UNIVERSIDADE FEDERAL DE LAVRAS

MARIA ANGÉLICA ONO

BIOTIC AND ABIOTIC EFFECTS OF THE COMMUNITY ON THE FUNCTIONALITY AND STRUCTURE OF A HOST-PARASITOID MULTITROPHIC FOOD WEB IN THE LONG TERM

LAVRAS – MG

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Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecologia e Conservação de Recursos Naturais em Ecossistemas Fragmentados e Agrossistemas, para a obtenção do título de Doutora.

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Prof. Dr. Lucas Del Bianco Faria
Orientador

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MARIA ANGÉLICA ONO

EFEITOS BIÓTICOS E ABIÓTICOS DA COMUNIDADE SOBRE A FUNCIONALIDADE E ESTRUTURA DE UMA REDE MULTITRÓFICA HOSPEDEIRO-PARASITÓIDE EM LONGO PRAZO

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E sobre o fato de não sermos imortais. Eu nunca quis acreditar que meu pai fosse partir. Também não imaginava o quanto a sua presença me implicava em segurança. Ainda que no meio de tantas fragilidades, ele me imprimia coragem. Sento agora em sua cadeira e vejo que está vaga, uma tentativa de preencher o vazio que ele me deixou. Na minha frente vejo o horizonte por onde devo seguir forte e segura com seus ensinamentos. "Aos trancos e barrancos" , cambaleante eu vou. E quando parece tudo estar sem sentido, surge o alarme do despertador, vulgo mãe para me acordar. Mãe ensina que a vida é fluxo contínuo e mesmo que a gente endureça com os tombos, sempre existirá dentro de nós um colo de mãe para lembrar que a vida não precisa ser dura, basta passar "merthiolate" e dar uma "assopradinha". Amor e gentileza também são um jeito sutil e eficaz de nos fazer crescer.

Aos meus pais, **Teresa** e **Getúlio** (*in memorian*)

que nunca mediram esforços para que eu chegasse até aqui

Dedico

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"Bom, às vezes a vida é dura, mas eu tenho muita coisa para agradecer."

(William P. Young- A Cabana)

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E lá vou eu, nas minhas tentativas, às vezes meio cegas, às vezes meio burras, tentar acertar os passos. Sem me preocupar se a próxima etapa será o tombo ou o voo...

(Caio Fernando Abreu)

No Final sempre dá certo...

RESUMO

Toda rede trófica apresenta métricas estruturais em comum, onde metaforicamente pode ser considerada como um "mapa" que mostra a localização das espécies, no entanto, a localização não é tão clara, porque as espécies estão conectadas por elos de alimentação que podem arrebentar ou flexibilizar, devido a intensidade da interação exercida. O que pode comprometer a estabilidade e a complexidade da rede por meio da composição funcional entre os níveis tróficos. Compreender como cada espécie responde à variações no ambiente impulsionadas por fatores bióticos e abióticos a longo prazo é relevante para estudar a diversidade funcional das espécies no ecossistema. No entanto, as ramificações potenciais de mudanças mais amplas nas redes tróficas no que condiz às interações hospedeiro-parasitoide por meio de interações diretas e indiretas, da qual as espécies são afetadas são amplas, mas pouco documentadas, principalmente em relação à composição funcional, estrutura, estabilidade e complexidade. Nesta tese, foram abordadas questões sobre dinâmica funcional e sua relação com o meio e a rede trófica. No capítulo 1, foi investigado se a composição funcional dos níveis tróficos está correlacionada com a estrutura, complexidade e estabilidade da rede. No capítulo 2, foi explorado a relação da funcionalidade das espécies com fatores bióticos e abióticos. Em ambos os capítulos, foi utilizado um conjunto de dados de cinco anos sobre a rede trófica hospedeiro-parasitoide hospedada por *Senegalia tenufolia*. Os resultados do capítulo 1 mostraram que a estrutura, complexidade e estabilidade da rede trófica estão correlacionadas às taxas funcionais, principalmente com o nível trófico mais alto. No capítulo 2, demonstramos que a temperatura e a precipitação atuam de forma diferenciada nas taxas de herbivoria e parasitismo e, sobretudo, há uma combinação de fatores abióticos e bióticos que impulsionam a funcionalidade das espécies. Os resultados em conjunto, de ambos os capítulos nos dão a ideia de que a diversidade funcional e a estrutura da rede estão correlacionadas para garantir sua estabilidade e complexidade, na qual composição funcional dos níveis tróficos é impulsionada pela sinergia entre biótico e abiótico. As principais implicações encontradas no contexto do funcionamento do ecossistema são discutidas ao final da tese.

