UNIVERSIDADE ESTADUAL PAULISTA
"JÚLIO DE MESQUITA FILHO"
INSTITUTO DE BIOCIÊNCIAS – RIO CLARO

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA, EVOLUÇÃO E BIODIVERSIDADE

INVASÕES POR GRAMÍNEAS AFRICANAS E RESTAURAÇÃO DE FORMAÇÕES ABERTAS DE CERRADO: UMA ABORDAGEM DE MODELO DE ESTADO-E-TRANSIÇÃO

GABRIELLA DE FARIA OLIVEIRA DAMASCENO RIBEIRO

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Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutor em Ecologia, Evolução e Biodiversidade

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RESUMO

Espécies exóticas invasoras (EEI) representam um dos grandes desafios do Antropoceno. A presença de gramíneas invasoras é mais um obstáculo à conservação de savanas tropicais, já ameaçadas pela conversão de áreas naturais e em menor grau por iniciativas equivocadas de restauração. Esta tese teve o objetivo de construir um modelo conceitual de estado-e-transição a respeito da degradação e restauração de savanas tropicais invadidas por gramíneas exóticas. Especificamente, utilizamos experimentos em campo para entender como a abundância de uma gramínea exótica invasora, *Urochloa decumbens*, está relacionada a alterações em ecossistemas abertos de Cerrado. Além disso, também investigamos como a abundância da EEI pode modular os efeitos de queimada prescritas nas comunidades vegetais e funcionamento desses ecossistemas. Os experimentos foram implementados em Itirapina/SP e Brasília/DF e envolveram a coleta de dados em distintos níveis ecológicos: micro-habitat (luminosidade, umidade e temperatura), indivíduo (área foliar específica), comunidade (riqueza, diversidade e estrutura) e ecossistema (acúmulo de biomassa, fluxo de carbono e taxa de decomposição). Foram estabelecidas parcelas (25 m^2) representando gradientes de abundância de *Urochloa decumbens* (0, 25, 50, 75 e 100% de cobertura). Em cada área, foram estabelecidos três blocos, cada um composto por um gradiente queimado e outro controle (sem queima). A partir da junção das informações observadas em campo com as obtidas da literatura, nós propusemos um modelo de estado-e-transição composto por sete estados, sendo três estados estáveis e quatro transientes. O processo de degradação resultante da invasão por gramíneas exóticas pode ser revertido ou minimizado através de ações de manejo, capazes de manter o sistema em estados com menor cobertura pela EEI ou menos impactados pela sua presença. Esperamos que este modelo sirva de base para a tomada de decisões relativas ao manejo de gramíneas exóticas invasoras em savanas tropicais. Acreditamos que somente baseada em ciência a prática de ecologia aplicada pode enfrentar os desafios que a humanidade encontrará em decorrência das mudanças globais.

Palavras-chave: invasões biológicas, restauração ecológica, Cerrado, gramíneas africanas, espécies exóticas invasoras

ABSTRACT

Invasive alien species (IAS) represent one of the major challenges of the Anthropocene. The presence of invasive grasses is an obstacle to the conservation of tropical savannas, which are already threatened by the conversion of natural areas and, to a lesser extent, by misguided restoration initiatives. This thesis aimed to build a state-and-transition model regarding the degradation and restoration of tropical savannas. Specifically, we used field experiments to understand how the abundance of an invasive alien grass, *Urochloa decumbens* is related to changes in open Cerrado ecosystems. In addition, we also investigated how the IAS's abundance can modulate the effects of prescribed burning in vegetation and functioning of these ecosystems. Fire experiments were implemented in Itirapina/SP and Brasília/DF where we sampled data at different levels of ecological organization: micro-habitat (luminosity, humidity, and temperature), individuals (specific leaf area), community (richness, diversity, and structure) and ecosystem (biomass accumulation, carbon flux and decomposition rate). Plots (25 m²) were established in each area representing *Urochloa decumbens* abundance gradients (0, 25, 50, 75 and 100% cover). In each area, three blocks were established, each one composed of a burnt gradient and another control. From the combination of information obtained in the field with those retrieved from the literature, we proposed a state-and-transition model composed of seven states, three stable states and four transient states. The degradation process resulting from the invasion by alien grasses can be reversed or minimized through management actions, capable of maintaining the system in states with less coverage by the IAS or less impacted by its presence. We hope that this model will serve as a basis for decision-making regarding the management of invasive alien grasses in tropical savannas. We believe that the science-based practice of applied ecology can help us overcome the challenges that humanity will face because of global changes.

Keywords: biological invasions, ecological restoration, Cerrado, African grasses, invasive alien species

SUMÁRIO

INTRODUÇÃO GERAL

1. REVISÃO DE LITERATURA

Espécies exóticas invasoras (EEI) são uma das principais ameaças à conservação da biodiversidade (Butchart et al., 2010) e por este motivo são reconhecidas como um desafio global para a sobrevivência das populações humanas (Pyšek et al., 2020). Devido aos impactos que causam nos sistemas invadidos, EEI causam prejuízos ecológicos (Bellard, Cassey, & Blackburn, 2016; Kumschick et al., 2015), sanitários (Ogden et al., 2019), sociais (Jones, 2017) e econômicos (Diagne et al., 2021). No Brasil, os custos econômicos associados a 16 EEI foram de 105 bilhões de dólares nos últimos 35 anos (Adelino et al., 2021). Entretanto, são registradas 254 EEI no Brasil (Ziller et al., 2020) e, portanto, estes custos certamente são subestimados.

A maior parte das EEI no Brasil são plantas terrestres (68%, n =173), das quais 25 são pertencentes à família Poaceae (Ziller et al., 2020). Estas espécies geralmente estão associadas a ambientes abertos e ameaçam sobretudo a conservação da biodiversidade no Pantanal (Alho, Mamede, Bitencourt, & Benites, 2011), nos Campos Sulinos (Fonseca et al., 2013) e no Cerrado (Damasceno et al., 2018; Durigan, De Siqueira, & Franco, 2007; Musso et al., 2019). Gramíneas utilizadas como forrageiras para alimentação de animais estão entre as EEI mais problemáticas, como por exemplo, *Eragrostis plana, Andropogon gayanus*, *Megathyrsus maximus*, *Melinis minutiflora* e diversas espécies do gênero *Urochloa*, como *U. decumbens, U. humidicola* e *U. brizantha*.

Urochloa decumbens (Stapf) R.D. Webster, assim como as demais espécies de gramíneas exóticas invasoras, causa impactos negativos em áreas invadidas de

Cerrado, como a exclusão de espécies nativas e alterações na estrutura das comunidades vegetais (Damasceno et al., 2018; Hoffmann & Haridasan, 2008; Musso et al., 2019; Pivello, Shida, & Meirelles, 1999; Zenni et al., 2020). Espécies deste gênero são utilizadas como pastagens para bovinos em todo o Brasil (Brossard & Barcellos, 2005); tendo sido amplamente introduzidas a partir da década de 1960 devido à sua alta produtividade, palatabilidade e conteúdo nutricional (Milles et al. 1996). Além disso, estas espécies são alvo de seleções artificiais e melhorias genéticas desde a década de 1980, visando incrementos na qualidade e quantidade dos produtos de origem bovina (Valle, Jank, & Resende, 2009). Consequentemente, espécies de *Urochloa* possuem características que facilitam tanto sua utilização como forrageiras quanto seu sucesso como espécies invasoras, como por exemplo, acúmulo de biomassa área (até 16 toneladas.ha^{-1}.ano^{-1}, Baptistella, de Andrade, Favarin, & Mazzafera, 2020) e rápido crescimento após distúrbios (Geissianny B Assis, Pilon, Siqueira, & Durigan, 2021; Damasceno & Fidelis, 2020; Fisher & Kerridge, 1996).

A preocupação com espécies de gramíneas exóticas invasoras torna-se ainda maior no Cerrado, onde a vegetação nativa vem sendo convertida para a formação de pastagens plantadas (Brossard & Barcellos, 2005), que aumentam a pressão de propágulo das invasoras sobre áreas naturais remanescentes O Cerrado é uma savana tropical e, devido à coexistência entre os estratos herbáceo e arbóreo, apresenta um gradiente de fitofisionomias, que vão desde campos abertos até formações florestais (Ribeiro & Walter, 2008). Esta diversidade de fitofisionomias reflete-se também na quantidade de suas espécies vegetais. O Cerrado abriga mais de 12000 espécies de plantas, das quais 35% são endêmicas deste bioma (BFG, 2015). Em virtude desta riqueza e da crescente conversão de áreas naturais para

fins agrícolas (Alencar et al., 2020), o Cerrado é considerado um hotspot para a conservação da biodiversidade (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Este reconhecimento, porém, não impediu a continuidade de sua devastação; dentre os hotspots mundiais, o Cerrado é um dos três mais convertidos para fins agrícolas (Kong, Zhou, & Jiao, 2021).

Os ecossistemas abertos de Cerrado são especialmente ameaçados pois sua conversão é estimulada por políticas públicas que priorizam a conservação de ecossistemas florestais às custas de ecossistemas abertos (Bonanomi et al., 2019), incluindo o plantio de árvores exóticas invasoras (Fernandes et al., 2016). Por muito tempo, savanas e campos naturais foram entendidos como resultado da degradação de ambientes florestais (Parr, Lehmann, Bond, Hoffmann, & Andersen, 2014; Pausas & Bond, 2020). A correção desse equívoco é recente, por meio da sistematização do conhecimento sobre os processos históricos de formação de vegetações abertas (Veldman, Buisson, et al., 2015), bem como pelo reconhecimento da alta biodiversidade de campos tropicais (Murphy, Andersen, & Parr, 2016).

Infelizmente, a supervalorização de ambientes florestais ainda hoje influencia políticas e práticas de restauração equivocadas em sistemas abertos (Buisson et al., 2021; Silveira et al., 2021), causando perdas de biodiversidade e de funções ecossistêmicas (Buisson et al., 2019; Veldman, Overbeck, et al., 2015). Devido a todas estas ameaças à sua conservação, a necessidade de manejar fisionomias abertas do Cerrado é cada vez mais premente (Strassburg et al., 2017). Nesse sentido, o entendimento de savanas como ecossistemas dinâmicos e guiados por distúrbios é essencial para o sucesso do manejo (Buisson et al., 2021, 2019; Mayer & Rietkerk, 2004).

Savanas tropicais são ecossistemas que dependem da ocorrência de distúrbios naturais, como fogo e herbivoria, para sua existência e manutenção (Walker, 1987). Em virtude da recorrência destes distúrbios, savanas possuem múltiplos pontos de estabilidade ecológica, chamados de estados alternativos estáveis (May, 1977). Estes estados alternativos estáveis (EAE) resultam da retroalimentação de variáveis estruturantes do sistema, que podem ser abióticas, como a disponibilidade de nutrientes, mas também bióticas, como a riqueza e diversidade de espécies. Nesse contexto, alterações das variáveis estruturantes podem levar à desestabilização de mecanismos de retroalimentação do sistema, causando sua transição a outro estado alternativo (Figura 1; Beisner, Haydon, & Cuddington, 2003).

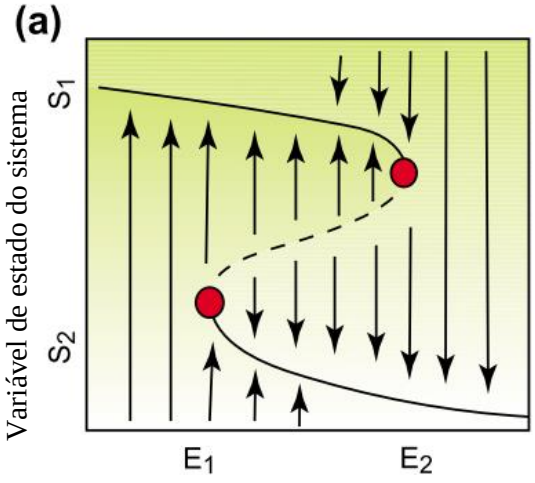

Figura 1. Representação de dois estados alternativos estáveis (círculos vermelhos) mantidos por combinações de condições ambientais (eixo x) e variáveis de estado do sistema (eixo y). Alterações em um ou ambos os eixos podem causar a transição entre os dois estados. Modificado de Suding et al. 2004.

Dentre outras forças transformadoras, invasões biológicas são capazes de causar transições entre EAE ao conduzir o sistema a um estado alternativo degradado (Wilsey, Daneshgar, Hofmockel, & Polley, 2014). De forma geral, essas

transições estão atreladas a um aumento da abundância da espécie exótica invasora à medida que o processo de invasão avança (Blackburn et al. 2011). Nas fases iniciais e intermediárias do processo de invasão, a abundância da EEI é moderada, acarretando modificações das interações entre espécies (Kuebbing, Souza, & Sanders, 2014), promovendo assim alterações na trajetória da comunidade e na riqueza e diversidade de espécies (Kuebbing, Classen, Sanders, & Simberloff, 2015). Nas fases finais do processo de invasão, porém, a EEI geralmente domina a comunidade, ocasionando mudanças subsequentes nas propriedades do ecossistema, como produtividade, ciclagem de nutrientes (Ehrenfeld, 2003) e alterações do regime de distúrbio (D'Antonio & Vitousek, 1992).

A transição a um estado invadido degradado, portanto, acontece a partir de alterações dos mecanismos de feedback atuantes nas comunidades invadidas à medida que a espécie exótica invasora aumenta em abundância. Comunidades não invadidas são mantidas por feedbacks negativos, que promovem sua resiliência frente a distúrbios e perturbações (Beisner et al., 2003; Suding & Hobbs, 2009). As transformações resultantes da presença de EEI, entretanto, criam mecanismos de feedback positivo que retroalimentam sua expansão nessas áreas. Finalmente, quando a EEI é dominante na comunidade, novos feedbacks negativos são estabelecidos, resultando na resiliência do sistema invadido frente a ações de manejo. (King & Hobbs, 2006; Wilsey et al., 2014)

Devido a essas transformações, pode não ser mais possível reverter o estado degradado às condições ecológicas anteriores à invasão, quando se considera a escala de tempo antrópica. Nestes casos, o controle da espécie exótica invasora e a adoção de medidas de restauração conduzem o sistema a um terceiro estado alternativo, que possui seus próprios mecanismos de retroalimentação (Hobbs,

Higgs, & Harris, 2009). Utilizando modelos conceituais de estado-e-transição, essa situação foi identificada em casos de invasões de ecossistemas abertos por plantas (Bestelmeyer, Herrick, Brown, Trujillo, & Havstad, 2004), incluindo gramíneas africanas em savanas tropicais (Brooks, Setterfield, & Douglas, 2010).

Modelos conceituais de estado-e-transição permitem a aplicação prática de conhecimentos científicos ao sintetizar informações sobre processos ecológicos e seus mecanismos subjacentes (Hobbs & Norton, 1996). Neste sentido, a elaboração de modelos conceituais sobre a dinâmica de sistemas abertos invadidos por gramíneas exóticas é de fundamental importância para orientar as práticas de conservação e restauração destes ecossistemas (Bestelmeyer et al., 2003), incluindo o manejo de gramíneas invasoras (Hobbs, 2007). Quando aplicados a savanas tropicais, modelos de estado-e-transição permitem identificar os mecanismos responsáveis pela manutenção e/ou transições entre EAE, influenciado assim o sucesso de ações de manejo de EEI (Suding & Hobbs, 2009) e de restauração ecológica (Suding, Gross, & Houseman, 2004).

A utilização de modelos conceituais para o entendimento da dinâmica das formações de Cerrado foi iniciada por Pivello e Coutinho (1996), que consideraram um modelo de estado-e-transição para esse bioma, inclusive com transições causadas por espécies de gramíneas exóticas invasoras. Apesar de os autores deixarem claro que seu modelo foi um primeiro protótipo e alertarem sobre a necessidade de novos estudos sobre o assunto, pouco se avançou ao longo destes 25 anos. Os problemas ocasionados por gramíneas exóticas invasoras, por outro lado, intensificaram-se, tornando-se um desafio cada vez maior para a conservação destes ecossistemas (Guimarães-Silva, Zenni, Rosse, Bastos, & van den Berg, 2020), dada a dificuldade de seu controle (Damasceno & Fidelis, 2020), o legado de

seus efeitos negativos (Zenni et al., 2020) e a ausência de regeneração natural da vegetação nativa após seu controle (Assis et al., 2021).

Atualmente, existem evidências que apontam tanto para a eficácia (Aires, 2009; Assis et al., 2021; Barbosa, 2009; Castillioni, 2015; Damasceno & Fidelis, 2020; Martins, Hay, Walter, Proença, & Vivaldi, 2011; Sampaio et al., 2015; Zenni et al., 2020) quanto a ineficácia do controle de espécies de gramíneas no Cerrado (Geissianny B Assis et al., 2021; Barbosa, 2009; Castillioni, 2015; Damasceno & Fidelis, 2020; Gorgone-Barbosa, 2016; Martins et al., 2011). A ausência de uniformidade dos resultados de manejo pode resultar de diversos fatores, incluindo diferenças inerentes a cada técnica, ao tempo de monitoramento e à escala do estudo. Entretanto, mesmo limitando-se os estudos apenas aos que avaliaram a eficácia de queimadas prescritas, resultados distintos também são encontrados. Uma possível explicação para essas divergências é o fato de que os resultados de ações de manejo são dependentes do contexto, como, por exemplo, do momento e da qualidade da execução das ações (Shea, Kelly, Sheppard, & Woodburn, 2005). Além disso, apesar de serem funcionalmente similares, espécies de gramíneas exóticas invasoras no Cerrado são diferentemente influenciadas pelas condições climáticas após seu controle pelo fogo (Damasceno & Fidelis, 2020).

Um fator ainda a ser investigado e que também pode afetar o resultado de ações de manejo de gramíneas exóticas invasoras em savanas tropicais é a abundância da espécie indesejada no momento do controle (porém veja Martins et al., 2011). Isto pode se dar de duas formas: diretamente, pela influência da abundância nas técnicas de manejo adotadas; e indiretamente, a partir dos efeitos da abundância nos impactos causados no sistema. Consequentemente, a abundância da EEI, dentre outras características como capacidade de rebrote, por

exemplo, influencia a escolha das técnicas de manejo a serem adotadas.

Em áreas em início de invasão (quando a abundância da invasora é baixa), técnicas direcionadas a erradicar os indivíduos invasores (Blackburn et al., 2011; Robertson et al., 2020), como capina, arranquio e corte são preferíveis, por sua maior eficácia e menor impacto na vegetação nativa (Aires, 2009; Assis et al., 2021; Barbosa, 2009; Martins et al., 2011). Em áreas dominadas pela espécie exótica invasora (nas quais sua abundância é alta) é preferível a utilização de técnicas aplicáveis em larga escala e que permitam seu controle em longo prazo (García-Díaz et al., 2021), como queimadas prescritas, associadas (Assis et al., 2021; Castillioni, 2015; Martins et al., 2011) ou não (Damasceno & Fidelis, 2020; Gorgone-Barbosa, 2016) à aplicação de herbicidas e/ou à semeadura direta de espécies nativas.

Por outro lado, a abundância de espécies exóticas invasoras também influencia o resultado das ações de manejo através de impactos per-capita dependentes da densidade (Dresseno, Guido, Balogianni, & Overbeck, 2018; Iannone, Heneghan, Rijal, & Wise, 2015; Pearse, Sofaer, Zaya, & Spyreas, 2019; Tererai, Gaertner, Jacobs, & Richardson, 2013; Zhang et al., 2020). Por impacto per-capita referimo-nos às alterações ecológicas resultantes do processo de invasão ponderadas pela abundância da invasora, assim fornecendo um indicativo de como os efeitos e/ou impactos são dependentes da densidade da invasora (Pearse et al., 2019; Sofaer, Jarnevich, & Pearse, 2018). Ao longo de um gradiente de abundância, os impactos per-capita podem se manter constantes, resultando em um impacto total linear e diretamente proporcional à abundância da invasora. Entretanto, é possível que o impacto per-capita varie ao longo do gradiente de abundância. Nesse caso, a curva abundância-impacto é não-linear e pode apresentar mudanças de sentido e

direção, o que indica limiares de abundância da invasora que causam descontinuidade na variável impactada (Figura 2).

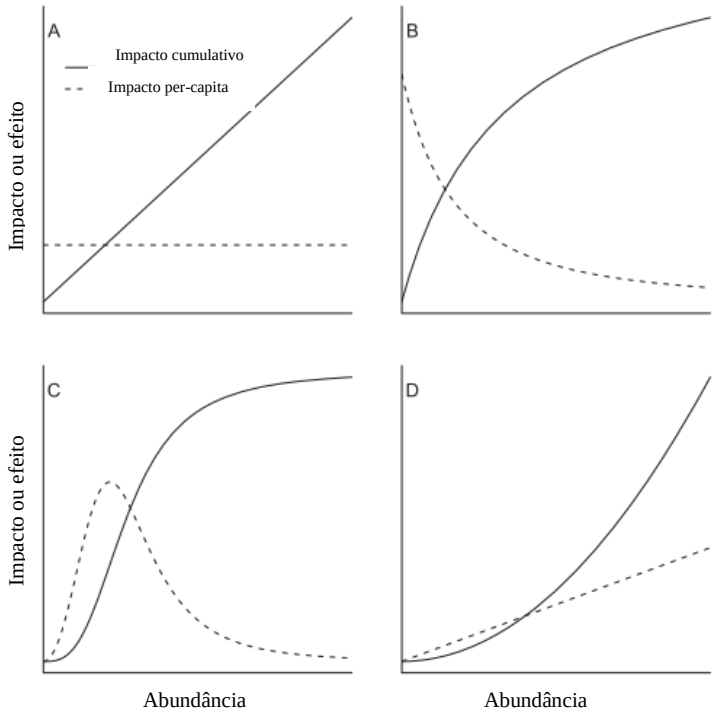

Figura 2. Representação de possíveis curvas de abundância-impacto de uma espécie invasora. A curva pode ser linear (A), quando o impacto per-capita é constante, ou não-linear quando os impactos per-capita não são constantes (B,C,D). Nestes casos, os pontos de mudança de direção da curva indicam limiares de abundância da invasora que podem resultar em mudanças abruptas no impacto total causado no sistema invadido, indicando um possível limiar entre estados alternativos estáveis (C, pico da curva pontilhada). Modificado de Sofaer et al. (2018).

Em decorrência da relação entre abundância, impactos e limiares de transição, curvas de impacto-abundância são ferramentas úteis em estudos que pretendem investigar o efeito de espécies exóticas invasoras na dinâmica do sistema invadido (Pearse et al., 2019). Nesse sentido, esta tese de doutorado avaliou como a abundância da gramínea *Urochloa decumbens*, ao longo de um gradiente de invasão, afeta a degradação e a restauração de ecossistemas abertos de Cerrado.

2. OBJETIVOS

O objetivo geral desta tese de doutorado foi investigar como a gramínea exótica invasora *Urochloa decumbens* influencia a degradação e restauração de ecossistemas abertos de Cerrado, a partir de uma abordagem de modelo de estado-e-transição. Objetivamos construir um modelo conceitual que represente os possíveis estados alternativos de um sistema invadido, bem como as transições entre estes estados, considerando abundância da espécie invasora como variável estruturante do sistema. O objetivo geral foi dividido em três objetivos específicos, que abordam sequencialmente 1) a degradação causada pelo processo de invasão; 2) a restauração do sistema invadido; e 3) a construção do modelo conceitual.

No primeiro objetivo, investigamos de que forma a abundância da gramínea exótica invasora está relacionada com os impactos causados em propriedades do sistema, desde o nível de micro-habitat até o nível de ecossistema. Ao longo de um gradiente de invasão, avaliamos como a abundância da EEI (avaliada por sua cobertura) relaciona-se com características de micro-habitat (cobertura de solo nu, luminosidade, temperatura e umidade do ar); com a performance dos indivíduos, mensurada a partir da área foliar específica, um atributo funcional relacionado à capacidade fotossintética; com as comunidades vegetais (estrutura, composição e diversidade); e com propriedades do ecossistema (biomassa acumulada, taxa de decomposição, e emissão de CO_2 do solo).

Esperamos encontrar, no nível de micro-habitat, curvas de abundância-impacto lineares negativas para a luminosidade e temperatura do ar no nível do solo devido à alta produtividade da EEI. No nível de indivíduo, esperamos que os valores de área foliar específica (SLA) de *Urochloa decumbens* aumentem de forma não-linear devido à intensificação da competição intraespecífica e às limitações

fisiológicas e ambientais ao SLA (Lambers & Oliveira, 2019). Esperamos que o SLA das espécies nativas dominantes aumente por causa da maior competição interespecífica; porém de forma linear, já que apenas boas competidoras se manteriam em áreas completamente invadidas. Esperamos decréscimos não-lineares na abundância, riqueza e diversidade de espécies devido aos impactos da EEI sobre a biodiversidade (Almeida-Neto et al., 2010; Damasceno et al., 2018). Esperamos aumentos lineares no acúmulo de biomassa área e no efluxo de CO_2 do solo devido à alta capacidade fotossintética de gramíneas exóticas invasoras. (Baruch, Hernandez, & Montilla, 1989). Entretanto, esperamos aumentos não-lineares das taxas de decomposição da serrapilheira, já que este processo é fortemente limitado pela comunidade de agentes decompositores (Bradford et al., 2002).

No segundo objetivo, avaliamos de que forma os impactos detectados poderiam ser revertidos a partir do uso de queimadas prescritas para a restauração desses ecossistemas. Para tanto, ao longo do gradiente de invasão mensuramos como duas queimadas prescritas afetaram os impactos causados por *Urochloa decumbens*, explorados no primeiro objetivo do estudo. Esperamos que as queimas prescritas resultem em maiores alterações do impacto da EEI em níveis intermediários de abundância por *Urochloa decumbens*. Essa expectativa deriva de três premissas: 1) comunidades não invadidas serão resilientes aos distúrbios causados pelo fogo, dada a presença desse elemento ao longo de sua história evolutiva (Simon et al., 2009); 2) em níveis intermediários de invasão, o fogo temporariamente alteraria as relações competitivas entre a invasora e as espécies nativas, facilitando sua coexistência; 3) áreas muito invadidas já teriam sido massivamente impactadas pela presença de *Urochloa decumbens*.

Assim, esperamos que as queimadas prescritas sejam mais eficazes em minimizar os impactos da invasora em sistemas menos degradados (até cerca de 75% de cobertura por *Urochloa decumbens*), e que, portanto, não teriam transicionado em direção a um estado alternativo degradado (Figura 3, retângulo 1). Isto porque nestes sistemas ainda não degradados os mecanismos de retroalimentação responsáveis por manter o estado alternativo conservado ainda não haveriam sido alterados pela presença da EEI, possibilitando minimização dos impactos e manutenção de um estado ecológico íntegro ou pouco modificado. Esperamos, em contrapartida, ii) que em sistemas que tenham transicionado para um estado degradado, com alta abundância da EEI (Figura 3, retângulo 2), as queimadas prescritas não mais restaurariam as condições de um sistema não-invadido, mas sim dariam origem a um outro distinto estado alternativo (Figura 3, retângulo 3).

Para atingir o terceiro objetivo específico, elaboramos um modelo de estado-e-transição para invasões por gramíneas exóticas invasoras em savanas tropicais. A construção do modelo baseou-se tanto em aspectos ecológicos teóricos quanto em resultados primários obtidos a partir das análises relacionadas aos dois primeiros objetivos. Em relação à fundamentação teórica, apoiamo-nos nas teorias de estados alternativos estáveis (Stringham, Krueger, & Shaver, 2003) e de invasões biológicas (Blackburn et al., 2011), bem como nas interrelações entre elas e em suas implicações para a ecologia aplicada (Hobbs & Humphries, 1995; Suding et al., 2004; Suding & Hobbs, 2009). Construímos o modelo conceitual visando sua utilização por gestores de unidades de conservação envolvidos no controle de espécies invasoras e restauração ecológica.

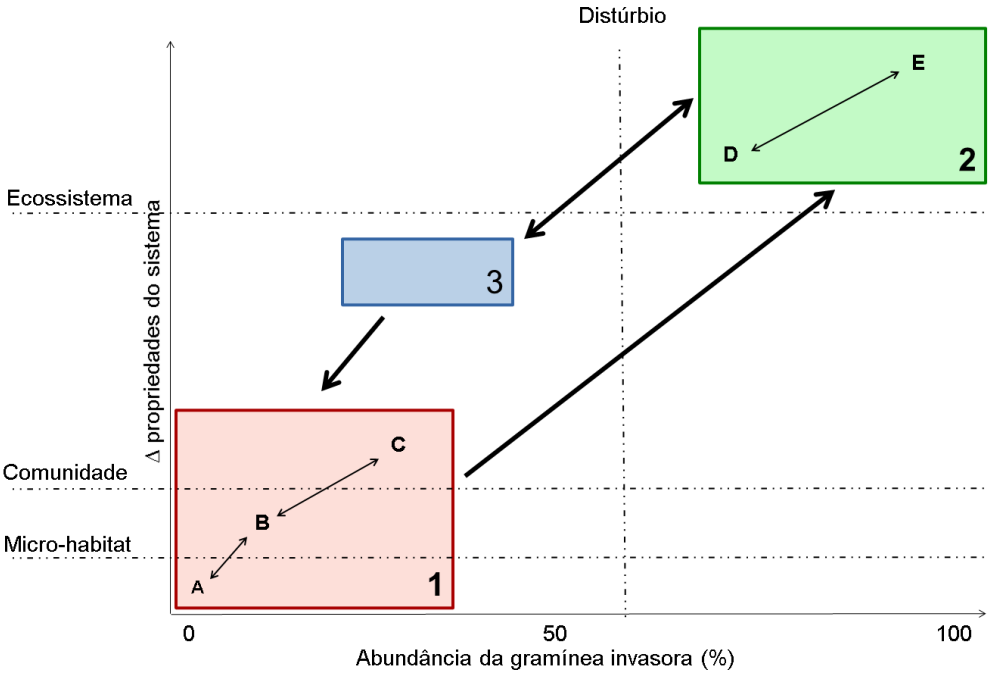

Figura 3. Representação de um modelo teórico relacionando a abundância de gramíneas exóticas invasoras com as alterações de propriedades do sistema invadido, induzindo à transição entre três estados alternativos estáveis (EAE; retângulos 1 [vermelho], 2 [verde] e 3 [azul]) e entre diferentes configurações de um mesmo estado (A, B ou C no estado 1; D e E no estado 2). As linhas tracejadas indicam pontos a partir dos quais alterações das propriedades do sistema em diferentes níveis de organização (eixo y; micro-habitat, comunidade e ecossistema) bem como do regime de distúrbio (eixo x) estão associadas às transições entre configurações e estados (setas no interior dos retângulos e entre eles, respectivamente). Antes de transpor o limiar ecológico entre dois EAE's, a espécie exótica invasora atinge abundâncias capazes de modificar as características físicas do sistema (micro-habitat), bem como a composição de espécies (comunidade). As transições entre diferentes configurações de um mesmo EAE (setas bidirecionais no interior de cada retângulo) seriam reversíveis mediante a implementação de ações de restauração. Por outro lado, o aumento da abundância da gramínea exótica invasora promove a transposição do limiar ecológico entre dois EAE's (seta unidirecional entre os retângulos 1 e 2), causando alterações no funcionamento e nas propriedades do ecossistema que podem ser irreversíveis na escala de tempo antrópica. Entretanto, seria possível ainda a ocorrência de um terceiro estado alternativo menos degradado (retângulo 3), originário de ações de restauração que reduzissem a abundância da gramínea invasora e que recuperassem parte das características anteriores do sistema. Neste caso, o sistema poderia retornar ao estado degradado, caso a abundância da gramínea exótica invasora não fosse mantida dentro dos limites que permitem a ocorrência do EAE 3 (seta bidirecional entre os retângulos 2 e 3). Além disso, é possível ainda que as características iniciais do sistema sejam restauradas a partir do novo estado alternativo em uma escala de tempo geológica (seta unidirecional entre os retângulos 1 e 3).

