest (mainly in the west of Espírito Santo and east of Minas Gerais states). The geographic pattern of expansion-retraction in the 2.6/70 scenario was basically the same than described above, but with expansion area slightly larger and retraction slightly smaller (Fig. 2b). The climatic suitable area for *A. mangium* changed from 24.0% of the Atlantic Forest area to 24.5%, in the comparison between 2.6/50 and 2.6/70 scenarios, respectively (Table 1).

Acacia mangium suitable area in 8.5/50 presented expansion in the same geographic regions than 2.6/50 scenario (Fig. 2c). However, the expanded areas in the 8.5/50 scenario are much larger than in the scenario with RCP 2.6 of gas emission. Beyond the larger size of the areas, the 8.5/50 scenarios presented a large area of expansion in the western of Atlantic forest, from the south of Mato Grosso do Sul until northwest of Parana and northwest of São Paulo states. The retraction area in the 8.5/50 was distributed in eastern Minas Gerais and in southwestern of Espírito Santo state. The 8.5/70 scenario bit different distribution with smaller expansion areas in the south (in Santa Catarina and Rio Grande do Sul states) and larger expansion areas in the western and northern of Atlantic Forest (Fig. 2d). Although more spread, the retraction area occupied a similar distribution than in the other cases. The climatic suitable area for *A. mangium* increased from 37.3% of the Atlantic Forest area to 44.3%, in the comparison between 8.5/50 and 8.5/70 scenarios, respectively (Table 1).

The future climatic suitable area for *A. auriculiformis* occupied mainly a small region between southern Bahia and Espírito Santo states and presented small fluctuations among the different climatic scenarios, from 8,588 to 17,416 (13,083 ± 3,391 SD; Fig. 2a, b, c, d, Table 1). Additionally, all models for the future presented an expansion area in the coastal northeastern Bahia varying slightly in area, and the two models of RCP 8.5

presented an expansion area in the southern Rio de Janeiro state. The climatic suitable area for *A. auriculiformis* changed from 0.8% in 2.6/50 to 1.2% of the Atlantic Forest area in the 2.6/70, while the suitable area between 8.5/50 and 8.5/70 scenarios changed from 1.6% to 1.4% of the Atlantic Forest area, respectively (Table 1).

Potential restoration vs. potential invasion

Approximately 31,425 km^2 of the potential areas for restauration are distributed over the area of climatic suitable area of *A. mangium* in the current climate conditions. The future scenarios shown an increase of the overlapped area from the year 2050 to 2070 and from RCP 2.6 to 8.5. The overlapping between suitable area and potential areas for restoration was approximately 31,760 km^2 for current-2.6/50 scenarios (22.9% of the potential areas for forest restoration), 32,458 km^2 for current-2.6/70 scenarios (23.5%), 45,889 km^2 for current-8.5/50 (33.1%), and 54,342 km^2 for current-8.5/70 (39.3%) (Fig. 3, Table 2). For *A. auriculiformis*, around 797 km^2 of the potential area for restoration were overlapped with current suitable area. *Acacia auriculiformis* had an overlapping of approximately 450 km^2 for current-2.6/50 scenarios (0.3%), 783.7 km^2 for current-2.6/70 (0.5%), 946 km^2 for current-8.5/50 (0.7%), 966 km^2 for current-8.5/70 (0.7%) (Table 2).

DISCUSSION

Suitable areas

Acacia mangium and *A. auriculiformis* are largely distributed in Brazil and were reported invading degraded and open areas (Aguiar Jr. et al. 2014; Lehmann et al. 2017; Meira-Neto et al. 2017; Supplementary material, Fig. S4). In Atlantic Forest between Espírito Santo and Bahia states, can be found invading roadside, pasture, open ecosystems, and eucalyptus plantation understory (field observations; Supplementary material, Fig. S4). In the fragmented context, the large climatic suitable area for *A. mangium* found in this study shown a potential increase of invaded areas in Atlantic Forest. Atlantic Forest present suitable climatic conditions for *A. mangium* through Atlantic coast and in three large inland areas. This is particularly worrying because Atlantic Forest is a predominantly deforested domain (Ribeiro et al. 2009) and can be invaded by *Acacia* species. Additionally, the continuous suitable area in Atlantic coast found here associated with the high fragmented landscape with large road network and the acacia's plantation (Heringer et al. unpublished) may promote fast spread of these invasive species and increase the invaded areas. In contrary, the restricted suitable area for *A. auriculiformis* suggest this species would not be a problem beyond the current distribution area.

Regarding the climate change for the years of 2050 and 2070, our models shown a possible expansion of suitable area for *A. mangium* in both scenarios of greenhouse emissions (RCP 2.6 and 8.5). Further, the suitable area increased from current to the year 2050, and from 2050 to 2070, as well as increased from current to RCP 2.6, and from RCP 2.6 to RCP 8.5, indicating great impact of climate change in the expansion of *A. mangium* distribution. On the other hand, the suitable area for *A. auriculiformis* oscillated between expansion and retraction and, despite two coastal regions in Espírito Santo and Bahia states, this species could not become invasive in other regions of Atlantic Forest.

The area expansion found here can be explained because *A. mangium* is adapted to high temperatures, high mean annual rainfall, and short dry period (National Research Council - US 1983; Delnatte and Meyer 2012), therefore, its potential distribution would be affected by the temperature increasing in the next years. These can be observed by the large area of expansion toward areas with few records of *A. mangium* currently, such as the southwestern Atlantic Forest, São Paulo state, and southern of Minas Gerais state. In the opposite sense, in high altitude vegetation-types, such as *campos de altitude* (Neri et al. 2016), would restrict *A. mangium* invasion even in expansion areas in the scale of this study due the temperate microclimate and freezing.

As expected, the larger suitable area than the locally invaded areas by *A. mangium* indicate other factors are restricting the distribution of the species, mainly regionally and locally factor such as introduction events, propagule pressure, dispersion limitations, disturbance, and landscape structure (Donaldson et al. 2014; Heringer et al. unpublished). Indeed, few studies shown source of propagule, fragmentation, and disturbance could affect biological invasion by *A. mangium* and *A. auriculiformis* (Aguiar Jr. et al. 2014; Heringer et al. unpublished). Therefore, we highlight the need to construct models to predict *Acacia* invasion considering a multi-scale framework, where landscape, source of propagule, and disturbance may be used as predictors. These models would allow stablish areas of high risk of invasion with higher accuracy that could be target of preventive monitoring and, therefore, increase the success and reduce the costs with eradication policies (Lehmann et al. 2017).

Potential impacts in restauration projects

A set of governmental and non-governmental policies indicates an increment of restoration projects in Atlantic Forest. The Native Vegetation Law (NVPL; Brazilian Laws nº 12,651 and 12,727 from 2012), the National Plan for Native Vegetation Recovery (in Portuguese PLANAVEG), and the Atlantic Forest Restoration Pact (AFRP; http://www.pactomataatlantica.org.br/) are the most relevant on a large scale. The first one determines the register the boundaries of all rural propriety with their protected areas, native vegetation areas, and land-use areas in a georeferenced database called (in Portuguese SiCAR) that allow the establishment of programs for incentives, technical assistance, and monitoring of the restoration projects (Soares-filho et al. 2014; Brancalion et al. 2016a). National Plan for Native Vegetation Recovery, in turn, aim to expand and strengthen public policies for restoration and has a goal to restore around 125,000 km^2 in the next 20 years. Finally, PRAF is a multi-stakeholders group that aim integrate actions to restore the Atlantic Forest in large scale, with a goal of achieving 150,000 km^2 of restored area until 2050.

The achievement of these goals would be essential to revert the status of fragmentation, biodiversity loss, and disruption of ecosystem functioning in the Atlantic Forest (Magnago et al. 2014; Magnago et al. 2015). However, even whether these programs are carried out, the local conditions could make the restauration a challenge. Based in our founds, *A. mangium* has a large suitable area and, therefore, can invade deforested areas and hence restoration programs in Atlantic Forest. At least 22.7% of the potential areas for restoration are overlapped with current suitable climate and up to 39.3% of overlapping could occur in the future (current-8.5/70 scenarios). Additionally, the fast spread of this species due economic value (Griffin et al. 2011), fragmentation and roads network (Heringer et al. unpublished), the high number of seeds production and fast grow (National Research Council - US 1983), and the capacity to transform the ecosystem and became dominant (Lehmann et al. 2017; Meira-Neto et al. 2017), make *A. mangium* an additional barrier to forest restauration in Atlantic Forest. Contrarily, we cannot ignore that a window of opportunities for restoration projects will open in retraction areas already invaded by *A. mangium*. As suggested by Bradley et al. (2009), retraction areas currently invaded may reduce the competitivity of the invasive species and make future invasions less probable and, therefore, may benefit restoration actions. For instance, approximately 23,477 km^2 (±3,847 SD) of the Atlantic Forest domain are composed by retraction areas and of these around 6,348 km^2 (±1,303 SD) are overlapped with potential areas for restoration (Table 1, 2).