Palavras-chaves: Complexidade. Diversidade. Rede Trófica. Taxa de Herbivoria. Taxa de Parasitismo. Taxa de hiperparasitismo.

ABSTRACT

Every food web has structural metrics in common, where metaphorically can be considered as a "map" that shows the species location however, the location of them is not so clear because the species are linked by feeding links that can be breakable or flexible due to the intensity of the interaction between them in the web, which can compromise the stability and complexity of the web through the functional composition between trophic levels. Understanding how each species respond to variations in the environment driven by biotic and abiotic factors in the long term is relevant for studying the diversity function of species in the ecosystem. However, the potential ramifications of wider changes to food webs on host-parasitoid interactions through both direct and indirect interactions that are affected are wide-ranging but poorly documented, mainly regarding trophic level functionality, structure, stability, and complexity. In this thesis, questions about functional dynamics and their relationship with the environment and the trophic network were addressed. Manuscript 1, was investigated whether the functional composition of the trophic levels that are correlated with the structure, complexity, and stability of the food web. Manuscript 2, was explored the relationship of species functionality with biotic and abiotic factors. In both manuscripts, was used a dataset for the long term of the five years about the host-parasitoid food web hosted by Senegalia tenuifolia. The results of manuscript 1, showed that the structure, complexity, and stability of the food web are correlated to herbivory, parasitism, and hyperparasitism rate, especially the highest trophic level. In manuscript 2, was found that temperature and precipitation act differently on herbivory and parasitism rates, and above all, there is a combination of abiotic and biotic factors that drive the species functionality. Taken together the results from both chapters give us the idea that the functional diversity and structure of the network are correlated to ensure its stability and complexity, in which the functional composition of the trophic levels is driven by the synergy between biotic and abiotic. The main implications found in the context of the functioning of the ecosystem are discussed at the end of the thesis.

KEYWORDS: Complexity. Diversity**.** Food Web. Herbivory Rate. Hyperparasitism Rate. Parasitism Rate.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

Metaforicamente redes tróficas são semelhantes a um grande mapa, onde sinaliza a localização das espécies (PIMM et al., 1991; THOMPSON et al., 2012). Em se tratando de comunidade natural, múltiplos herbívoros e parasitoides se ligam para formar uma complexa rede de interação, onde sob processos dinâmico a localização da espécie pode não ser tão clara, simplesmente porque ao interagir com as demais espécies, se torna susceptível às mais diversas condições que podem flexibilizar ou até mesmo romper o elo inicial, devido a intensidade das interações (MCCANN; HASTINGS; HUXEL, 1998; EVELEIGH et al., 2007).

Considerando a topologia das interações direcionais, toda rede trófica apresenta métricas quantitativas em comum que determinam a sua estrutura, na qual podemos citar: as espécies de topo (%Topo), intermediária (%Intermediária) e também a parte basal (%Basal) que são marcadas por uma razão consumidor-recurso, com propriedades de vulnerabilidade e generalidade, o qual foi introduzido por Schoener (1989) para mensurar a média do número de consumidor por presa e o número de presa por consumidor, respectivamente. A rede tem em comum também, uma proporção de ligações tróficas (i.e. elos de alimentação) entre os diferentes tipos de espécies com uma variação funcional (i. e. taxas de funcionalidade que caracteriza a função da espécie), na qual são marcados por uma escala dependente responsável por configurar a estrutura da rede trófica com diferentes comprimentos de cadeias e complexidade (BERSIER et al., 2002; COHEN et al., 1978; LANDI et al., 2018; MARTINEZ, 1994; MARTINEZ; LAWTON, 1995; PASCUAL; DUNNE, 2005; PIMM; LAWTON; COHEN, 1991; VAN DER PLAS, 2019).