3. DESCRIÇÃO GERAL DOS MÉTODOS

3.1. ÁREAS DE ESTUDO

Este estudo foi desenvolvido no interior de duas unidades de conservação de Cerrado – o Parque Nacional de Brasília (PNB) e a Estação Ecológica de Itirapina (EcEI). As duas áreas de estudo estão localizadas na mesma longitude (47º53'W) e são separadas por 800 km em linha reta, no sentido norte-sul (Figura 4). O PNB situa-se no Distrito Federal, no Planalto Central Brasileiro, em região central do Cerrado (15º41'S e 47º53'W), enquanto a EcEI encontra-se no estado de São Paulo, na porção marginal do bioma (22º14'S e 47º53'W). Os solos das duas áreas são oligotróficos e intemperizados, sendo dominantes os argissolos vermelhos e os arenossolos no PNB e EcEI, respectivamente (IBAMA & FUNATURA., 1998; Zanchetta et al., 2006).

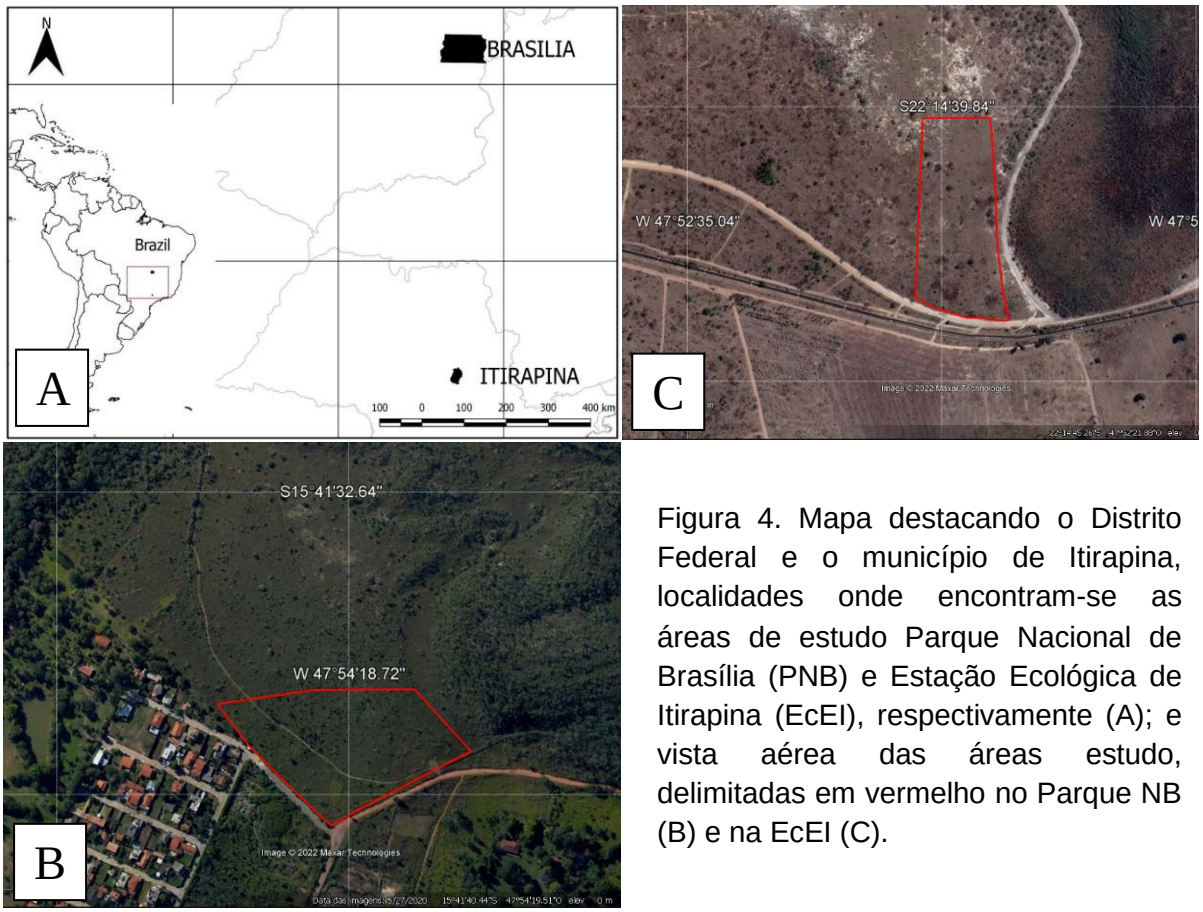

Figura 4. Mapa destacando o Distrito Federal e o município de Itirapina, localidades onde encontram-se as áreas de estudo Parque Nacional de Brasília (PNB) e Estação Ecológica de Itirapina (EcEI), respectivamente (A); e vista aérea das áreas estudo, delimitadas em vermelho no Parque NB (B) e na EcEI (C).

Ambas as áreas apresentam clima do tipo Cw, com verões quentes e chuvosos e invernos secos. As médias mensais de temperatura e precipitação durante o verão e o inverno são 23ºC e 300mm e 18ºC e 150mm para o PNB e 22ºC e 188mm e 17ºC e 55mm para a EcEI (IBAMA & FUNATURA 1998; Zanchetta et al. 2006). A vegetação das duas áreas de estudo é composta por distintas formações de Cerrado, que vão desde campos abertos até áreas florestais (IBAMA & FUNATURA., 1998; Zanchetta et al., 2006). Como este estudo busca avaliar a influência de gramíneas exóticas invasoras em ecossistemas abertos de Cerrado, selecionamos, em ambas as localidades, áreas de campo sujo invadidas por *Urochloa decumbens* (introdução não-intencional). Similarmente a outras formações abertas do Cerrado, o campo sujo é caracterizado por um estrato herbáceo dominado por gramíneas, mas também composto por diversas espécies não-graminóides. Nesta matriz herbácea estão inseridos indivíduos arbustivos e arbóreos isolados, que representam até 25% da cobertura de copa nesses ambientes (Ribeiro & Walter, 1998).

3.2. DELINEAMENTO EXPERIMENTAL

Para o estudo, selecionamos uma área de campo sujo invadida (introdução não-intencional da invasora) em cada uma das unidades de conservação (Figura 5). O histórico indica que as invasões se iniciaram nas décadas de 1980 no PNB e de 1990 na EcEI. As unidades amostrais do estudo foram parcelas de 5 x 5 m escolhidas para representar um gradiente de invasão de acordo com a cobertura por *Urochloa decumbens*. Estabelecemos três blocos de parcelas em cada área, sendo cada bloco composto por dois gradientes pareados, um destinado às queimas prescritas e outro para ser utilizado como controle não queimado.

Cada gradiente foi composto por cinco parcelas representando 0%, 25%, 50%, 75% e 100% de cobertura pela invasora (Figura 6 A). Estabelecemos um total de 60 parcelas: 5 parcelas x 2 gradientes x 3 blocos x 2 áreas. Cada parcela foi estabelecida em uma mancha de invasão que correspondesse à cobertura desejada e nenhuma mancha foi utilizada para mais de uma parcela; i.e., as maiores manchas selecionadas tinham 5 x 5 metros, correspondendo às parcelas 100% invadidas. Em um mesmo bloco, as parcelas foram espaçadas entre si por, no mínimo, 5 metros. Entre os blocos, a distância mínima foi de 100 m.

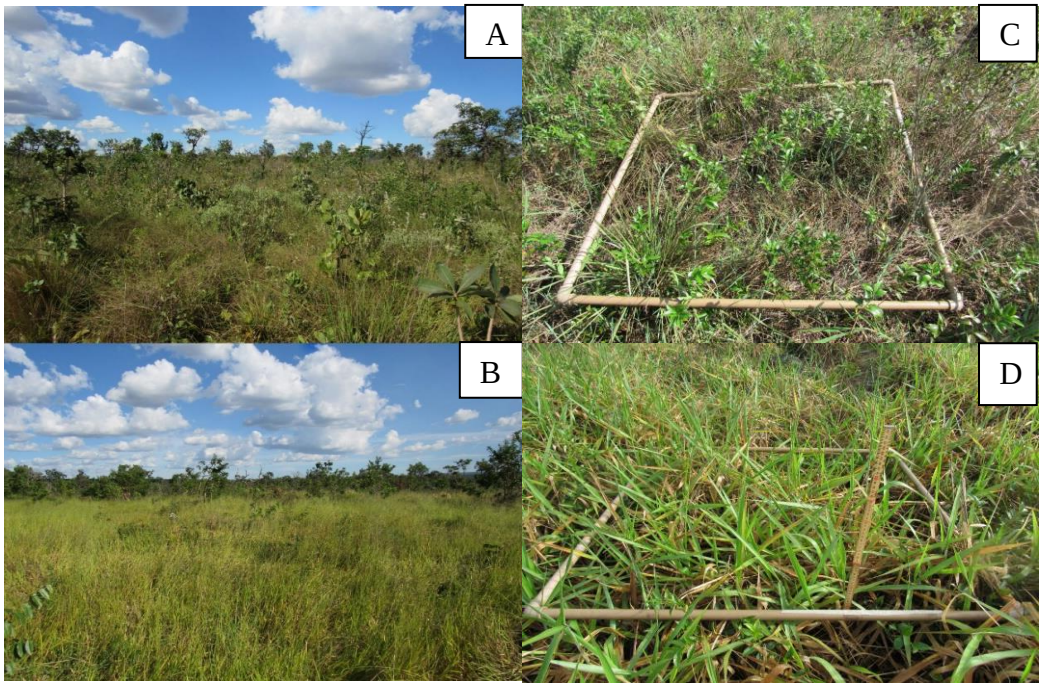

Figura 5. Aspecto geral (A, B) e detalhe (C, D) de áreas abertas de Cerrado não-invadidas (A, C) e sob invasão por *Urochloa decumbens* (B, D). Apesar de não resultar em transformações fisionômicas, a presença da invasora causa impactos estruturais na vegetação que são visualmente perceptíveis, como a redução de cobertura por espécies nativas. As fotografias foram tiradas nas áreas de estudo desta pesquisa: as fotos A e B são registros tomados do Parque Nacional de Brasília; e as fotos C e D na Estação Ecológica de Itirapina.

Os levantamentos da comunidade vegetal e a caracterização do micro-habitat foram realizadas na porção central de cada parcela (núcleo de 3 x 3 m), que foi

subdividida em 9 subparcelas de 1 m² (Figura 6B) visando diminuir o efeito da heterogeneidade espacial do estrato herbáceo (Augustine, 2003). A zona de bordadura (1 m ao redor da área central, em direção às bordas da parcela) foi utilizada para amostragens que demandaram remoção da vegetação, como coleta de biomassa e de folhas para área foliar específica, bem como as taxas de decomposição e o efluxo de CO_2 do solo.

3.3. COLETA DE DADOS

Foram realizadas duas campanhas de amostragem em cada área: uma anterior (2019) e outra posterior (2021) à execução das duas queimadas prescritas, realizadas no meio da estação seca em 2019 e 2020. Cada gradiente destinado ao tratamento de fogo foi queimado de forma independente. Desse modo, garantimos a independência entre os blocos e minimizamos as variações nas condições de queima experienciadas pelas parcelas de um mesmo gradiente. Todas as amostragens foram realizadas ao final da estação chuvosa, nos meses de março e abril.

O registro das condições microclimáticas (iluminância, temperatura e umidade do ar ao nível do solo) foi realizado de hora em hora, utilizando kits de sensores do tipo HOBO (cada kit foi composto por um HOBO Pendant e um HOBO Pro v2). Devido à limitação no número de kits disponíveis, dois blocos de cada área foram sorteados para receberem os sensores (20 kits por área, 40 kits no total). Para evitar viés relativo ao local de instalação dos kits, os sensores foram sistematicamente instalados sempre no mesmo vértice de cada parcela. Em cada amostragem (em 2019 e em 2021), os kits permaneceram no campo por pelo menos 130 dias, desde

a transição da estação chuvosa para a estação seca (março/abril) até o final da estação seca (agosto/setembro).

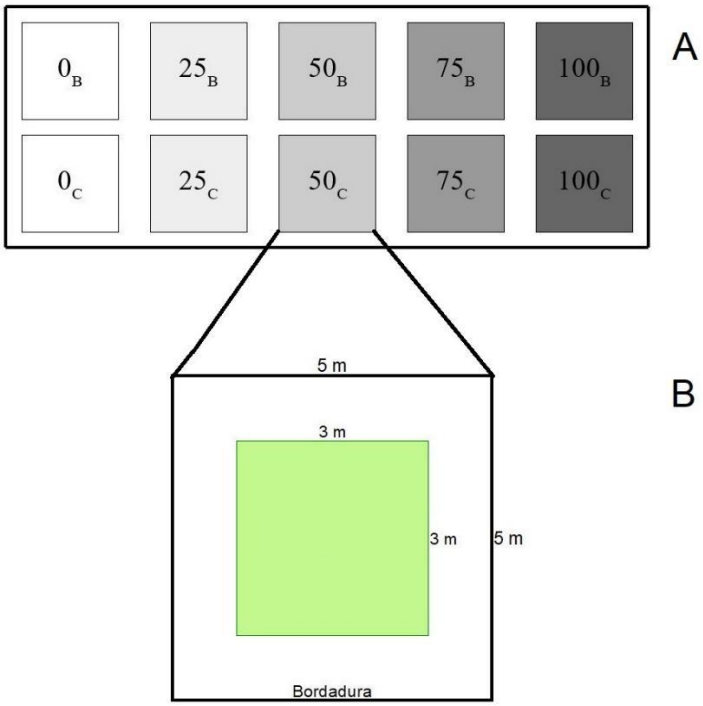

Figura 6. Esquema do delineamento experimental utilizado (a localização das parcelas em campo não seguiu o alinhamento mostrado na figura, por limitações técnicas). A) Cada bloco de parcelas é composto por dois gradientes pareados em relação à abundância de *Urochloa decumbens* (0, 25, 50, 75 e 100% de cobertura pela invasora). Em cada bloco, um gradiente foi destinado ao tratamento de queima e outro permaneceu inalterado como controle (índices B e C na identificação das parcelas na figura). B) Em cada parcela (25 m²), os levantamentos da comunidade vegetal foram feitos em uma área central (9 m², em verde), enquanto as demais variáveis foram amostradas na bordadura de 1 m de largura.

Em cada subparcela (1 x 1m), a amostragem da vegetação foi feita por meio da estimativa visual da cobertura percentual de cada espécie. Esta amostragem foi realizada sempre pela mesma pessoa em ambas as áreas experimentais. Utilizamos uma escala com porcentagem de cobertura de 0, 1, 5, 10 e, a partir daí, a cada 10 pontos percentuais até o máximo de 100% para estimar o somatório da projeção da parte aérea de todos os indivíduos de cada espécie. A estimativa de cobertura foi realizada tanto para espécies nativas quanto para *Urochloa decumbens* e outras

espécies exóticas invasoras quando ocorrentes, tais como *Melinis minutiflora* e *Andropogon gayanus.* Devido ao arranjo tridimensional dos indivíduos, a cobertura total da comunidade dentro de uma subparcela (soma de todas as espécies) eventualmente ultrapassou 100%. Além disso, dentro de cada subparcela, estimamos também a porcentagem de solo exposto (solo nu) ou coberto por biomassa morta (serrapilheira + biomassa morta ainda aderida aos indivíduos) de espécies nativas e exóticas invasoras. Nós agrupamos as espécies nativas em grupos funcionais de acordo com sua forma de crescimento: graminóides, herbáceas e arbustos.

No nível de indivíduos, analisamos a área foliar específica de espécies dominantes em cada parcela. Ranqueamos, do maior para a menor valor de cobertura, todas as espécies encontradas em uma parcela. Para isso, utilizamos os valores médios de cobertura de cada espécie calculados a partir da média simples de sua cobertura nas nove subparcelas que compõem uma parcela. Além da espécie mais abundante, selecionamos também as espécies seguintes até que a soma de sua cobertura atingisse pelo menos 80% da cobertura de cada parcela, independentemente de serem nativas ou invasoras. Seguindo o protocolo estabelecido por Pérez-Harguindeguy e colaboradores (2013), coletamos folhas de dez indivíduos (3 folhas por indivíduo) que foram temporariamente estocadas em sacos de papel. Em laboratório, as folhas foram reidratadas e tiveram sua área mensurada utilizando um equipamento LI-COR LI-3000C. Folhas compostas foram escaneadas em um scanner Epson V800 e medidas utilizando-se o software P-trap (Al-Tam et al., 2013). Após mensurações da área, as folhas foram secas em estufa (80ºC, 48h) e pesadas em balança eletrônica com precisão de 0.1 mg.

A biomassa acumulada foi quantificada através da coleta de todo o material

vegetal acima do solo em uma área de 0.5 x 0.5 m. Aleatoriamente, coletamos três subamostras por parcela (na faixa de bordadura), de modo a minimizar os efeitos da heterogeneidade espacial. A biomassa coletada foi armazenada em sacos de papel e posteriormente separada e pesada em laboratório. Separamos a biomassa em *Urochloa decumbens* viva ou morta; biomassa viva nativa (gramíneas, herbáceas ou arbustos); biomassa nativa morta (não separada por grupo funcional). Quando ocorrentes, quantificamos separadamente a biomassa de outras gramíneas invasoras. Após triada, a biomassa foi seca em estufa (80ºC, 48h) e pesada em balança eletrônica.

Mensuramos taxas de decomposição do ecossistema por meio de experimentos com bolsas de decomposição (20 x 20 cm) confeccionadas em aço inoxidável. Em cada parcela, nas duas amostragens, três bolsas foram deixadas sobre o solo e sob incidência direta de radiação solar, conforme protocolo descrito por Karberg e colaboradores (2008). Em cada parcela, uma das três bolsas foram resgatadas aos 90, 120 e 160 dias após sua instalação, entre abril e agosto. Objetivando a padronização do material parental ao longo do gradiente de invasão, utilizamos 5g de biomassa morta de *Urochloa decumbens* coletada antes de sua queda e incorporação na serrapilheira.

Os dados de efluxo de CO_2 do solo foram coletados utilizando-se câmaras de incubação com cal sodada (Ca/NaOH), conforme protocolo de Keith e Wong (2006). Em cada amostragem, instalamos uma câmara por parcela, sistematicamente posicionada em relação aos vértices delimitadores da parcela. A cal sodada permaneceu encubada por um período de 24 horas, sendo então recolhida, seca em estufa (105ºC, 24h) e pesada em balança eletrônica de precisão. As atividades executadas em campo e em laboratório ao longo da pesquisa estão ilustradas nas

Figuras 7 e 8, respectivamente. A análise dos dados foi realizada por meio de diferentes abordagens nos capítulos e, portanto, essas não são descritas aqui.

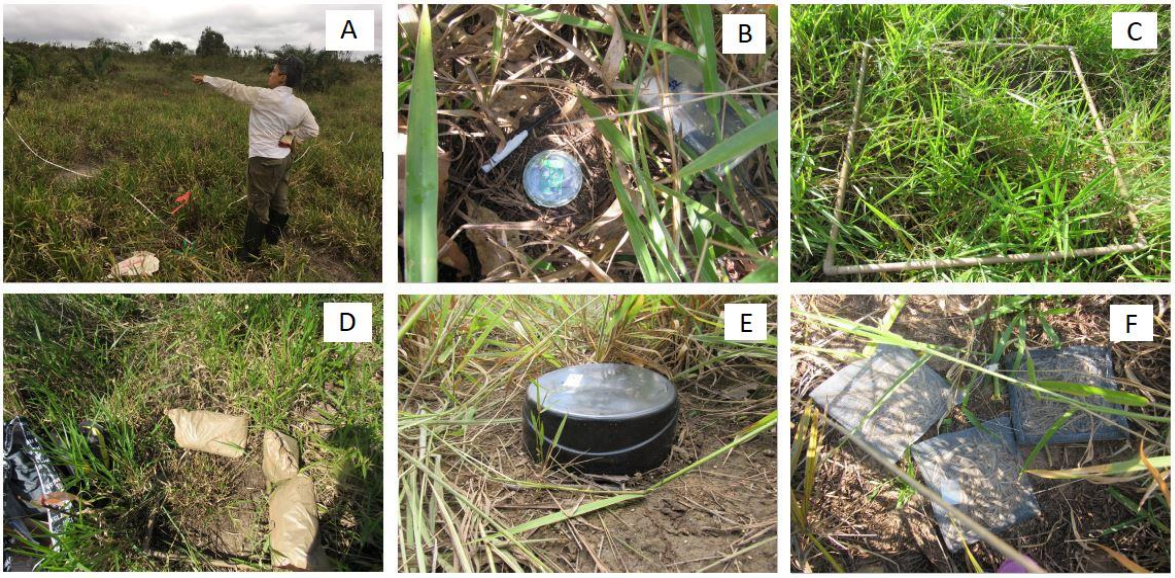

Figura 7. Amostragens em campo: A) montagem dos experimentos; B) sensores de micro-habitat; C) levantamento de vegetação; D) coleta de biomassa; E) amostragem do efluxo de CO_2; F) bolsas de decomposição.

Figura 8. Processamento de material em laboratório. Triagem de biomassa (A) e medição de área foliar específica através da reidratação (B), preparação (C) e escaneamento (D) das folhas.

3.4. OPERAÇÕES DE QUEIMA

As queimas experimentais foram realizadas no meio da estação seca, em agosto e outubro de 2019 e agosto e setembro de 2020 (Figura 9). Optamos por realizar as queimas nesta época do ano para maximizar sua eficácia na redução da abundância de gramíneas invasoras (Damasceno & Fidelis, 2020). Todas as queimas aconteceram durante o dia e foram iniciadas a favor do vento. As queimas foram conduzidas pelas brigadas de incêndio das unidades de conservação. As cinco parcelas de queima de cada bloco foram queimadas em uma mesma operação de queima de forma a garantir a independência amostral entre os blocos, bem como a similaridade de condições de queima experenciadas pelas parcelas ao longo de um mesmo gradiente.

Figura 9. Imagens das operações de queima em Itirapina em agosto de 2019 (A) e agosto de 2020 (B) e em Brasília em outubro de 2019 (C) e setembro de 2020 (D).

4. ORGANIZAÇÃO DA TESE

Esta tese está organizada em três seções: introdução, desenvolvimento e conclusão. Tanto a introdução quanto a conclusão estão redigidas em português de forma a contextualizar a questão abordada e apresentar os resultados e as implicações decorrentes do trabalho. Estas seções visam ainda facilitar a leitura e utilização da tese dentro do país, especialmente por pessoas interessadas na conservação da biodiversidade brasileira e no manejo de espécies exóticas invasoras, como, por exemplo, gestores de unidades de conservação.

A seção de desenvolvimento da tese é dividida em três capítulos, redigidos no formato de artigos científicos em língua inglesa. Cada capítulo corresponde a um dos objetivos específicos do estudo, todos os três convergindo para o objetivo principal da tese: elucidar como gramíneas exóticas invasoras influenciam na degradação e na restauração de formações abertas do Cerrado a partir de uma abordagem de modelo de estado-e-transição. Nesse tipo de abordagem, a abundância da espécie exótica invasora é aspecto chave para o entendimento dos processos, sendo por isso abordada diretamente nos dois primeiros capítulos.

O primeiro capítulo, intitulado ***"Per-capita impacts of an invasive grass vary across levels of ecological organization in a tropical savanna"*** será enviado para publicação na revista *Biological Invasions*. Este capítulo avalia como a abundância de *Urochloa decumbens* está relacionada a seus impactos sobre o ecossistema em diversos níveis de organização ecológica. Consideramos modificações resultantes nas características de micro-habitat, em atributos funcionais de plantas nativas, na diversidade de comunidades vegetais e no ciclo do carbono. Dessa forma, este capítulo destina-se à compreensão do processo de degradação de um sistema invadido por *Urochloa decumbens*, que é a primeira

etapa necessária para construção de um modelo de estado-e-transição.

O segundo capítulo, intitulado "***Abundance of an invasive grass modulates short-term effects of fire in a tropical savanna"*,** contribui para a segunda etapa da construção do modelo, referente aos processos de restauração desses sistemas invadidos. Neste capítulo avaliamos de que forma a abundância da espécie exótica invasora modula os efeitos de queimadas prescritas. Com o objetivo de unir os panoramas de degradação e restauração, mensuramos o efeito das ações de manejo sobre as mesmas variáveis ecológicas consideradas no primeiro capítulo. Assim, avaliamos como duas queimadas anuais influenciaram as condições de micro-habitat, a área foliar específica (SLA) das espécies dominantes, a estrutura e composição de comunidades, a biomassa acumulada e a taxa de decomposição, bem como o efluxo de CO_2 do solo. Este capítulo será submetido para publicação na revista *Applied Ecology.*

O último capítulo sintetiza e integra os anteriores, ao apresentar um modelo conceitual da degradação e restauração de formações abertas do Cerrado em função da abundância de gramíneas exóticas invasoras. Este capítulo fornece embasamento científico para o planejamento de políticas públicas e ações de conservação do Cerrado. Esperamos ainda que o modelo proposto seja utilizado por gestores como uma ferramenta de aplicação prática no manejo de unidades de conservação. Este capítulo, intitulado "***A state-and-transition model for the restoration of grass-invaded open tropical savannas"*** será submetido para publicação na revista *Journal of Applied Ecology*.

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Per-capita impacts of an invasive grass vary across levels of ecological organization in a tropical savanna

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Abstract

Invasive alien plants can negatively impact biodiversity and ecosystem functioning through alterations of microhabitat conditions, plant traits, community diversity, and ecosystem processes. These negative impacts are directly determined by the abundance of the invasive alien species (IAS), a relationship that usually does not follow simple linear trends due to the complexity of ecological interactions. Abundance-impact curves are key to inform evidence-based management interventions since they can reveal how per-capita impact changes as the invader becomes more abundant. Across 12 invasion gradients occurring in two areas, we constructed abundance-impact curves of the invasive grass *Urochloa decumbens* in a tropical savanna (Cerrado). Each gradient was composed of five 25 m² with 0, 25, 50, 75 and 100% of cover by the invader. We used generalized additive models to assess how increases in the invader's abundance influenced system properties from the microhabitat to the ecosystem level. At the microhabitat level, increasing invader's abundance resulted in non-linear effects on bare soil cover and illuminance on the ground but a linear reduction in temperature fluctuations. Specific-leaf area of dominant species (native and invasive pooled together) linearly increased with invader's abundance due to its growing dominance in communities. At community level, we found higher per-capita effect of *Urochloa decumbens* on native graminoids' cover when the invader was at low levels of abundance. Conversely, per-capita effect on native species richness were higher at moderate levels of invasion. These results indicate prompt impacts of the invader on abundance of functionally similar native grasses, but greater impacts on species richness only at moderate levels of invasion. Total biomass increased through the invasion gradient reflecting the combination of an increase in invader's biomass and a loss of natives' biomass. Despite these

changes, ecosystem properties (CO_2 soil efflux and decomposition rates) were not influenced by the abundance of the IAS. These findings support the functional redundancy between *Urochloa decumbens* and native dominant grasses in relation to carbon cycle, as expected from their C_4 metabolisms. Despite being functionally similar to the native species it excludes, *Urochloa decumbens* promotes negative impacts at microhabitat, individual and community levels. Varying per-capita impacts on community composition and richness might misguide implementation of management actions to a moment when biodiversity loss is already occurring.

keywords: abundance-impact curve, biological invasion, Cerrado, invasive grasses, per-capita impact, tropical savanna, *Urochloa decumbens*

Introduction

Invasive alien plants usually cause a range of ecological impacts in the invaded system, including negative, positive or neutral outcomes (Pyšek et al., 2012). Due to density-dependent per-capita effects (Parker, Simberloff, & Lonsdale, 1999; Pearse et al., 2019), the abundance of an invasive alien species (IAS) influences both direction and magnitude of its impacts in the recipient system (Strayer, 2020). Per-capita impacts are derived from the steadiness of slopes in abundance-impact curves (Sofaer et al., 2018). Linear relationships, i.e., with constant slope, imply a constant per-capita effect of IAS on the impact being accessed. Diversely, non-linear abundance-impact curves have varying slopes and then a changing per-capita impact throughout the invasion gradient. Implications of how per-capita impacts of an IAS could vary is paramount for science-based planning of management actions (Yokomizo, Possingham, Thomas, & Buckley, 2009), since long-term management of IAS should focus on reducing its negative impacts and sharped towards limiting its spread into new areas instead of pure eradication (Diagne et al., 2021; García-Díaz et al., 2021).

Abundance-impact curves differ depending on the impact being measured, including variations in impacts accessed at the same ecological level of organization. For invaders at the same trophic level, abundance-impact curves at the population level can follow linear or non-linear trends, whereas trends at community level tend to be linear (Bradley et al., 2019). At ecosystem level, impacts of invasive alien plants seems to be context-dependent (Vila et al., 2011), but despite their effects on ecosystem functioning (Vila et al., 2010), abundance-impact curves for invasive alien plants at this level of organization are poorly understood. Notwithstanding the need for appropriate abundance-impact curves to guide management actions (Yokomizo et al., 2009), as far as we know, no study has evaluated how abundance-impact curves of an IAS might differ depending on the level of ecological organization at which impacts are being accessed.

Our study also addresses an important knowledge gap in applied ecology, that is the study of biological invasions in tropical ecosystems (Nuñez et al., 2019), in which the high diversity does not seem to prevent plant invasions by limiting similarity (Chong et al., 2021). This is the case of tropical savannas invaded by perennial exotic C_4 grasses, where these species can modify ecosystem properties and drive the system towards a non-reversible process of degradation, as conceptually suggested (Pivello & Coutinho, 1996) and empirically demonstrated (Brooks et al., 2010; Rossiter-Rachor et al., 2009). In these systems, driven by state-and-transition dynamics (D'Odorico, Laio, & Ridolfi, 2006), characterization of abundance-impact curves resulting from alien plant invasions is fundamental to anticipate the crossing of ecological thresholds thus, preventing the system to transition towards new degraded stable states (Wilsey et al., 2014).

Tropical savannas and grasslands are present mainly in the southern

hemisphere, covering about 20% of land on Earth (Brian J. Huntley & Walker, 1982) providing home for millions of people and important ecosystem services at the global scale (Parr et al., 2014), but also being underrepresented in ecology scientific literature (Nuñez, Chiuffo, Pauchard, & Zenni, 2021). The biodiversity of tropical savannas is high in number of species and in their uniqueness (Murphy et al., 2016) and because of the threats to their conservation (Parr et al., 2014), these ecosystems are recognized as globally endangered (Bond & Parr, 2010). One of the main threats these ecosystems face is biological invasions (Foxcroft, Richardson, Rejmánek, & Pyšek, 2010; Milton, 2004). In savannas of South America and Australia, invasive alien grasses are one of the predominant groups of invaders (Foxcroft et al., 2010), where they cause modifications in community structure (Damasceno et al., 2018), functional diversity (Almeida-Neto et al., 2010), ecosystem processes (Rossiter-Rachor et al., 2009), and fire regimes (Gorgone-Barbosa et al., 2015; N. A. Rossiter, Setterfield, Douglas, & Hutley, 2003).

Using *Urochloa decumbens* (Hochst. ex A. Rich.) as a focal species we investigated how the abundance-impact curves and the per-capita impacts of an invasive alien grass varies across levels of ecological organization in the Cerrado (Neotropical savanna). Cerrado is the second largest biome in South America, covering originally more than 2 million km² (IBGE, 2004) and having more than 12,000 plant species, of which 30% are endemic to this system (BFG, 2015). However, nearly a half of its area has been converted into agricultural uses, mostly planted pastures, which now cover 31% of Cerrado original area (Souza et al., 2020). *Urochloa decumbens* is the commonest used species for forming planted pastures for cattle grazing (Brossard & Barcellos, 2005), representing a high risk for non-invaded areas (Guimarães Silva et al., 2020) as well as causing negative impacts on

biodiversity where they are already established (Damasceno et al., 2018; Pivello, Shida, & Meirelles, 1999). As invasive alien grasses have negative impacts on both abiotic (Assis, 2017) and biotic properties of Cerrado (Dairel & Fidelis, 2020); are resilient to management actions at high densities (Assis, Pilon, Siqueira, & Durigan, 2020; Damasceno & Fidelis, 2020), and can lead to legacy effects (Zenni et al., 2020), understanding their abundance-impact curves on recipient ecosystem is key to inform when management actions should be taken to prevent possible transitions to degraded states.