Therefore, restauration projects into suitable area for *A. mangium*, should use synergistic strategies that allow the restauration process while prevents and control biological invasion. At the same time, forest restauration and tree plantation are an interesting alternative for *A. mangium* and *A. auriculiformis* control, once forest act as a barrier to these species and they are not able grow under dense canopy (Delnatte and Meyer 2012; Heringer et al. unpublished). Yet, in regions where *A. mangium* is not reported as invasive currently, but presented suitability in the future scenarios, should be careful evaluated regarding acacia's plantations, because these plantations increase propagule pressure (Richardson and Thuiller 2007; Donaldson et al. 2014) in a hotspot full of pathways for invasive acacias due deforestation and land-use (Ribeiro et al. 2009; Heringer et al. unpublished).

CONCLUSION

Atlantic forest is a large suitable area for the invasive species *A. mangium*, while for *A. auriculiformes* the suitable area is much more concentrated. Further, the difference of current distribution data and suitable area indicate local factor are also affecting the distribution of these species and more studies to detect invasion areas should be done. The large expansion of suitable areas in the future scenarios suggest Atlantic Forest will suffer with one more degradation factor and, additionally, the needed restoration projects can be hampered by biological invasion. Therefore, the map of suitable area should be applied to land management policies, such as, priories early detection, monitoring, and eradication actions. Furthermore, the map of suitable area would favor to discouraging the use of *A. mangium* in the restauration of area with suitable climatic conditions, to predict costs in prevention or eradication of this invasive species during restoration, and to use alternatives of management that allow both restore the ecosystem and prevent invasion, such as promote fast cover of bare soil and reduce *A. mangium* and *A. auriculiformis* population.

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REFERENCES

Aguiar Jr. A, Barbosa RI, Barbosa JBF, Mourao Jr. M (2014) Invasion of Acacia mangium in Amazonian savannas following planting for forestry. PLANT Ecol Divers 7:359–369. doi: 10.1080/17550874.2013.771714

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232. doi: 10.1111/j.1365-2664.2006.01214.x

Arruda DM, Fernandes-Filho EI, Solar RRC, Schaefer CEGR (2017) Combining climatic and soil properties better predicts covers of Brazilian biomes. Sci Nat. doi: 10.1007/s00114-017-1456-6

Bradley B a., Wilcove DS, Oppenheimer M (2010) Climate change increases risk of plant invasion in the Eastern United States. Biol Invasions 12:1855–1872. doi: 10.1007/s10530-009-9597-y

Bradley BA, Oppenheimer M, Wilcove DS. (2009) Climate change and plant invasions: restoration opportunities ahead? 15:1511–1521. doi: 10.1111/j.1365-2486.2008.01824.x

Brancalion PHS, Garcia LC, Loyola R, et al (2016a) A critical analysis of the Native Vegetation Protection Law of Brazil (2012): Updates and ongoing initiatives. Nat e Conserv 14:1–15. doi: 10.1016/j.ncon.2016.03.003

Brancalion PHS, Pinto SR, Pugliese L, et al (2016b) Governance innovations from a multi-stakeholder coalition to implement large-scale Forest Restoration in Brazil. World Dev Perspect 3:15–17. doi: 10.1016/j.wdp.2016.11.003

Broennimann O, Treier U a., Müller-Schärer H, et al (2007) Evidence of climatic niche shift during biological invasion. Ecol Lett 10:701–709. doi: 10.1111/j.1461-0248.2007.01060.x

Bueno ML, Pennington RT, Dexter KG, et al (2016) Effects of Quaternary climatic fluctuations on the distribution of Neotropical savanna tree species. Ecography (Cop) 40:403–414. doi: 10.1111/ecog.01860

Delnatte C, Meyer J-Y (2012) Plant introduction, naturalization, and invasion in French Guiana (South America). Biol Invasions 14:915–927. doi: 10.1007/s10530-011-0129-1

Donaldson JE, Hui C, Richardson DM, et al (2014) Invasion trajectory of alien trees: the role of introduction pathway and planting history. Glob Chang Biol 20:1527–1537. doi: 10.1111/gcb.12486

Elith J (2002) Quantitative methods for modeling species habitat: Comparative 31 performance and an application to Australian plants. In: Ferson S, Burgman M (eds) Quantitative methods for conservation biology. Springer, New York, pp 39–58

Elith J, Graham CH, Anderson RP, et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography (Cop) 29:129–151. doi: 10.1111/j.2006.0906-7590.04596.x

ESRI (2012) ArcGIS desktop: release 10.1. Environmental Systems Research Institute, Redlands

Ferro VG, Lemes P, Melo AS, Loyola R (2014) The reduced effectiveness of protected areas under climate change threatens atlantic forest tiger moths. PLoS One. doi: 10.1371/journal.pone.0107792

Fridley JD, Stachowicz JJ, Naeem S, et al (2007) The invasion paradox: reconciling pattern and process in species invasions. Ecology 88:3–17. doi: 10.1890/0012-9658(2007)88[3:Tiprpa]2.0.Co;2

Gaertner M, Biggs R, Te Beest M, et al (2014) Invasive plants as drivers of regime shifts: Identifying high-priority invaders that alter feedback relationships. Divers Distrib 20:733–744. doi: 10.1111/ddi.12182

Griffin AR, Midgley SJ, Bush D, et al (2011) Global uses of Australian acacias - recent trends and future prospects. Divers Distrib 17:837–847. doi: 10.1111/j.1472-4642.2011.00814.x

Hellmann C, Sutter R, Rascher KG, et al (2011) Impact of an exotic N2-fixing Acacia on composition and N status of a native Mediterranean community. Acta Oecologica 37:43–50. doi: 10.1016/j.actao.2010.11.005

Hijmans RJ, Cameron SE, Parra JL (2005) Very high resolution interpolated climate surfaces for global land areas. Int J Climatol 25:1965–1978. doi: 10.1002/joc.1276

Hulme PE (2009) Trade, transport and trouble: Managing invasive species pathways in an era of globalization. J Appl Ecol 46:10–18. doi: 10.1111/j.1365-2664.2008.01600.x

I3N Brazil – National Database of Invasive Alien Species Brazil (2017) Instituto Hórus de Desenvolvimento e Conservação Ambiental, Florianópolis, Brazil. Available at: http://i3n.institutohorus.org.br/www (accessed June 30, 2017)

Jones CC, Acker S a, Halpern CB (2010) Combining local-and large-scale models to predict the distributions of invasive plant species. Ecol Appl 20:311–326. doi: 10.1890/08-2261.1

Kamino LHY, Stehmann JR, Amaral S, et al (2012) Challenges and perspectives for species distribution modelling in the neotropics. Biol Lett 8:324–326. doi: 10.1098/rsbl.2011.0942

Kennedy TA, Naeem S, Howe KM, et al (2002) Biodiversity as a barrier to ecological invasion. Nature 417:636–638. doi: 10.1038/nature00776

Le Maitre DC, Gaertner M, Marchante E, et al (2011) Impacts of invasive Australian acacias: implications for management and restoration. Divers Distrib 17:1015–1029. doi: 10.1111/j.1472-4642.2011.00816.x

Lehmann JR, Prinz T, Ziller SR, et al (2017) Open-Source processing and analysis of aerial imagery acquired with a low-cost Unmanned Aerial System to support invasive plant management. Front Environ Sci. doi: 10.3389/fenvs.2017.00044

Lemes P, Melo AS, Loyola RD (2014) Climate change threatens protected areas of the Atlantic Forest. Biodivers Conserv 23:357–368. doi: 10.1007/s10531-013-0605-2

Magnago LFS, Edwards DP, Edwards FA, et al (2014) Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J Ecol 102:475–485. doi: 10.1111/1365-2745.12206