Desde que foi inserida por May (1972), conectância (C) tem sido amplamente usada como um indicador de complexidade (NEWMAN, 2010; ESTRADA, 2012), mensurando a riqueza de espécies e a proporção de interações realizadas entre todas as interações possíveis na rede trófica (LANDI et al., 2018). Este fato, remete ao fato de que a diversidade funcional da população pode ser decomposta em três características principais: a variabilidade individual com traços múltiplos, a força das correlações entre esses traços e a direção dessas correlações (BOUCHER et al., 2013). Dessa forma, a questão que mais tem intrigado a comunidade cientifica é se a diversidade e complexidade da comunidade também está

relacionada com a função do ecossistema (GRIME, 1998; HUSTON, 1997; RODRÍGUEZ; HAWKINS, 2000; VAN DER PLAS, 2019). Uma vez que, redes tróficas são consideradas mais do que a soma de suas espécies componentes e podem responder às mais diversas mudanças do meio, de uma maneira imprevisível e não refletida de forma adequada na abundância e diversidade de suas espécies (TYLIANAKIS et al., 2007).

As interações entre herbívoros e seus respectivos inimigos naturais podem influenciar as populações biológicas de maneira direta ou indireta, refletindo-se em conseqüências para o sistema dinâmico (WOOTTON, 1994). Interações fracas entre consumidor e recurso podem assegurar maior estabilidade em teias e garantir a persistência das espécies, pela mera minimização de efeitos oscilatórios no sistema trófico (McCANN et al., 1998). Interações competitivas são aquelas em que organismos influenciam-se de forma a possibilitar uma espécie limitar a densidade populacional da outra, seja pela mera exploração de recursos ou interferência direta sobre a outra espécie culminando em exclusão com significativa regulação intra ou interespecífica (GOTELLI, 2001). A competição atua como importante força estrutural dentro de uma comunidade ecológica (LAW; WATKINSON, 1989). Ela pode ainda desempenhar ação direta sobre o sistema interativo (LAWTON; HASSELL, 1981), causar também efeito indireto, ou apresentar-se no formato de competição aparente, quando competidores compartilham um mesmo predador ou parasitoide (HOLT, 1977).

Dessa forma, a abundância e riqueza tanto de herbívoros como de parasitoides podem afetar a interação entre as espécies, promovendo distúrbios e acentuando a competição intra e interespecífica nas comunidades naturais, na qual a presença do inimigo natural pode minimizar os resultados competitivos entre a duas ou mais espécie de herbívoros (DENNO et al., 1995; RIBEIRO-COSTA, 1998). De acordo com Denno et al. (1995), o aumento do ataque e a eficiência do parasitoide sobre o herbívoro competidor mais fraco, pode minimizar os efeitos negativos provindos da competição. O mesmo ocorre quando as espécies herbívoras compartilham o mesmo parasitoide, através de efeitos indiretos à presença do inimigo natural pode aumentar a pressão em atacar uma determinada espécie herbívora que é mais susceptível ao parasitismo (DENNO et al., 1995; ABRAMS & MATSUDA, 1996; ABRAMS et al., 1998; HIERRY; HRČEK; LEWIS, 2019).

Este cenário pode ser atribuído ao fato de que a taxa de parasitismo altera as competições entre herbívoros, simplesmente por modificarem a força da interação e a riqueza de espécies na estrutura da rede trófica (THIERRY; HRČEK; LEWIS, 2019), na qual a estrutura da rede trófica também pode se comportar de maneira dinâmica em muitos níveis tróficos, mudando no tempo e no espaço como resultado da plasticidade das interações entre

as espécies e a variação do ambiente (EVELEIGH et al., 2007; GIBERT, 2019; PASCUAL; DUNNE, 2005). A interação entre hospedeiro-parasitoide pode fornecer um interessante caso de estudo para fatores abióticos e bióticos, uma vez que há condições que podem atrapalhar ou favorecer a taxa de encontro e seleção do hospedeiro para que o parasitismo seja bem sucedido, o que pode causar uma alteração no padrão observado de variabilidade da comunidade e sua funcionalidade (MICHELI et al., 1999; HUGHES, 2000; THIERRY; HRČEK; LEWIS, 2019).