We adopted a hierarchical approach (Noss, 1990) to investigate the relationship between the abundance of *Urochloa decumbens* and 1) microhabitat (luminosity; air temperature and humidity at ground level); 2) plant traits (specific-leaf area); 3) community structure, composition, and diversity; and 4) ecosystem characteristics (biomass accumulation, carbon soil efflux and litter decomposition rates). We expected to find linear negative effects of invader's abundance on luminosity, and temperature and humidity fluctuations at the ground level owed to its increased productivity (Fig. 1A). Using specific leaf area (SLA) values as a proxy for plant photosynthetic efficiency, we hypothesized that as *Urochloa decumbens* becomes more abundant in the community, its SLA would non-linearly increase due to the intensification of intraspecific competition (Fig. 1B). We expect this curve to reach a plateau at intermediate levels of invasion because of the physiological and environmental constraining in SLA values (Lambers & Oliveira, 2019). As a result of enhanced interspecific competition, we hypothesized the SLA of native dominant species to increase through the invasion gradient. However, we expect this relationship to be linear because only good competitors (high SLA) will persist in heavily invaded communities (Fig 1C).

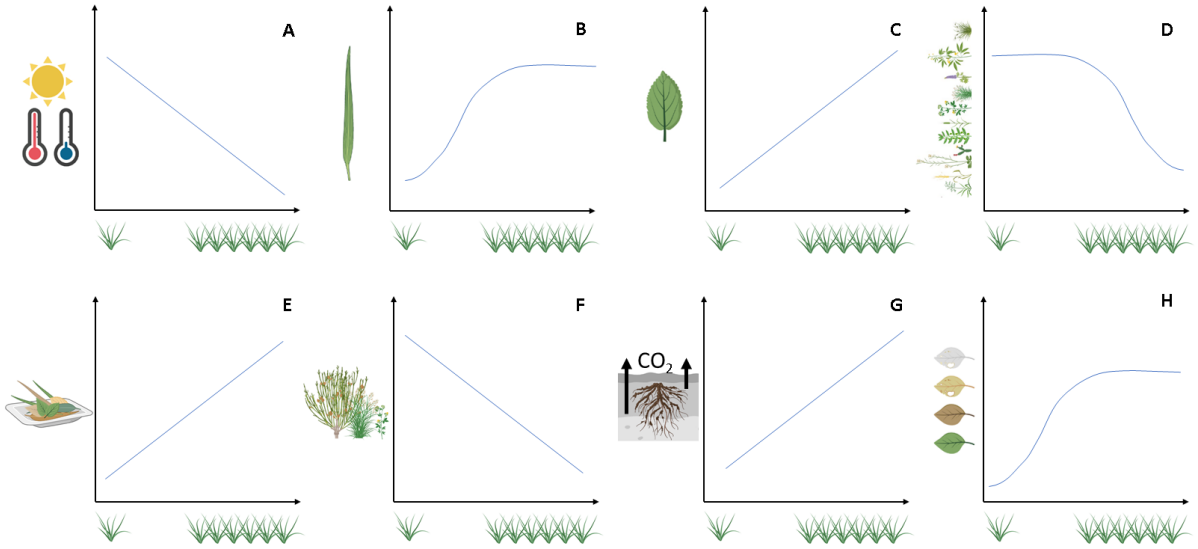

Figure 1. Hypothesis suggested for the abundance-curve of *Urochloa decumbens* in relation to properties of an invaded tropical savanna at distinct levels of ecological organization. A) microhabitat (daily illuminance and air temperature at the ground level); B) *Urochloa decumbens* specific leaf-area; C) specific leaf-area of dominant native species; D) abundance, richness and diversity of plant communities; E) total aboveground biomass; F) native aboveground biomass; G) CO_2 soil efflux; H) litter decomposition rates.

From the attenuation of the impacts of an IAS toward more complex levels of ecological organization (Vila et al., 2011), we expected greater per-capita effects of *Urochloa decumbens* at community than at ecosystem levels. We hypothesized non-linear decreases of native plant abundance, richness, and diversity (Fig. 1D) with increasing *Urochloa decumbens* abundance due to *Urochloa* negative impacts on Cerrado biodiversity (Almeida-Neto et al., 2010; Damasceno et al., 2018). We expected linear increases in aboveground biomass accumulation (Fig. 1E), as well as in soil carbon efflux (Fig. 1F), across the invasion gradient due to higher photosynthetic capacity of invasive alien grasses (Baruch et al., 1989). However, we expected non-linear increases in litter decomposition rates (Fig. 1G) as it is a process strongly limited by decomposition agents and chemical content of leaves (Bradford et al., 2002).

Materials and methods

Study areas

Fieldwork was conducted in two areas in the Cerrado (Neotropical savanna) located inside protected areas: Estação Ecológica de Itirapina (EcEI; 700 meters a.s.l; 22º14'40"S 47º52'29"W, Southeastern Brazil) and Parque Nacional de Brasília (PNB; 100 meters a.s.l; 15º41'43"S 47º54'18"W, Central Brazil). In both areas, we chose non-converted landscapes invaded by *Urochloa decumbens*. Vegetation is characterized by a continuous herbaceous layer dominated by C_4 grasses (*Gymnopogon foliosus* is the commonest species in EcEI and *Arthropogon villosus* in PNB) with scattered shrubs and small trees and locally known as *campo sujo*. At both sites, invasion started more than 30 years ago, during the 80's in EcEI and the 90's in PNB. The two study sites have deep (> 5 m) P-limited soils; EcEI presents sandy Entisols while PNB have clay Oxisols (IBAMA & FUNATURA., 1998; Zanchetta et al., 2006). The climate is classified as Cw inboth areas, with dry winters and rainy summers. Monthly mean values of temperature and precipitation during summer and winter are 23 ºC and 300 mm and 18 ºC and 150 mm for the PNB; and 22º C and 188 mm and 17 ºC and 55 mm for the EcEI (IBAMA & FUNATURA 1998; Zanchetta et al. 2006). EcEI is in the southern part of Cerrado, where the dry season is shorter (Macena, Assad, Steinke, & Gustavo Müller, 2008) and mild frost events are common (Brando & Durigan, 2004). Fire history during the last 20 years (1999 – 2019) differs between the two areas: PNB had burned five times in this period while EcEI had experienced no fire due to a fire exclusion policy.

Experimental design

We adopted a horizontal design (Sofaer et al., 2018) based on gradients of invasion considering ground cover by *Urochloa decumbens*. As spatial heterogeneity

of herbaceous vegetation varies according to scale in tropical savannas (Augustine, 2003), we adopted a two-step approach to better characterize the abundance of the IAS. At a coarser scale, we defined an invasion gradient composed by five plots (5 x 5 m) representing 0, 25, 50, 75 and 100% of the IAS cover (Figure 1, Supporting Information). We placed six gradients in each study area, totaling 12 gradients and 60 plots (5 plots x 6 gradient x 2 areas). Each plot was established at an independently invaded patch that matched the expected cover by *Urochloa decumbens*; *i.e.* the bigger invasion patches selected were sized 5 x 5 m, corresponding to a totally invaded plot (100% of cover by the invasive species). Plots within a gradient were separated apart by at least 10 m, gradients were distant from each other by at least 50 m. To characterize the abundance of plant species at a finer scale, every plot was divided into a core zone (3 x 3 m in the center) and a marginal zone (a 1 m strip at every size of the plot). The core zone was then subdivided into nine subplots (1 x 1 m) where vegetation surveys were conducted. We then calculated the mean cover at the plot level using the values from its nine $1m^2$ subplots. All samplings were conducted in March and April 2019, at the end of the rainy season.

Data sampling

To evaluate the abundance-impact curve of the IAS on distinct levels of ecological organization, we sampled data to characterize microhabitat conditions, plant individual's performance, plant community and ecosystem properties. Considering microhabitat conditions, we took hourly measurements of light incidence and air temperature and humidity at soil surface using a kit composed of one HOBO Pendant and one HOBO Pro v2 sensors. We chose to place one kit per plot to avoid

pseudo-replication at the plot level. To minimize the effect of environmental heterogeneity, we systematically placed the sensors at the same location in every plot in relation to its vertices. Due to limitations in the number of sensors (40 kits were available), we randomly selected four gradients in each area for this purpose (5 plots x 4 gradient, total 20 kits/area). Sensors simultaneously remained in the field in both areas for at least 130 days from the transition between rainy and dry seasons until the mid of the dry season (April to August 2019).

Vegetation surveys were conducted at nine 1 m^2 subplots in the core zone of plots (9 m^2). We used a modified Braun-Blanquet method (Wikum & Shanholtzer, 1978) to assess community structure and composition. We visually estimated the percentage of cover by every species using values of 0, 1, 5 and then every 10% until 100%. Ground cover of herbaceous plants is traditionally used as an estimate for plant abundance because it accounts for the varying size of individuals (Damgaard, 2014). We classified native plant species in functional groups according to their growth form: graminoids, forbs and shrubs. We also recorded the percentage of bare soil and cover by dead biomass (standing dead biomass + litter), separately for native species (total) and *Urochloa decumbens*.

Specific-leaf area measurements followed Pérez-Harguindeguy and collaborators (2013). From vegetation surveys, we identified the dominant species in the community, which together summed up to 80% of ground cover in the plot. For those species, we collected fully-expanded and not damaged leaves from 10 distinct random individuals (three leaves/individual). Leaves were carefully stored, re-hydrated at the laboratory using petri dishes filled with water; and then measured using a LI-COR LI-3000C. Species with delicate leaflets were measured using a scanner Epson V800 and the P-trap software (Al-Tam et al., 2013). After being dried

at 80ºC for 48 hours in a drying oven, all leaves were individually weighted in an electronic balance with 0.1 mg precision.

We quantified three ecosystem properties: biomass accumulation, CO_2 soil efflux and litter decomposition rates. Biomass accumulation was assessed by sampling the aboveground biomass (three samples/plot) in 0.25 m² plots. At the laboratory, biomass was sorted out into dead and live *Urochloa decumbens*; native live grasses, forbs and shrubs; and total native dead biomass. CO_2 soil efflux, a proxy to carbon dynamics, was estimated by soda-lime incubation for 24 h as proposed by Keith & Wong, (2006). We systematically placed one incubation chamber in every plot after removing aboveground biomass. We used petri dishes containing 25 mg of dried soda-lime incubated under opaque plastic chambers with a diameter of 24 cm. Litter decomposition rates were assessed using litterbags containing 5 g of *Urochloa decumbens* standing dead biomass. We opted to use biomass of the IAS instead of litter from the plot-level community to standardize the parental material across the invasion gradient. Litterbags were left directly on the ground for 90, 120 and 160 days following the methodology described in Karberg, Scott, & Giardina (2008).

Statistical analysis

We used the mean percentage cover by *Urochloa decumbens* in every plot (obtained from its nine 1m² subplots) as the fixed continuous predictor variable. Every response variable was set to depend on *Urochloa decumbens* cover by a generalized additive mixed model (GAMM) to allow non-linear abundance-impact relationships. For every response variable, we used the gamm function from mgcv package to create an additive model with the maximum number of base functions (k)

as suggested by Wood (2011). We specified a penalized cubic regression spline by the Penalized Quasi-Likelihood estimation method for the smooth function of the predictive variable. Frequency distribution of response variables depended on their characteristics as presented afterwards. We included gradient within area as random effects in all models due to nested design of the experiment.

Before analysis, data from microhabitat conditions was summarized by calculating the daily total illuminance (sum of all measured values during a 24 h period) and daily amplitudes of air temperature and humidity (the maximum values minus the minimum values registered during a 24 h period). We then considered these entities as response variables in relation to the abundance of *Urochloa decumbens*. We used a Gamma distribution with a log link.

To separately understand how SLA of *Urochloa decumbens* and of native dominant species varied across the invasion gradient, we constructed three models for the abundance-impact relationship between the invader and SLA values. First, we investigated how the SLA of *Urochloa decumbens* varied throughout the invasion gradient. Secondly, we selected the dominant native species (species which together summed up to 80% of ground cover in the plot) to investigate how the increase in cover by the IAS would affect the SLA of native species. Finally, we investigated the SLA of the dominant species in the communities independently of their origin (*Urochloa decumbens* and native species pooled together). We considered data at the level of leaves, including plant individual, species, and plot as random effects within gradient and area.

At the community level, we modeled *Urochloa decumbens* effect on ground cover by functional components: live native grasses, forbs, and shrubs; native dead biomass; and bare soil. These response variables were set to follow a negative

binomial distribution with automated estimation of the theta dispersion parameter. Due to the experimental design (subplots nested inside plots), we included plot as a nested random variable within gradient and area for models considering ground cover. Still at the community level, we investigated the effect of *Urochloa decumbens* abundance on total native species richness and on richness considered by plant growth form (grasses, forbs, and shrubs); as well as Shannon's diversity and Pielou's evenness.

Litter decomposition rates (k) were calculated using the equation $X_t/X_0 = e^{-kt}$, where X_t is the mass at time t and X_0 is the mass at the beginning of the experiment (Karberg et al., 2008). All analyses were conducted in R software (R Core Team, 2020) using the packages mgcv (Wood, 2011), ggplot2 (Wickham, 2009) and cowplot (Wilke, 2019).

Results

Throughout the abundance gradient, abundance-impact curves and per-capita effects of *Urochloa decumbens* on Cerrado varied across and within levels of ecological organization (Table 1). At microhabitat level, for example, we found non-linear, linear and no relationship between the invader's abundance and bare soil cover, daily illuminance, and daily range of air relative humidity; respectively.

Abundance-impact curve of *Urochloa decumbens* on bare soil cover followed a non-monotonic relationship, evidencing changing per-capita impact in relation to the cover of the invader. The relationship was positive when the invasion increased up to moderate levels (40%) and negative afterwards, with higher per-capita impact (steeper slope) after the inflexion point (Fig. 2A). Conversely, per-capita impacts on daily illuminance were higher at invader lower densities (Fig. 2B) and constant on

daily range of air temperature (Fig. 2C); both variables were negatively related to *Urochloa decumbens* abundance. We did not find an abundance-impact curve for the daily range of air relative humidity.

Table 1. Summary statistics of generalized additive mixed models (GAMM) evaluating the relationships between abundance by the invasive alien grass *Urochloa decumbens* and properties of the invaded Cerrado (Neotropical savanna).

Level of organization	Response variable	*Urochloa decumbens* cover	
		F-statistic	p-value
Microhabitat	Bare soil cover (%)	4.71	**0.02**
	Total daily illuminance (lx)	6.91	**0.01**
	Temperature daily range (°C)	5.95	**0.01**
	Humidity daily range (°C)	2	0.16
Individual	SLA of *Urochloa decumbens* ($mm^2.mg^{-1}$)	0.11	0.40
	SLA of native dominant species ($mm^2.mg^{-1}$)	0.97	0.32
	SLA of dominant species ($mm^2.mg^{-1}$)	33.73	**<0.01**
Community	Cover by native shrubs (%)	39.31	**<0.01**
	Cover by native graminoids (%)	4.05	**<0.01**
	Cover by native forbs (%)	5.93	**0.04**
	Cover by native dead biomass (%)	74.76	**<0.01**
	Native grass richness (n)	32.38	**<0.01**
	Native forb richness (n)	4.34	**0.04**
	Native shrub richness (n)	1.91	0.2
	Total native richness (n)	19.11	**<0.01**
	Shannon's diversity index	3.74	0.06
	Pielou's evenness index	1.41	0.24
Ecosystem	*Urochloa decumbens* biomass ($kg.m^{-2}$)	54.38	**<0.01**
	Native biomass ($kg.m^{-2}$)	31.24	**<0.01**
	Total biomass ($kg.m^{-2}$)	3.95	**0.05**
	Soil CO_2 efflux ($g.C.m^{-2}.day^{-1}$)	0.15	0.72
	Decomposition rate (day^{-1})	0.4	0.53

We did not find relationships between *Urochloa decumbens* abundance and its specific-leaf area (SLA), which was around 20 $mm^{-2}.mg^{-1}$ across the invasion gradient (Fig. 3A). The SLA values of native dominant species (that together summed up to 80% of cover) were also not related to the abundance of the invasive

species (Fig. 3B). However, when we considered the invader and native species pooled together to represent the dominant species, we found a positive linear abundance-impact curve, and therefore a constant per-capita impact of *Urochloa decumbens* on SLA values at community level (Fig. 3C).

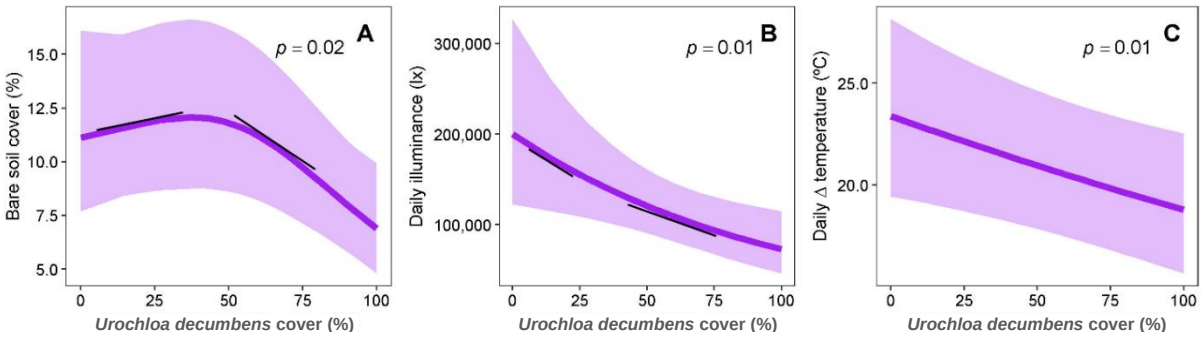

Figure 2. Abundance-impact curves of *Urochloa decumbens* on microhabitat conditions in a tropical savanna. A) bare soil cover (%); B) daily illuminance (lx); and C) daily range of air amplitude at soil level (ºC) in relation to cover by *Urochloa decumbens*. Solid lines are the predicted values from the GAMM models, smooths are the 95% confidence intervals. Black segments are tangents to the abundance-impact curve and represent the curve's slope.

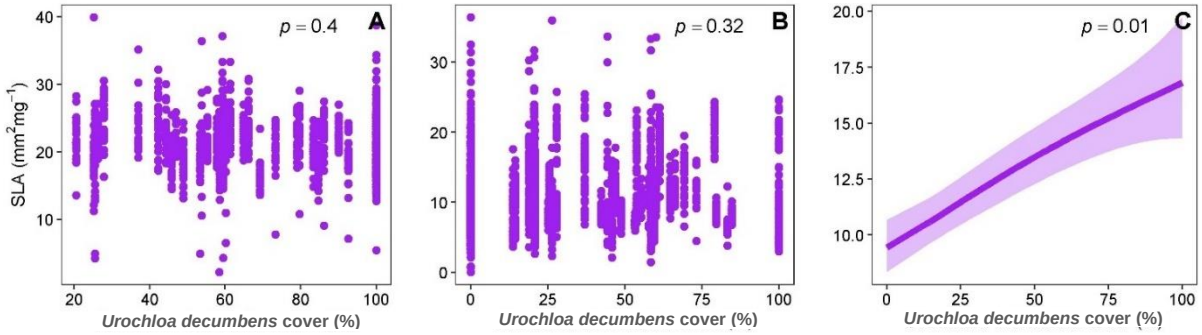

Figure 3. Effects of invasive grass abundance on specific-leaf area values (mm^2 mg^{-1}) of plant species in a tropical savanna. Specific-leaf area of A) *Urochloa decumbens*; B) native dominant species; and C) dominant species in the community (invasive and native species pooled together) in relation to cover by *Urochloa decumbens*. Solid line is the predicted values from the GAMM model, smooth is the 95% confidence interval.

We found varying per-capita impacts of *Urochloa decumbens* on ground cover by native growth forms. Per-capita effect on native shrubs cover varied from positive to negative, with an inflexion point around 30% of cover by the invasive species (Fig. 4A). Abundance-impact curves on ground cover by native graminoids (Fig. 4B),

native forbs (Fig. 4C), and native dead biomass (Fig. 4D) were negatively monotonical and revealed higher per-capita impacts of *Urochloa decumbens* up to intermediate levels of invasion (60%). Conversely, per-capita impacts on richness of native graminoids and native forbs were negative and constant along the invasion gradient (Fig. 5A and 5B). Negative per-capita effects of *Urochloa decumbens* on total plant richness became more pronounced from low to high levels of invasion (Fig. 5C). Despite decreases in plant richness, we only detected a marginally significant reduction in diversity, measured as Shannon's index, in relation to cover by *Urochloa decumbens* (Table 1). We did not find an effect of *Urochloa decumbens* abundance on the richness of native shrubs or on Pielou's evenness index.

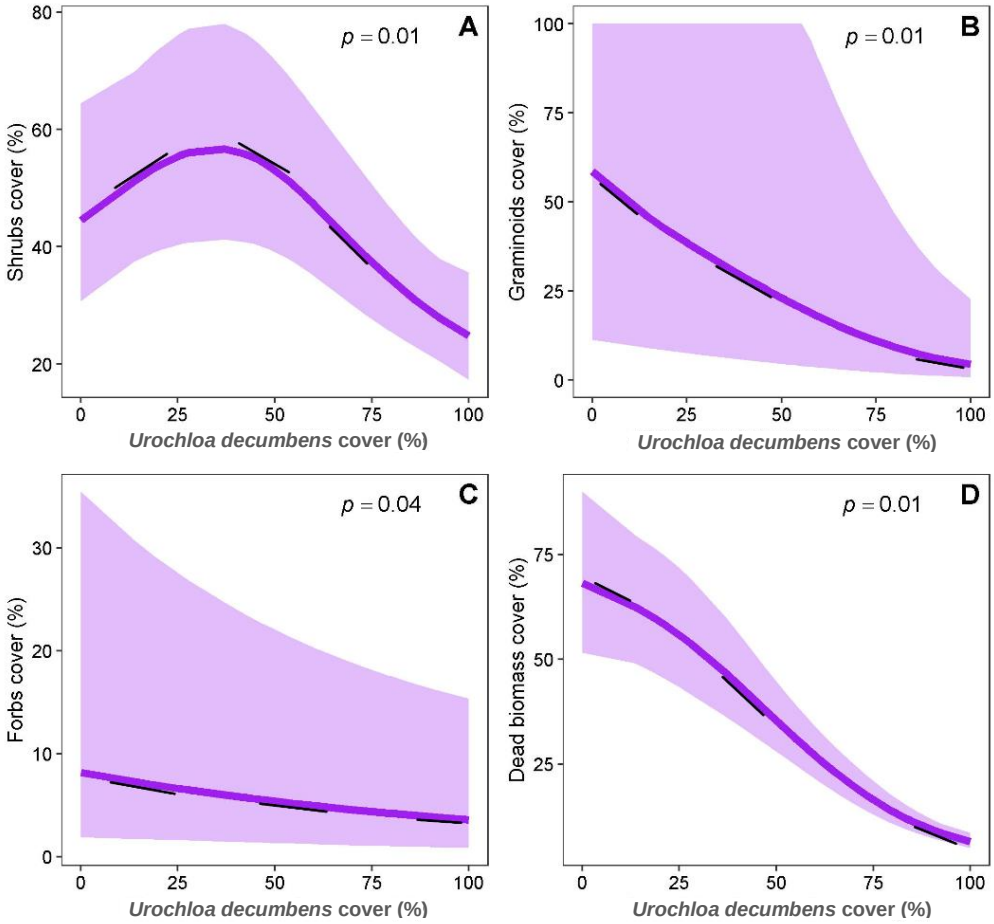

Figure 4. Abundance-impact curves of *Urochloa decumbens* on ground cover (%) by growth forms in a tropical savanna. Ground cover by native A) shrubs; B) graminoids; C) forbs; and D) dead biomass in relation to cover by *Urochloa decumbens*. Solid lines are the predicted values from the GAMM models, smooths are the 95% confidence intervals. Black segments are tangents to the abundance-impact curve and represent the curve's slope.

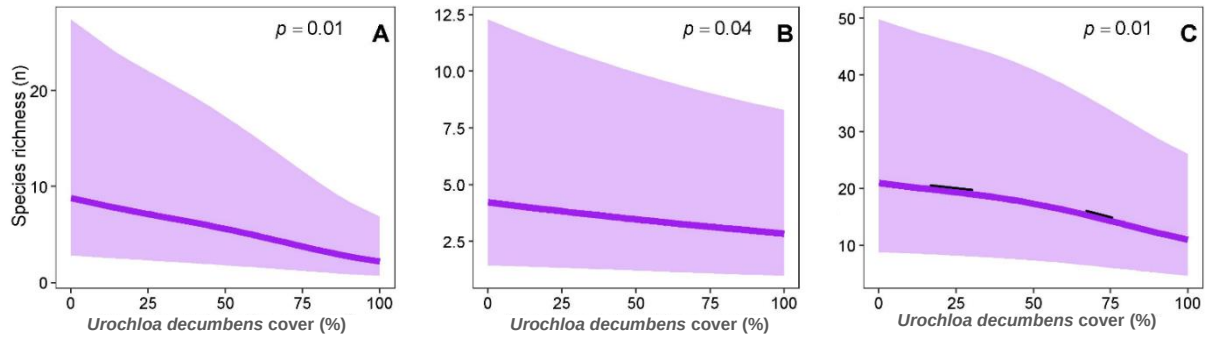

Figure 5. Abundance-impact curves of *Urochloa decumbens* on native plant species richness (n) in a tropical savanna. Plant richness of A) graminoids; B) forbs; and C) total species in relation to cover by *Urochloa decumbens* in plots of 9 m^2. Solid lines are the predicted values from the GAMM models, smooths are the 95% confidence intervals. Black segments are tangents to the abundance-impact curve and represent the curve's slope.

At the ecosystem level, we only found abundance-impact curves of *Urochloa decumbens* on biomass accumulation. We found varying per-capita impacts of invader when we considered only invasive or only native biomass (Fig. 6A and 6B). Despite following opposite trends, per-capita impacts on these variables were attenuated at higher densities of invader, where slopes approached to zero. We also detected a constant positive per-capita impact of the invader on total biomass (Fig. 6C). Considering the other ecosystem properties, neither CO_2 soil efflux nor decomposition rates were related to the invasive species abundance (Fig. 7).

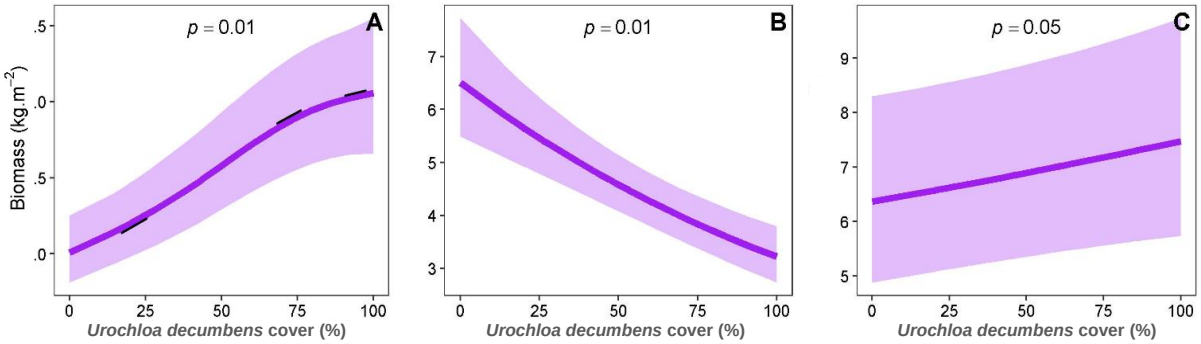

Figure 6. Abundance-impact curves of *Urochloa decumbens* on plant aboveground biomass ($kg.m^{-2}$) in a tropical savanna. Biomass of A) *Urochloa decumbens*; B) native species and C) total (native + invasive alien species) biomass in relation to cover by *Urochloa decumbens*. Solid lines are the predicted values from the GAMM models, smooths are the 95% confidence intervals. Black segments are tangents to the abundance-impact curve and represent the curve's slope.

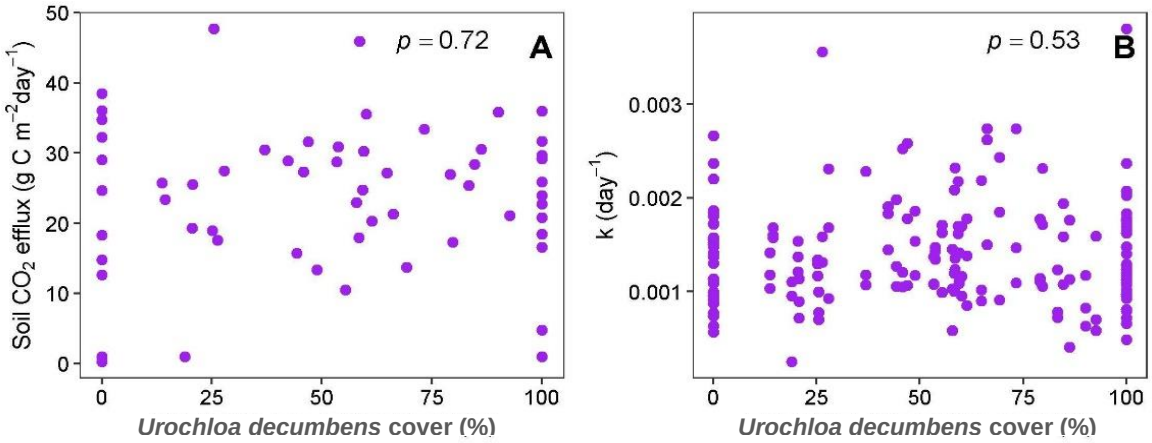

Figure 7. Effects of invasive alien grass abundance on carbon cycle in a tropical savanna. A) CO_2 soil efflux ($gCm^{-2}day^{-1}$); and B) decomposition rate (day^{-1}) in relation to cover by *Urochloa decumbens*.

Discussion

Across an invasion gradient, the per-capita effects of *Urochloa decumbens* on invaded areas of open savannas of the Cerrado varied depending on the level of ecological organization at which impacts were accessed. The most varying effects were detected on community composition (abundance of native plants), but also on community structure and microhabitat. At organism (SLA values) and ecosystem levels, abundance-impact curves tended to be linear or non-existent.

Per-capita effect of *Urochloa decumbens* varied the most on ground cover by bare soil and native shrubs, going from positive to negative across the invasion gradient. Both variables were positively affected by increases in invader's cover up to intermediate levels of invasion (~40%) and linearly decreased afterwards. Despite expecting non-linear trends, we did not expect the per-capita effects of *Urochloa decumbens* on any of the variables measured to change between positive and negative values. However, the pattern found for bare soil can be understood considering the invasion dynamics (*sensu* Hui & Richardson, 2017) of *Urochloa*

species (Assis, 2017). In tropical savannas, the expansion of these grasses usually relies on colonization by seeds (but see Dias-Filho, 1983), resulting in many sparse individuals being established around a founder individual. Due to greater per-capita effect on native graminoids (Fig 3B), these isolated *Urochloa decumbens* individuals reduced the cover by native grasses thus, increasing bare soil cover. At intermediate levels of invasion, the isolated tussocks have grown and started to amalgamate into a continuous layer, resulting in linear decreases of bare soil cover (Assis, 2017) and homogenization in the structure of the herbaceous layer in savannas (Lindsay & Cunningham, 2012).

Interestingly, we found different per-capita effects of *Urochloa decumbens* on total daily illuminance and on daily temperature amplitude. The former was reduced the most when the invader was at lower densities and per-capita effect did not vary on the latter. These results can be explained by the small-scale heterogeneity of herbaceous communities in savannas (Augustine, 2003). Differently from evaluation of ground cover, which was repeatedly sampled inside a plot (nine 1m² subplots) to account for small-scale heterogeneity of the herbaceous layer, microclimatic variables were assessed with one sensor per plot due to limitation in the number of sensors. The greater per-capita impact of *Urochloa decumbens* on daily illuminance at low levels of abundance of the invader could be due to the replacement of native grasses by the invader's tussocks, which are denser (Fisher & Kerridge, 1996; Pilon, Durigan, et al., 2021). Contrary to illuminance, which is spatially dependent on the surrounding vegetation, variations in air temperature are not spatially structured at the microscale, which resulted in a constant per-capita effect of *Urochloa decumbens* in buffering daily range of air temperatures.