Magnago LFS, Magrach A, Laurance WF, et al (2015) Would protecting tropical forest fragments provide carbon and biodiversity co-benefits under redd+? Glob Chang Biol 44:n/a–n/a. doi: 10.1111/gcb.12937

Marchante H, Freitas H, Hoffmann JH (2011) Assessing the suitability and safety of a well-known bud-galling wasp, Trichilogaster acaciaelongifoliae, for biological control of Acacia longifolia in Portugal. Biol Control 56:193–201. doi: 10.1016/j.biocontrol.2010.11.001

Matos FAR, Magnago LFS, Gastauer M, et al (2016) Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. J Ecol 105:265–276. doi: 10.1111/1365-2745.12661

Meira-Neto JAA, da Silva MCNA, Tolentino GS, et al (2017) Early Acacia invasion in a sandy ecosystem enables shading mediated by soil, leaf nitrogen and facilitation. Biol Invasions 1–9. doi: 10.1007/s10530-017-1647-2

Melo FPL, Pinto SRR, Brancalion PHS, et al (2013) Priority setting for scaling-up tropical forest restoration projects: Early lessons from the Atlantic Forest Restoration Pact. Environ Sci Policy 33:395–404. doi: DOI 10.1016/j.envsci.2013.07.013

Meyerson L a, Mooney H a (2007) Invasive alien species in an era of globalization. Front Ecol Environ 5:199–208. doi: 10.1890/1540-9295(2007)5[199:IASIAE]2.0.CO;2

Myers N, Mittemeier RA, Mittemeier CG, et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858. doi: 10.1038/35002501

National Research Council - US (1983) Mangium and other fast-growing Acacias for the humid tropics. National Academy Press, Washington, D.C., National A. Washington DC

Neri AV, Borges GRA, Meira-Neto JAA, et al (2016) Diversity and functioning on Brazilian Páramos. J Plant Ecol 10:771–779. doi: 10.1093/jpe/rtw088

Pena JCDC, Kamino LHY, Rodrigues M, et al (2014) Assessing the conservation status of species with limited available data and disjunct distribution. Biol Conserv 170:130–136. doi: 10.1016/j.biocon.2013.12.015

Pereira HM, Leadley PW, Proença V, et al (2010) Scenarios for global biodiversity in the 21st century. Science (80-) 330:1496–1501. doi: 10.1126/science.1196624

Peterson AT, Soberón J, Pearson RG, et al (2011) Ecological Niches and Geographic Distributions. Princeton University Press, New Jersey

Phillips S, Anderson R, Schapire R (2006) Maximum entropy modeling of species geographic distributions. Ecol Modell 190:231–259. doi: 10.1016/j.ecolmodel.2005.03.026

Quantum GIS Development Team (2017) Quantum GIS geographic information system. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Rascher KG, Große-Stoltenberg a., Máguas C, et al (2011) Acacia longifolia invasion impacts vegetation structure and regeneration dynamics in open dunes and pine forests. Biol Invasions 13:1099–1113. doi: 10.1007/s10530-011-9949-2

Ribeiro MC, Metzger JP, Martensen AC, et al (2009) The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biol Conserv 142:1141–1153. doi: 10.1016/j.biocon.2009.02.021

Richardson DM, Rejmánek M (2011) Trees and shrubs as invasive alien species - a global review. Divers Distrib 17:788–809. doi: 10.1111/j.1472-4642.2011.00782.x

Richardson DM, Thuiller W (2007) Home away from home - Objective mapping of high-risk source areas for plant introductions. Divers Distrib 13:299–312. doi: 10.1111/j.1472-4642.2007.00337.x

Rodrigues RR, Gandolfi S, Nave AG, et al (2011) Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. For Ecol Manage 261:1605–1613. doi: 10.1016/j.foreco.2010.07.005

Sala OE., Chapin III FS. S, Armesto JJ., et al (2000) Global Biodiversity Scenarios for the Year 2100. Science 287:1770–1774. doi: 10.1126/science.287.5459.1770

Soares-filho B, Rajão R, Macedo M, et al (2014) Cracking Brazil's Forest Code. Science 344:363–400.

Urban MC (2015) Accelerating extinction risk from climate change. Science 348:571–573. doi: 10.1126/science.aaa4984

Van Kleunen M, Dawson W, Essl F, et al (2015) Global exchange and accumulation of non-native plants. Nature 525:100–103. doi: 10.1038/nature14910

Wei J, Zhang H, Zhao W, Zhao Q (2017) Niche shifts and the potential distribution of Phenacoccus solenopsis (Hemiptera: Pseudococcidae) under climate change. PLoS One 12:1–17. doi: 10.1371/journal.pone.0180913

Wisz MS, Hijmans RJ, Li J, et al (2008) Effects of sample size on the performance of species distribution models. Divers Distrib 14:763–773. doi: 10.1111/j.1472-4642.2008.00482.x

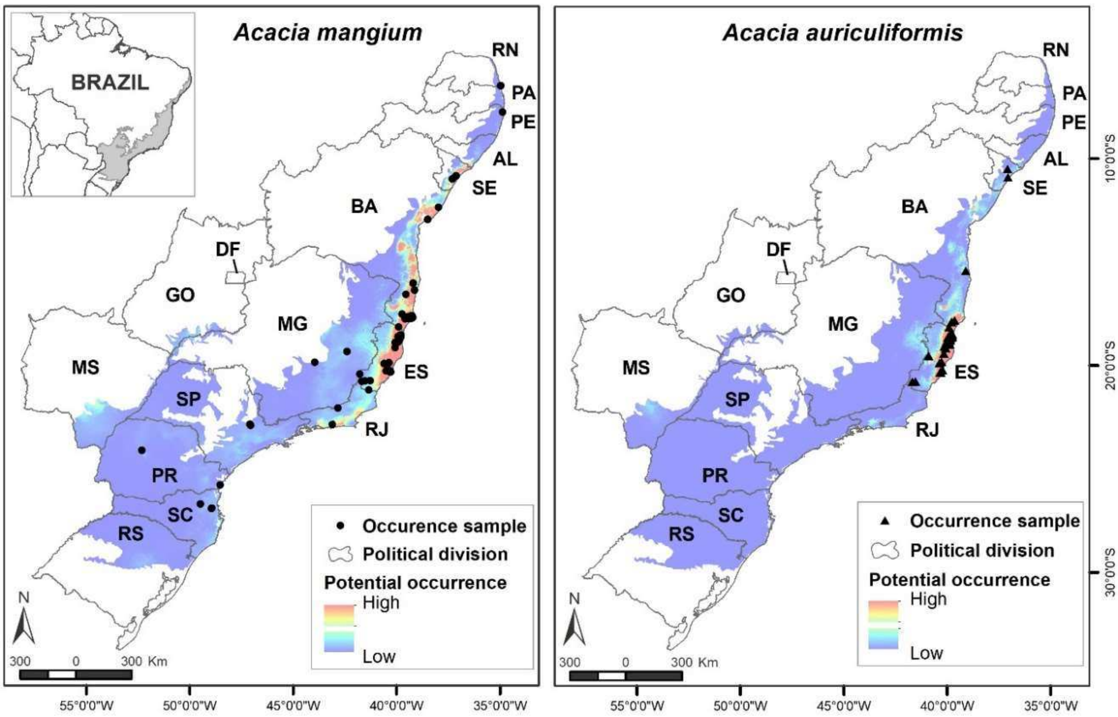

Fig. 1 Map of potential occurrence of *A. mangium* and *A. auriculiformis* in Brazilian Atlantic Forest