Compreender a relação dinâmica entre a estrutura, complexidade da rede trófica e o seu funcionamento tem sido uma questão fundamental na ecologia, na qual se torna uma importante aplicação para predizer respostas do ecossistema frente as variações climáticas (WANG, 2020), onde cada população de inseto pode responder de maneira idiossincrática para as variações ambientais, que pode impactar de forma direta ou indireta o seu crescimento, desenvolvimento e também a interação com outras espécies (DAVIS et al., 1998; BALE et al., 2002).

Variações ambientais podem alterar as abundâncias absolutas e relativas dos táxons (CARDINALE et al., 2006), onde as variações climáticas além de afetar a produtividade primária e as características do recursos podem também causar uma relação positiva entre a planta e a diversidade do grupo funcional (LOREAU, 1998; MICHELI et al., 1999). Neste quesito, frutos maiores podem ser mais atrativos para a colonização dos insetos (COPE & FOX, 2003; ÖSTERGÅRD et al., 2007; DE SOUSA-LOPES et al., 2019). Temperatura e precipitação (i.e. fatores abióticos) parece combinar com as características do recurso, abundância e riqueza de espécies (i. e. fatores bióticos) para determinar a dinâmica das interações e complexidade das redes tróficas (MICHELI et al., 1999). Por um lado, temperatura pode aumentar o metabolismo de insetos herbívoros e acelerar a mortalidade de insetos parasitoides. Em outro ângulo, precipitações em excesso podem prejudicar a sobrevivência e aumentar o tempo de desenvolvimento de artrópodes, podendo interromper o vôo e até mesmo reduzir a eficiência do forrageamento de herbívoros e parasitóides (BALE et al., 2002; STIREMAN et al., 2005; GILMAN et al., 2010).

O sistema multitrófico que engloba a espécie *Senegalia tenuifolia* BRITTON & ROSE (Fabaceae: Mimosoideae) e suas respectivas sementes pode funcionar como um modelo de estudo para explorar o forrageio na herbivoria e parasitismo em relação as variações climáticas em longo prazo. Pode servir também como alicerce para investigar e compreender a variabilidade funcional (i.e. variabilidade dos traços funcionais das espécies) que pode assegurar a estrutura e estabilidade da rede trófica. Tendo em vista que a espécie

arbórea hospeda diferentes grupos taxonômicos de insetos que consomem frutos e sementes, entre eles se destacam as ordens Lepidoptera, Coleoptera e Hymenoptera. *Merobruchus terani* e *Stator maculatopygus* (Coleoptera: Chrysomelidae, Bruchinae) estão comumente associados à predação de sementes de *S. tenuiflolia* evidenciando o significativo consumo da planta. As duas espécies de Bruchinae representaram mais de 90% da abundância total de insetos que se alimentam de sementes (TULLER et al., 2015). Cada espécie do besouro é capaz de explorar a semente de forma diferenciada. *Merobruchus terani* é o primeiro a ovipositar no fruto ainda na planta mãe, sendo assim o consumidor primário da semente, enquanto que *S. maculatopygus* se comporta como o segundo consumidor, já que oviposita em frutos deiscentes, isto é, quando os frutos atingem o ápice da sua maturação (DAN-JOHNSON & ROMERO, 2004*). Senegalia tenuifolia* também é composto pelo terceiro e quarto nível trófico, na qual abriga uma diversidade de espécie de parasitoides, em sua grande maioria generalistas (TULLER et al., 2015; MAIA et al., 2017, 2018).

Usando um banco de dados de cinco anos que remete a rede trófica composta por *S. tenuifolia* e suas interações tróficas e dentro do escopo que abrange a tese exploramos e investigamos os efeitos que estão atrelados ao processo funcional das espécies herbívoras e parasitoides e como esses efeitos impactam a rede trófica. A tese está organizada em dois capítulos. Cada capítulo está formatado em uma versão preliminar de manuscrito para a divulgação do artigo científico.