The abundance of *Urochloa decumbens* was neither related to the specific-leaf area of dominant native species, nor with its own SLA values. The presence of the invasive species seemed to not affect the investment that co-occurring native plants are putting into photosynthetic tissues. Moreover, the constant SLA values of *Urochloa decumbens* across the invasion gradient indicates that this species is consistently at high photosynthetic rates, a common trait found in invasive species (Feng, Fu, & Zheng, 2008). Accordingly, our results are similar to SLA values registered for *Urochloa decumbens* in optimal growth conditions at planted pastures (Dias-Filho, 2000) as well as for other species from the same genus (Zanchi et al., 2009). However, when the whole community was considered together (invasive and native dominant species pooled together), we found a constant per-capita effect of *Urochloa decumbens* on SLA values, which reached a maximum of circa 20 mm^2mg^{-1} on totally invaded communities. This results from the replacement, across the invasion gradient, of native species with lower SLA by *Urochloa decumbens*. Because of the relationship between SLA and photosynthetic efficiency, the increase in SLA values indicates that totally invaded have greater primary productivity than non-invaded areas (Lambers & Oliveira, 2019). This is expected since invasive grasses usually have higher photosynthetic rates and higher productivity than native species in invaded savannas (Setterfield et al., 2013; Silva & Haridasan, 2007).

Changes in community composition and biomass accumulation

The per-capita effect of *Urochloa decumbens* on communities' composition varied among the different growth forms. Invasive alien plants occupy niches already existing in the functional space of invaded communities (Loiola et al., 2018) and,

therefore, due to niche overlapping, invasive alien grasses are more detrimental to functionally similar grasses on recipient savannas (Damasceno et al., 2018; Foxcroft et al., 2010). Our results evidence that these negative effects are more pronounced at initial and intermediate levels of invasion, when the per-capita effect of the invader on native grasses abundance is greater. Conversely, per-capita impact on the richness of native grasses is constant across the invasion gradient. This indicates that despite causing higher impacts on cover by native grasses at lower levels of invasion, *Urochloa decumbens* promotes exclusion of local species independent of its abundance across the invasion gradient. In other words, *Urochloa decumbens* is not only reducing the abundance of dominant invasive grasses, like *Gimnopogon foliosus* in EcEI and *Arthropogon vilosus* in PNB, but also of the less common grasses, which are lost even at low levels of invasion, like *Andropogon leucostachyus* in EcEI and *Paspalum pectinatum* in PNB. This result is fundamental to inform management plans for the endangered biodiversity of Cerrado (Strassburg et al., 2017) as rare species might be lost since initial levels of invasion.

Per-capita impact of *Urochloa decumbens* on cover by forbs was greater at the beginning of the invasion gradient. This is consistent with the sensibility of forbs to shading by invasive alien grasses (Coleman & Levine, 2007), which from the beginning of the invasion processes decrease light availability at the ground layer. However, forb richness decreases steadily across the invasion gradient, suggesting that rare and specialist species are being lost at lower levels of invasion and common and generalist species at higher levels of invasion (Almeida-Neto et al., 2010). Shrubs, which in general are less impacted by invasive alien grasses (Flory & Clay, 2010a, 2010b), benefitted from the reduction in grasses' abundance, and had their cover increased up to intermediate levels of invasion. However, contrary to previous

studies (Assis, 2017; Hoffmann & Haridasan, 2008), our study led to the detection of a negative effect of invasive alien grasses on Cerrado shrubs at highly invaded areas. This reduction seems to be caused by belowground competitive interactions (Levine et al., 2003), since shrubs are usually taller than *Urochloa* species and do not suffer from modifications of aboveground abiotic conditions (Assis, 2017). Plant richness, as well as cover by native biomass, was reduced the most at intermediate levels of invasion. These results are similar to the effects of *Urochloa decumbens* on bare soil and seems to derive from the mechanics of invasion by *Urochloa* species (Assis, 2017). Moreover, the higher per-capita effects of *Urochloa decumbens* individuals on native plant richness at intermediate levels of invasion alerts for the caveats of monitoring impacts of IAS only by diversity metrics. If these impacts were accessed using only total species richness, management actions could be wrongly delayed to a moment when rare grass and forb species could already be lost.

We found lower per-capita effect of *Urochloa decumbens* on its total biomass at higher levels of invasion, suggesting a stagnation in the system primary productivity (Lambers & Oliveira, 2019). Moreover, it also indicates that the IAS is not facing strong intraspecific limitations, what was also observed from its optimum photosynthetic activity (high and constant SLA values) even in highly invaded areas. Due to local exclusion of native species, per-capita effects of *Urochloa decumbens* on native biomass were constant, causing a linear decrease of total, dead, graminoids, forbs and shrubs biomass across the invasion gradient, whether they were considered together or independently. Despite this decrease in native biomass, system total biomass linearly increased, implying a higher productivity of invaded areas.

Stability of carbon cycling

Contrary to studies in which invasive alien grasses have altered biogeochemical cycles in different types of ecosystems (Drenovsky & Batten, 2007; Evans, Rimer, Sperry, & Belnap, 2001; Litton, Sandquist, & Cordell, 2006; Reed, Seastedt, & Blair, 2005; Rossiter-Rachor et al., 2009), including changes of carbon and nitrogen distributions across the soil profile (Garcia, Xavier, Camargo, Vieira, & Pivello, 2022), we did not find the abundance of *Urochloa decumbens* to alter soil CO_2 efflux and litter decomposition rates. This result indicates that the impacts of invasive grasses on ecosystem properties are more complex than at the community level, as described for invasive plants (Vila et al., 2011) and expected by us. However, our findings could also reflect the choice to use *Urochloa decumbens* biomass as the parent material for the litter decomposition experiment, since it has been demonstrated the presence of chemical allelopathic compounds in *Urochloa* dead biomass (Barbosa, Pivello, & Meirelles, 2008).

Those results indicate that despite increasing the accumulated aerial biomass and transforming the microhabitat and plant communities, *Urochloa decumbens* does not affect the carbon cycle in invaded areas. This ecosystem stability can be attributed to the functional redundancy between the C_4 invader and C_4 native dominant grass (Rosenfeld, 2002), as similarly found for another IAS (Castro-Díez, Pauchard, Traveset, & Vilà, 2016). Finally, decomposition is a process driven by many factors (García-Palacios, Shaw, Wall, & Hättenschwiler, 2016) being the community of decomposer agents one of the most important in open physiognomies (Bradford et al., 2002; Smith & Bradford, 2003). Despite some evidence that invasive grasses may alter microbial communities (Batten, Scow, & Espeland, 2008; Sartori,

2012) including by legacy effects (Zenni et al., 2020) the presence of *Urochloa decumbens* did not alter decomposition rates.

Apparently, the stability of carbon efflux and decomposition is contradictory to the increases in biomass accumulation promoted by *Urochloa decumbens*. Nevertheless, when these processes are considered altogether, an unexpected conclusion emerges, that productivity of invaded areas would be greater during early stages of invasion but would return to pre-invasion levels once the area is completely covered by the invasive alien grasses. This conclusion is driven by the facts that 1) decomposition rates are not altered by the IAS; 2) biomass accumulation stabilizes at completely invaded areas; 3) there is no consumption of the accumulated biomass by fire or herbivores. Consequently, productivity would be reduced by the immobilization of nutrients and by the lack of empty spaces resulting from biomass accumulation.

Conclusions

In an invaded tropical savanna, *Urochloa decumbens* promoted negative impacts at microhabitat, individual and community levels, but did not alter the carbon cycle (carbon soil efflux and decomposition rates). This indicates that despite the functional redundancy between *Urochloa decumbens* and the native dominant grasses it excludes, it exerts negative impacts on biodiversity. Moreover, due to its varying per-capita effects on community composition and species loss, management actions should be taken at early stages of invasion to prevent negative impacts. Despite not altering carbon cycle, indirect impacts of *Urochloa decumbens* on ecosystem functioning could occur via trophic cascades, already documented for planted pastures (Almeida, Louzada, Sperber, & Barlow, 2011; de Queiroz et al.,

2020), but not for invaded areas. Finally, studies designed to address impacts of invasive alien grasses on functioning of the Cerrado are needed to evaluate if other biogeochemical cycles are being altered, as already identified for C_4 invasive grasses in other open ecosystems (Holly, Ervin, Jackson, Diehl, & Kirker, 2009; Reed et al., 2005) including tropical savannas (Douglas, Setterfield, Rossiter, Barratt, & Hutley, 2004; Rossiter-Rachor et al., 2009).

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Abundance of an invasive grass modulates short-term effects of fire in a tropical savanna

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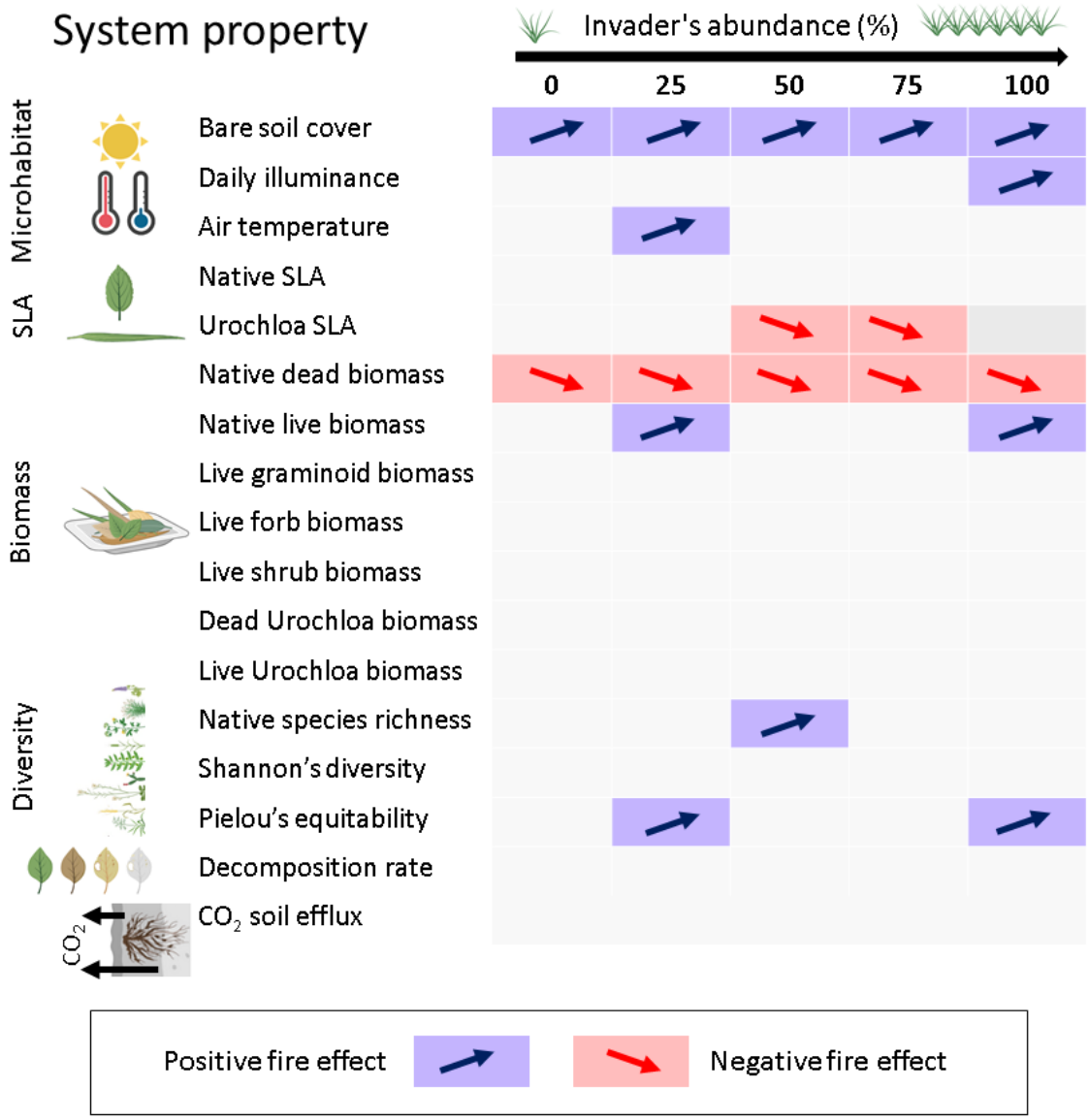
Abstract

The ecological impacts of an invasive alien species (IAS) are associated with its abundance. In South American savannas, the abundance of invasive alien grasses is related to changes in ecological properties from microhabitat to ecosystem level. Due to the natural occurrence of fire, prescribed burnings could be used as a management tool to control these invasions, with experimental studies revealing mixed evidence of its efficacy. Invader's abundance could be one of the unmeasured factors driving divergent fire outcomes. We evaluated how the abundance of the invasive African grass *Urochloa decumbens* modulated fire outcomes in the Cerrado, the Brazilian savanna. Across invasion gradients, we sampled microhabitat, specific-leaf area, community composition and ecosystem process in control/fire plots before and after (seven months post-fire) two annual prescribed burnings. The abundance of the invader modulated fire effects on microhabitat, individual and community levels, as well as in the accumulation of live native biomass. We found invader's abundance to not influence unambiguous effects of fire, like the reduction of accumulated dead biomass and the increase in gaps within vegetation. Also, *Urochloa decumbens* abundance did not influence fire effects on its own biomass, as well as on decomposition rates and CO_2 soil efflux. We found fires to benefit, in the short-term, native biodiversity in communities with all levels of invasion by *Urochloa decumbens*. Altogether, prescribed burnings could be considered as a management option for management plans tailored to reduce the negative impacts of invasive alien grasses in tropical savannas.

Key-words: invader's abundance; invasive alien grass; fire management; prescribed burning; tropical savanna

Graphical abstract



Introduction

From the beginning of the invasion process the abundance of an invasive alien species (IAS) tends to increase through time (Hui & Richardson, 2017). Directly related to its abundance are the ecological impacts caused by invasive alien plants, irrespective of their growth-form or invaded system (Dresseno et al., 2018; Iannone

et al., 2015; Tererai et al., 2013; Zhang et al., 2020). Among the ecological impacts driven by invasive alien plants' abundance are changes in soil microorganism communities (Grace et al., 2019; Zhang et al., 2020); mycorrhizal (Sun, Gao, & Guo, 2013) and root-rhizobium associations (Le Roux, Mavengere, & Ellis, 2016), as well as community structure and composition (Tererai et al., 2013) and on ecosystem functions like pollination and food networks(Dietzsch, Stanley, & Stout, 2011; Gillespie & Elle, 2018) and disturbance regimes (Taylor et al., 2017).

Alien grass invasions in tropical savannas occur mainly in Australia and South America, being caused by species native to the African continent (Foxcroft et al., 2010). Invasion by alien grasses have been recognized as threats for the conservation of tropical savannas in Australia (Rossiter, Setterfield, Douglas, Hutley, & Cook, 2004) and in South (Martins et al., 2011; Pivello et al., 1999; Williams & Baruch, 2000) and North America (Brewer, 2008). In these ecosystems, they cause plenty of negative ecological impacts, such as changes in community structure (Hoffmann & Haridasan, 2008) and composition (Damasceno et al., 2018); ecosystem functioning (Rossiter-Rachor et al., 2009); food webs (Cook & Grice, 2013) and disturbance regimes (Gorgone-Barbosa et al., 2015; Setterfield et al., 2013). Moreover, due to the non-equilibrium dynamics of tropical savannas (D'Odorico et al., 2006), invasive alien grasses can drive invaded ecosystems towards a degraded stable state by modifying system's feedback mechanisms (Brooks, Setterfield, & Douglas, 2010) and thus, influencing its degradation and restoration (Suding et al., 2004).

The abundance of IAS is also key to inform management plans (García-Díaz et al., 2021) and restoration efforts (D'Antonio, August-Schmidt, & Fernandez-Going, 2016). At low levels of invasion, the management of invasive alien plants usually

aims at its eradication with punctual actions tailored towards invader's individuals. However, in heavily invaded areas, management actions are generally broader in scope, both in space and time, and aim for reduction of invader's abundance and spread into new areas instead of eradication of the IAS, which is difficult to reach at these stages (Blackburn et al., 2011). Accordingly, management of invasive alien grasses at low levels of invasion focus on removing the established individuals without hampering native vegetation by, among others, hoeing, cutting and local herbicide application. When the IAS is widespread and covers large areas, the high costs of using such techniques might prevent their adoption despite their high efficacy (Assis, Pilon, Siqueira, & Durigan, 2021). Thus, management techniques that are cheaper and can be applied to large areas are usually preferred, like the use of prescribed burnings, singly or in association to other techniques (Assis et al., 2021; DiTomaso et al., 2006; Symstad, Buhl, & Swanson, 2021).

Despite the importance of invader's abundance on the selection of management techniques, few studies have addressed this question (Symstad et al., 2021). In this sense, invader's abundance could be one of the underlying – but not assessed – factors influencing diverging results of prescribed burnings to control IAS, such as invasive alien grasses in tropical savannas. There is mixed evidence on the efficacy and utility of using prescribed burnings to manage this type of invasion. Since fires are an element present in their evolutive history (Frost & Robertson, 1985); positive and negative feedbacks between invasive grasses and fire have been documented (Alba, Skálová, Mcgregor, D'Antonio, & Pyšek, 2015; Assis et al., 2021; M. L. Brooks et al., 2004; Damasceno & Fidelis, 2020; Holzmueller & Jose, 2012; Lippincott & Johns River, 2000; Rossiter, Setterfield, Douglas, & Hutley, 2003).

Using a BACI (before-after, control-impact) design, we evaluated how the

abundance of *Urochloa decumbens*, an African grass invasive in South American tropical savannas, influences the effect of prescribed burnings in the Cerrado. We compared burned and unburned plots across gradients considering the abundance of the IAS. Specifically, we evaluated how two annual burnings changed *Urochloa decumbens* impacts on microhabitat conditions, specific-leaf area of dominant species, community structure and composition, biomass accumulation, CO_2 soil efflux, and decomposition rates. We hypothesized that annual prescribed fires would result in greater changes in invader's impacts at intermediate levels of *Urochloa decumbens* abundance. Our reasoning derives from three tenets: 1) non-invaded communities will be resilient to the disturbance caused by prescribed burnings, since they had evolved under natural fires (Simon et al., 2009); 2) at intermediate levels of invasion fire would enable co-existence between invader and native species by temporarily altering competitive relationships, allowing system's recovery from invader negative impacts; and 3) heavily invaded areas would be already impacted by the presence of *Urochloa decumbens* and with less potential to recover from invader's negative impacts (Damasceno & Fidelis, in preparation).

Material and Methods

Study area

Our study was conducted in Parque Nacional de Brasília (PNB; 15º41'43" S 47º54'18" W), a protected area in the Cerrado. The Cerrado is the richest savanna in the world in plant species and it is classified as one of the world hotspots for biodiversity conservation due to its unique flora and to the permanent threats to its conservation (Colli, Vieira, & Dianese, 2020). PNB has a seasonal climate with dry

winters (23ºC and 185 mm) from April to September and rainy summers from October to March (18ºC and 25mm; Macena, Assad, Steinke, & Gustavo Müller, 2008). PNB has deep (> 5 m) clayish Oxisols, with low contents of phosphorus and nitrogen (IBAMA & FUNATURA., 1998). The study area is characterized as *campo sujo* (Ribeiro & Walter, 2008), an open savanna vegetation with a continuous herbaceous layer dominated by C_4 grasses, where small shrubs (< 2 m) and scattered trees (< 5 m) can also be found. During the last 20 years the experimental area has been burnt five times, the last one in 2017, two years before the establishment of the experiment.

Experimental design

We chose an open savanna site invaded by *Urochloa decumbens* for 20 years (non-intentional introduction). Our experimental design followed a BACI type (Smith, 2012) and had the plot (5 x 5 m) as the sampling unit. We established six invasion gradients based on the cover by the IAS. Each gradient was composed by five plots representing 0, 25, 50, 75 and 100% ground cover by *Urochloa decumbens.* Every two gradients formed a block, one gradient to be left unmanaged (control) and one to be burned (fire treatment). We had a total of 30 plots divided into three blocks (5 plots x 6 gradients). Plots were established into independent invaded patches corresponding to the desired cover by the invasive species, from non-invaded (0% of cover by *Urochloa decumbens*) to totally invaded plots (100% cover by *Urochloa decumbens*). Blocks were at least 50 m apart while plots inside a gradient were 10 m apart.

We collected vegetation data in the central portion of the plot (3 x 3 m) and

destructive sampling, like biomass sampling, in remaining one-meter strip towards plot's borders. We conducted two experimental burnings in the middle of the dry season, in October in 2019 and in September in 2020. We opted for this fire season in order to maximize fire effects on reducing invader's biomass (Damasceno & Fidelis, 2020). Aiming to apply the same fire conditions to all plots within a gradient, we burned the entire gradient at once using head-fires lit during the day by PNB fire brigade.

Sampling

We collected data in two sampling seasons (2019 and 2021) to characterize the ecological system before and after the execution of the prescribed burnings. Both samplings were conducted at the end of the rainy season (March/April), after vegetation had achieved its growing peak. Pre-fire sampling was conducted five and six months before burning. The post-fire sampling was collected seven months after the execution of the last prescribed burning. In every sampling season, we recorded ecological variables from microhabitat to ecosystem level as described below.

We used HOBO kits (composed by one HOBO Pendant and one HOBO Pro v2 sensors) to obtain hourly measurements of illuminance and temperature at the ground level. Because of the limitation in the numbers of kits (20 kits), we randomly selected two blocks to be sampled. To avoid biases in the location in which kits were left, we systematically placed one kit per plot at the same point in relation to its vertices. Kits remained in the field for at least 130 days, from the transition between the rainy-dry season (March/April) to the end of the dry season (August/September).

We assessed community composition by visual estimation of cover by every

species present in the plots, including *Urochloa decumbens*. Due to the spatial heterogeneity of the herbaceous layer in tropical savannas (Augustine, 2003) and to follow the Braun-Blanquet method (Wikum & Shanholtzer, 1978), we divided the core zone of plots (9 m²) into nine 1 m² subplots where vegetation cover was always estimated by the same person. We visually estimated the cover by plant species using values of 0, 1, 5 and then every 10 up to 100% of cover from the projection of its canopy to the ground layer. Therefore, the total cover of a plot was allowed to surpass 100% due to the tridimensional organization of plant individuals. We also assessed the bare soil percentage and cover by dead biomass (standing + litter); the latter was estimated for the native and invasive biomass separately. We grouped native plant species according to their growth-form: grasses, forbs, and shrubs.

At the plant's individual level, we sampled the specific-leaf area of dominant species in the communities. These dominant species were selected based on their abundance: we ranked down all species by their cover and starting from the most abundant, we sampled additional species until they had represented at least 80% of cover in every community. Following Pérez-Harguindeguy and collaborators (2013), we collected three leaves/individual and ten individuals/species to account for trait plasticity. After collection, leaves were carefully stored in paper bags; at the laboratory they were rehydrated and had their area measured using a LI-COR LI-3000C equipment. Delicate leaflets were scanned using a scanner Epson V800 and had their area quantified using the P-trap software (Al-Tam et al., 2013). After measurements, all leaves were dried in a drying oven at 80ºC for 48 hours and weighted in an electronic scale with 0.1 mg precision.

We randomly sampled plant aboveground biomass on the marginal zone of plots using 0.5 x 0.5 m quadrats. We sampled three subplots per plot to minimize the

effects of spatial heterogeneity. We collected every sample by cutting all standing biomass at the ground level and by gathering the litter inside the subplot. At the laboratory, biomass was sorted out into *Urochloa decumbens* biomass (live or dead); native graminoids, forbs and shrubs (all live biomass); and native dead biomass. After that, biomass was dried in a drying oven at 80ºC for 48 hours and then weighted.

We measured CO_2 soil efflux by placing incubation chambers with soda lime (CaO/NaOH) in every plot following Keith & Wong (2006). We used 7 cm petri dishes with 25 mg of soda lime incubated for 24 hours inside opaque plastic chambers with a radius of 12 cm. The CO_2 efflux was calculated from the difference in soda lime weight before and after incubation. We assessed decomposition rates using aluminum litter bags (20 cm x 20 cm) left on bare ground for 90, 120 and 160 days (Karberg et al., 2008) from April to August. We standardized parent material across the invasion gradient by using 5 g of *Urochloa decumbens* biomass in all bags.

Statistical analysis

We used generalized linear mixed models (GLMM) to analyze the main effects of annual fires. As we were interested in comparing the effect of management action (burning x control) at every level of invasion (0, 25, 50, 75 and 100% of cover by IAS) in two sampling seasons (before and after the experiment, in 2019 and 2021 respectively), we set a fixed effect with treatment within invasion level within sampling occasion for all models. We added random effects accounting for the nested design of gradients within the block. When measurements were carried out at the subplot level (microhabitat, SLA, biomass, and decomposition), we used the plot weighted

mean as a response variable. Despite losing predictive power in doing so, we opted to use plot-level data to reduce the complexity of nested effects in models, which already accounted for gradient and block. For community multivariate analysis, we also calculated the mean cover of every species at the plot level from its nine 1 m^2 subplots. We compared the effect of treatment within the invasion level within a year by pairwise comparisons corrected for multiple comparisons using the Monte Carlo method. We used the Gamma and Negative Binomial distributions for continuous and discrete numeric variables, respectively.

Considering every plot as a community, we counted native plant richness, and calculated Shannon's diversity and Pielou's evenness indices. We also conducted a Principal Coordinate Analysis (PCoA) to evaluate how plant composition caused the differentiation of communities. For this analysis we considered every sampling of a plot as a community (30 plots sampled twice; 60 communities in total) to be included in the PCoA analysis. We used the mean cover by every species at the plot level (calculated from plot's nine subplots) to generate the dissimilarity matrix using the Bray-Curtis distance. We used the R software (R Core Team, 2020) and the packages lme4 (Bates, Mächler, Bolker, & Walker, 2015), emmeans (Lenth, 2021), multcomp (Hothorn, Bretz, & Westfall, 2008), and vegan (Oksanen et al., 2016).

Results

Overall, the effects of burning were modulated by the abundance of *Urochloa decumbens* for most of the ecological properties assessed in this study (Supplementary material, Table 1). Fires did not influence the cover of live *Urochloa decumbens* across its invasion gradient (Supplementary Material, Fig. 1). The

influence of invader's abundance on the effects of fire varied among the microhabitat conditions (Fig. 1). Seven months after fire, burned plots presented greater bare soil percentage throughout the invasion gradient (Fig. 1A). However, this increment in gaps did not increase light conditions in all plots. Prescribed burnings resulted in increased light availability in plots with the highest abundance of the invader (Fig. 1B) and in increased air temperatures at ground level in communities with 25% cover by *Urochloa decumbens* (Fig. 1B). Prescribed burnings did not affect SLA values of native species across the invasion gradient (Fig. 2A). Alternatively, fire decreased SLA of *Urochloa decumbens* in communities where the invasive species had 50% and 75% cover (Fig. 2B).

Fire greatly influenced native biomass accumulation across the invasion gradient (Fig. 3). Dead biomass of native plants was reduced by fires in all burned plots independently of the invader's abundance (Fig. 3C). Distinctly, native live biomass was promoted by fires in communities with low levels of invasion (25%) or totally invaded by *Urochloa decumbens* (Fig. 3D). Live biomass of native graminoids was promoted by fire only in totally invaded communities (100% of invasive species cover, Fig. 3E). Fire affected neither live biomass of native forbs nor shrubs, as well as total, live or dead biomass of *Urochloa decumbens* independently of invader's abundance across the invasion gradient (Supplementary material, Fig.2 and Fig. 3). Despite their effect on native biomass accumulation, fires did not interact with *Urochloa decumbens* abundance to influence decomposition rates or CO2 soil efflux (Supplementary material, Fig. 4, Fig. 5). Considering community diversity (Fig. 4), fires only increased species richness in communities with 50% cover by *Urochloa decumbens* (Fig. 4A). In these plots (9 m^2), mean native plant richness increased from 21 to 45 species from 2019 (before) to 2021 (seven months after the second

burning), while in unburned plots it decreased from 32 to 29. Despite not affecting Shannon-Weaver's index, prescribed burnings increased Pielou's evenness in communities with 25% or 100% of cover by *Urochloa decumbens* (Fig. 4B and 4C).

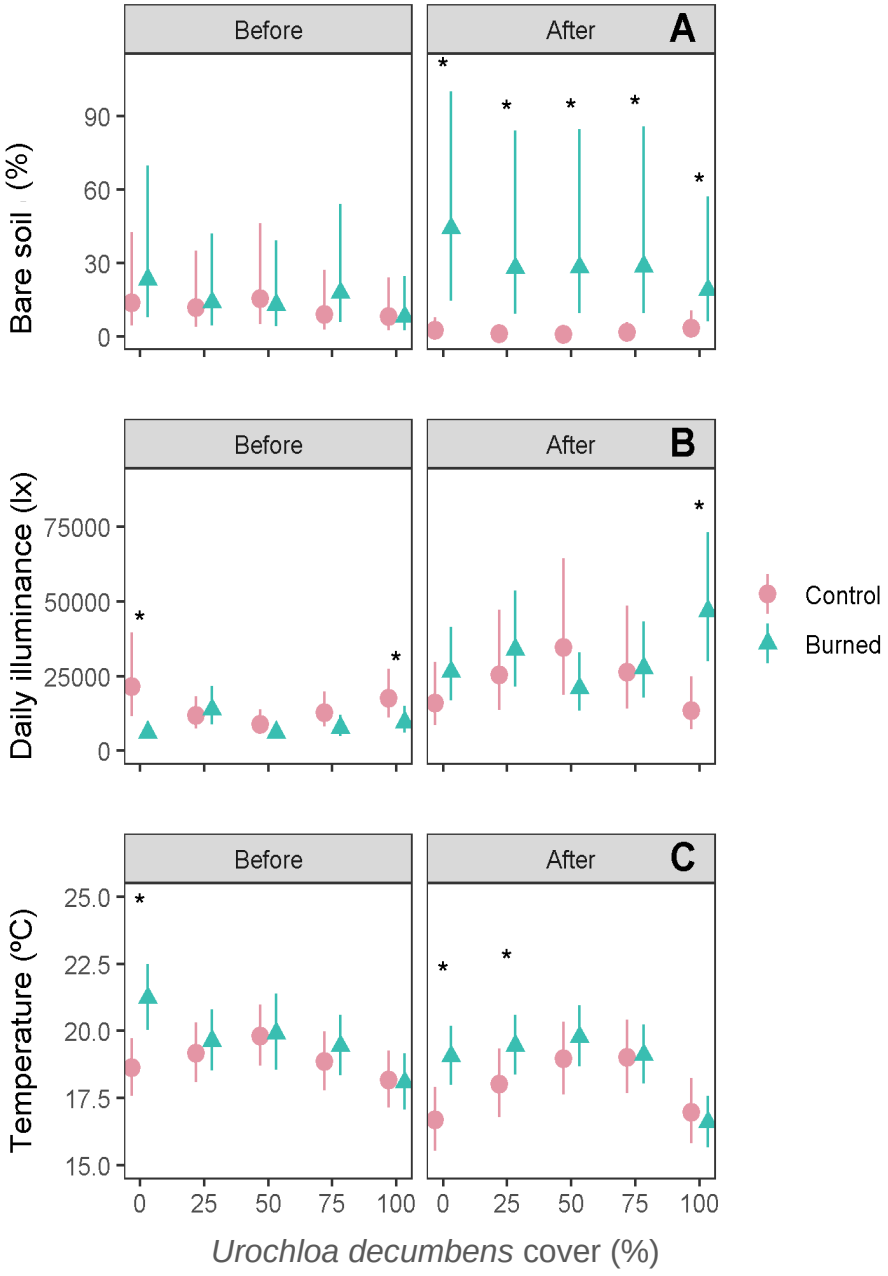


Figure 1. Effects of two annual prescribed burnings on microhabitat conditions at ground level in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% cover by the invasive species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. A) bare soil (%); B) total daily illuminance (lx) and C) mean daily temperature (ºC); in relation to a gradient of cover by *Urochloa decumbens* (%). Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks show significant differences between control and burned plots within every invasion level.