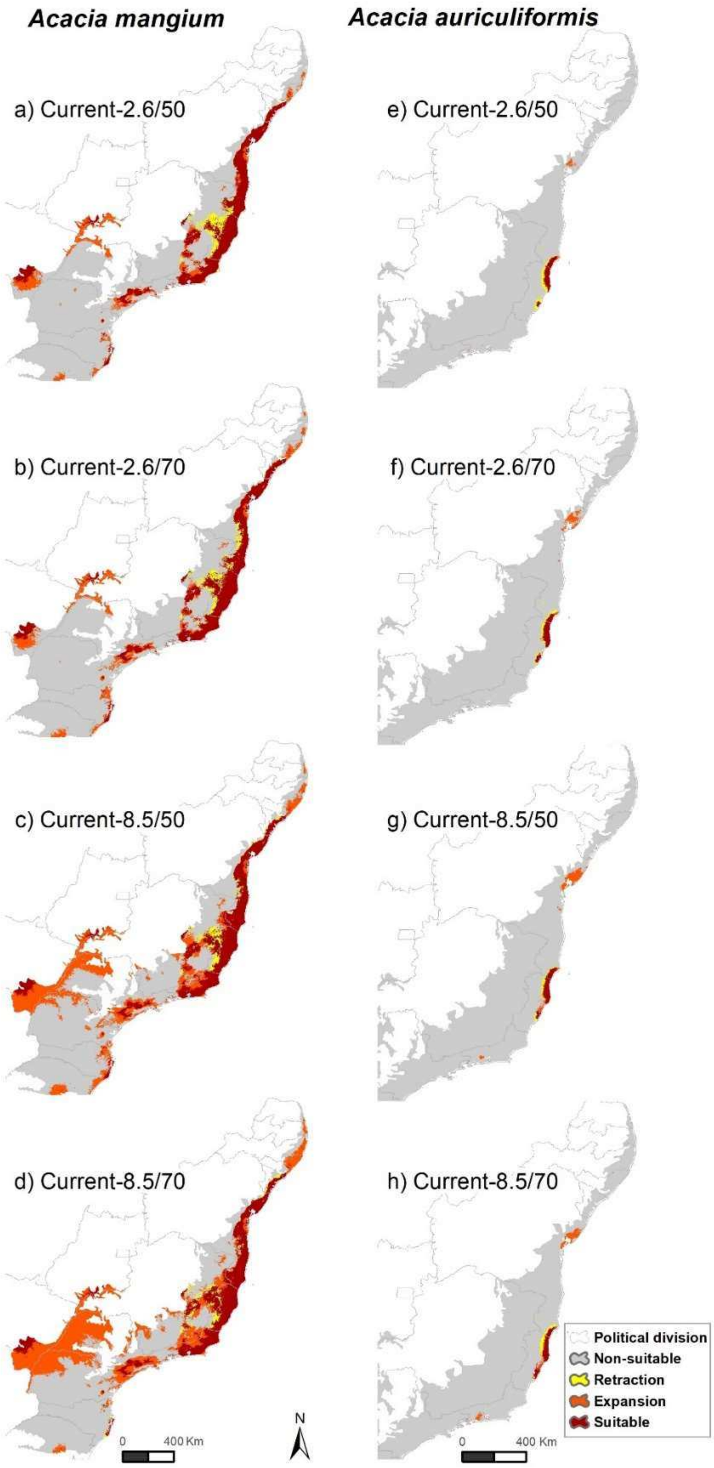

Fig. 2 Map of non-suitable, retraction, expansion, and suitable niches for *A. mangium* and *A. auriculiformis* in Brazilian Atlantic Forest. **a** map of expansion-retraction for *A. mangium* with the greenhouse gas emission scenario of RCP 2.6, in 2050. **b** map of expansion-retraction for *A. mangium* with the greenhouse gas emission scenario of RCP 2.6, in 2070. **c** map of expansion-retraction for *A. mangium* with the greenhouse gas emission scenario of RCP 8.5, in 2050. **d** map of expansion-retraction for *A. mangium* with the greenhouse gas emission scenario of RCP 8.5, in 2070. **e** map of expansion-retraction for *A. auriculiformis* with the greenhouse gas emission scenario of RCP 2.6, in 2050. **f** map of expansion-retraction for *A. auriculiformis* with the greenhouse gas emission scenario of RCP 2.6, in 2070. **g** map of expansion-retraction for *A. auriculiformis* with the greenhouse gas emission scenario of RCP 8.5, in 2050. **h** map of expansion-retraction for *A. auriculiformis* with the greenhouse gas emission scenario of RCP 8.5, in 2070.

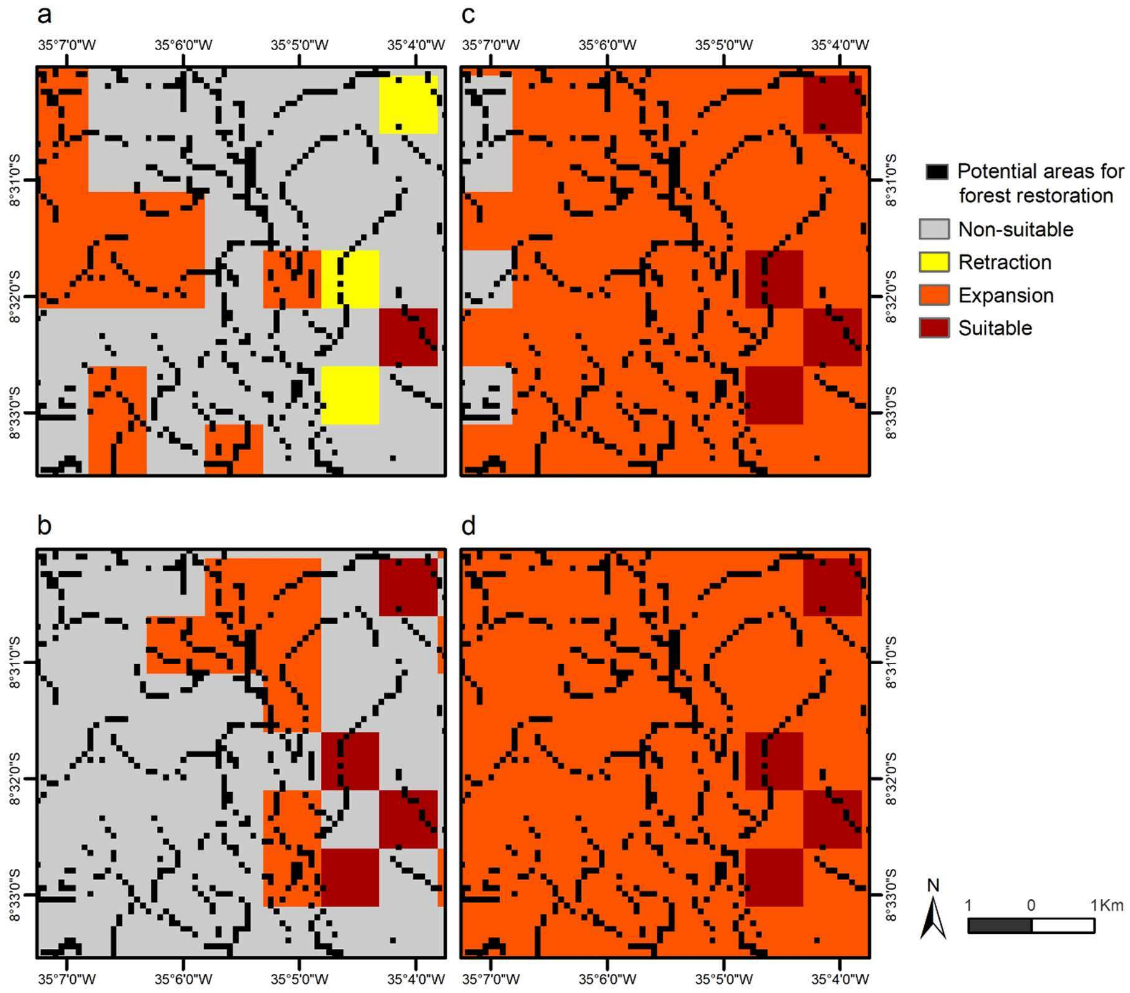

Fig. 3 Map showing the overlap between the map of potential area for forest restoration and the map of non-suitable, retraction, expansion, and suitable niches for *A. mangium*. **a** overlapping in the greenhouse gas emission scenario of RCP 2.6, in 2050. **b** overlapping in the greenhouse gas emission scenario of RCP 2.6, in 2070. **c** overlapping in the greenhouse gas emission scenario of RCP 8.5, in 2050. **d** overlapping in the greenhouse gas emission scenario of RCP 8.5, in 2070.

Table 1 Area of not suitable, retraction, expansion, and suitable niche for *A. mangium* and *A. auriculiformis* in Brazilian Atlantic Forest (km^2) for current climate and four scenarios of greenhouse gas emission. The percentage refers to the area of Atlantic Forest.