No primeiro capítulo, usando como motivação a lacuna bibliográfica existente em relação à composição funcional das redes tróficas no que rege a sua dinâmica e estrutura (MONTEIRO & FARIA, 2018), investigamos o papel funcional da estrutura e complexidade da rede trófica. Por meio de uma estatística descritiva e usando análise de correlação não paramétrica proposta por Zar (2005), nós respondemos as seguintes questões: (*i*) as taxas de herbivoria, parasitismo e hiperparasitismo estão correlacionadas com as métricas da rede trófica?, (*ii*) se correlacionado, através das taxas de funcionalidade (i.e. taxa de herbivoria e parasitismo) dos níveis tróficos pode causar algum efeito que compromete a estrutura, estabilidade e complexidade da rede trófica?

No segundo capítulo, por meio de modelagem de regressão, propostos por Stasinopoulos e Rigby (2007), na qual usa modelos aditivos generalizados para locação, escala e forma (generalized additive models for location, scale and shape – GAMLSS), exploramos os efeitos dos fatores abióticos e bióticos que podem estar atrelados as taxas de herbivoria e parasitismo. Neste estudo usamos um banco de dados meteorológicos captados por diferentes satélites e sistemas sensores pertencentes à NASA's Earth para responder as

seguintes perguntas levantadas: (*i*) temperatura e precipitação afetam as taxas de herbivoria e parasitismo da mesma maneira?; (*ii*) como as características dos frutos, abundancia e riqueza de herbivoros e parasitoides agem sobre as taxas de herbivoria e parasitismo?

Finalizando a tese eu apresento uma sessão de conclusão geral, onde eu discuto as implicações encontradas em ambos os capítulos, fazendo referência aos principais contextos da ecologia no que remete a funcionalidade das espécies, estrutura, complexidade e estabilidade de redes tróficas complexas. O presente trabalho pode servir de base para outros estudos visando a compreensão do funcionamento das redes tróficas e suas interações.

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SEGUNDA PARTE: Artigos

**ARTIGO 1: Food web map: the route between the four trophic levels concerning
functionality, structure, and complexity**

"Este artigo está formatado nas normas do periódico Functional Ecology (versão preliminar)"

Acknowledgments

Abstract

1. Every food web has structural metrics in common, which can be metaphorically considered as a "map" that shows the species location. However, the location of them is not so clear because the species are linked by feeding links that can be breakable or flexible due to the intensity of the interaction between them in the food web, which can compromise the stability and complexity of the web through the functional composition between levels trophic.

2. This study assesses the combination metrics of food web and herbivory, parasitism, and hyperparasitism rates to establish a correlation between structure, stability, the complexity of food web, and functional composition of the levels trophic.

3. We find that the herbivory rate is negatively associated with fractions of the top species and positively associated with intermediate species and ratio consumer-resource. The parasitism rate is negatively correlated to the fractions of links between intermediate-basal, on other hand is positively correlated to the fractions of links intermediate-intermediate and also the max chain length. Hyperparasistism rate has a negative correlation with fraction basal, the fractions of links intermediate-basal and connectance, however it has a positive correlation between fractions of the intermediate links and max chain length.

4. It is concluded that the level trophic functionality is correlated with food web metrics, where the structure, complexity, and stability of the food web can be modulated by the functional composition, where the complexity of the food web could be matching the connectivity of the habitat over of the dynamic interaction between species, mostly from the upper level.

Keywords: interaction, herbivory rate, hyperparasitism rate, metrics of the food web top-level, parasitism rate

Introduction

Metaphorically a food web can be considered as a "map" that shows the species location (Pinn *et al.*, 1991, Thompson *et al.*, 2012). However, the location of them is not so clear because the species are linked by feeding links that can be breakable or flexible due to the intensity of the interaction among organisms in the food web (McCann *et al.*, 1998, Eveleigh *et al.*, 2007). Further, all food web has in common characteristics -i.e. suite of metrics which can be calculated to describe food web structure (Thompson *et al.*, 2012), such as fractions of all species in a web, top (%Top), intermediate (%Intermediate), and basal (%Basal), that include also a ratio of consumer-resource. Additionally, the fractions of links between top and intermediate species (%Top-Intermediate), top and basal species (%Top-Basal), intermediate species (%Intermediate-Intermediate), and intermediate and basal species (%Intermediate-Basal), as well as the properties of vulnerability and generality that were introduced by Mougi & Kondoh, 2016 as the mean number of consumers per prey, and the mean number of prey per consumer, respectively. It is also integrated by common characteristics with different lengths of the chain and connectance that are related to their complexity (Pinn et al., 1991; Martinez, 1994; Martinez & Lawton, 1995; Besier et al., 2002; Pascual & Dunne, 2005, Landi et al., 2018). However, the structure is dynamic at many scales, changing in time and space as the result of the plasticity of interactions between the composition of species and environment variation (Mougi & Kondoh, 2016).