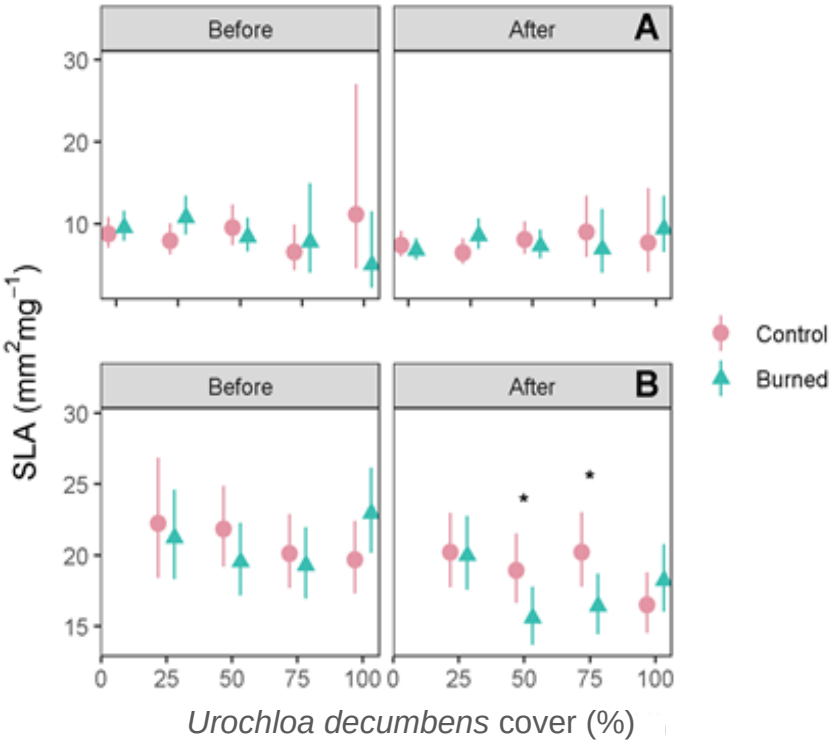


Figure 2. Effects of two annual prescribed burnings on specific-leaf area (mm² mg^{-1}) values of plant species in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. Specific-leaf area of A) native dominant species; and B) *Urochloa decumbens* in relation to a gradient of cover by *Urochloa decumbens* (%). Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

The invasion gradient by *Urochloa decumbens* was represented in the first PCoA axis, where communities were positioned according to the abundance of this species (Fig. 5). Fire effects were represented in PCoA second axis, with the differentiation of burned and unburned communities across it (Fig. 5). Moreover, fire effects on community dissimilarities were modulated by the abundance of the invasive alien species: the distances between burned and unburned communities with lower levels of invasion (0, 25 and 50% of cover by *Urochloa decumbens*) were greater than the distance between burned and unburned communities with higher

levels of invasion (75 and 100% cover by the invasive alien species).

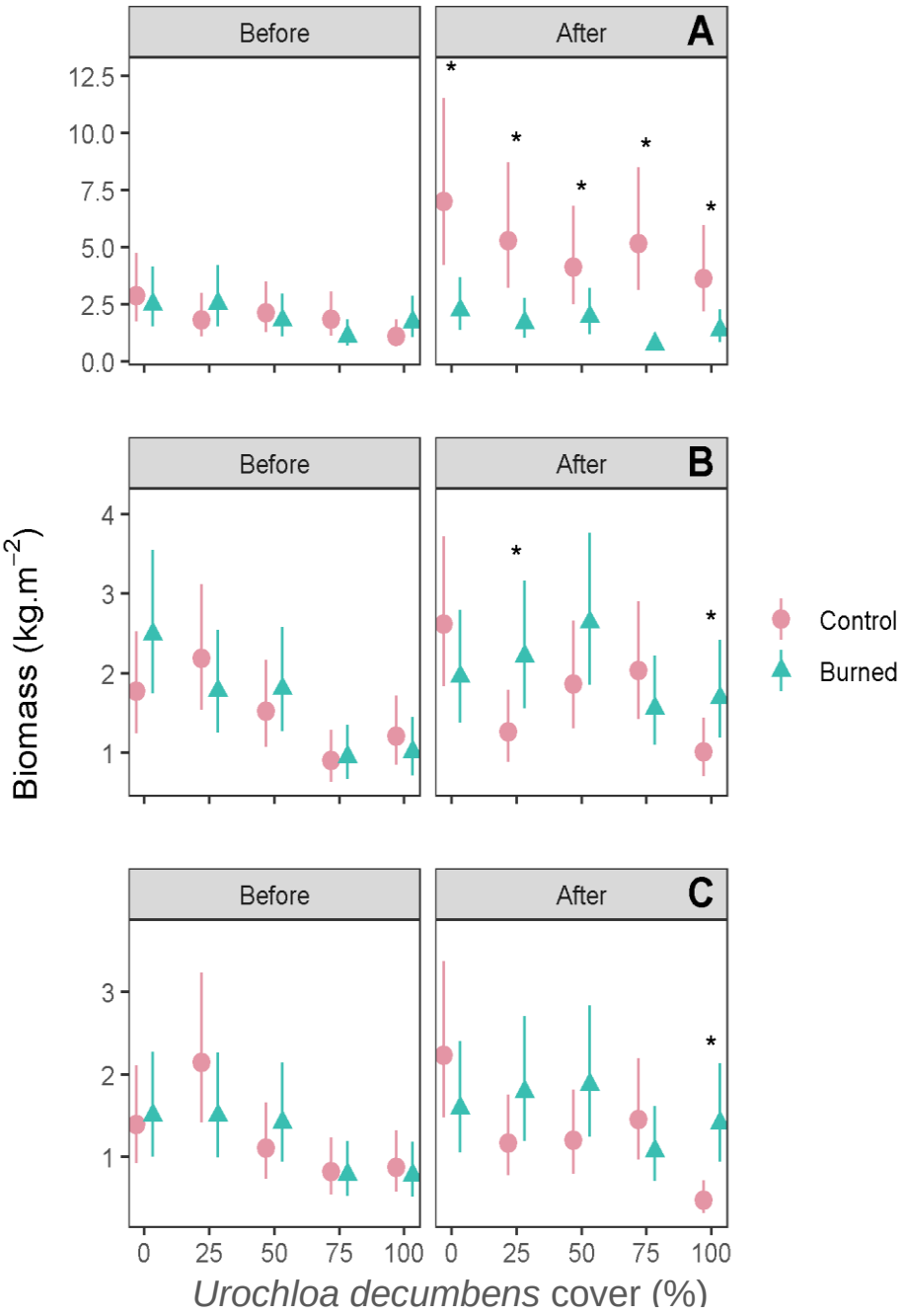


Figure 3. Effects of annual prescribed burnings on plant aboveground biomass (kg m^{-2}) in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. A) Native dead; B) native live; and C) native graminoids biomass in relation to a gradient of cover by *Urochloa decumbens* (%). Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

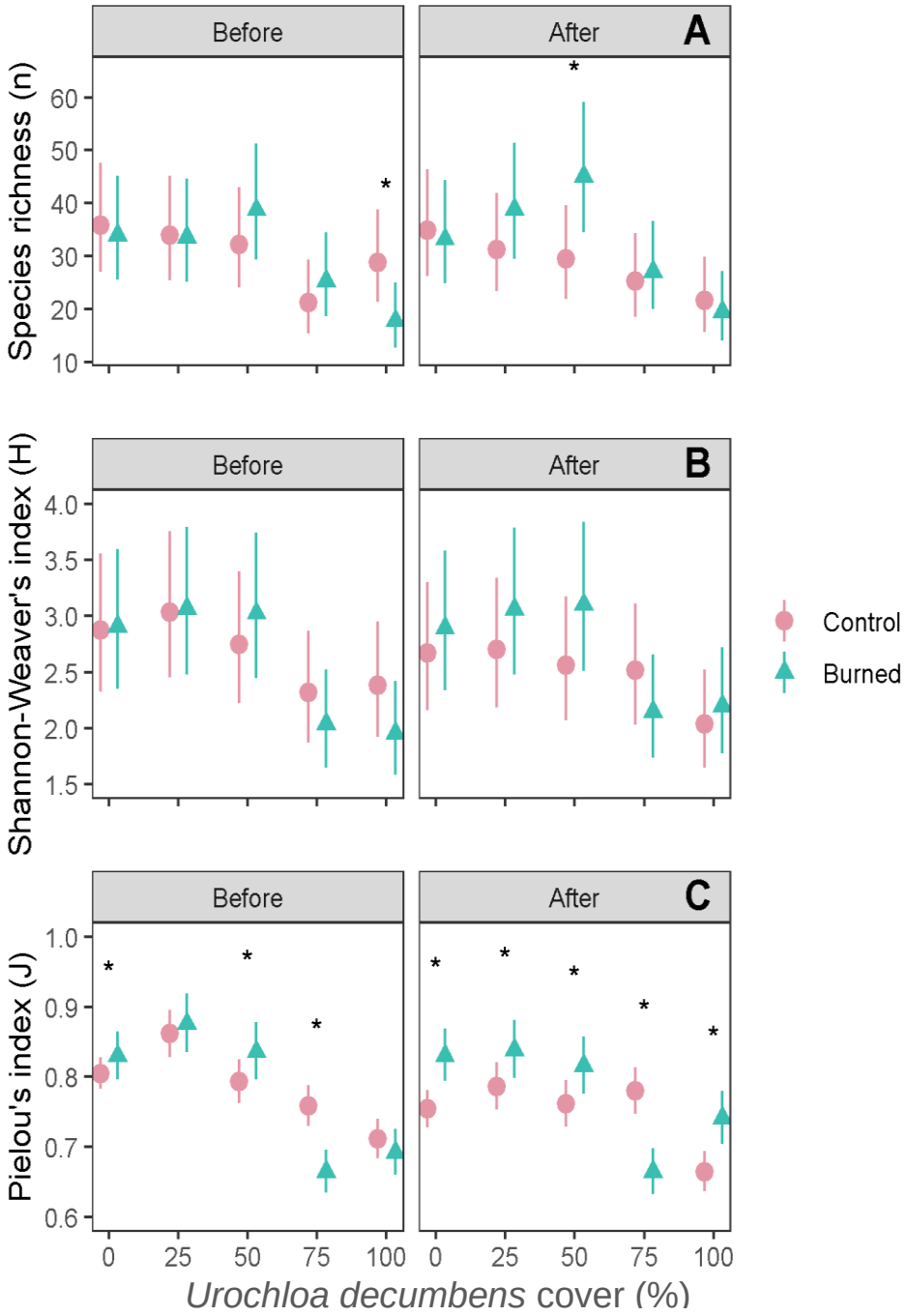


Figure 4. Effects of annual prescribed burnings on diversity of plant communities in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. A) native species richness (n); B) Shannon-Weaver's index (H); C) Pielou's evenness (J) in relation to a gradient of cover by *Urochloa decumbens* (%). Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

This pattern was driven mainly by the bare soil percentage, which increased more in burned communities at the beginning than at the end of the invasion gradient. The cover of native dead biomass also contributed to the divergence between burned and unburned communities in less invaded communities (up to 50% cover by the invader). Invasive dead biomass was less influential in separating burned from unburned communities, as this component was more related to the PCoA first axis.

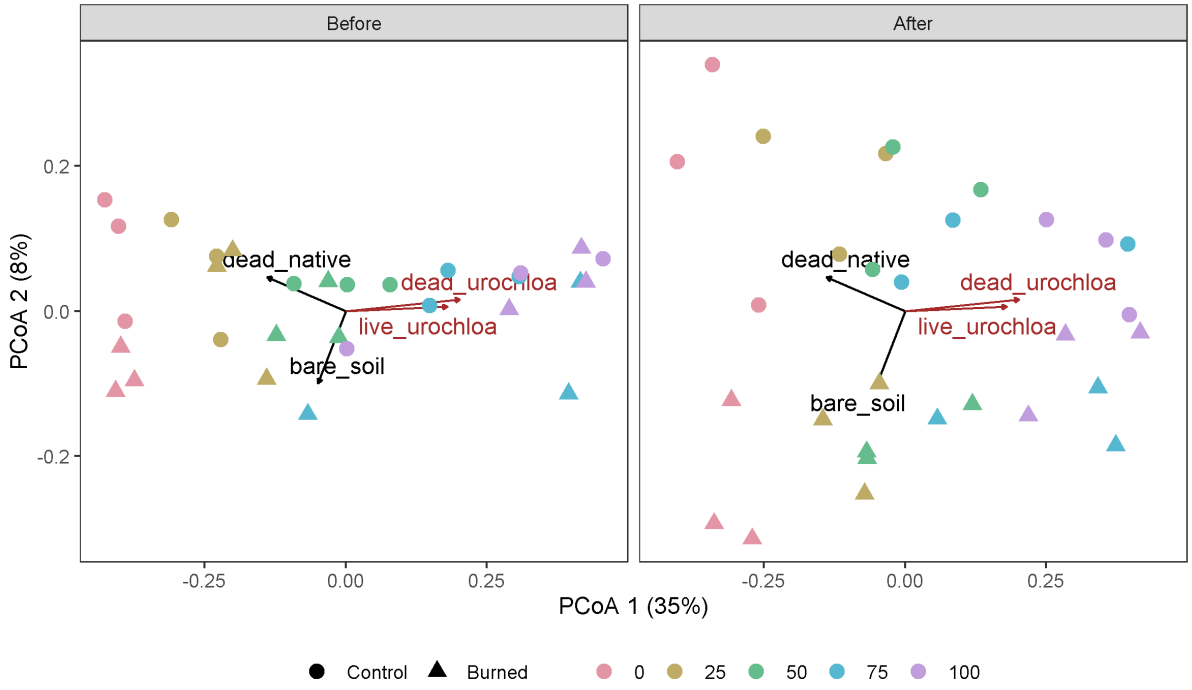


Figure 5. Principal Coordinate Analysis (PCoA) of plant communities invaded by *Urochloa decumbens* in a tropical savanna. Each point represents a plant community (9 m²) where species abundance was visually estimated by ground cover, as well as bare soil percentage and cover by dead (invasive and native) biomass. The influences of species abundance, bare soil and dead biomass cover on the spatial distribution of communities are shown as vectors. The orientation of a vector indicates its influence on communities' positions in the PCoA; the abundance of a given species increases towards its vector's head. Vectors of A) graminoids; and B) structural components. Native and invasive components are showed in black and red, respectively. Dissimilarities were calculated using Bray-Curtis distance.

Discussion

Fire effects on invaded tropical savanna were modulated by the abundance of *Urochloa decumbens*. Invader's abundance influenced fire effects on microhabitat (daily illuminance and mean air temperature), *Urochloa decumbens* specific leaf-area, live biomass of native species, species richness and Pielou's equitability index. However, *Urochloa decumbens* abundance did not influence common fire effects in tropical savannas, like the creation of gaps within vegetation and the reduction of dead biomass accumulated. *Urochloa decumbens* abundance also did not interact with fire to result in effects in decomposition rates and CO_2 soil efflux.

Prescribed burnings increased bare soil percentage independently of *Urochloa decumbens* abundance, which can be attributed to the moment the post-fire samplings were carried out: seven months after the last burning and by the end of the first rainy season. In open ecosystems of the Cerrado, ground cover is driven by seasonality, as the dry season causes the accumulation of dead herbaceous biomass (Eiten, 1972). After burning, both dead biomass of native species and of invasive alien grasses need at least one dry season to accumulate and cover the gaps left by fires (Damasceno & Fidelis, 2020; Rodrigues, 2019). As we sampled vegetation cover before the first dry season, dead biomass did not have enough time to accumulate in burned plots thus, leading to gaps within the vegetation independently of *Urochloa decumbens* cover.

However, *Urochloa decumbens* abundance influenced fire effects on microhabitat conditions, specifically daily illuminance, and mean air temperatures. Daily illuminance increased only in totally invaded burned communities. Across an invasion gradient, as the abundance of the invader increases, so does the amount of

total biomass blocking the entrance of sunlight to the ground (Damasceno & Fidelis, in preparation). Fire effects on illuminance were more pronounced in totally invaded communities. This results from the greater difference between pre- and post-fire conditions at these plots, which have the greatest amount of biomass accumulated in pre-fire conditions (Damasceno & Fidelis, in preparation). Additionally, the higher abundance of *Urochloa decumbens* and an increased intraspecific competition within these plots might have favored the post-fire regrowth of many small individuals due to alleviation of competitive asymmetries (Dar & Reshi, 2014; Despres et al., 2017; Hui & Richardson, 2017). Moreover, studies about fire effects on population dynamics of invasive alien grasses in tropical savannas are still scarce, being a knowledge gap in the understanding of management actions toward these invasions.

Urochloa decumbens abundance also influenced fire effects on air temperatures on the ground, which increased only in plots with 25% cover by the invader. In non-invaded communities, native plants can recover their live biomass after the first post-fire rainy season (Rodrigues, 2019), buffering temperatures increases in relation to pre-fire conditions. In communities with cover of 50%, 75% or 100% by *Urochloa decumbens*, the native species are replaced by the invader, which can also recover its live biomass after the first rainy season after fires (Damasceno & Fidelis, 2020), also preventing post-fire temperature changes. In invaded communities with 25% cover by *Urochloa decumbens*, however, the abundance of the invader seems to be insufficient to buffer these changes due to its sparse distribution among native species like found for other *Urochloa* species (Assis, 2017); and despite being abundant, native plants cannot prevent temperature increases because its recovery is hampered by the coexistence with the invader (Damasceno et al., 2018).

Fires did not interact with the abundance of *Urochloa decumbens* to influence the specific leaf area of native species. This indicates that, contrary to its effects in the long-term (Scalon & Rossatto, 2021), fires do not influence allocation of photosynthetic resources in herbaceous native species in the short-term. Alternatively, *Urochloa decumbens* abundance interacted with fire by decreasing its SLA values only in communities where its cover was 50% and 75%. This can be attributed to an increased intraspecific competition perceived by *Urochloa decumbens* individuals in the post-fire environment at these communities. By consuming aboveground biomass, fire could alleviate competitive asymmetries perceived by *Urochloa decumbens* individuals in the pre-fire environment of these communities. We suggest that this effect occurred only at these communities and not also in communities with 100% cover by the invader because is at intermediate levels of invasion when the interference between invader's tussocks starts because of the amalgamation process (Assis, 2017) thus, resulting in increased intraspecific competition perceived by invasive individuals. The non-effect of invader's abundance and fires on native species' SLA, together with the decrease in *Urochloa decumbens* SLA in communities where it covered 50% and 75% signalizes for a management opportunity to favor native species at these levels of invasion, as the competitive advantage of the invader (considered as the difference between it's and native's SLA values) decreased in the post-fire environment.

Urochloa decumbens abundance modulated fire effects on native species richness and Pielou's equitability, despite not influencing Shannon-Weaver's diversity index. These results derive from the counterbalance between positive effects of fire on native species (Frost & Robertson, 1985; Pilon, Cava, et al., 2021) and negative effects of invasive alien grasses (Damasceno & Fidelis, in preparation; Damasceno

et al., 2018) on community diversity in tropical savannas. In communities with 25% cover by the invader, fire might have increased equitability by increasing abundance of co-occurring native species (Pilon, Cava, et al., 2021), given the small negative effects of *Urochloa decumbens* on community diversity at this level of invasion (Damasceno & Fidelis, in preparation). In communities with 50% of cover by the IAS, fires preempted the loss of native species caused by *Urochloa decumbens* at this level of abundance (Damasceno & Fidelis, in preparation). In totally invaded communities, fire probably increased equitability by temporarily reducing the cover of the dominant invasive alien species as already found by previous studies (Damasceno & Fidelis, 2020; Martins et al., 2011).

Dissimilarities in community composition between burned and unburned communities were modulated across the invasion gradient: the lower the *Urochloa decumbens* abundance, the greater the divergence between them. This results from vigorous post-fire resprout of *Urochloa* species (Assis et al., 2021; Damasceno & Fidelis, 2020); as *Urochloa decumbens* abundance increases, its individuals occupy the gaps left by fires. Also, the post-fire recovery of *Urochloa decumbens* dead biomass is quicker than native dead biomass (Damasceno & Fidelis, 2020; Rodrigues, 2019), decreasing the dissimilarities between burned and unburned heavily invaded communities.

However, the amount of *Urochloa decumbens* biomass was not affected by fires in any community across the invasion gradient. This extends the quick recovery of *Urochloa* species in heavily invaded areas (Damasceno & Fidelis, 2020) as being independent of its abundance. It also enhances the appeal for using fire as a toll to manage these invasions, since the invasive alien grass was not benefited by fires at any level of its abundance. Nevertheless, further studies are needed to clarify if

prescribed fires influence or not the susceptibility of native communities to new *Urochloa* invasions. Additionally, experiments addressing how fire influences the relationships among invasive alien grasses are also needed to avoid the replacement of one invader by another, as already found for *Melinis minutiflora* (Damasceno & Fidelis 2020).

Urochloa decumbens abundance did not interact with fire to affect the accumulation of dead biomass of native species, which was always lower in burned plots. Despite invasive alien grasses can alter community structure (Damasceno et al., 2018) and modify biomass accumulation (Damasceno & Fidelis, in preparation), fire absence remains the main driver of the amount of native dead biomass accumulated in the herbaceous layer of tropical savannas (Frost & Robertson, 1985; Gomes, Miranda, Silvério, & Bustamante, 2020; Rodrigues, 2019). On the other hand, *Urochloa decumbens* abundance influenced the accumulation of total native live biomass, which increased in burned communities with 25% and 100% of *Urochloa decumbens* cover. In totally invaded plots, it is due to the greater biomass of live native graminoids, which seems to have been benefited by the higher illuminance in the post-fire environment and by a temporary alleviation of competition with the invader. In plots with 25% of cover by the invader, although, this increase seems to collectively represent small increases in live biomass of grasses, forbs, and shrubs, as we did not detect fire effects in these components in isolation.

Urochloa decumbens abundance did not influence fire effects on decomposition rates and CO_2 soil efflux in the Cerrado, similarly to its non-effects on these ecosystem properties in invaded communities without fire (Damasceno & Fidelis, in preparation). Fire is an important driver of nutrient fluxes in tropical savannas, including carbon cycles (Jiang et al., 2021); however, its effects on

decomposition rates are dependent on medium-term changes in fire regime towards increased fire frequency (Ficken & Wright, 2017; Hopkins, Huffman, Platt, & Sikes, 2020; Pellegrini et al., 2020). Although we had increased fire frequency, our study assessed only the short-term effects of two prescribed burnings and long-term experiments are still needed to better understand the interaction of invasive alien grasses and fire on ecosystem processes.

Conclusions

The abundance of the invader did not influence well-recognized effects of fires in tropical savannas, like reduction in the accumulated biomass and the creation of gaps within vegetation (Coutinho, 1982). However, invader's abundance modulated, in the short-term, other fire effects on invaded tropical savannas. Fires exerted stronger effects on communities with the lowest (25%) and the highest (100%) levels of invasion. In both communities, fires can benefit native biodiversity by increasing its live biomass and community evenness. Fires were also beneficial to native biodiversity in moderately invaded communities (50% and 75% of *Urochloa decumbens* cover). In these communities, fires reduced the invader's specific leaf-area, probably alleviating the competition suffered by native species; indeed, species richness increased in burned communities with 50% of cover by the invader.

Fires did not benefit the performance of *Urochloa decumbens* in any invaded community; as well it did not enhance *Urochloa decumbens* entrance in non-invaded communities. This suggests that despite the failure in using prescribed burnings to reduce the abundance of invasive alien grasses (Assis et al., 2021; Damasceno & Fidelis, 2020; Martins et al., 2011) it does not seem to favor their spread in the short-term. However, studies specifically designed to evaluate the existence of a grass-fire

cycle in Neotropical savannas are urgently needed, so we can better understand the role of fire, both as prescribed burnings and as wildfire, in the population dynamics of invasive alien grasses. Finally, given the positive effects fire had on native biodiversity, it could be considered a management toll, among other techniques, within management plans tailored to reduce the abundance and negative impacts of invasive alien grasses in tropical savannas.

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Supplementary information for Damasceno, Durigan and Fidelis: *"Abundance of an invasive grass modulates short-term fire effects in a tropical savanna"*

Table 1. Statistical output of generalized linear mixed models evaluating the effect of prescribed burnings on the properties of a tropical savanna with distinct levels of invasion by *Urochloa decumbens*. Letters compare paired burned/control plots within invasion level (0, 25, 50, 75 and 100% cover by the invader) within sampling event (before and after the prescribed burnings). Samplings were conducted in 2019 (before) and 2021 (after).

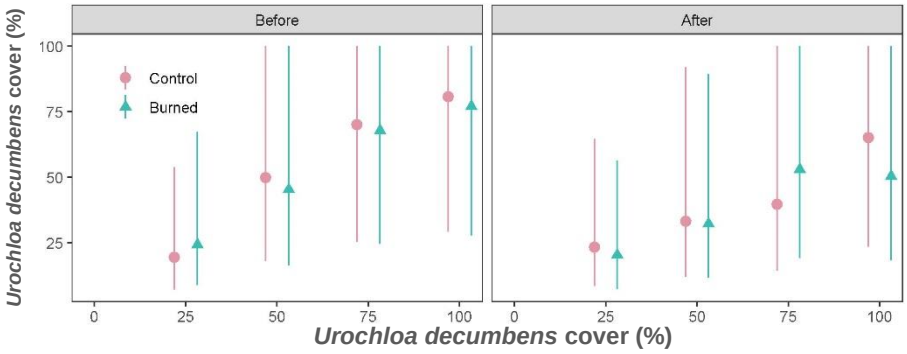
Sampling	Invasion level (%)	Treatment	Bare soil cover (%)	Illuminance (lx)	Temperature (ºC)	Specific leaf-area ($mm^2.mg^{-1}$)	
						Native species	*Urochloa decumbens*
Before	0	Control	13.88 ± 1.77 a	21419.1 ± 1.37 b	18.64 ± 1.03 a	8.8 ± 1.11 a	---
Before	0	Burned	23.41 ± 1.75 a	6168.36 ± 1.26 a	21.23 ± 1.03 b	9.61 ± 1.1 a	---
Before	25	Control	11.8 ± 1.75 a	11712.46 ± 1.26 a	19.18 ± 1.03 a	8.01 ± 1.13 a	22.25 ± 1.1 a
Before	25	Burned	14.07 ± 1.75 a	13839.87 ± 1.26 a	19.64 ± 1.03 a	10.84 ± 1.12 a	21.26 ± 1.08 a
Before	50	Burned	13.21 ± 1.75 a	6130.72 ± 1.26 a	19.92 ± 1.04 a	8.49 ± 1.13 a	19.55 ± 1.07 a
Before	50	Control	15.42 ± 1.75 a	8804.96 ± 1.26 a	19.82 ± 1.03 a	9.58 ± 1.14 a	21.86 ± 1.07 a
Before	75	Control	9.05 ± 1.75 a	12748.62 ± 1.26 a	18.86 ± 1.03 a	6.64 ± 1.23 a	20.13 ± 1.07 a
Before	75	Burned	17.99 ± 1.76 a	7749.26 ± 1.26 a	19.45 ± 1.03 a	7.88 ± 1.39 a	19.31 ± 1.07 a
Before	100	Control	8.14 ± 1.75 a	17455.67 ± 1.26 b	18.18 ± 1.03 a	11.14 ± 1.57 a	19.7 ± 1.07 a
Before	100	Burned	8.22 ± 1.76 a	9544.91 ± 1.26 a	18.09 ± 1.03 a	5.09 ± 1.52 a	22.96 ± 1.07 a
After	0	Control	2.53 ± 1.79 a	16001.29 ± 1.37 a	16.69 ± 1.04 a	7.48 ± 1.11 a	---
After	0	Burned	44.32 ± 1.75 b	26487.08 ± 1.26 a	19.06 ± 1.03 b	6.87 ± 1.1 a	---
After	25	Control	1.18 ± 1.83 a	25363.84 ± 1.37 a	18.03 ± 1.04 a	6.55 ± 1.13 a	20.2 ± 1.07 a
After	25	Burned	28.09 ± 1.75 b	33951.19 ± 1.26 a	19.46 ± 1.03 b	8.63 ± 1.12 a	20 ± 1.07 a
After	50	Control	0.95 ± 1.76 a	34649.68 ± 1.37 a	18.95 ± 1.04 a	8.13 ± 1.13 a	18.93 ± 1.07 b
After	50	Burned	28.43 ± 1.75 b	20923.14 ± 1.26 a	19.78 ± 1.03 a	7.37 ± 1.13 a	15.6 ± 1.07 a
After	75	Control	1.88 ± 1.79 a	26174.72 ± 1.37 a	19.01 ± 1.04 a	9.01 ± 1.23 a	20.24 ± 1.07 b
After	75	Burned	28.84 ± 1.74 b	27684.94 ± 1.26 a	19.12 ± 1.03 a	6.97 ± 1.31 a	16.44 ± 1.07 a
After	100	Control	3.52 ± 1.76 a	13401.34 ± 1.37 a	16.98 ± 1.04 a	7.76 ± 1.37 a	16.53 ± 1.07 a
After	100	Burned	19.1 ± 1.75 b	46752.09 ± 1.26 b	16.61 ± 1.03 a	9.45 ± 1.2 a	18.24 ± 1.07 a

(Table 1. Continuation)

Sampling	Invasion level (%)	Treatment	Biomass (kg.m^{-2})						
			Total	Native total	Native dead	Native live	Native grasses	Native forbs	Native shrubs
Before	0	Control	4.62 ± 1.14 a	4.63 ± 1.2 a	2.88 ± 1.29 a	1.77 ± 1.2 a	1.39 ± 1.23 a	0.01 ± 2.23 b	0.35 ± 1.72 a
Before	0	Burned	5.01 ± 1.14 a	5.03 ± 1.2 a	2.51 ± 1.29 a	2.49 ± 1.2 a	1.51 ± 1.23 a	0 ± 2.23 a	1.08 ± 1.72 a
Before	25	Control	4.43 ± 1.14 a	4.03 ± 1.2 a	1.81 ± 1.29 a	2.19 ± 1.2 a	2.14 ± 1.23 a	0 ± 2.23 a	0.05 ± 1.72 a
Before	25	Burned	4.53 ± 1.14 a	4.31 ± 1.2 a	2.54 ± 1.29 a	1.78 ± 1.2 a	1.5 ± 1.23 a	0 ± 2.23 a	0.25 ± 1.73 b
Before	50	Burned	4.75 ± 1.14 a	3.64 ± 1.2 a	1.81 ± 1.29 a	1.81 ± 1.2 a	1.42 ± 1.23 a	0.01 ± 2.23 a	0.4 ± 1.71 a
Before	50	Control	4.38 ± 1.14 a	3.66 ± 1.2 a	2.12 ± 1.29 a	1.52 ± 1.2 a	1.1 ± 1.23 a	0.01 ± 2.23 a	0.43 ± 1.71 a
Before	75	Control	5.26 ± 1.14 a	2.79 ± 1.2 a	1.84 ± 1.29 a	0.9 ± 1.2 a	0.82 ± 1.23 a	0 ± 2.23 a	0.09 ± 1.72 a
Before	75	Burned	4.78 ± 1.14 a	2.06 ± 1.2 a	1.11 ± 1.29 a	0.95 ± 1.2 a	0.79 ± 1.23 a	0 ± 2.23 b	0.13 ± 1.75 a
Before	100	Control	5.22 ± 1.14 a	2.32 ± 1.2 a	1.1 ± 1.3 a	1.21 ± 1.2 a	0.87 ± 1.23 a	0.02 ± 2.23 a	0.34 ± 1.72 a
Before	100	Burned	4.59 ± 1.14 a	2.75 ± 1.2 a	1.74 ± 1.29 a	1.01 ± 1.2 a	0.78 ± 1.23 a	0.01 ± 2.23 a	0.25 ± 1.76 a
After	0	Control	9.71 ± 1.14 b	9.66 ± 1.2 b	6.99 ± 1.29 b	2.61 ± 1.2 a	2.23 ± 1.23 a	0.01 ± 2.23 a	0.33 ± 1.72 a
After	0	Burned	4.25 ± 1.14 a	4.2 ± 1.2 a	2.24 ± 1.29 a	1.96 ± 1.2 a	1.59 ± 1.23 a	0.01 ± 2.23 a	0.34 ± 1.73 a
After	25	Control	7.89 ± 1.14 b	6.53 ± 1.2 b	5.29 ± 1.29 b	1.26 ± 1.2 a	1.16 ± 1.23 a	0.01 ± 2.23 a	0.09 ± 1.72 a
After	25	Burned	4.54 ± 1.14 a	3.91 ± 1.2 a	1.69 ± 1.29 a	2.22 ± 1.2 b	1.79 ± 1.23 a	0 ± 2.23 a	0.42 ± 1.72 b
After	50	Control	7.62 ± 1.14 a	5.97 ± 1.2 a	4.13 ± 1.29 b	1.86 ± 1.2 a	1.2 ± 1.23 a	0.05 ± 2.23 a	0.55 ± 1.72 a
After	50	Burned	6.29 ± 1.14 a	4.64 ± 1.2 a	1.96 ± 1.29 a	2.64 ± 1.2 a	1.88 ± 1.23 a	0.11 ± 2.23 a	0.66 ± 1.71 a
After	75	Control	11.19 ± 1.14 b	7.27 ± 1.2 b	5.16 ± 1.29 b	2.03 ± 1.2 a	1.45 ± 1.23 a	0.02 ± 2.23 a	0.49 ± 1.76 a
After	75	Burned	6.32 ± 1.14 a	2.31 ± 1.2 a	0.75 ± 1.29 a	1.56 ± 1.2 a	1.07 ± 1.23 a	0.02 ± 2.23 a	0.41 ± 1.72 a
After	100	Control	8.89 ± 1.14 a	4.6 ± 1.2 a	3.61 ± 1.29 b	1.01 ± 1.2 a	0.47 ± 1.23 a	0.03 ± 2.23 b	0.54 ± 1.73 a
After	100	Burned	6.72 ± 1.14 a	3.06 ± 1.2 a	1.39 ± 1.29 a	1.69 ± 1.2 b	1.41 ± 1.23 b	0 ± 2.23 a	0.22 ± 1.73 a