	Current	**Current-2.6/50**	**Current-2.6/70**	**Current-8.5/50**	**Current-8.5/70**
A. mangium					
Suitable	203,778.7 (18.4%)	175,924.8 (15.9%)	178,319.3 (16.1%)	182,741.3 (16.5%)	184,220.4 (16.7%)
Non-suitable	900,758.6 (81.6%)	811,445.2 (73.5%)	807,904.5 (73.1%)	671,884.4 (60.8%)	595,190.5 (53.9%)
Expansion	–	89,313.5 (8.1%)	92,854.2 (8.4%)	228,874.2 (20.7%)	305,568.1 (27.7%)
Retraction	–	27,853.9 (2.5%)	25,459.5 (2.3%)	21,037.5 (1.9%)	19,558.3 (1.8%)
A. auriculiformis					
Suitable	11,315.1 (1.0%)	6,956.2 (0.6%)	7,829.7 (0.7%)	8,388.8 (0.8%)	7,628.8 (0.7%)
Non-suitable	1,093,222.3 (99.0%)	1,091,590.7 (98.8%)	1,088,011.2 (98.5%)	1,084,194.8 (98.2%)	1,085,795.3 (98.3%)
Expansion	–	1,631.6 (0.1%)	5,211.1 (0.5%)	9,027.4 (0.8%)	7,426.9 (0.7%)
Retraction	–	4,358.9 (0.4%)	3,485.4 (0.3%)	2,926.3 (0.3%)	3,686.3 (0.3%)

Table 2 Areas of non-suitable, retraction, expansion, and suitable niche for *A. mangium* and *A. auriculiformis* that overlap with potential areas for forest restoration of Atlantic Forest (km^2). The percentage refers to the potential area for forest restoration.

	Current-2.6/50	**Current-2.6/70**	**Current-8.5/50**	**Current-8.5/70**
A. mangium				
Suitable	23548.7 (17%)	24749.5 (17.9%)	25321.7 (18.3%)	26686.7 (19.3%)
Non-suitable	98960.6 (71.4%)	99463.4 (71.8%)	86604.9 (62.5%)	79517.2 (57.4%)
Expansion	8211.7 (5.9%)	7708.9 (5.6%)	20567.4 (14.8%)	27655.1 (20%)
Retraction	7876.4 (5.7%)	6675.7 (4.8%)	6103.5 (4.4%)	4738.5 (3.4%)
A. auriculiformis				
Suitable	323.4 (0.2%)	439.2 (0.3%)	442 (0.3%)	520.1 (0.4%)
Non-suitable	137674.2 (99.3%)	137456 (99.2%)	137296.5 (99.1%)	137354.4 (99.1%)
Expansion	126.3 (0.1%)	344.5 (0.2%)	504.1 (0.4%)	446.2 (0.3%)
Retraction	473.6 (0.3%)	357.7 (0.3%)	355 (0.3%)	276.8 (0.2%)

SUPPLEMENTARY MATERIAL

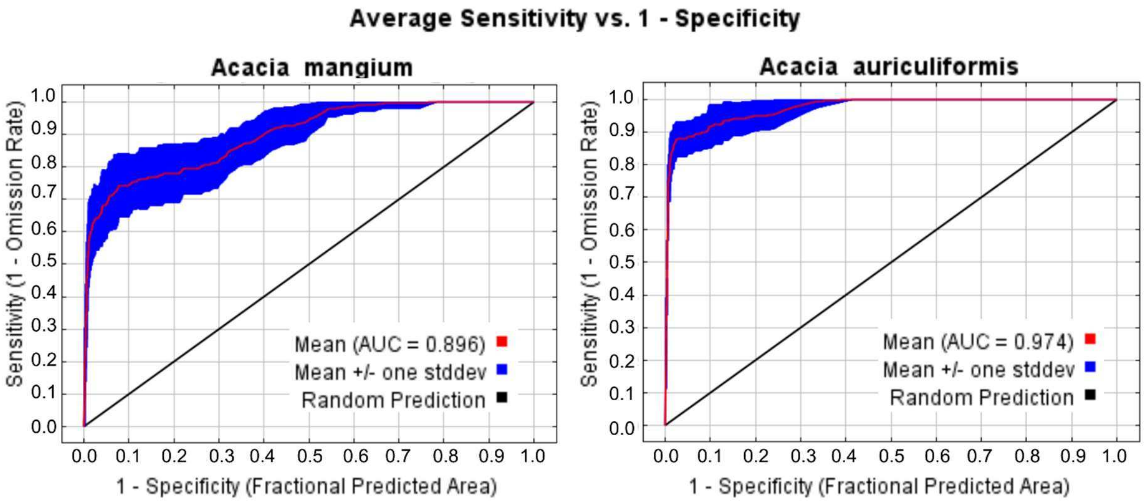

Fig. S1 Receiver operating characteristic (ROC) curve for *A. mangium* and *A. auriculiformis*. The curves were draw based in ten running for each specie

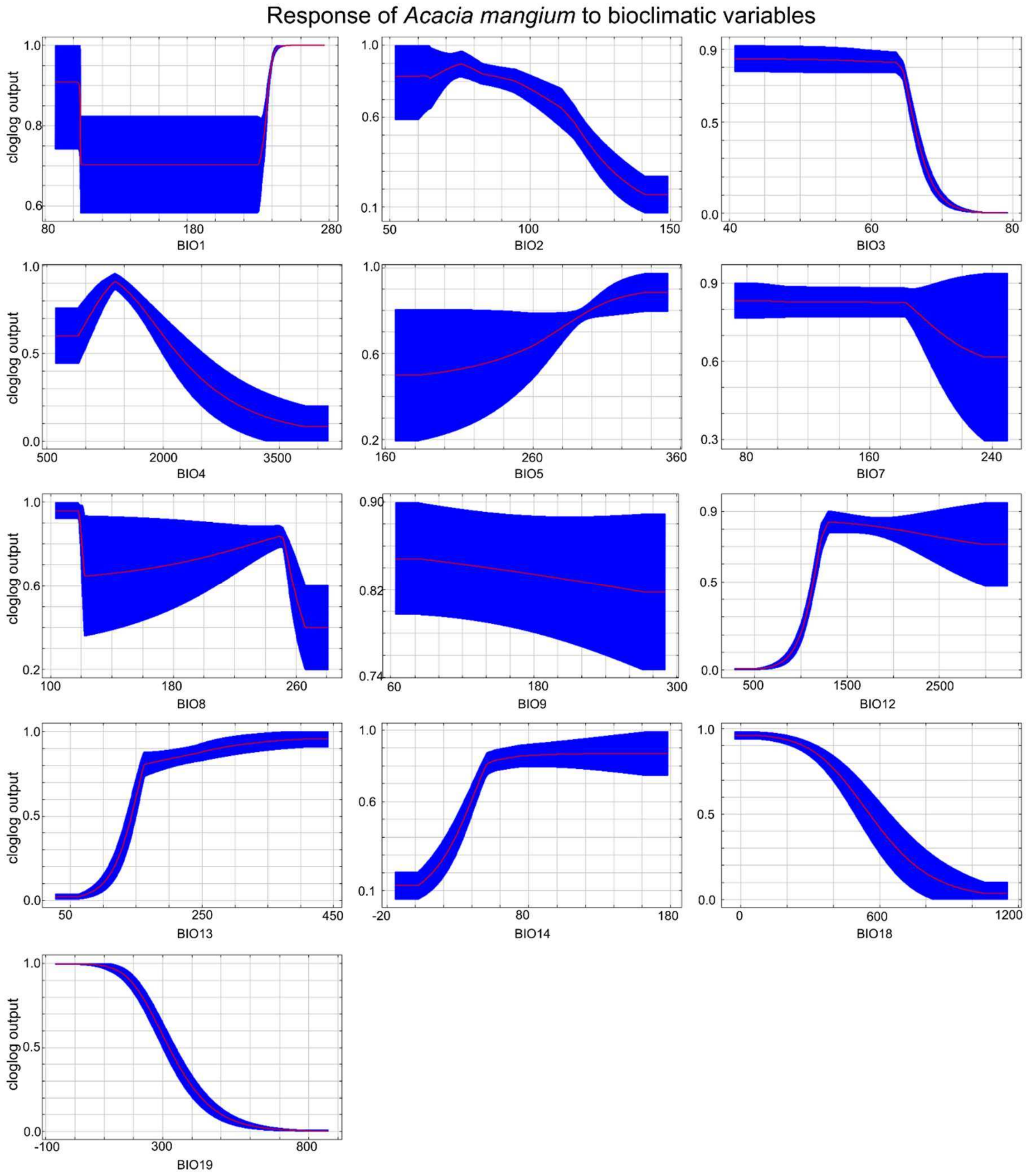

Fig. S2 Response curves for *A. mangium* showing the relationship between probability of presence and 13 bioclimatic variables. The curves shown the output for 10 running: blue area show the ±SD calculated for the 10 replicates