However, the nature of the relationship between the species diversity of food web and its stability is a long standing problem in ecology (Pinn, 1984, McCann et al., 1998, Mougi & Kondoh, 2016). A closely related question that intrigues the scientific community is whether the diversity of communities is also related to ecosystem function (Huston, 1997; Grime, 1998; Rodríguez & Hawkins, 2000; van der Plas, 2019), which include the presence or relative abundance a top species, a combination of species, beyond variation in functional composition (van der Plas, 2019). Studies of model webs has demonstrated that stability and function are integrated across all trophic levels (Naeem et al., 1994, Naeem & Li, 1997), where increasing species richness generally raised the number of functions that species-rich communities maintained multiple functions at higher levels (Lefcheck et al., 2015).

The functional composition - i.e. herbivory, parasitism, and hyperparasitism of the community has a direct effect on the food web through the effects of species identity and an indirect effect through its impact on the structure of the food web (Gravel et al., 2016). There is, however, currently a gap that relating the functional composition of food webs to their

dynamics and structure, making it hard to measure and understand the y (Monteiro & Faria, 2018), mainly when it involves a more diverse array of interactions such as herbivory, parasitism, and hyperparasitism (Gravel et al., 2016). Specification of the functionality that species played is necessary allowing the determination if some communities have unusual properties of the food web to support more species than their size constraints in dynamic scale dependencies (Martinez & Lawton, 1995).

Multitrophic host-parasitoid food web supported for *Senegalia tenuifolia* (L.) BRITTON & ROSE (Fabaceae: Mimosoideae) is assumed as a model to explore the structure and complexity concerning the functionality level trophic that host herbivores, parasitoids, and hyperparasitoids in which they can interact with each other. The plant species is a host of several herbivorous insect taxa consuming fruits and seeds, such as Lepidoptera, Coleoptera, and Hymenoptera. The third and fourth trophic levels represent different species of parasitoids in the vast majority of generalists- i. e. sharing the same host (Tuller et al., 2015; Maia et al., 2017, 2018). Here, we used long-term data of the multitrophic food web to investigate the functional role of the structure and complexity of the food web. (*i*) is there any correlation between the trophic level functionality (i.e. herbivory, parasitism, and hyperparasitism rates) and metrics of the food web? (*ii*) whether correlated it can, through functionality level trophic, cause effects on other interactions, compromising the structure, stability, and complexity of the food web?

Material and Methods

Field description

We carried out this study at the municipalities of Lavras and Luminarias in fragments of Brazilian cerrado (savanna) in the south of Minas Gerais state, southeastern Brazil. The study was divided into three main areas (i. e. sites) as a unit of logistic reachability, called A (located in the municipality of Luminárias-MG), B, and C (located in the municipality of Lavras-MG). Across these three sites, nine collection spots which are our true replica, were established which were at least 400 m from each other (**A1:** 21∘31′ 1.36″S, 044∘53′ 1.78″W; **A2:** 21∘31′ 5.13″S, 044∘52′ 6.32″W; **A3:** 21∘31′ 5.31″S, 044∘52′ 3.84″W; **A4:** 21° 31'32.3" S, 044° 52'24.3" W; **B1:** 21∘18′ 3.46″S, 044∘58′ 0.53″W; **B2:** 21∘19′ 4.85″S, 044∘57′ 8.66″W; **C1:** 21∘14′ 4.57″S, 044∘57′ 6.38″W; **C2:** 21∘14′ 5.71″S, 044∘57′ 8.66″W; **C3:** 21∘14′ 7.87″S, 044∘58′ 0.06″W), (Fig. 1). According to the Köppen-Geiger climate

classification, this region's climate is classified as Cwa and Cwb, being defined by a subtropical altitude climate with dry winter and mild summer (Köppen, 1900.; Kottek et al., 2006; Reboita et al., 2015). The average temperature of 19.4°C, and the annual average rainfall of 1529.5mm - Brazilian National Institute of Meteorology (INMET) (BRAZIL, 1992).