(Table 1. Continuation)

Sampling	Invasion level (%)	Treatment	Biomass (kg.m-²)			Richness (n)	Shannon-Weaver's index (H)	Pielou's index (J)	Decomposition rate (k.day-¹)	CO2 soil efflux (g.C.m-²day-¹)
			Total *U. decumbens*	Dead *U. decumbens*	Live *U. decumbens*					
Before	0	Control	---	---	---	1.77 ± 1.2 a	1.39 ± 1.23 a	0.01 ± 2.23 b	0.35 ± 1.72 a	26.19 ± 5.88 a
Before	0	Burned	---	---	---	2.49 ± 1.2 a	1.51 ± 1.23 a	0 ± 2.23 a	1.08 ± 1.72 a	19.08 ± 6.94 a
Before	25	Control	0.4 ± 2.03 a	0.26 ± 1.95 a	0.14 ± 2.09 a	2.19 ± 1.2 a	2.14 ± 1.23 a	0 ± 2.23 a	0.05 ± 1.72 a	22.96 ± 5.88 a
Before	25	Burned	0.24 ± 2.03 a	0.18 ± 1.95 a	0.06 ± 2.09 a	1.78 ± 1.2 a	1.5 ± 1.23 a	0 ± 2.23 a	0.25 ± 1.73 b	25.12 ± 5.88 a
Before	50	Burned	1.14 ± 2.03 a	0.78 ± 1.95 a	0.36 ± 2.09 a	1.81 ± 1.2 a	1.42 ± 1.23 a	0.01 ± 2.23 a	0.4 ± 1.71 a	32.08 ± 5.88 a
Before	50	Control	0.71 ± 2.03 a	0.4 ± 1.95 a	0.32 ± 2.09 a	1.52 ± 1.2 a	1.1 ± 1.23 a	0.01 ± 2.23 a	0.43 ± 1.71 a	25.89 ± 5.88 a
Before	75	Control	2.46 ± 2.03 a	1.93 ± 1.95 a	0.53 ± 2.09 a	0.9 ± 1.2 a	0.82 ± 1.23 a	0 ± 2.23 a	0.09 ± 1.72 a	23.29 ± 5.88 a
Before	75	Burned	2.75 ± 2.03 a	1.69 ± 1.95 a	1.06 ± 2.09 a	0.95 ± 1.2 a	0.79 ± 1.23 a	0 ± 2.23 b	0.13 ± 1.75 a	29.06 ± 5.88 a
Before	100	Control	2.91 ± 2.03 a	2.14 ± 1.95 a	0.77 ± 2.09 a	1.21 ± 1.2 a	0.87 ± 1.23 a	0.02 ± 2.23 a	0.34 ± 1.72 a	28.68 ± 6.91 a
Before	100	Burned	1.82 ± 2.03 a	1.41 ± 1.95 a	0.41 ± 2.09 a	1.01 ± 1.2 a	0.78 ± 1.23 a	0.01 ± 2.23 a	0.25 ± 1.76 a	24.43 ± 5.88 a
After	0	Control	---	---	---	2.61 ± 1.2 a	2.23 ± 1.23 a	0.01 ± 2.23 a	0.33 ± 1.72 a	0.1 ± 5.88 a
After	0	Burned	---	---	---	1.96 ± 1.2 a	1.59 ± 1.23 a	0.01 ± 2.23 a	0.34 ± 1.73 a	2.91 ± 6.94 a
After	25	Control	1.13 ± 2.03 a	0.77 ± 1.95 a	0.37 ± 2.09 a	1.26 ± 1.2 a	1.16 ± 1.23 a	0.01 ± 2.23 a	0.09 ± 1.72 a	1.24 ± 5.88 a
After	25	Burned	0.66 ± 2.03 a	0.28 ± 1.95 a	0.38 ± 2.09 a	2.22 ± 1.2 b	1.79 ± 1.23 a	0 ± 2.23 a	0.42 ± 1.72 b	-0.56 ± 6.94 a
After	50	Control	1.64 ± 2.03 a	1.18 ± 1.95 a	0.47 ± 2.09 a	1.86 ± 1.2 a	1.2 ± 1.23 a	0.05 ± 2.23 a	0.55 ± 1.72 a	0.03 ± 5.88 a
After	50	Burned	1.74 ± 2.03 a	0.67 ± 1.95 a	1.07 ± 2.09 a	2.64 ± 1.2 a	1.88 ± 1.23 a	0.11 ± 2.23 a	0.66 ± 1.71 a	-3.17 ± 6.93 a
After	75	Control	3.92 ± 2.03 a	2.68 ± 1.95 a	1.24 ± 2.09 a	2.03 ± 1.2 a	1.45 ± 1.23 a	0.02 ± 2.23 a	0.49 ± 1.76 a	0.49 ± 5.88 a
After	75	Burned	3.99 ± 2.03 a	1.79 ± 1.95 a	2.2 ± 2.09 a	1.56 ± 1.2 a	1.07 ± 1.23 a	0.02 ± 2.23 a	0.41 ± 1.72 a	1.35 ± 6.94 a
After	100	Control	4.4 ± 2.03 a	2.87 ± 1.95 a	1.53 ± 2.09 a	1.01 ± 1.2 a	0.47 ± 1.23 a	0.03 ± 2.23 b	0.54 ± 1.73 a	1.6 ± 5.88 a
After	100	Burned	3.61 ± 2.03 a	1.91 ± 1.95 a	1.7 ± 2.09 a	1.69 ± 1.2 b	1.41 ± 1.23 b	0 ± 2.23 a	0.22 ± 1.73 a	0.3 ± 5.88 a



Fgure 1. Effects of two annual prescribed burnings on live *Urochloa decumbens* cover (%) in a tropical savanna across its invasion gradient (0, 25, 50, 75 and 100% cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

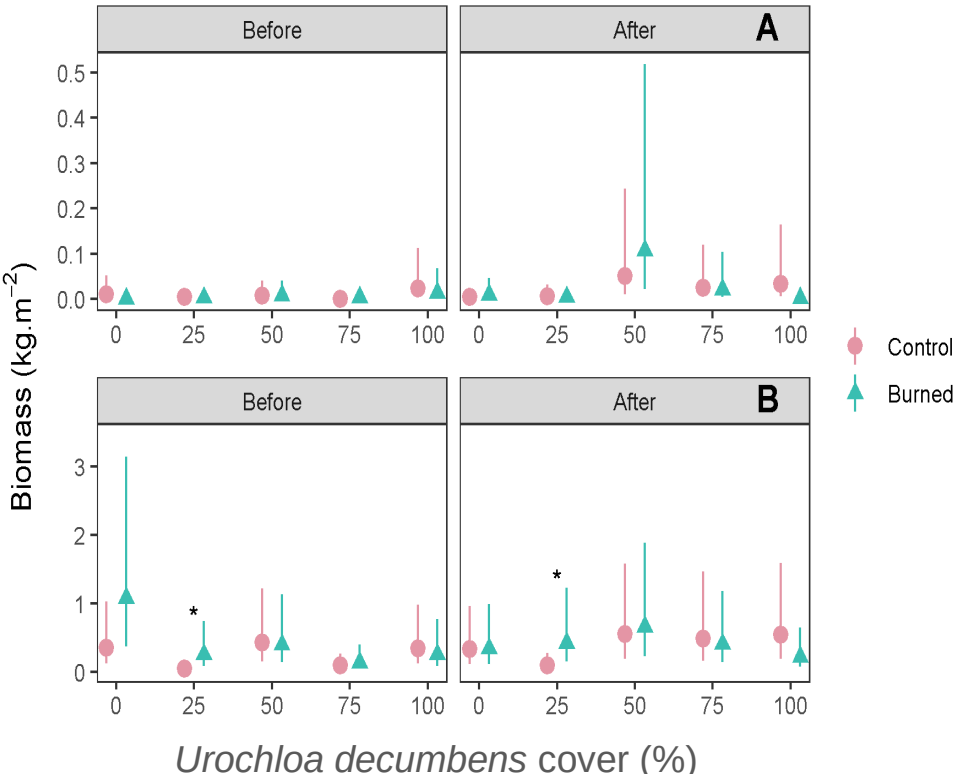


Figure 2. Effects of two annual prescribed burnings on plant aboveground biomass (kgm^{-2}) in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. Native biomass of A) forbs; and B) shrubs in relation to a gradient of cover by *Urochloa decumbens* (%). Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

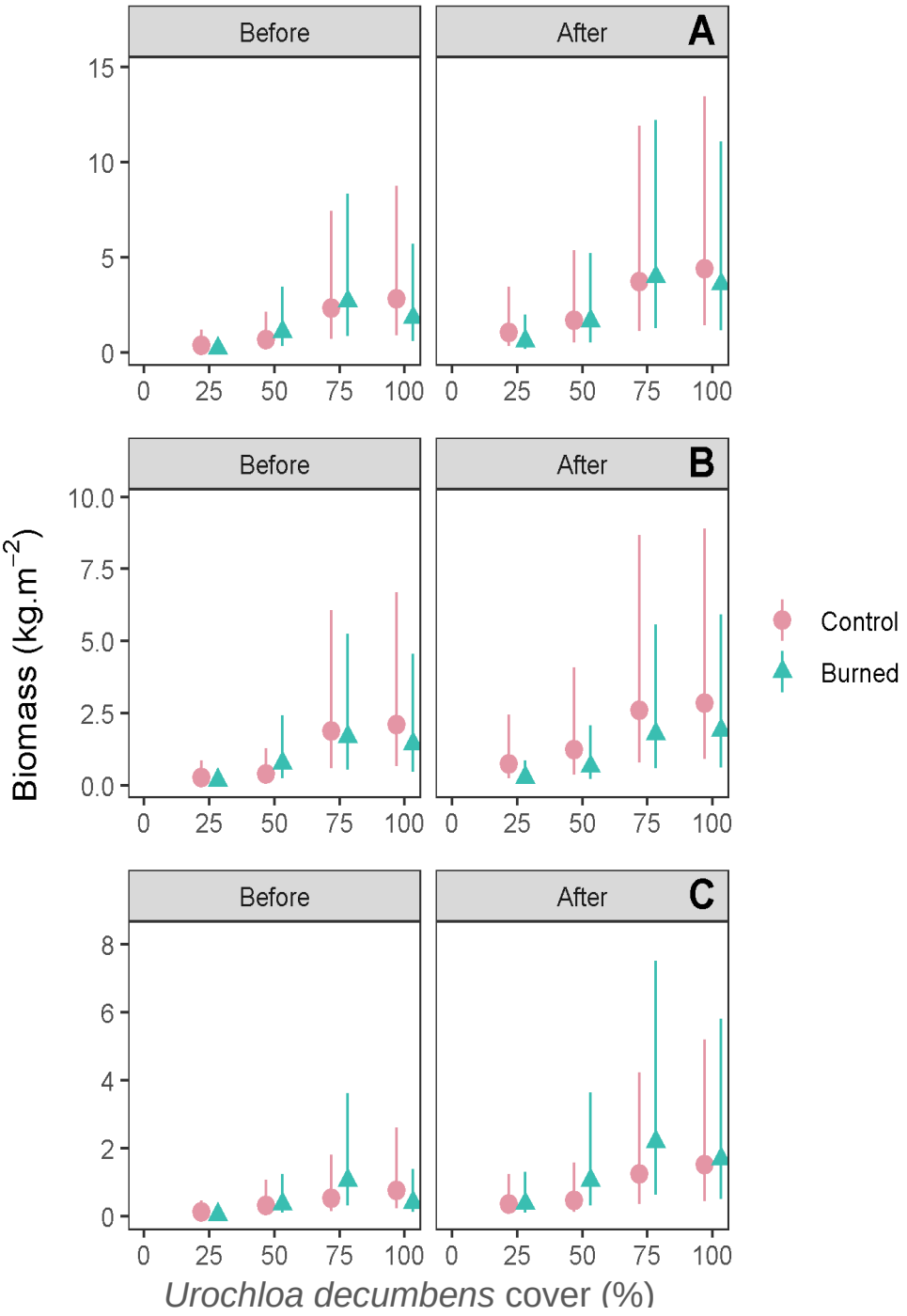


Figure 3. Effects of two annual prescribed burnings on plant aboveground biomass (kgm^{-2}) in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% of cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. A) total; B) dead; and C) live biomass of *Urochloa decumbens* in relation to a gradient of its cover (%). Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

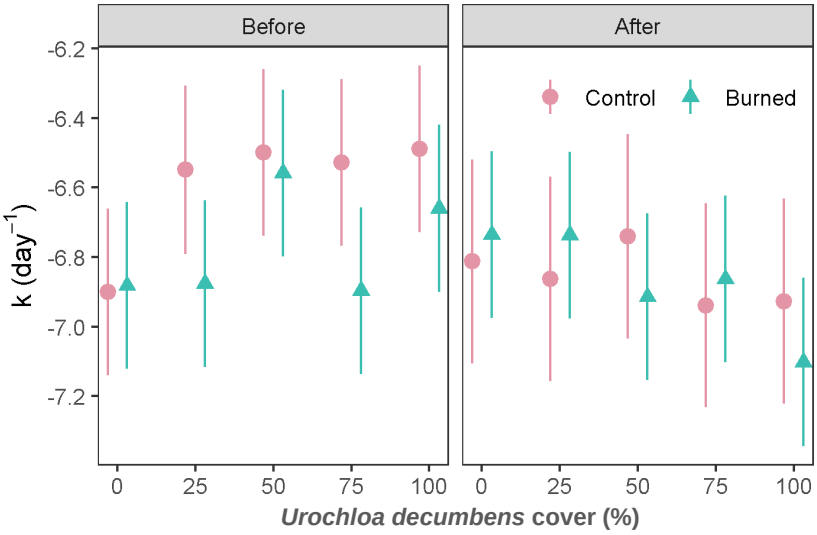


Figure 4. Effects of two annual prescribed burnings on decomposition rates (day^{-1}) in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% of cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

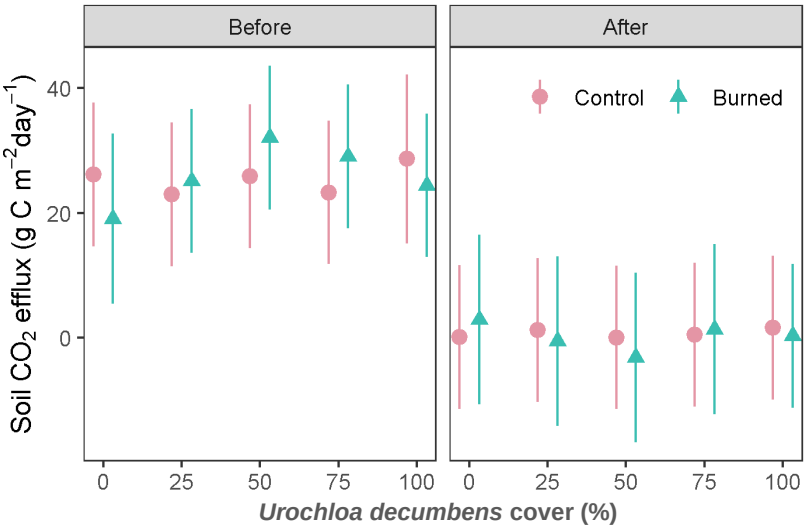


Figure 5. Effects of two annual prescribed burnings on CO_2 soil efflux (gCm^{-2}day) in a tropical savanna across an invasion gradient by *Urochloa decumbens* (0, 25, 50, 75 and 100% of cover by the invasive alien species). Measurements were carried out before (March/April 2019) and seven months after (March/April 2021) the experimental burnings, applied in August/October 2019 and August/September 2020. Dots are the fitted values for group means from GLMM models; lines are the mean's 95% confindence intervals. Markers are the fitted values for group means from GLMM models; lines are the mean's 95% confidence intervals. Asterisks mark significant differences between control and burned plots within every invasion level.

A state-and-transition model for the restoration of grass-invaded open tropical savannas

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Abstract

The negative impacts of invasive alien species pose them as one of the main threats to biodiversity conservation and a great challenge for human populations. We propose a unified state-and-transition model to aid in the management of invasive alien grasses and restoration of invaded open tropical savannas. We used primary data from field experiments with *Urochloa decumbens* to describe how the invader's abundance can influence its impacts and management outcomes in these systems. We also retrieved and included information about these invasions from a systematic search in scientific databases (Web of Science and SciELO). We found a total 108 scientific studies, most of which about the impacts caused by invasive alien grasses in tropical savannas. The resulting conceptual model was represented by seven states, three stable states and four transient states; plus 20 possible transitions. We hope that the model will help managers in making decisions for the management of biological invasions by grasses in open tropical savannas.

Keywords: conceptual model; invasive grasses; ecological restoration; state-and-transition; tropical savanna

Introduction

Invasive alien species (IAS) are one of the main threats to biodiversity conservation worldwide (Butchart et al. 2010) and the mitigation of their ecological

and socioeconomic negative impacts pose a great challenge for human populations (Pysek et al. 2020). Hopefully, new perceptions about the strengths and weaknesses of the management of biological invasions are originating new approaches to deal with this problem (Robertson et al., 2020). In general, the management of long-established IAS is becoming more centered on adaptive management tailored towards reducing invader's negative impacts in the long-term (García-Díaz et al., 2021). For this, the management actions need to be planned to maximize efficiency and reduce costs, which can be titanic at both global (Diagne et al., 2021) or regional scales (Adelino et al., 2021).

Conceptual models are a useful tool in aiding the planning and execution of management actions because they synthesize the theoretical and practical aspects of degradation, restoration and biological invasions (Novoa et al., 2020, 2018; Robertson et al., 2020; Firn, House, & Buckley, 2010). State and transition models started to be used for the management of open ecosystems in 1989 (Westoby, Walker & Noy-meier 1989) and they are still adopted nowadays (Andrade et al. 2015; Jackson & Boartolome). New developments of these models occurred within the field of restoration ecology, expanding their utilization for the restoration and degradation of systems with complex dynamics like tropical savannas (Briske, Fuhlendorf, & Smeins, 2006; Mayer & Rietkerk, 2004; Suding & Hobbs, 2009). Savannas are systems driven by non-equilibrium dynamics, in which alternative stable states are possible depending on physical characteristics of the environment, like soil composition, but also on system properties like the abundance of dominant species or the frequency of disturbances (Beckage, Gross, & Platt, 2011; Beisner, Haydon, & Cuddington, 2003; D'Odorico, Laio, & Ridolfi, 2006).

The restoration of complex systems is dependent on the establishment of

realistic goals that can be monitored by the adoption of clear indicator variables to inform management options and results (Hobbs & Norton, 1996; King & Hobbs, 2006). In this sense, the abundance of an invasive alien species can be considered an important variable because it influences system transition from one state to another, given the creation of new feedback mechanisms between the invader and other system's properties (Beisner et al., 2003; Suding, Gross, & Houseman, 2004). This is the case for alien grass invasions in tropical savannas, where these invaders can alter system properties and create new feedback mechanisms by starting a grass-fire cycle beneficial to their persistence (Gorgone-Barbosa et al., 2015; Rossiter et al., 2003). However, despite some investigations about the role of invasive alien grasses in influencing the degradation of these ecosystems (Brooks, Setterfield, & Douglas, 2010; Pivello & Coutinho, 1996), a general state-and-transition model addressing the restoration possibilities, which also considers the invader abundance is still lacking.

The importance of a general model to aid in the management of invasions and restoration of these systems is both highlighted and enabled by the growing scientific efforts on this topic. Recent studies have started to elucidate the mechanisms and drivers of successful alien grass invasions in tropical savannas (Ens, Hutley, Rossiter-Rachor, Douglas, & Setterfield, 2015; Guimarães Silva, Zenni, Rosse, Bastos, & van den Berg, 2020; Musso et al., 2015; Paredes et al., 2018; Xavier, Leite, & da Silva Matos, 2019; Xavier, Christianini, Pegler, Leite, & Silva-Matos, 2021), including future trends predicted to occur due to climate change (Barbosa, 2016; Baruch & Jackson, 2005; Damasceno & Fidelis, 2020; de Faria, Fernandes, & França, 2015; Fulgêncio-Lima et al., 2021). Another indication for the need of a synthetic model is the accumulating evidence of distinct management techniques

already tested but not framed together under the ecological theories explaining their results found (Assis, Pilon, Siqueira, & Durigan, 2021; Damasceno & Fidelis, 2020; Martins, Hay, Walter, Proença, & Vivaldi, 2011; Musso et al., 2019; Palermo et al., 2007; Zenni et al., 2020).

Therefore, we propose a unified state-and-transition model to assist in the management of invasive alien grasses and restoration of invaded tropical savannas. We used primary data from field experiments with *Urochloa decumbens* carried out to describe how the invader's abundance can influence its impacts (Damasceno & Fidelis, in preparation) and management outcomes (Damasceno, Durigan, & Fidelis, in preparation) in the Cerrado, the Neotropical savanna. We also retrieved and included information about alien grass invasion in tropical savannas from a systematic search in scientific databases (Web of Science and SciELO). By using the abundance of the IAS as an indicator variable, we aim to link field observations and management actions to the theory of biological invasions and ecological restoration. We expect the model to be used by managers in decision-making and management planning regarding the restoration of grass-invaded tropical savannas.

Material and Methods

We adopted two complimentary approaches to create a threshold model aimed to guide decision making and management of invaded tropical savannas in the short timescale (Suding & Hobbs 2009). We systematically reviewed the scientific literature on invasive alien grasses in tropical savannas and implemented field experiments to evaluate how invader's abundance relates to the degradation and restoration of these ecosystems.

Literature review

We conducted a systematic search in the ISIS Web of Science and SciELO scientific databases. Whereas the first is the largest database for scientific manuscripts, the second one is a regional database commonly used by Latin American scientists to publish articles in Portuguese and Spanish. Therefore, we used English search terms in ISIS Web of Science and Portuguese and Spanish terms in the SciELO bases. The inclusion of both databases and three languages intended to decrease the knowledge gaps caused by ignoring publications in other languages than English (Nuñez & Amano, 2021) which can result in biased results also in invasion science (Angulo et al., 2021).

We conducted all searches in November 2018 and checked for updates in the results in January 2021. We used the following search terms: ALL FIELDS = (grass* OR weed* OR poaceae OR gramineae) AND (invasi* OR alien* OR exotic* OR non-native*) AND (“tropical savanna*” OR "neotropical savanna*") in ISIS Web of Science; and ALL FIELDS = (gram* OR praga* OR daninha* OR pasto* OR cesped* OR hierba* OR poaceae OR gramineae) AND (invas* OR alien* OR exotic* OR n*-nativa* OR mala*) AND (savana* OR sabana OR cerrado OR llanos OR chaco) in SciELO. We did not include native species, even when behaving as superdominants (Vânia Regina Pivello, Vieira, Grombone-Guaratini, & Matos, 2018).

From the abstract and main text, we classified all articles found into one of four categories regarding their predominant theme: 1) impact of invasive alien grasses on plants, animals, ecological processes or restoration efforts (impact); 2) traits, characteristics or environmental factors that had the potential to influence the invasion success (mechanism); 3) management actions to control or reduce the

abundance of the invader, as well as to reduce their negative impacts (management); and 4) articles that had proposed theoretical models for savanna dynamics including or not invasive alien grasses in their scope (theoretical). We further classified every article according to its main topic, within the four themes (Table 1). Instead of extracting data from the manuscripts found, we use the categorized list as an enlistment for the *ad-hoc* construction of the model.

Field experiments

We implemented field experiments to quantitatively evaluate how the abundance of an invasive grass affects system properties and could modulate the outcome of management actions. We selected two areas naturally invaded by *Urochloa decumbens* inside protected areas in the Cerrado, Parque Nacional de Brasília (PNB, 5º41'S 47º53'W) and Estação Ecológica de Itirapina (EcEI, 22º14'S 47º53'W). Both areas have a Cw climate with dry winters and rainy summers. Monthly mean values of temperature and precipitation during summer and winter are 23 ºC and 300 mm and 18 ºC and 150 mm for the PNB; and 22º C and 188 mm and 17 ºC and 55 mm for the EE (IBAMA & FUNATURA 1998; Zanchetta et al. 2006). In each area we established plots (25 m^2) forming a gradient of cover by the invader (0, 25, 50, 75 and 100% cover). We had six gradients per area, divided into three blocks, each of them formed by a burning and an unburned (control) gradient. We had a total of 60 plots (5 plots x 2 gradients x 3 blocks x 2 areas); further details of the study area and the experimental design can be found in Damasceno & Fidelis (in preparation) and in Damasceno, Durigan, & Fidelis (in preparation).

Results

We found 157 and 38 papers in ISIS and SciELO databases, respectively. After excluding those not related to the topic (considering other invasive species, for example), we retained a total of 108 articles (Supplementary Information, Table 1). Most of the articles found addressed the impacts caused by invasive alien grasses in tropical savannas (43%, n = 47), followed by papers about the mechanisms underlying these invasions (37%, n = 40). Articles about management accounted for 13% (n = 14) while theoretical papers summed up 7% (n = 7; Figure 1; Table 1).

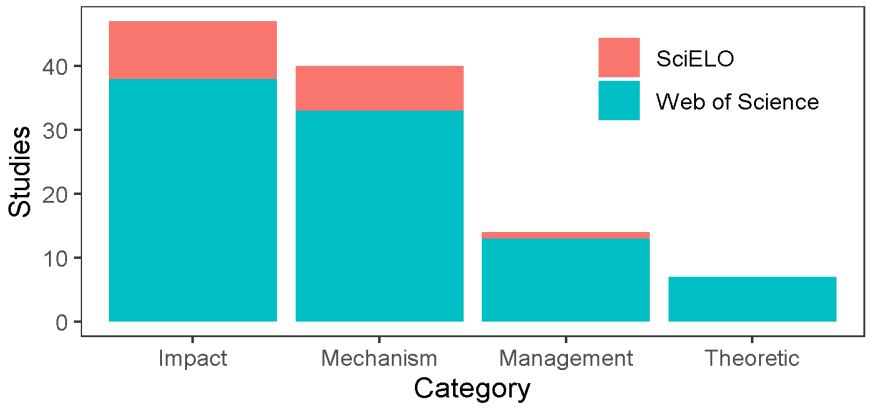

Figure 1. Number of scientific articles about grass invasions in tropical savannas retrieved from SciELO and The Web of Science databases (n = 108).

We developed a model of tropical savannas invaded by alien grasses composed by seven stages and 20 transitions (Figure 2). We defined a state to be stable if it is maintained by structuring negative feedbacks, which promote its stability in terms of community composition and function in the anthropic time-scale (Beisner et al., 2003). Alternatively, we considered a state to be transient if it was characterized by destabilizing positive feedbacks, which put the system in a succession pathway with varying communities. Consequently, the transient states could only be maintained by the input of stabilizing forces from management actions.

Table 1. List of scientific articles about invasive grasses in tropical savannas classified according to the issues addressed (impact, mechanism, management or theoretical), and topics within each theme.

Category	Topic	References[1]
Impact	Microhabitat	1,6,7,10,11,23,32,35,53
	Native plant populations	7,47,73
	Plant communities	1,6,7,11,16,21,23,27,31,32,101,102,103
	Animal communities	5,9,12,15,19,20,21,27,30
	Trophic networks	25
	Ecosystem	3,7,13,21,23,35,90, 108
	Disturbance	1,2,3,4,6,10,26,68,87,90,101
	Restoration	11,24,29,36,80,82,86,87,88,89,91,94,97
	Conservation	83,95,98
Mechanism	Invasiveness	12,18,28,33,40,47,48,49,52,54,55,57,61,63,65, 67,70,71,72,74,79,106,107
	Recruitment	24,40,49,51,54,56,60,64,67,77
	Growth	22,38,41,45,47,55,57,61,65,67,69
	Reproduction	50,62,64
	Dispersal	24,59,66,75,76,77,78,92,98,99,105
Management	Chemical control	46, 36, 39,100
	Physical control	21,32,34,36,38,40,45,46,100
	Biological control	85
	Long-term management	2,44
	Socioeconomic aspects	17, 37,42,44

[1]According to Table 1, Supplementary Material

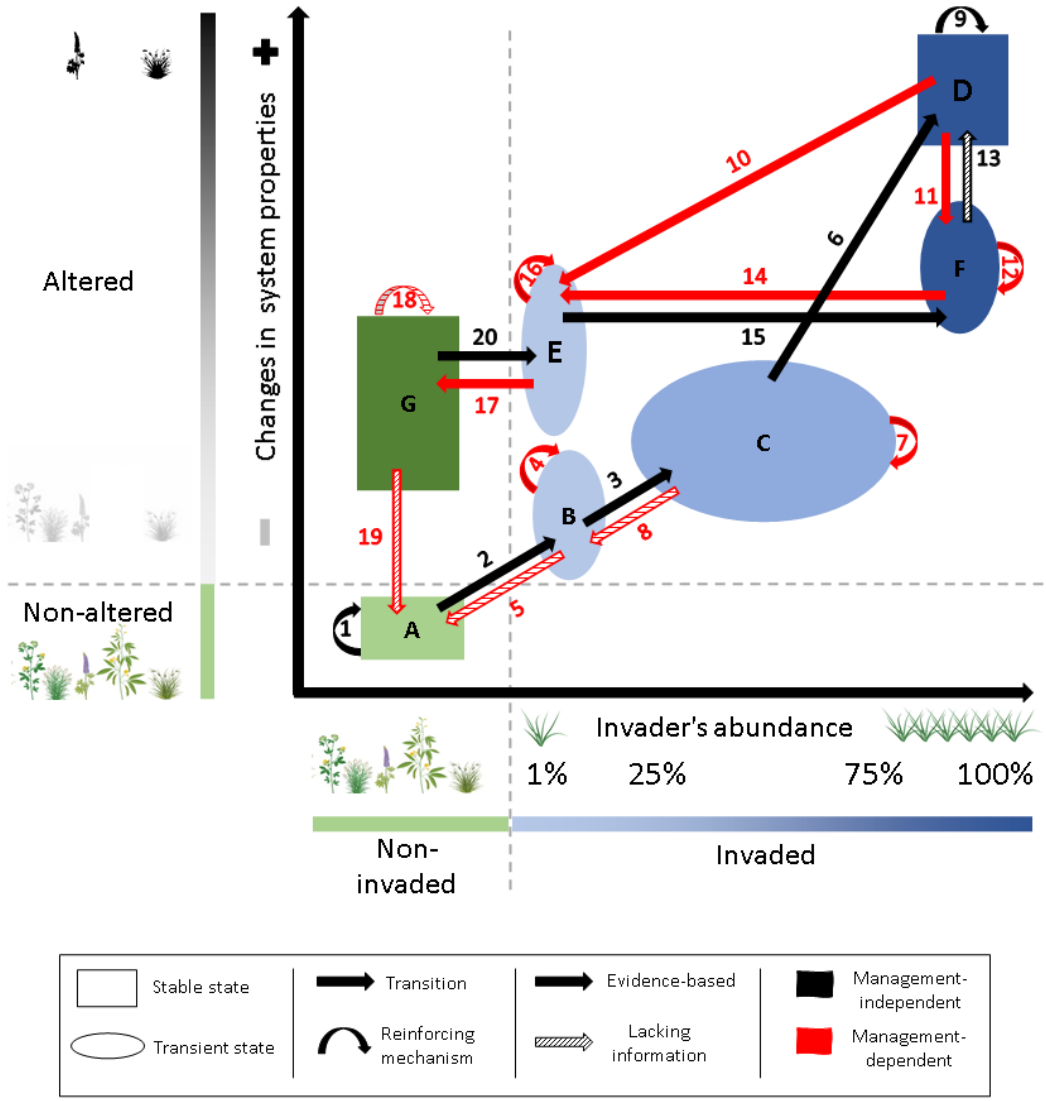

Figure 2. State-and-transition model of tropical savannas invaded by alien grasses. The x axis represents the abundance of the invasive alien grasses, which is related to the changes caused in the recipient system as represented in the y axis. Combinations of both axis results in alternative states (see Box 1 below); transitions (see Box 2 below) between states represent invasion progression and the use of management actions.