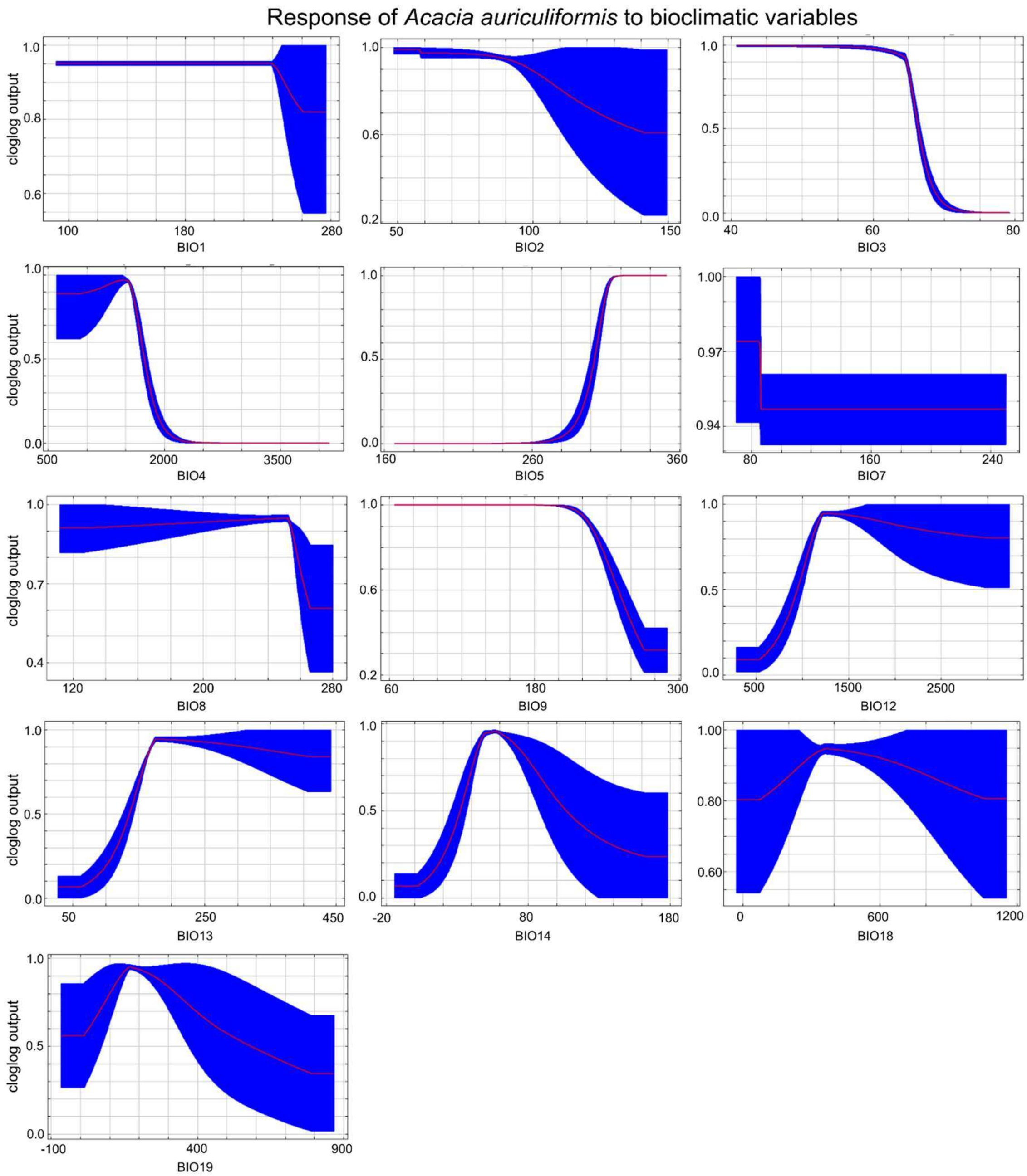

Fig. S3 Response curves for *A. auriculiformis* showing the relationship between probability of presence and 13 bioclimatic variables. The curves shown the output for 10 running: blue area show the ±SD calculated for the 10 replicates

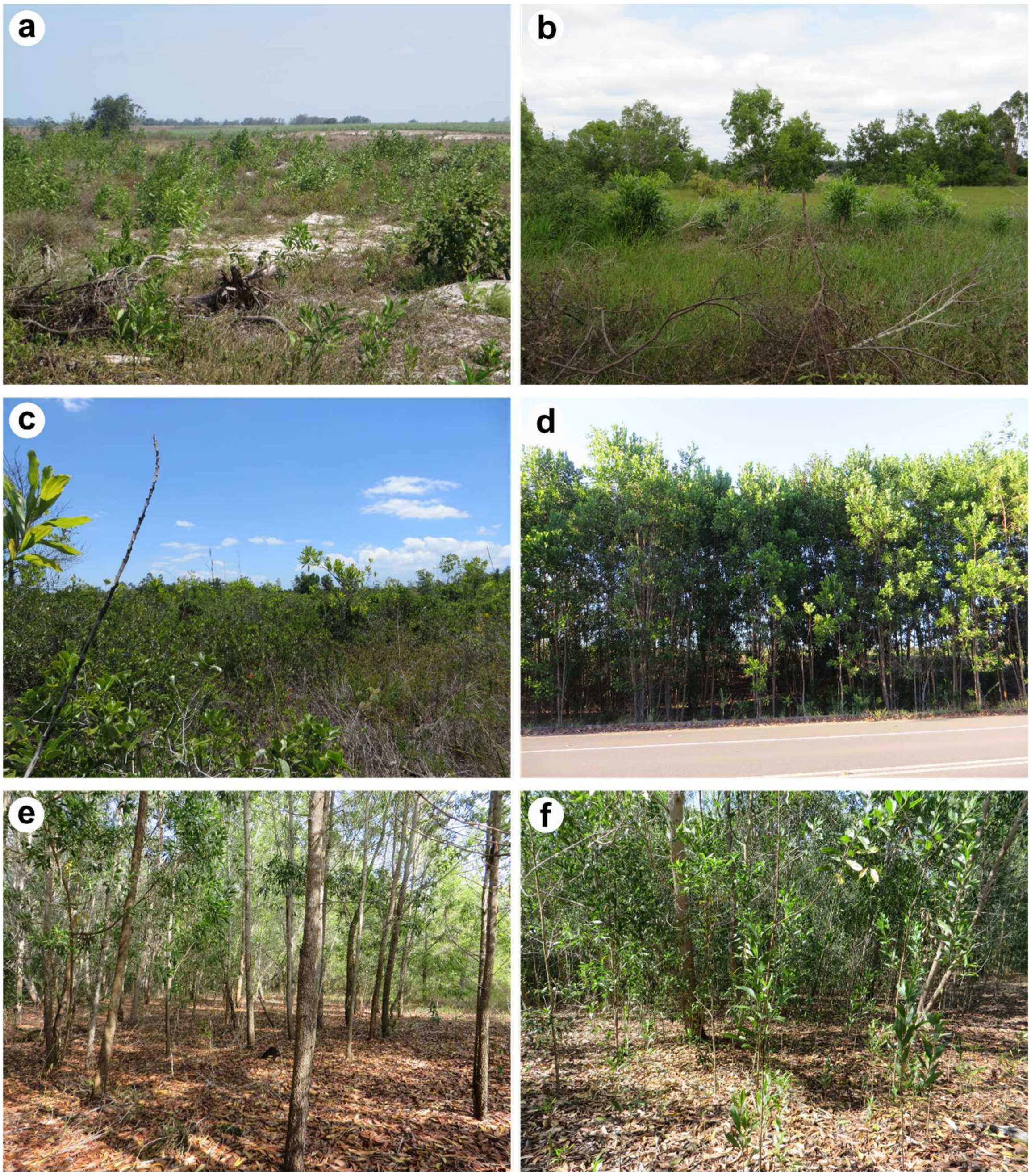

Fig. S4 *Acacia mangium* and *A. auriculiformis* invading open and degraded ecosystems in Atlantic Forest domain. **a** saplings of *Acacia* spp. growing in a degraded area; **b** adults and saplings of *Acacia* spp. growing in a pasture; **c** saplings and adults of *Acacia* spp. invading a savanna-type *Mussununga* ecosystem; **d** monodominant forest of *Acacia* spp. troadside; **e** monodominant forest of *Acacia* spp.; **f** monodominant forest of *Acacia* spp. with saplings recruiting.