Fig. 1. A- Map of Brazil, highlighting the state of Minas Gerais.
B - Map of Minas Gerais, highlighting the municipalities of Lavras and Luminárias.
C-Location of the sampling sites from where we collected *Senegalia tenuifolia* fruits. Extracted from Maia et al., 2017. A1, A2, A3, A4 correspond to spots the municipality of Luminárias-MG. B1, B2, C1, C2 and C3 correspond to spots the municipality of Lavras

Senegalia tenuifolia (model plant) and dataset

Senegalia tenuifolia is known from almost all states of Brazil and several phytogeographic domains (Barros & Morim, 2014). However, in the Atlantic Domain, its altitudinal gradient varies between 250–847m. It has a wide distribution in the Americas (Rico-Arce, 2007). The plant is the host of the different taxonomic groups of insects, with predominance to order Coleoptera and Hymenoptera (Tuller et al., 2015; Maia et al., 2017). Among then, *Merobruchus terani* (Kingsolver, 1980), *Stator maculatopygus* (Pic, 1930) (Chrysomelidae: Bruchinae) and *Allorhogas vulgaris* (Zaldívar-Riverón & Martinez, 2018) (Hymenoptera: Braconidae: Doryctinae) are commonly associated with the predation of S. *tenuifolia* seeds, where *M. terani* is the most representative and abundant specie in this system (Tuller et al., 2015).

The data represent *S. tenuifolia* food web generated by different members of the Laboratory Laboratory of Ecology and Complexity of Federal University of Lavras, Minas Gerais, Brazil over a 5-year period (2011, 2012, 2013, 2014 and, 2017). *Senegalia tenuifolia* fruits were sampled in three sites within nine spots collection (Fig. 1). All fruits were collected between July and August. The months corresponding to the season of greater development and ripening of fruits. We collected approximately 25 fruits per spots collection each month, totaling 1896 fruits (Table 1). As *Senegalia. tenuifolia* is a liana, we could not distinguish the number of different plants at each site, so we opted to collect the fruits randomly in each collection spots (Maia et al., 2017, 2018). For the removal of fruits, we used pruning shears with a long stem. In the field, fruits were stored in paper packages properly identified by plant and later moved to the Laboratory of Ecology and Complexity of Federal University of Lavras, Minas Gerais, Brazil. Each fruit was individually stored in labeled PVC tubes, and sealed at both ends with voile fabric, fixed by rubber, to allow the entry of oxygen and balance moisture, which prevents the proliferation of fungi and permits the development of organisms contained in fruits and their containment after emergence, it is also avoiding the attack of natural enemies in the laboratory environment. The fruits were stored for 3 months to allow the insects inside the seeds to complete their development and emerge as adults.

To determine the interactions between beetles and parasitoids, we dissected the seeds and examined the cephalic capsule and the host remnants (according to Maia et al., 2018; Morales-Silva et al., 2018). We established the interactions involving the seed-feeding species using information from previous works (Tuller et al., 2015, Zaldívar-Riverón et al., 2018) and

observed in the laboratory. The genus *Paracrias* sp is a gregarious parasitoid, which from only one host can emerge in about 10/12 adults of the parasitoid, then we consider this count of the parasitoid in the host to be just one individual of the genus *Paracrias* sp.

After that information seeds were separated and characterized qualitatively in the general categories as follows: consumed or not by herbivores, and with the presence or not of parasitoid that is, the seed at the first moment was consumed by the herbivore, but herbivores were death by attack parasitoid, that registered by the presence of the host's head capsule. The aborted seeds were disregarded. We gathered information on fruits after the emergence of adult insects. The emerged insects of each fruit were identified to the lowest taxonomical level possible. The voucher specimens were deposited in the Entomological Collection of the Laboratory of Ecology and Complexity at the Federal University of Lavras, Minas Gerais, Brazil.