Overall, as a viable population of the invader is established, the non-invaded stable state A transitions towards the completely invaded stable state D. As management actions are applied to control the invasive alien grass, the invaded system can be actively maintained within the transient invaded states B, C, E, and F. It is also possible to eradicate the invader, returning the system to the pre-invasion conditions (state A) or to the alternative stable state G depending on the impacts already caused when eradication is carried out.

Box 1. Catalogue of states

State A: Non-invaded stable state determined by climatic conditions, soil properties and occurrence of natural fires. Naturally maintained by negative feedbacks between vegetation and system abiotic properties.

State B: Transient invaded state. Represents the beginning of alterations in system properties, as caused by initial levels of invader's abundance (< 25% of cover). This promotes destabilizing positive feedbacks, as for example, between the invader's cover and the proportion of bare soil in the community. Due to these positive feedbacks, this state naturally progresses towards state C if management is not adopted.

State C: Transient state derived from the intensification of the invasion process. The invasive species cover between 25% and 75% and produce more impacts in system properties, like community diversity. Destabilizing positive feedbacks between the invader cover and the abundance of native species act to promote this state towards the state D if management is not adopted.

State D: Stable state completely dominated by the invasive species, where it covers > 90% of the community. There is a massive transformation of the system's biotic properties like community composition and associated soil microbiota. Due to new stabilizing negative feedbacks between the invader and system properties, like modifications of fire regimes and nutrient cycles, this state will maintain itself if unmanaged.

State E: A transient state characterized by low levels of invasion (< 25% cover) but intermediate changes in system properties. It results from reduction of invader's abundance by management actions in heavily invaded states (D, F). Because of positive feedbacks like those acting on state B, it will return to the state D if not stabilized by management actions.

State F: Transient state resulting from management of totally invaded areas (D). These management actions are tailored to attenuate invader's impact instead of focused in reducing its abundance. These impacts will be resumed if management is ceased thus, creating positive feedbacks that will lead to further modifications of the system towards its return to state D.

State G: Non-invaded state resulting from eradication of the invader after it had achieved high levels of abundance. At such densities, the invader might have caused irreversible transformations of system properties (soil mineral content, plant-soil feedbacks), preventing the restoration of the former non-invaded state A. The stability of this state depends on the reestablishment of negative feedbacks like those acting in state A thus, guarantying its resistance to re-invasion.

Box 2. Catalogue of transitions

1: Self-reinforcing mechanisms of tropical savannas responsible for avoiding invasion by exotic grasses, like the system's natural dynamics and diversity.

2: Successful invasion of tropical savannas by exotic grasses. This transition occurs when a viable population of the invader establishes within the native vegetation, causing changes in the system properties like microclimatic conditions and the abundance of native species.

3: Unassisted intensification of the invasion process by increased abundance of the invader. This transition results from further modification of the system properties, like native species richness and community composition.

4: Management-based maintenance of the transient state B by containment of the invasive species population, i.e., no liquid population increase. This can be achieved by the prevention of new individual's recruitment and/or by the removal of established individuals. Independently of the management actions chosen, they should be applied annually to guarantee the invader's population containment through time.

5: Eradication of the invasion in systems with low levels of invader's abundance (< 25% cover). It can only be achieved by killing all established individuals and the depletion of invader's seed bank. These actions can be executed simultaneously or sequentially, but after their results are guaranteed (the system is resilient), no additional intervention is needed and the restored system stays within the stable state A unless a new invasion starts.

6: Further intensification of the invasion process. The unassisted increase in invader's abundance results in massive transformations of native communities and ecosystem process, like primary productivity, disturbance regimes and biogeochemical cycles; and possibly, impacts on higher trophic levels due to altered feeding by animals.

7: Similarly to number 4, these stabilizing mechanisms result from management actions tailored to limit invader's population growth. Management actions must be applied periodically (every 1-2 years) to keep the system within state C.

8: Transition resulting from management actions aiming to the suppression of the invader from intermediate (25 ~ 75% cover) to low levels of abundance (< 25% cover). Invader's suppression must be achieved by the removal of established individuals, together or not with actions tailored to prevent the establishment of new individuals. If management is successful in reducing the invader's cover, management actions are needed to be applied only once. However, further management of state B (transitions 4 or 5) will be required to prevent the system from progressing to state D.

9: Newly established feedback mechanisms, like altered competitive hierarchies and changed disturbance regimes can maintain the system within the degraded state D. Management actions are needed to promote transitions towards less impacted states like in E or F.

10: Transition resulting from the suppression of the invasive species in heavily invaded areas. Despite the decrease in invader's abundance, the restoration of pre-invasion properties of the system, like community structure and soil chemical composition might be no longer possible because of the massive negative impacts of the invader. If management is successful in suppressing the invader, management actions are needed to be applied only once. However, further management of state E (transitions 16 or 17) will be required to prevent the system from returning to state D.

11: Transition resulting from the alleviation of the negative impacts of the invader on native co-occurring species, without reductions in its abundance. If management is successful in reducing invader's negative impacts, management actions are needed to be applied only once. However, further management of state F (transitions 12 or 14) will be required to prevent the system from returning to state D.

12: Maintenance of the transient state F using management actions to attenuate negative impacts of the invasive species. Long-term monitoring of the management outcomes should be adopted to prevent further degradation of system properties.

13: Unassisted transition from the transient state F back to the degraded stable stated D with the cessation of management actions. Without the alleviation of impacts caused by management actions, the invader resumes its negative impacts on the recipient system.

14: Similarly to transition 10, this transition is dependent on management actions aimed to reduce the abundance of the invasive species. A pathway from state D to state E throughout state F represents the association of management actions to reduce invader's negative impacts (transition 11) with other techniques applied to suppress its abundance. If management is successful in reducing invader's abundance, management actions are needed to be applied only once. However, further management of state C (transitions 16 or 17) will be required to prevent the system to return to state D.

15: Transition resulting from the unassisted increasing in abundance of the invasive species in the absence of management actions to stabilize the system within state E.

16: Similarly to the management-based reinforcing mechanisms applied to the state B (transition 4) and state C (transition 7), management actions to contain invader populations should be applied for the stabilization of state E. Management actions should be applied periodically (1-2 years) to guarantee no increment of the invader's population size.

17: Eradication of the invader from a state with low levels of invasion but with altered conditions caused by the past dominance of the invasive species. Differently from transition 5, this eradication does not result in restoration of pre-invasion conditions, given the legacy left in the system even after complete removal of invasive individuals. The management actions required for this transition are related to the restoration of the native community (transition 17) and the feedback mechanisms acting to stabilize the non-invaded system (transition 18). If management is successful in eradicating the invader, management actions are needed to be applied only once.

18: Management-based maintenance mechanisms of the altered non-invaded system. The former dominance of the invader results in legacy effects, requiring the monitoring for the need of further restoration efforts aimed to increase the resilience of this state. If needed, management actions could involve manipulations of abiotic conditions, like soil chemical characteristics, and the re-introduction of native species locally excluded by the invader. Timely, the application of restoration efforts could be punctual or periodical (every year) depending on the re-establishment of state self-reinforcing mechanisms.

19: Restoration of pre-invasion conditions from an altered non-invaded system. This can only be achieved by overcoming the invader's legacy in the system after its eradication, including the seed bank and seed sources around. Although theoretically possible, this transition is potentially unfeasible in practice, given the complexity of ecological systems.

20: Re-invasion of a non-invaded altered area where the invader was eradicated after achieving high densities. The reinvasion might be facilitated by the failure in guaranteeing the stability of state G with management actions aimed to increase its resilience.

Discussion

The degradation process

The degradation process caused by the invasive alien grass is characterized

by changes in the feedback mechanisms acting on the recipient system. The successful establishment of the invader is the trigger leading to these changes, promoting the transition of the non-invaded stable state towards the completely invaded stable state. In intransitive networks where there is no clear competitive hierarchy between species, like species-rich tropical savannas, the system is stabilized by negative feedbacks determined by the self-organized structure of the community, (Beisner et al., 2003; Suding & Hobbs, 2009), which decreases community invasibility by biotic resistance and limiting similarity mechanisms (Enders et al., 2020). The introduction of the invasive alien species starts cascading positive feedbacks between the invader and the proportion of bare cover at the ground level (Damasceno & Fidelis, in preparation). At initial levels of cover (state B), the invasive alien grass can create gaps within vegetation, thus increasing the availability of space for its own expansion (Damasceno & Fidelis, in preparation).

New positive feedbacks, as a density-dependent population increase, appear in the system as the invader's abundance become higher (Hui & Richardson, 2017; Suding & Hobbs, 2009). At intermediate levels of cover (state C), the invader can reduce the abundance of native species, thus temporarily decreasing the interspecific competition it faces (Damasceno & Fidelis, in preparation). Beyond the community level, the invader also promotes impacts at the ecosystem level, thus further promoting the degradation process (Damasceno & Fidelis, in preparation; Douglas, Setterfield, Rossiter, Barratt, & Hutley, 2004; Garcia, Xavier, Camargo, Vieira, & Pivello, 2022; Rossiter-Rachor et al., 2009, 2017; Setterfield, Clifton, Hutley, Rossiter-Rachor, & Douglas, 2018a; Zenni et al., 2020).

As the invader completely dominates the community, there is a reversion of positive to negative feedbacks stabilizing the degraded invaded state (state D). When

the invasive alien species reaches high levels of abundance, its competitive advantages (Ens et al., 2015; Lawes & Grice, 2010; Musso et al., 2021), modifications of abiotic conditions (Holly, Ervin, Jackson, Diehl, & Kirker, 2009) and fire regimes (Gorgone-Barbosa et al., 2015; Rossiter-Rachor et al., 2009, 2017; Rossiter et al., 2003) create negative feedbacks between its dominance and the establishment of native species, thus stabilizing the invaded state as already found for other grassy systems (Wilsey, Daneshgar, Hofmockel, & Polley, 2014). Empirically, the resilience of the completely invaded state (state D) is attested by its ecological resistance in absorbing disturbances from management actions (Assis et al., 2021; Damasceno & Fidelis, 2020; Martins et al., 2011).

The maintenance of transient states by management actions

Since management actions can reduce both the abundance (Assis et al., 2021; Damasceno & Fidelis, 2020) and the impacts of invasive alien grasses (Damasceno, Durigan, & Fidelis, in preparation.; Zenni et al., 2020), we propose the adoption of management actions to stabilize transient invaded states. The type of actions taken will be determined by the local context, being guided by the aims of the management (Robertson et al. 2020) and limited by constrains of financial, socioeconomic and logistic origins (Crowley, Hinchliffe, & McDonald, 2017). In this sense, the use of decision analysis can help managers optimize adaptive management plans according to their reality (Maguire, 2004) in face of the myriad of actions been tested for the management of invasive alien grasses in tropical savannas. From the labor-consuming uprooting (Zenni et al. 2020) to the cheap use of prescribed burnings (Damasceno et al. 2020), every technique has its pro and

cons, and the combined use of them will probably result in the maximization of results while decreasing the financial costs (Assis et al. 2021). Nevertheless, the expected outcome of management, in terms of the status of the invasive alien species (Robertson et al. 2020), can help narrow down the list to a few best candidates.

Interventions tailored to the containment of the invader must impede its population growth either by preventing the recruitment of new individuals or by removing established individuals. In the first case, avoiding seed production is paramount and can be achieved by mechanical, chemical or biological ways. The cutting (Martins et al. 2011) or burning of adult individuals (Damasceno & Fidelis 2020) before they disperse seeds are examples of mechanical interventions; while the use of pre-emerge herbicides (Sebastian, Nissen, & Rodrigues, 2016) is a chemical option. There is also the potential for preventing seed dispersion by cattle grazing, giving cattle preference for these grasses used as planted forages (Miles et al., 1996). Cattle grazing damage the established individuals, reduce their competitive ability and might prevent reproduction (Beck et al. 2015; Ramirez-Yañez, Ortega-S, Brennan, & Rasmussen, 2007). However, due to possible negative impacts of cattle on native vegetation (Kimball & Schiffman, 2003; Ash et al. 2011), further studies considering this possibility are needed, especially regarding the abundance of the invader.

The containment of the invader's population is also possible by the removal of established individuals, and this is desired for the reduction of its abundance, i.e, suppression. Management techniques tailored to remove established invasive individuals must kill them, what can be achieved by uprooting (Zenni et al. 2021), hoeing or use of post-emergence herbicide (Assis et al. 2021). It could also involve

the use of parasites (Sutton et al., 2019); however, due to lack of information, biological control must be further investigated by scientific studies before its application.

Impact accommodation involves the attenuation of invader's negative impacts, what can be achieved by damaging established individuals via disturbance. In this sense, the use of prescribed burnings (Damasceno & Fidelis 2020), post-emergence herbicides (Assis et al. 2021) and cattle grazing (Ramirez-Yañez et al., 2007) can decrease the competitive advantage of invasive alien grasses over native species, thus reducing invader's impact on community diversity (Damasceno et al., in preparation). Moreover, these three techniques can be used as a first action in combined management, increasing the effectiveness and reducing the costs of following actions (Assis et al. 2021). Nevertheless, it is essential to closely monitor the invaded system during and after the application of management actions to detect opportunity windows and avoid undesirable outcomes.

The restoration processes

After the invader successfully establishes, the potential for system restoration derives from the gradual accumulation of the invader's negative impact as the invasion progresses. In the state B, system modifications are incipient, and eradication of the invader would revert the degradation process. As invader's impacts become more pronounced due to its increasing abundance, biotic and abiotic conditions are further altered (Bilbao & Medina, 1990; Garcia et al., 2022; Rossiter-Rachor et al., 2009, 2017; Setterfield, Clifton, Hutley, Rossiter-Rachor, & Douglas, 2018b; Zenni et al., 2020). Nevertheless, the absence of massive abiotic

alterations promoted by the invasive alien grasses, like modifications of hydrological cycles and soil destabilization and erosion, enables the restoration of the degraded stable state (Briske et al., 2006; King & Hobbs, 2006).

For restoration to succeed, the newly established negative feedbacks that maintain the invasion in the long-term must be overcome (Rossiter et al., 2003). However, the eradication of the invader in areas where it is completely dominant will not lead the system back to its non-invaded condition because of the invader's legacy (Zenni et al., 2020). Therefore, the restoration of a completely invaded area might lead to a different non-invaded stable state from the pristine one (state G). In these cases, the need for the re-introduction of native species should be evaluated in loco. As taxonomic and functional diversity help to increase community resistance to invasions (Enders et al. 2020), active introduction of native species would, hypothetically, help to reestablish self-reinforcing mechanisms and guarantee the maintenance of the restored state. However, the efficacy of this action is yet to be proved and it will certainly depend on the balance between positive (increased resistance to invasion) and negative effects of active re-introduction of native species (disturbance caused by interventions).

Conclusions

We created a threshold model resulting from short-term modifications of biotic and abiotic components by the intensification of the invasion process, represented by the invader's abundance (Beisner, Haydon, & Cuddington, 2003; Briske et al., 2006; Damasceno & Fidelis, in preparation; Suding, Gross, & Houseman, 2004; Suding & Hobbs, 2009). We also considered our model to follow a hysteretic dynamic where

the degradation and restoration pathways are not the same (*sensu* Suding & Hobbs, 2009). However, due to uncertainties about the effectiveness of restoration techniques, we also included the possibility of the stable restored state (state G) being brought back to the initial condition of the pre-invasion ecosystem (state A). By including the possibility for both a non-hysteresis and hysteresis threshold model, we minimized undesirable outcomes resulting from possible wrong assumptions about the system (Suding & Hobbs, 2009).

We considered the model to be framed in the short-medium timescale based on the life-cycle of invasive alien grasses. From the perspective of population dynamics of the invader, a period of five years is enough for successive generations to be incorporated in the system (Xavier et al., 2019; 2021). In the long-term, the management of invasive alien grasses in tropical savannas should be considered under the paradigm of adaptive management, in which the reduction of invader's impacts is the tenet (García-Díaz et al., 2021). Therefore, we recommend the careful monitoring of management actions outcome to guide future actions in the long-term.

We envisioned our model to be applied at a local scale because this is the scale at which the management of grass-invaded tropical savanna is usually adopted. However, we are aware that cross-scale dependencies might alter the dynamics of these ecosystems (Suding & Hobbs, 2009). Hence, we suggest comparisons of management actions taken under distinct contexts to investigate the general applicability of the model at distinct spatial scales. We emphasize the model was developed for the management of invasions in natural areas. Therefore, because of the great potential of native species to recover from belowground structures (Zupo et al. 2021), we did not include management techniques that revolve the soil, as is performed in planted pastures (Sampaio et al. 2019).

We suggest future studies to use a probabilistic approach (Briske et al., 2006) to address the states and transitions as proposed here. The probabilities of a trigger to occur in an area of interest might be estimated from information about the propagule pressure (Guimarães Silva et al., 2020), seed dispersal (Rebolo et al., 2021; Xavier et al., 2021) and the germination and establishment of invasive alien grasses (Musso et al., 2019). The occurrence of a trigger could also be estimated for different scenarios resulting from intentional management of the system (Gorgone-Barbosa, Daibes, Novaes, Pivello, & Fidelis, 2020; Gorgone-Barbosa, Pivello, Baeza, & Fidelis, 2016) or extreme climate conditions (Damasceno & Fidelis, 2020). Other probabilities for the model could be derived from manipulative experiments aiming to quantify the effect of management actions on population parameters.

Nevertheless, we identified population studies of invasive alien species as well as the investigation of their belowground impacts as being the major knowledge gap to the understanding and management in tropical savannas. Although some authors have looked at aspects of invasive alien grasses populations, most of them addressed questions related to seed dispersal and seedlings recruitment (Dairel & Fidelis, 2020; Gorgone-Barbosa et al., 2020, 2016; Musso et al., 2019, 2015; Paredes et al., 2018; Rebolo et al., 2021). Additionally, we also noted the lack of studies considering plant–plant and plant-microorganism interactions, as well as trophic consequences of grass invasion in tropical savannas.

We expect our model to be useful for managers dealing with the restoration of grass-invaded tropical savannas. However, as any model, we recognize it will not cover all aspects of reality. Above all, we hope to foster biodiversity conservation to promote a healthier world. Beyond looking for simple eradication, we believe that management should be carried out aiming to reduce the negative impacts of

widespread invasive alien species, as is the case of exotic grasses in tropical savannas.

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Zenni, R. D., Cunha, W. L., Musso, C., Souza, J. V., Nardoto, G. B., & Miranda, H. S. (2020). Synergistic impacts of co-occurring invasive grasses cause persistent effects in the soil-plant system after selective removal. *Functional Ecology*, *34*(5), 1102–1112. doi: 10.1111/1365-2435.13524

Zupo, T., Daibes, L. F., Pausas, J. G., & Fidelis, A. (2021). Post-fire regeneration strategies in a frequently burned Cerrado community. *Journal of Vegetation Science*, *32*(1), e12968. doi: 10.1111/JVS.12968

Supplementary information for Damasceno, Durigan and Fidelis: *"A state-and-transition model for the restoration of grass-invaded open tropical savannas"*

Table 1. Scientific publications retrieved from the literature search on Web of Science and Scopus. Search conducted in 2018 and updated in January 2021.

Number	Category	Title	Authors	Journal/Book	Year
1	Impact	A grass-fire cycle eliminates an obligate-seeding tree in a tropical savanna	Bowman, DMJS; MacDermott, HJ; Nichols, SC; Murphy, BP	Ecology And Evolution	2014
2	Management	Adding Fuel to the Fire: The Impacts of Non-Native Grass Invasion on Fire Management at a Regional Scale	Setterfield, SA; Rossiter-Rachor, NA; Douglas, MM; Wainger, L; Petty, AM; Barrow, P; Shepherd, IJ; Ferdinands, KB	Plos One	2013
3	Impact	Andropogon gayanus (Gamba grass) invasion increases fire-mediated nitrogen losses in the tropical savannas of northern Australia	Rossiter-Rachor, NA; Setterfield, SA; Douglas, MM; Hutley, LB; Cook, GD	Ecosystems	2008
4	Impact	Assessing fire potential in a Brazilian savanna nature reserve	Mistry, J; Berardi, A	Biotropica	2005
5	Impact	Complex mammal species responses to fire in a native tropical savannah invaded by non-native grader grass (Themeda quadrivalvis)	Abom, R; Parsons, SA; Schwarzkopf, L	Biological Invasions	2016
6	Impact	Ecological impacts of buffel grass (Cenchrus ciliaris L.) invasion in central Australia - does field evidence support a fire-invasion feedback?	Miller, G; Friedel, M; Adam, P; Chewings, V	Rangeland Journal	2010
7	Impact	Exotic grass invasion alters microsite conditions limiting woody recruitment potential in an Australian savanna	Setterfield, SA; Clifton, PJ; Hutley, LB; Rossiter-Rachor, NA; Douglas, MM	Scientific Reports	2018

Number	Category	Title	Authors	Journal/Book	Year
8	Impact	Fire Regimes and Invasive Species: A Changing Landscape	Stewart, PLF; Moss, PT; Stewart, DA; Farrell, R	International Journal Of Ecology & Development	2017
9	Impact	Habitat Complexity and Invasive Species: The Impacts of Gamba Grass (Andropogon gayanus) on Invertebrates in an Australian Tropical Savanna	Parr, CL; Ryan, BJ; Setterfield, SA	Biotropica	2010
10	Impact	How can an invasive grass affect fire behavior in a tropical savanna? A community and individual plant level approach	Gorgone-Barbosa, E; Pivello, VR; Bautista, S; Zupo, T; Rissi, MN; Fidelis, A	Biological Invasions	2015
11	Impact	Impact of invasive grasses on Cerrado under natural regeneration	Damasceno, G; Souza, L; Pivello, VR; Gorgone-Barbosa, E; Giroldo, PZ; Fidelis, A	Biological Invasions	2018
12	Impact	Increased grazing and dominance of an exotic pasture (Bothriochloa pertusa) affects vertebrate fauna species composition, abundance and habitat in savanna woodland	Kutt, AS; Fisher, A	Rangeland Journal	2011
13	Impact	Invasive Andropogon gayanus (Gamba grass) alters litter decomposition and nitrogen fluxes in an Australian tropical savanna	Rossiter-Rachor, NA; Setterfield, SA; Hutley, LB; McMaster, D; Schmidt, S; Douglas, MM	Scientific Reports	2017
14	Mechanism	Invasive Andropogon gayanus (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna	Rossiter-Rachor, NA; Setterfield, SA; Douglas, MM; Hutley, LB; Cook, GD; Schmidt, S	Ecological Applications	2009
15	Impact	Mechanisms of the impact of a weed (grader grass, Themeda quadrivalvis) on reptile assemblage structure in a tropical savannah	Abom, R; Vogler, W; Schwarzkopf, L	Biological Conservation	2015

Number	Category	Title	Authors	Journal/Book	Year
16	Impact	Native plant diversity in tropical savannas decreases when exotic pasture grass cover increases	Kutt, AS; Kemp, JE	Rangeland Journal	2012
17	Management	Permits to burn: weeds, slow violence, and the extractive future of northern Australia	Neale, T; Macdonald, JM	Australian Geographer	2019
18	Mechanism	Phytotoxicity and allelopathic potential of extracts from rhizomes and leaves of Arundo donax, an invasive grass in neotropical savannas	Girotto, L; Franco, AC; Nunez, CV; Oliveira, SCC; Scheffer de Souza, MC; Fachin-Espinar, MT; Ferreira, CS	Notulae Botanicae Horti Agrobotanici Cluj-Napoca	2021
19	Impact	Red-backed fairywrens adjust habitat use in response to dry season fires	Sommer, NR; Moody, NM; Lantz, SM; Leu, M; Karubian, J; Swaddle, JP	Austral Ecology	2018
20	Impact	Short-term responses of reptile assemblages to fire in native and weedy tropical savannah	Abom, R; Schwarzkopf, L	Global Ecology And Conservation	2016
21	Impact	Synergistic impacts of co-occurring invasive grasses cause persistent effects in the soil-plant system after selective removal	Zenni, RD; da Cunha, WL; Musso, C; de Souza, JV; Nardoto, GB; Miranda, HS	Functional Ecology	2020
22	Impact	The effects of tree cover and soil nutrient addition on native herbaceous richness in a neotropical savanna	Massi, KG; Eugenio, CUO; Franco, AC; Hoffmann, WA	Biotropica	2021
23	Impact	The invasive grass, Melinis minutiflora, inhibits tree regeneration in a Neotropical savanna	Hoffmann, WA; Haridasan, M	Austral Ecology	2008
24	Mechanism	The presence of invasive grasses affects the soil seed bank	Dairel, M; Fidelis, A	Journal Of Environmental	2020

Number	Category	Title	Authors	Journal/Book	Year
		composition and dynamics of both invaded and non-invaded areas of open savannas		Management	
25	Impact	Tracking dietary habits of cave arthropods associated with deposits of hematophagous bat guano: A study from a neotropical savanna	Salgado, SS; Motta, PC; Aguiar, LMD; Nardoto, GB	Austral Ecology	2014
26	Impact	Turning up the heat: the impacts of Andropogon gayanus (gamba grass) invasion on fire behaviour in northern Australian savannas	Setterfield, SA; Rossiter-Rachor, NA; Hutley, LB; Douglas, MM; Williams, RJ	Diversity And Distributions	2010
27	Impact	Why do lizards avoid weeds?	Hacking, J; Abom, R; Schwarzkopf, L	Biological Invasions	2014
28	Impact	Seeds of weeds as an alternative host of phytopathogens	Oliveira, Emerson Flores de, Santos, Patricia Resplandes Rocha dos, Santos, Gil Rodrigues dos	Arquivos Do Instituto Biol??O	2018
29	Impact	Avaliação do banco de sementes de uma área em processo de recuperação em cerrado campestre	Machado, V.M., Santos, J.B., Pereira, I.M., Lara, R.O., Cabral, C.M., Amaral, C.S.	Planta Daninha	2013
30	Impact	Habitat use by Collared Crescentchest (Melanopareia torquata) in a Cerrado in southeastern Brazil: implications for management	Kanegae, MF., Levy, G., Freitas, SR.	Brazilian Journal Of Biology	2012
31	Impact	Estrutura da comunidade de plantas lenhosas em fragmentos de cerrado: relação com o tamanho do fragmento e seu nível de perturbação	Carmo, A.B., Vasconcelos, H.L., Arajo, G.M.	Brazilian Journal Of Botany	2011
32	Impact	Impacto da invasão e do manejo do capim-gordura (Melinis minutiflora) sobre a riqueza e biomassa da flora nativa do Cerrado sentido restrito	Martins, C.R., Hay, J.D.V., Walter, B.M.T., Proen? C.E.B., Vivaldi, L.J.	Brazilian Journal Of Botany	2011

Number	Category	Title	Authors	Journal/Book	Year
33	Impact	Allelopathic evidence in Brachiaria decumbens and its potential to invade the Brazilian Cerrados	Barbosa, Elizabeth Gorgone, Pivello, V?a Regina, Meirelles, S?io Tadeu	Brazilian Archives Of Biology And Technology	2008
34	Management	Banco de sementes em cerrado sensu stricto sob queimada e sistemas de cultivo	Ikeda, Fernanda Satie, Mitja, Danielle, Vilela, Lourival, Silva, Jos?arlos Sousa	Pesquisa Agropecu?A Brasileira	2008
35	Impact	Acmulo de biomassa aérea e concentração de nutrientes em Melinis minutiflora P. Beauv. e gramíneas nativas do cerrado	Silva, Jos?alom?Oliveira, Haridasan, Mundayantan	Brazilian Journal Of Botany	2007
36	Impact	Capim - gordura (Melinis minutiflora P. Beauv.), uma gramínea exótica que compromete a recuperação de áreas degradadas em unidades de conservação	Martins, Carlos Romero, Leite, La?io Leonel, Haridasan, Mundayatan	Revista Rvore	2004
37	Management	A Sea of Gamba: Making Environmental Harm Illegible in Northern Australia	Neale, T	Science As Culture	2019
38	Management	Abundance of invasive grasses is dependent on fire regime and climatic conditions in tropical savannas	Damasceno, G; Fidelis, A	Journal Of Environmental Management	2020
39	Management	Allelopathy of a native shrub can help control invasive grasses at sites under ecological restoration in a Neotropical savanna	Lopes, PG; Oliveira, SCC; Salles, KA; Sampaio, AB; Schmidt, IB	Plant Ecology & Diversity	2018
40	Mechanism	Effects of fire and defoliation on the life history of native and invader C-4 grasses in a Neotropical savanna	Baruch, Z; Bilbao, B	Oecologia	1999
41	Management	Elevated carbon dioxide and fire reduce biomass of native grass	Tooth, IM; Leishman, MR	Biological Invasions	2014

Number	Category	Title	Authors	Journal/Book	Year
		species when grown in competition with invasive exotic grasses in a savanna experimental system			
42	Management	Entangled invasive lives: Indigineous invasive plant management in Northern Australia	Head, L; Atchison, J	Geografiska Annaler Series B-Human Geography	2015
43	Management	Fire and weeds: Interactions and management implications	Wilson, C; Mudita, W	Fire And Sustainable Agricultural And Forestry Development In Eastern Indonesia And Northern Australia, Proceedings	2000
44	Management	Governing invasive plants: Policy and practice in managing the Gamba grass (Andropogon gayanus) - Bushfire nexus in northern Australia	Head, L; Atchison, J	Land Use Policy	2015
45	Management	Native and exotic plant species respond differently to wildfire and prescribed fire as revealed by meta-analysis	Alba, C; Skalova, H; McGregor, KF; D'Antonio, C; Pysek, P	Journal Of Vegetation Science	2015
46	Management	Residual herbicide treatments reduce Andropogon gayanus (Gamba Grass) recruitment for mine site restoration in northern Australia	Luck, L; Bellairs, SM; Rossiter-Rachor, NA	Ecological Management & Restoration	2019
47	Mechanism	Responses of tropical native and invader C-4 grasses to water stress, clipping and increased atmospheric CO2 concentration	Baruch, Z; Jackson, RB	Oecologia	2005