Table S1 Environmental variables *A. mangium* and *A. auriculiformis*

Variable	**Percent contribution**	**Permutation importance**
Acacia mangium		
Annual Mean Temperature (BIO1)	18	7.1
Temperature Annual Range (BIO7)	15.4	2.3
Mean Diurnal Range (BIO2)	13.1	6.4
Temperature Seasonality (BIO4)	11.4	19.1
Mean Temperature of Wettest Quarter (BIO8)	11.3	1.4
Isothermality (BIO3)	9.4	10.3
Annual Precipitation (BIO12)	6.8	7.4
Precipitation of Driest Month (BIO14)	6.4	7.7
Precipitation of Coldest Quarter (BIO19)	3.9	25.5
Precipitation of Wettest Month (BIO13)	3.4	3.9
Precipitation of Warmest Quarter (BIO18)	0.7	7.1
Max Temperature of Warmest Month (BIO5)	0.1	1.6
Mean Temperature of Driest Quarter (BIO9)	0.1	0.1
Acacia auriculiformis		
Temperature Annual Range (BIO7)	28.5	0
Mean Temperature of Wettest Quarter (BIO8)	21.7	0.1
Temperature Seasonality (BIO4)	14.7	65.4
Precipitation of Driest Month (BIO14)	11.1	5
Precipitation of Wettest Month (BIO13)	5.9	0.2
Isothermality (BIO3)	4.5	4.1
Mean Diurnal Range (BIO2)	4	1
Annual Precipitation (BIO12)	4	0.5
Precipitation of Coldest Quarter (BIO19)	2.5	1
Precipitation of Warmest Quarter (BIO18)	1.1	0.1
Mean Temperature of Driest Quarter (BIO9)	0.8	1.9
Max Temperature of Warmest Month (BIO5)	0.7	20.6
Annual Mean Temperature (BIO1)	0.5	0.1

Table S2 True skill statistics (TSS) results for *A. mangium* based in the comparison with *Eugenia uruguayensis* distribution

	Training samples	**External test presence points**	**External test absence points**	**Sensitivity**	**Specificity**	**TSS**
Running 0	59	19	89	1.000	0.947	0.947
Running 1	59	19	89	0.800	0.966	0.766
Running 2	59	19	89	1.000	0.927	0.927
Running 3	59	19	89	0.889	0.967	0.856
Running 4	59	19	89	0.818	0.988	0.807
Running 5	59	19	89	1.000	0.947	0.947
Running 6	59	19	89	0.833	0.956	0.789
Running 7	59	19	89	0.850	0.977	0.827
Running 8	59	19	89	1.000	0.947	0.947
Running 9	59	19	89	0.923	0.926	0.849
Average				0.911	0.955	0.866

Table S3 True skill statistics (TSS) results for *A. auriculiformis* based in the comparison with *Eugenia uruguayensis* distribution

	Training samples	**External test presence points**	**External test absence points**	**Sensitivity**	**Specificity**	**TSS**
Running 0	55	18	89	1.000	0.967	0.967
Running 1	55	18	89	1.000	0.967	0.967
Running 2	55	18	89	1.000	0.967	0.967
Running 3	55	18	89	1.000	0.947	0.947
Running 4	55	18	89	1.000	0.967	0.967
Running 5	55	18	89	1.000	0.989	0.989
Running 6	55	18	89	1.000	1.000	1.000
Running 7	55	18	89	1.000	0.967	0.967
Running 8	55	18	89	1.000	0.967	0.967
Running 9	55	18	89	1.000	0.967	0.967
Average				1.000	0.971	0.971

Table S4 Areas of non-suitable, retraction, expansion, and suitable niche for *A. mangium* and *A. auriculiformis* that overlap with potential areas for forest restoration of Atlantic Forest by state of Brazil. Alagoas = AL, Bahia = BA, Espírito Santo = ES, Minas Gerais = MG, Mato Grosso do Sul = MS, Pernambuco = PE, Paraná = PR, Rio de Janeiro = RJ, Rio Grande do Sul = RS, Santa Catarina = SC, Sergipe = SE, and São Paulo = SP. Rio Grande do Norte (RN) and Paraíba (PB) are not included because the data were not available.

			Area (km^2) / Percentage of the State			
State	**Species**	**Scenarios**	**Suitable**	**Non-suitable**	**Expansion**	**Retraction**
AL	*A. mangium*	Current-26/50	72.3 (5.6%)	929.1 (72.3%)	278.8 (21.7%)	5.3 (0.4%)
		Current-26/70	76.3 (5.9%)	781.8 (60.8%)	426.1 (33.1%)	1.4 (0.1%)
		Current-85/50	66.5 (5.2%)	543.5 (42.3%)	664.4 (51.7%)	11.1 (0.9%)
		Current-85/70	64.1 (5%)	270.9 (21.1%)	937 (72.9%)	13.6 (1.1%)
	A. auriculiformis	Current-26/50	0 (0%)	1285.5 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	1285.5 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	1285.5 (100%)	0 (0%)	0 (0%)
		Current-85/70	0 (0%)	1284.2 (99.9%)	1.4 (0.1%)	0 (0%)
BA	*A. mangium*	Current-26/50	5052.1 (47.4%)	4826.8 (45.3%)	549.2 (5.2%)	224.2 (2.1%)
		Current-26/70	4366.4 (41%)	5093.3 (47.8%)	282.7 (2.7%)	909.9 (8.5%)
		Current-85/50	4730.4 (44.4%)	5025.6 (47.2%)	350.4 (3.3%)	545.9 (5.1%)
		Current-85/70	4824 (45.3%)	4772.7 (44.8%)	603.2 (5.7%)	452.3 (4.2%)
	A. auriculiformis	Current-26/50	90.3 (0.8%)	10407 (97.7%)	120.4 (1.1%)	34.5 (0.3%)
		Current-26/70	68.1 (0.6%)	10201.2 (95.8%)	326.2 (3.1%)	56.7 (0.5%)
		Current-85/50	93.3 (0.9%)	10155.8 (95.3%)	371.6 (3.5%)	31.6 (0.3%)
		Current-85/70	67.1 (0.6%)	10300.6 (96.7%)	226.8 (2.1%)	57.7 (0.5%)
ES	*A. mangium*	Current-26/50	6215.1 (62.4%)	1155 (11.6%)	12.9 (0.1%)	2578.1 (25.9%)
		Current-26/70	7022.4 (70.5%)	1115.9 (11.2%)	51.9 (0.5%)	1770.8 (17.8%)
		Current-85/50	6702.4 (67.3%)	1000.4 (10%)	167.4 (1.7%)	2090.8 (21%)
		Current-85/70	7192.1 (72.2%)	776 (7.8%)	391.9 (3.9%)	1601.1 (16.1%)
	A. auriculiformis	Current-26/50	233.1 (2.3%)	9289.1 (93.3%)	0.1 (0%)	438.8 (4.4%)
		Current-26/70	371.1 (3.7%)	9275.6 (93.1%)	13.5 (0.1%)	300.7 (3%)
		Current-85/50	348.7 (3.5%)	9206.2 (92.4%)	83 (0.8%)	323.1 (3.2%)
		Current-85/70	453.1 (4.5%)	9196.4 (92.3%)	92.8 (0.9%)	218.8 (2.2%)
MG	*A. mangium*	Current-26/50	5288.2 (10.9%)	34711.2 (71.8%)	3540.5 (7.3%)	4813.2 (10%)
		Current-26/70	6384.5 (13.2%)	35224.8 (72.8%)	3026.9 (6.3%)	3716.9 (7.7%)
		Current-85/50	6741.5 (13.9%)	29433.5 (60.9%)	8818.2 (18.2%)	3359.9 (6.9%)
		Current-85/70	7664 (15.9%)	25898.5 (53.6%)	12353.1 (25.5%)	2437.4 (5%)
	A. auriculiformis	Current-26/50	0 (0%)	48353.1 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	48353.1 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	48353.1 (100%)	0 (0%)	0 (0%)