Number	Category	Title	Authors	Journal/Book	Year
48	Mechanism	Alien plant invasions in tropical and sub-tropical savannas: patterns, processes and prospects	Foxcroft, LC; Richardson, DM; Rejmanek, M; Pysek, P	Biological Invasions	2010
49	Mechanism	Constraints to colonization and growth of the African grass, Melinis minutiflora, in a Venezuelan savanna	Barger, NN; D'Antonio, CM; Ghneim, T; Cuevas, E	Plant Ecology	2003
50	Mechanism	Distinctive seed dispersal and seed bank patterns of invasive African grasses favour their invasion in a neotropical savanna	Xavier, RO; Christianini, AV; Pegler, G; Leite, MB; Silva-Matos, DM	Oecologia	2021
51	Mechanism	Disturbance as a factor in breaking dormancy and enhancing invasiveness of African grasses in a Neotropical Savanna	Gorgone-Barbosa, E; Pivello, VR; Baeza, MJ; Fidelis, A	Acta Botanica Brasilica	2016
52	Mechanism	Dynamics of energy and nutrient concentration and construction cost in a native and two alien C-4 grasses from two neotropical savannas	Baruch, Z; Gomez, JA	Plant And Soil	1996
53	Mechanism	Ecophysiological aspects of the invasion by African grasses and their impact on biodiversity and function of neotropical savannas	Baruch, Z	Biodiversity And Savanna Ecosystem Processes: A Global Perspective	1996
54	Mechanism	Effects of canopy cover and ground disturbance on establishment of an invasive grass in an Australia savanna	Setterfield, SA; Douglas, MM; Hutley, LB; Welch, MA	Biotropica	2005
55	Mechanism	Effects of water and nutrient availability on morphological, physiological, and biochemical traits of one invasive and one native grass	Musso, C; Fontenele, HGV; Pinto, G; Oliveira, R; Correia, C; Moutinho-Pereira, JM; Soares, AMVM; Loureiro, S	Environmental And Experimental Botany	2021

Number	Category	Title	Authors	Journal/Book	Year
		of a Neotropical savanna			
56	Mechanism	Fire cues and germination of invasive and native grasses in the Cerrado	Gorgone-Barbosa, E; Daibes, LF; Novaes, RB; Pivello, VR; Fidelis, A	Acta Botanica Brasilica	2020
57	Mechanism	Fluctuating resources, disturbance and plant strategies: diverse mechanisms underlying plant invasions	Radford, IJ	Journal Of Arid Land	2013
58	Mechanism	Germinable soil seed banks in a tropical savanna: seasonal dynamics and effects of fire	Williams, PR; Congdon, RA; Grice, AC; Clarke, PJ	Austral Ecology	2005
59	Mechanism	Inferring habitat suitability and spread patterns from large-scale distributions of an exotic invasive pasture grass in north Australia	Petty, AM; Setterfield, SA; Ferdinands, KB; Barrow, P	Journal Of Applied Ecology	2012
60	Mechanism	Light affects the germination and normal seedling development of Neotropical savanna grasses	Pereira, CM; Figueiroa, RNA; Fontenele, HGV; Miranda, HS	Seed Science Research	2021
61	Mechanism	Low resource availability limits weed invasion of tropical savannas	Taylor, HR; Radford, IJ; Price, C; Grierson, P	Biological Invasions	2018
62	Mechanism	Phenological and reproductive traits and their response to environmental variation differ among native and invasive grasses in a Neotropical savanna	Xavier, RD; Leite, MB; Matos, DMD	Biological Invasions	2019
63	Mechanism	Positive frequency dependence undermines the success of restoration using historical disturbance regimes	Crandall, R; Knight, TM	Ecology Letters	2015
64	Mechanism	Seedling recruitment of the exotic grass Andropogon gayanus (	Flores, TA; Setterfield, SA; Douglas, MM	Australian Journal Of Botany	2005

Number	Category	Title	Authors	Journal/Book	Year
		Poaceae) in northern Australia			
65	Mechanism	Soil depth and fertility effects on biomass and nutrient allocation in jaraguagrass	Pieters, A; Baruch, Z	Journal Of Range Management	1997
66	Mechanism	Spatial pattern of invasive and native graminoids in the Brazilian cerrado	Dodonov, P; Harper, KA; Xavier, RD; Matos, DMS	Plant Ecology	2019
67	Mechanism	Stress responses of native and exotic grasses in a Neotropical savanna predict impacts of global change on invasion spread	Xavier, RD; Leite, MB; da Silva-Matos, DM	Austral Ecology	2017
68	Impact	Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia	Rossiter, NA; Setterfield, SA; Douglas, MM; Hutley, LB	Diversity And Distributions	2003
69	Mechanism	The superior re-sprouting performance of exotic grass species under different environmental conditions: the study case of Paspalum atratum (Swallen) and Urochloa brizantha (Hochst. ex A. Rich. - Stapf.)	Caramaschi, GMCL; Barbosa, ERM; da Silva, DA; Braga, VB; Borghetti, F	Theoretical And Experimental Plant Physiology	2016
70	Mechanism	Unassisted invasions: understanding and responding to Australia's high-impact environmental grass weeds	van Klinken, RD; Friedel, MH	Australian Journal Of Botany	2017
71	Mechanism	War of the weeds: Competition hierarchies in invasive species	Lawes, RA; Grice, AC	Austral Ecology	2010
72	Mechanism	Water relations of native and introduced C4 grasses in a Neotropical Savanna	BARUCH, Z; FERNANDEZ, DS	Oecologia	1993
73	Mechanism	Factors influencing seed germination in Cerrado grasses	Kolb, Rosana Marta, Pilon, Natashi Aparecida Lima, Durigan, Giselda	Acta Botanica Brasilica	2016

Number	Category	Title	Authors	Journal/Book	Year
74	Mechanism	Seasonal variation of soluble carbohydrates and starch in Echinolaena inflexa, a native grass species from the Brazilian savanna, and in the invasive grass Melinis minutiflora	Souza, A., Sandrin, CZ., Cali??FA., Meirelles, ST., Pivello, VR., Figueiredo-Ribeiro, RCL.	Brazilian Journal Of Biology	2010
75	Mechanism	Dormência e armazenabilidade de sementes de capim-gordura	Carmona, Ricardo, Martins, Carlos Romero	Revista Brasileira De Sementes	2010
76	Mechanism	Qualidade física, viabilidade e dormência de sementes recém-colhidas de capim-gordura (Melinis minutiflora P. Beauv.)	Carmona, Ricardo, Martins, Carlos Romero	Revista Brasileira De Sementes	2010
77	Mechanism	Potencial invasor de duas cultivares de Melinis minutiflora no cerrado brasileiro - características de sementes e estabelecimento de plântulas	Martins, Carlos Romero, Hay, John Du Vall, Carmona, Ricardo	Revista Rvore	2009
78	Mechanism	Efeito do local de coleta nas características de sementes de capim-gordura (Melinis minutiflora P. Beauv.) no Distrito Federal, Brasil	Carmona, Ricardo, Martins, Carlos Romero	Revista Brasileira De Sementes	2009
79	Mechanism	Diurnal variations of non-structural carbohydrates in vegetative tissues of Melinis minutiflora, Echinolaena inflexa and Lolium multiflorum (Poaceae)	Souza, Amanda de, Sandrin, Carla Z., Moraes, Moemy G., Figueiredo-Ribeiro, Rita de C?ia L.	Brazilian Journal Of Botany	2005
80	Theoretic	Abandoned pastures cannot spontaneously recover the attributes of old-growth savannas	Cava, MGB; Pilon, NAL; Ribeiro, MC; Durigan, G	Journal Of Applied Ecology	2018
81	Impact	Can native vegetation recover after slash pine cultivation in the Brazilian	de Abreu, RCR; de Assis, GB; Frison, S; Aguirre, A; Durigan, G	Forest Ecology And Management	2011

Number	Category	Title	Authors	Journal/Book	Year
		Savanna?			
82	Impact	Cerrado'' restoration by direct seeding: field establishment and initial growth of 75 trees, shrubs and grass species	Pellizzaro, KF; Cordeiro, AOO; Alves, M; Motta, CP; Rezende, GM; Silva, RRP; Ribeiro, JF; Sampaio, AB; Vieira, DLM; Schmidt, IB	Brazilian Journal Of Botany	2017
83	Impact	Conservation of the Brazilian Cerrado	Klink, CA; Machado, RB	Conservation Biology	2005
84	Theoretic	Exotic Grass Invasions: Applying a Conceptual Framework to the Dynamics of Degradation and Restoration in Australia's Tropical Savannas	Brooks, KJ; Setterfield, SA; Douglas, MM	Restoration Ecology	2010
85	Management	Grazing Management in Tropical Savannas: Utilization and Rest Strategies to Manipulate Rangeland Condition	Ash, AJ; Corfield, JP; McIvor, JG; Ksiksi, TS	Rangeland Ecology & Management	2011
86	Impact	How effective is direct seeding to restore the functional composition of neotropical savannas?	Giles, AL; Costa, PD; Rowland, L; Abrahao, A; Lobo, L; Verona, L; Silva, MC; Monge, M; Wolfsdorf, G; Petroni, A; D'Angioli, AM; Sampaio, AB; Schimidt, IB; Oliveira, RS	Restoration Ecology	2021
87	Theoretic	Invasive plants as drivers of regime shifts: identifying high-priority invaders that alter feedback relationships	Gaertner, M; Biggs, R; Te Beest, M; Hui, C; Molofsky, J; Richardson, DM	Diversity And Distributions	2014
88	Impact	Lessons on direct seeding to restore Neotropical savanna	Sampaio, AB; Vieira, DLM; Holl, KD; Pellizzaro, KF; Alves, M; Coutinho, AG; Cordeiro, A; Ribeiro, JF; Schmidt, IB	Ecological Engineering	2019
89	Impact	Plant colonization in a gravel mine revegetated with Stylosanthes spp. in a Neotropical savanna	Starr, CR; Correa, RS; Filgueiras, TD; Hay, JD; dos Santos, PF	Landscape And Ecological Engineering	2013
90	Theoretic	Plant invasion science in protected	Foxcroft, LC; Pysek, P; Richardson, DM; Genovesi, P;	Biological Invasions	2017

Number	Category	Title	Authors	Journal/Book	Year
		areas: progress and priorities	MacFadyen, S		
91	Impact	Savannas after afforestation: Assessment of herbaceous community responses to wildfire versus native tree planting	Haddad, TM; Viani, RAG; Cava, MGB; Durigan, G; Veldman, JW	Biotropica	2020
92	Impact	Seed characterization and direct sowing of native grass species as a management tool	Aires, SS; Sato, MN; Miranda, HS	Grass And Forage Science	2014
93	Theoretic	The 10 Australian ecosystems most vulnerable to tipping points	Laurance, WF; Dell, B; Turton, SM; Lawes, MJ; Hutley, LB; McCallum, H; Dale, P; Bird, M; Hardy, G; Prideaux, G; Gawne, B; McMahon, CR; Yu, R; Hero, JM; Schwarzkop, L; Krockenberger, A; Douglas, M; Silvester, E; Mahony, M; Vella, K; Saikia, U; Wahren, CH; Xu, ZH; Smith, B; Cocklin, C	Biological Conservation	2011
94	Impact	The recovery rates of secondary savannas in abandoned pastures are poorly explained by environmental and landscape factors	Cava, MGB; Pilon, NAL; Priante, CF; Ribeiro, MC; Durigan, G	Applied Vegetation Science	2020
95	Impact	Threats to the cerrado remnants of the state of Sao Paulo, Brazil	Durigan, G; de Siqueira, MF; Franco, GADC	Scientia Agricola	2007
96	Theoretic	Vegetation, Fire, and Feedbacks: A Disturbance-Mediated Model of Savannas	Beckage, B; Platt, WJ; Gross, LJ	American Naturalist	2009
97	Impact	Ocorrência de plantas não-nativas e exóticas em áreas restauradas de campos rupestres	FERNANDES, G. W., SANTOS, R., BARBOSA, N. P. U., ALMEIDA, H. A., CARVALHO, V., ANGRISANO, P.	Planta Daninha	2015
98	Mechanism	Landscape-level determinants of the spread and impact of invasive grasses in protected areas	Guimarães Silva, R., Zenni, R. D., Rosse, V. P., Bastos, L. S., & van den Berg, E.	Biological Invasions	2020
99	Impact	Andropogon gayanus Kunth invasion in the Cerrado: from seed	Musso, C., de Macedo, M. A., Almeida, N. N., de Melo Rodrigues, D., Camargo, M. E. M. S., Pôrto, A.	Biological Invasions	2019

Number	Category	Title	Authors	Journal/Book	Year
		production to seedling establishment along roadsides	C. C. Q., & Miranda, H. S.		
100	Management	Effectiveness and costs of invasive species control using different techniques to restore cerrado grasslands	Assis, G. B., Pilon, N. A., Siqueira, M. F., & Durigan, G	Restoration Ecology	2021
101	Impact	Impact of invasion by molasses grass (Melinis minutiflora P. Beauv.) on native species and on fires in areas of campo-cerrado in Brazil	Rossi, R. D., Martins, C. R., Viana, P. L., Rodrigues, E. L., & Figueira, J. E. C.	Acta Botanica Brasilica	2014
102	Impact	Alien grasses in Brazilian savannas: a threat to the biodiversity	Pivello, V. R., Shida, C. N., & Meirelles, S. T.	Biodiversity And Conservation	1999
103	Impact	Abundance and distribution of native and alien grasses in a "cerrado" (Brazilian savanna) biological reserve	Pivello, V. R., Carvalho, V. M. C., Lopes, P. F., Peccinini, A. A., & Rosso, S.	Biotropica	1999
104	Theoretic	A qualitative successional model to assist in the management of Brazilian cerrados	Pivello, V. R., Coutinho, L. M.	Forest Ecology And Management	1996
105	Mechanism	Native ants help to spread an invasive African grass in the Cerrado	Rebolo, I. F., Zirondi, H. L., Fidelis, A., & Christianini, A. V.	Biotropica	2021
106	Mechanism	Resource-use efficiency explains grassy weed invasion in a low-resource savanna in north Australia	Ens, E., Hutley, L. B., Rossiter-Rachor, N. A., Douglas, M. M., & Setterfield, S. A	Frontiers In Plant Science	2015
107	Mechanism	Effects of recent fire on soil conditions and nutrient use of a native and an invasive grass in the Brazilian savanna	Pereira-Silva, E. F. L., Hardt, E., Biral, M. B., Keller, V. C., & Delitti, W. B. C.	Écoscience	2019
108	Impact	Can an invasive African grass affect carbon and nitrogen stocks in open habitats of the Brazilian Cerrado?	Garcia, D. B., Xavier, R. O., Camargo, P. B., Vieira, S. A., & Pivello, V. R.	Flora	2022

CONSIDERAÇÕES FINAIS

O objetivo desta tese foi, utilizando como espécie modelo *Urochloa decumbens*, fornecer subsídios para o manejo de gramíneas exóticas invasoras em ecossistemas abertos de Cerrado. Visando a geração de informações que sejam facilmente aplicadas em campo, escolhemos estruturar nossa pesquisa considerando a abundância da invasora como uma variável indicadora do estado de degradação do sistema invadido. Dessa forma, conciliamos as teorias sobre invasões biológicas e restauração ecológica com a prática da ecologia aplicada no dia a dia, feita a partir de observações diretas em campo. Esperamos que nossos resultados influenciem o desenvolvimento de políticas públicas baseadas em evidências científicas para o manejo e restauração de ecossistemas abertos de Cerrado.

Sempre considerando a abundância da espécie exótica invasora como elemento central do estudo, organizamos a tese a partir de uma sequência linear de perguntas que correspondem aos três capítulos desenvolvidos. No primeiro capítulo, examinamos qual a relação entre a abundância da gramínea exótica invasora e as propriedades do sistema invadido; no segundo capítulo investigamos como a abundância da gramínea exótica invasora influencia o resultado de queimadas prescritas para seu controle; e no terceiro capítulo respondemos como a abundância da invasora relaciona-se com transformações (degradação e restauração) do sistema invadido por meio da elaboração de um modelo de estado-e-transição.

Nossos resultados corroboram os impactos negativos que gramíneas africanas exercem sobre as comunidades nativas de Cerrado, mas encontramos poucas evidências de que os processos ecossistêmicos estejam sendo alterados. Indo além do que outros trabalhos haviam demonstrado, porém, elucidamos como

esses impactos estão diretamente relacionados à abundância da invasora. Encontramos que os impactos da invasora nas comunidades nativas não aumentam de forma linear com sua abundância, implicando que pequenos aumentos de abundância da invasora podem acarretar grandes impactos.

Esta informação é crucial para o planejamento do manejo, pois é possível evitar que a invasora atinja níveis de abundância que resultem nos maiores impactos negativos para a comunidade nativa. Em relação à composição da comunidade, por exemplo, há uma diminuição na abundância de gramíneas nativas desde os níveis iniciais de invasão (< 25% cobertura pela invasora), mas o impacto na diversidade de espécies é amplificado em níveis intermediários de abundância da invasora (50 ~75% de cobertura pela invasora). Dessa forma, ainda que o impacto pareça pequeno quando a invasora está em baixas abundâncias, o manejo deve ser adotado tão rápido quanto possível para impedir que seus efeitos negativos se magnifiquem e causem a exclusão de espécies nativas.

Outra descoberta importante para fomentar o manejo dessas invasões é que a abundância da invasora modula o efeito do fogo nas propriedades do sistema invadido. Este resultado também tem importante aplicação prática, pois permite um melhor planejamento das ações de manejo em relação a seus objetivos, que são dependentes do contexto e podem variar desde a redução da abundância da invasora até a promoção de formas de crescimento específicas, como arbustos nativos. Entretanto, demonstramos também que queimadas prescritas são eficientes em atenuar os impactos da invasora sobre as comunidades nativas independentemente de sua abundância. Todavia, este favorecimento das espécies nativas dá-se de formas diferentes a depender da abundância da invasora, podendo acontecer por meio do aumento da riqueza de espécies ou da equitabilidade das

comunidades; ou por meio da redução da eficiência fotossintetizante da invasora. A partir desta informação, a execução de diferentes ações de manejo pode ser planejada para depois da realização das queimadas prescritas, visando promover ainda mais as espécies nativas em detrimento da invasora.

Por fim, a grande contribuição desta tese é o desenvolvimento de uma nova ferramenta, cientificamente embasada, para o planejamento e prática da restauração de ecossistemas abertos de Cerrado invadidos por gramíneas exóticas. Nosso modelo de estado-e-transição (Figura 1) demonstra as etapas da degradação dessas áreas ao longo do processo invasivo, destacando possibilidades para deter ou mesmo reverter esse processo. O ponto forte de nosso modelo é ser baseado na abundância da gramínea invasora, permitindo que uma avaliação em campo informe sobre a situação do sistema invadido e facilite a elaboração de um plano de manejo. Alternativamente a indicar ações de manejo específicas, apresentamos possíveis trajetórias de restauração que podem ser seguidas a depender dos interesses e possibilidades dos gestores em cada contexto. Recomendamos, porém, que as ações sejam tomadas o mais rápido possível pois, à medida que o tempo passa, a invasora aumenta em abundância, o sistema torna-se mais alterado e a restauração mais complexa. Assim, propomos que os gestores priorizem a manutenção do estado não-invadido (estado A) ao evitarem a primeira transição, qual seja o estabelecimento de populações viáveis da invasora. Além disso, propomos também que ações de manejo sejam priorizadas em áreas nas quais a invasora ainda esteja em níveis baixos de abundância (estado B), facilitando sua erradicação e a restauração do sistema não-invadido.

De forma mais ampla, esperamos que nosso modelo, para além de ser utilizado por gestores no manejo das gramíneas invasoras, seja também uma fonte

de inspiração para novos estudos científicos. Acreditamos que a ciência é construída de forma contínua e colaborativa: cada nova resposta traz consigo várias outras perguntas. E nesse processo dinâmico, esperamos que nosso modelo instigue perguntas e críticas que façam a ciência e a prática da ecologia avançarem ainda mais, criando alternativas para o enfrentamento dos desafios que a humanidade encontrará em decorrência das mudanças globais.

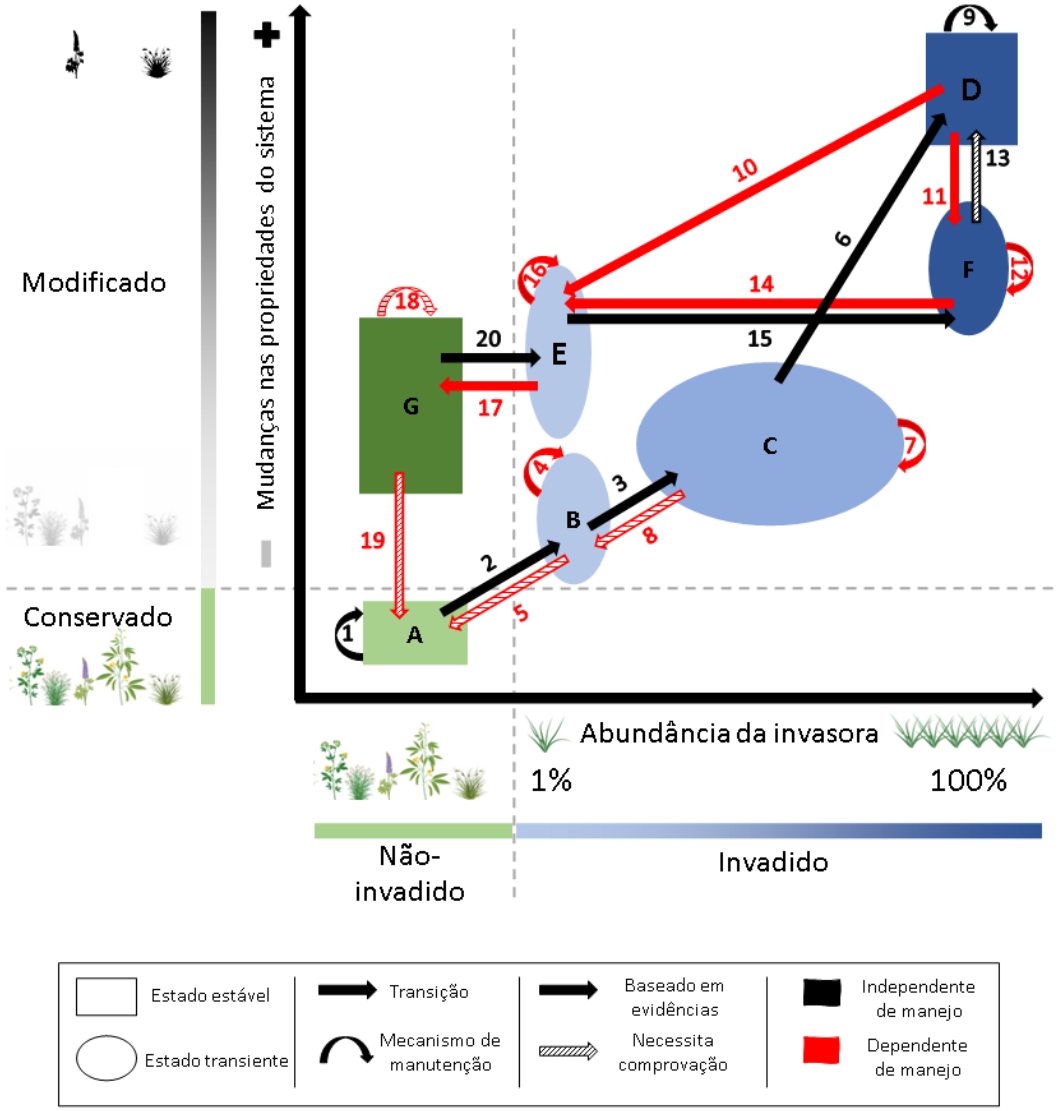

Figura 1. Modelo de estado-e-transição de savanas tropicais invadidas por gramíneas exóticas. O eixo x representa a abundância de gramíneas invasoras, que está relacionada às alterações das propriedades do sistema, representada no eixo y. Combinações dos dois eixos resultam em estados alternativos à medida que a invasão progride e ações de manejo são aplicadas.

Box 1. Lista de estados

Estado A: Estado não invadido estável; determinado por condições climáticas, propriedades do solo e ocorrência de queimadas naturais. Mantido por feedbacks negativos entre a vegetação e as propriedades abióticas do sistema.

Estado B: Estado invadido transiente. Representa o início de alterações nas propriedades do sistema, causadas por níveis iniciais de abundância da invasora (< 25% de cobertura). Estas alterações promovem a criação de feedbacks positivos que desestabilizam a comunidade, como entre a abundância da invasora e a cobertura por solo nu. Devido a estes feedbacks, este estado naturalmente progride para o estado C se não manejado.

Estado C: Estado transiente, resultante da Intensificação do processo de invasão. A invasora cobre entre 25% e 75% do solo e impacta mais propriedades do sistema, como a diversidade da comunidade. Feedbacks positivos desestabilizadores, entre a abundância da invasora e espécies nativas, promovem a transição deste estado ao estado D se o manejo não for adotado.

Estado D: Estado estável completamente dominado pela espécie invasora, que cobre mais de 90% da comunidade. Há transformações massivas de propriedades bióticas do sistema, como composição da comunidade vegetal e microbiota de solo associada. Devido ao estabelecimento de novos feedbacks negativos estruturadores, como modificações de regime de fogo e ciclos de nutrientes, este estado se mantém caso ações de manejo não sejam adotadas.

Estado E: Estado transiente caracterizado por níveis baixos de abundância da invasora (< 25%) porém níveis intermediários de alterações das propriedades do sistema. Este estado resulta da redução da abundância da invasora por meio de ações de manejo em estados muito invadidos (estados D, F). Devido a feedbacks positivos similares aos encontrados no estado B, este estado retorna ao estado D se não estabilizado por ações de manejo.

Estado F: Estado transiente resultante de ações de manejo em áreas totalmente invadidas (estado D). As ações de manejo objetivam a redução dos impactos da invasora ao invés de sua abundância. Tende a retornar ao estado D se não manejado continuamente devido à presença de feedbacks positivos.

Estado G: Estado não invadido resultante da erradicação da invasora em áreas onde sua abundância atingiu níveis altos (estados C e/ou F). Em tais abundâncias, a invasora pode ter promovido alterações irreversíveis nas propriedades do sistema, impossibilitando a restauração das condições anteriores à invasão (estado A). Sua estabilidade depende da criação de feedbacks negativos, como os encontrados no estado A, que aumentem sua resistência à novas invasões.

Box 2. Lista de transições

1: Mecanismos de automanutenção de savanas tropicais responsáveis por evitar a invasão por gramíneas exóticas, como a diversidade e a dinâmica natural do sistema.

2: Invasão bem-sucedida de savanas tropicais por gramíneas exóticas. Esta transição ocorre quando a invasora estabelece uma população viável em meio a vegetação nativa, causando alterações em propriedades do sistema como condições microclimáticas e afetando a abundância de espécies nativas.

3: Intensificação não-assistida do processo invasivo por meio do aumento da abundância da invasora. Esta transição resulta de posteriores alterações nas propriedades do sistema, como riqueza de espécies nativas e composição de comunidades.

4: Manutenção, por meio de ações de manejo, do estado transiente B, a partir da contenção da população da espécie invasora. Possíveis intervenções envolvem a prevenção da dispersão de sementes e/ou a remoção de novos indivíduos recrutados do banco de sementes. As ações de manejo devem ser aplicadas anualmente para garantir a contenção da população ao longo do tempo.

5: Erradicação da invasão em sistemas nos quais a abundância da invasora seja baixa (< 25% de cobertura). Somente pode ser atingida pela morte de todos os indivíduos estabelecidos e depleção do banco de sementes da invasora. Estas intervenções podem ser executadas simultaneamente ou sequencialmente; após a garantia do sucesso de suas ações, o sistema torna-se resiliente e nenhuma ação adicional é necessária. O sistema restaurado permanece no estado A até a ocorrência de uma nova invasão.

6: Intensificação do processo invasivo. O aumento não-assistido da abundância da invasora resulta em transformações massivas das comunidades nativas e de processos do ecossistema, como produtividade primária, regimes de distúrbio e ciclos biogeoquímicos; e possivelmente, impactos em níveis tróficos mais altos através da alimentação por animais.

7: Similarmente à transição 4, estes mecanismos de estabilização resultam da aplicação de ações de manejo delineadas para a limitar o crescimento da população da invasora. Ações de manejo devem ser aplicadas periodicamente (a cada um ou dois anos) para manter o sistema no estado C.

8: Transição resultante de ações de manejo objetivando a supressão da invasora de níveis intermediários (25 ~ 75% de cobertura) para níveis baixos de abundância (< 25%). A supressão da invasora deve ser atingida pela remoção de indivíduos estabelecidos, combinada ou não a ações que evitem o estabelecimento de novos indivíduos. Dado o sucesso em suprimir a invasora, ações de manejo devem ser aplicadas somente uma vez, Entretanto, outras ações de manejo aplicadas ao estado B (transições 4 ou 5) serão necessárias para evitar que o sistema progrida para o estado D.

9: Novos mecanismos de feedback, como hierarquias de competição modificadas e regimes de distúrbio alterados mantem o sistema no estado D. Ações de manejo são necessárias para promover transições em direção a estados menos impactados pela invasora, como os estados E ou F.

10: Transição resultante da supressão da invasora em áreas totalmente invadidas. Apesar da redução da abundância da invasora, a restauração de condições anteriores à invasão, como estrutura da comunidade e composição química do solo podem não ser mais viáveis em virtude dos impactos massivos já causados pela invasora. Dado sucesso em suprimir a invasora, ações de manejo podem ser aplicadas somente uma vez. Entretanto, o manejo do estado E (transições 16 e 17) será necessário para prevenir o sistema de retornar ao estado D.

11: Transição resultante da atenuação dos impactos negativos da invasora sobre espécies nativas, sem redução de sua abundância, entretanto. Dado o sucesso em reduzir os impactos da invasora, ações de manejo podem ser aplicadas somente uma vez. Entretanto, o manejo do estado F (transições 12 e 14) será necessário para prevenir o sistema de retornar ao estado D.

12: Manutenção do estado transiente F pela execução de ações de manejo destinadas a atenuar os impactos negativos da invasora. Monitoramento do sistema a longo-prazo é necessária para prevenir possíveis degradações resultantes da aplicação continuada de ações de manejo.

13: Transição não-assistida do estado transiente F de volta ao estado degradado estável D a partir da cessação do manejo. Sem a atenuação de impactos, a invasora volta a causar impactos negativos no sistema.

14: Similarmente à transição 10, esta transição depende da implementação de ações de manejo para a redução da abundância da invasora. A trajetória entre os estados D-E que passa pelo estado F representa a associação do manejo para a redução dos impactos negativos da invasora (transição 11) com outras técnicas direcionadas à sua supressão. Esta transição resulta de esforços de manejo pontuais, porém o manejo do estado E (transições 16 e 17) será necessário para evitar que o sistema retorne ao estado D.

15: Transição resultante do aumento não-assistido da abundância da invasora na ausência de ações de manejo que estabilizem o sistema no estado E.

16: Similarmente aos mecanismos de automanutenção dependentes de manejo aplicados no estado B (transição 4) e C (transição 7), ações de manejo para conter a população da invasora devem ser aplicadas para a estabilização do estado E. Ações de manejo devem ser aplicadas periodicamente (a cada um ou dois anos) para garantir que não haja um incremento populacional da invasora.

17: Erradicação da invasão a partir de um estado com baixa abundância da invasora, mas no qual as propriedades do sistema já foram alteradas pela anterior dominância da invasora. Diferentemente da transição 5, esta erradicação não resulta na restauração de condições anteriores à invasão, dado o legado da invasora após sua erradicação. Ações de manejo necessárias para promover esta transição estão relacionadas à restauração da comunidade nativa (transição 17) e dos mecanismos de feedback que estabilizam o estado não-invadido (transição 18)., Dado o sucesso em erradicar a espécie invasora, ações de manejo devem ser aplicadas somente uma vez.

18: Manutenção, por meio de ações de manejo, do estado G não invadido. A anterior dominância da espécie invasora deixa legados no sistema, ensejando o monitoramento da necessidade de ações adicionais de restauração visando o aumento da resiliência deste estado. Caso sejam necessárias, ações de restauração podem envolver a manipulação de condições abióticas, como conteúdo mineral do solo, e a reintrodução de espécies nativas localmente excluídas pela invasora. Temporalmente, as ações de restauração podem ser tanto pontuais ou periódicas (a cada ano) dependendo do reestabelecimento de mecanismos de automanutenção responsáveis por incrementar a resistência da comunidade a novas invasões.

19: Restauração de condições anteriores à invasão a partir de um sistema não-invadido, porém alterado pela prévia dominância da invasora. Somente pode ser alcançado a partir da eliminação do legado da invasora após sua erradicação, incluindo banco de sementes e fontes de sementes vizinhas. Apesar de teoricamente possível, esta transição é potencialmente impossível na prática, dada a complexidade de sistemas ecológicos.

20: Re-invasão de uma área onde a invasora foi erradicada após atingir uma alta abundância. A re-invasão pode ser facilitada pela falha em garantir a estabilidade do estado G por meio de ações de manejo direcionadas a aumentar sua resiliência.