		Current-85/70	0 (0%)	48352.9 (100%)	0.1 (0%)	0 (0%)
MS	*A. mangium*	Current-26/50	181.7 (38.3%)	97.6 (20.6%)	193.8 (40.9%)	0.8 (0.2%)
		Current-26/70	179.8 (37.9%)	150.3 (31.7%)	141.1 (29.8%)	2.7 (0.6%)
		Current-85/50	182.6 (38.5%)	1.2 (0.3%)	290.1 (61.2%)	0 (0%)
		Current-85/70	182.6 (38.5%)	0 (0%)	291.3 (61.5%)	0 (0%)
	A. auriculiformis	Current-26/50	0 (0%)	473.9 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	473.9 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	473.9 (100%)	0 (0%)	0 (0%)
		Current-85/70	0 (0%)	473.9 (100%)	0 (0%)	0 (0%)
PE	*A. mangium*	Current-26/50	9.6 (0.7%)	1232.5 (90%)	125.5 (9.2%)	2.4 (0.2%)
		Current-26/70	11.8 (0.9%)	1203.8 (87.9%)	154.2 (11.3%)	0.2 (0%)
		Current-85/50	12 (0.9%)	1020.5 (74.5%)	337.5 (24.6%)	0 (0%)
		Current-85/70	12 (0.9%)	714.8 (52.2%)	643.2 (46.9%)	0 (0%)
	A. auriculiformis	Current-26/50	0 (0%)	1370 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	1370 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	1370 (100%)	0 (0%)	0 (0%)
		Current-85/70	0 (0%)	1369.9 (100%)	0.1 (0%)	0 (0%)
PR	*A. mangium*	Current-26/50	9.9 (0%)	20988.4 (99.6%)	76.1 (0.4%)	0 (0%)
		Current-26/70	9.9 (0%)	20922.3 (99.3%)	142.3 (0.7%)	0 (0%)
		Current-85/50	9.9 (0%)	19795.8 (93.9%)	1268.8 (6%)	0 (0%)
		Current-85/70	9.9 (0%)	18123.1 (86%)	2941.4 (14%)	0 (0%)
	A. auriculiformis	Current-26/50	0 (0%)	21074.5 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	21074.5 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	21074.5 (100%)	0 (0%)	0 (0%)
		Current-85/70	0 (0%)	21074.5 (100%)	0 (0%)	0 (0%)
RJ	*A. mangium*	Current-26/50	5215 (57.2%)	2137.9 (23.5%)	1542.1 (16.9%)	220.2 (2.4%)
		Current-26/70	5172.1 (56.7%)	2859.4 (31.4%)	820.7 (9%)	263.1 (2.9%)
		Current-85/50	5370.3 (58.9%)	1315.7 (14.4%)	2364.4 (25.9%)	64.9 (0.7%)
		Current-85/70	5398.6 (59.2%)	862.4 (9.5%)	2817.7 (30.9%)	36.6 (0.4%)
	A. auriculiformis	Current-26/50	0 (0%)	9109.4 (99.9%)	5.8 (0.1%)	0 (0%)
		Current-26/70	0 (0%)	9113.2 (100%)	2.1 (0%)	0 (0%)
		Current-85/50	0 (0%)	9069.3 (99.5%)	45.9 (0.5%)	0 (0%)
		Current-85/70	0 (0%)	8990.8 (98.6%)	124.4 (1.4%)	0 (0%)
RS	*A. mangium*	Current-26/50	2.2 (0%)	9049.9 (96.3%)	345.5 (3.7%)	0 (0%)
		Current-26/70	2.2 (0%)	8830.4 (94%)	565 (6%)	0 (0%)
		Current-85/50	2.2 (0%)	8381.5 (89.2%)	1013.9 (10.8%)	0 (0%)
		Current-85/70	2.2 (0%)	9073.4 (96.6%)	322 (3.4%)	0 (0%)
	A. auriculiformis	Current-26/50	0 (0%)	9397.6 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	9397.6 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	9397.6 (100%)	0 (0%)	0 (0%)
		Current-85/70	0 (0%)	9397.6 (100%)	0 (0%)	0 (0%)

SC	*A. mangium*	Current-26/50	417.6 (2.9%)	13460.9 (93%)	588.4 (4.1%)	0 (0%)
		Current-26/70	417.6 (2.9%)	13094.3 (90.5%)	955 (6.6%)	0 (0%)
		Current-85/50	417.5 (2.9%)	12434.9 (86%)	1614.4 (11.2%)	0.2 (0%)
		Current-85/70	262.6 (1.8%)	13880.5 (95.9%)	168.8 (1.2%)	155 (1.1%)
	A. auriculiformis	Current-26/50	0 (0%)	14467 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	14467 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	14467 (100%)	0 (0%)	0 (0%)
		Current-85/70	0 (0%)	14467 (100%)	0 (0%)	0 (0%)
SE	*A. mangium*	Current-26/50	233.3 (83.5%)	31.1 (11.1%)	0.3 (0.1%)	14.8 (5.3%)
		Current-26/70	245.4 (87.8%)	28.3 (10.1%)	3.1 (1.1%)	2.7 (1%)
		Current-85/50	218.9 (78.3%)	30.9 (11.1%)	0.4 (0.2%)	29.2 (10.5%)
		Current-85/70	210 (75.2%)	31.3 (11.2%)	0 (0%)	38.1 (13.6%)
	A. auriculiformis	Current-26/50	0 (0%)	279.1 (99.9%)	0 (0%)	0.3 (0.1%)
		Current-26/70	0 (0%)	276.4 (98.9%)	2.7 (1%)	0.3 (0.1%)
		Current-85/50	0 (0%)	275.6 (98.6%)	3.5 (1.3%)	0.3 (0.1%)
		Current-85/70	0 (0%)	278.6 (99.7%)	0.5 (0.2%)	0.3 (0.1%)
SP	*A. mangium*	Current-26/50	851.7 (7%)	10340.3 (85%)	958.7 (7.9%)	17.3 (0.1%)
		Current-26/70	861 (7.1%)	10159 (83.5%)	1140 (9.4%)	7.9 (0.1%)
		Current-85/50	867.5 (7.1%)	7621.4 (62.6%)	3677.5 (30.2%)	1.4 (0%)
		Current-85/70	864.7 (7.1%)	5113.5 (42%)	6185.5 (50.8%)	4.3 (0%)
	A. auriculiformis	Current-26/50	0 (0%)	12167.9 (100%)	0 (0%)	0 (0%)
		Current-26/70	0 (0%)	12167.9 (100%)	0 (0%)	0 (0%)
		Current-85/50	0 (0%)	12167.9 (100%)	0 (0%)	0 (0%)
		Current-85/70	0 (0%)	12167.9 (100%)	0 (0%)	0 (0%)

CONCLUSÃO GERAL

Com base nos resultados encontrados nesse estudo e no conjunto de evidências reportados na literatura, podemos afirmar que *Acacia mangium* e *A. auriculiformes* podem se tornar uma grande ameaça às comunidades vegetais na Mata Atlântica. Essas espécies podem invadir ecossistemas abertos e, juntamente com outros fatores antrópicos, promover um conjunto de mudanças na diversidade, estrutura e fitofisionomia no ecossistema negligenciado de *Mussununga*. Ainda, mudanças ambientais promovidas pelo homem interferem positivamente na dispersão e estabelecimento dessas espécies na Mata Atlântica. A fragmentação florestal e o conjunto de rodovias dispersos pela Mata Atlântica aumentam a permeabilidade da paisagem para as espécies de *Acacia* e aumenta a chance de invasão biológica no ecossistema de *Mussununga*. Além disso, as mudanças climáticas esperadas para as próximas décadas irão promover um aumento na área de disponibilidade climática para essas espécies e poderão acarretar em mais um obstáculo para os programas de restauração da Mata Atlântica. Portanto, a utilização de modelos para prever ou detectar a invasão biológica por *Acacia* nessa região se fazem necessários e irão facilitar o estabelecimento de políticas públicas. Além disso, projetos de restauração, o desestímulo ao plantio de *Acacia* e controle e monitoramento de áreas invadidas serão de grande importância para diminuição dos efeitos causados pela invasão de espécies de *Acacia*.