Quantitative food web complexity and structure between herbivores host, parasitoid, and hyperparasitoids

We organized all nine collection spots of *S. tenuifolia* fruit into three large sites (i.e. A, B, and C sites), (Fig. 1). We also reorganized the food web only with signaled interactions between the herbivores and their parasitoids/hyperparasitoids. Other insects from the food web that are not part of host-parasitoid dynamics of seed consumption were discarded for this study, as decomposers, phytophagous, and defoliators insects. Thus, we pooled the data by the site each year and analyzed the qualitative structures of interaction herbivore-parasitoid-hyperparasitoid of the food web. This phase was documented based on laboratory observations of the presence and absence of insects contained in seeds and fruits to completed the *S. tenuifolia* food web. We based, also on previous studies on S. *tenuifolia* food web that were carried out by other members of the laboratory (Tuller et al., 2015; Maia et al., 2017, 2018). Moreover, we used a literature review to clarify the link among species. The next step was measured the quantitative metrics of the food web by *Cheddar* package (Hudson et al., 2013) in software R (R Developed Core team 2019).

We include the fractions of all species present in the *S. tenuifolia* food web: top species (%Top), intermediate species (%Intermediate), and basal species (% Basal) (Briand & Cohen, 1984; Martinez, 1994), the ratio resource-consumer (Bersier et al., 2002), as well as the link density (Tylianakis et al., 2007; Landi et al., 2018). Additionally, the fractions of links between top and intermediate species (%Top-Intermediate), top and basal (%Top-Basal), intermediate species (%Intermediate-Intermediate), and intermediate and basal

(%Intermediate-Basal) (Martinez, 1994, Martinez &.Lawton, 1995). Also, generality and vulnerability that was introduced by Schoener (1989), as the mean number of consumers per prey, and the mean number of prey per consumer, respectively, together can measure the asymmetry of the food web (Dong et al., 2019). Finally, we estimated the max chain length and connectance, that measures the structure and complexity of the food web, respectively (Bersier et al., 2002, Landi et al., 2018).

The trophic level functionality (herbivory, parasitism, and hyperparasitism rates) and data analysis

The first step was to calculate the herbivory, parasitism, and hyperparasitism rates in the seeds. Considering the seed numbers consumed by herbivores (*SC*) in total seeds (*TS*) we could express the herbivory rates (*HR*), as following:

$$HR = (SC)/(TS) \qquad\qquad\qquad \text{eqn 1}$$

Parasitism rates (*PR*) was determined by herbivores abundance (*HA*) and parasitoids abundance (*PA*) contained in the fruit, as following:

$$PR = (PA)/(PA + HA) \qquad\qquad\qquad \text{eqn 2}$$

Similarly, the hyperparasitism rates (*HYR*) was determined by primary parasitoids abundance (*PPA*) and secondary parasitoids abundance (*SPA*) contained in the fruit, as following:

$$HYR = (PPA)/(PPA + SPA) \qquad\qquad\qquad \text{eqn 3}$$

Separately we pooled system-wide herbivory, parasitism, and hyperparasitism rates at all sites and years collecting of the *S. tenuifolia* fruits, we adopted the non-parametric correlation proposed by Zar (2005), to ascertain the relationship between trophic level functionality (i. e. herbivory, parasitism, and hyperparasitism rates) and quantitative metrics of the food web. For this, we used the Spearman's coefficient (*r*) and *p-value* to measure the strength of the correlation, which expresses how closely a change in the magnitude of one of the variables is accompanied by a change in the magnitude of the other variable. Whether the *p-value* for correlation between two variables is less than the 0.05 significance level, it indicates that the correlation coefficients (*r*) are significant. Thus, each of the functionality rates measurements of the components of the food web may represent the rank of values of the function, where each rank is an integer, from 0 through 1, indicating relative magnitude. Similarly, each of the quantitative matrices of the food web may represent the rank of values of the quantitative metrics of the food web. If *r* = 0 ("no correlation") indicates that the magnitudes of the ranks of the variability in function are independent of the magnitudes of the

ranks of the quantitative matrices of the food web. A positive value of r ("positive correlation") indicates that both variables tend to increase together; a negative r ("negative correlation") indicates that one variable tends to decrease as other variable increases.

Results

The *Senegalia tenuifolia* quantitative food web

We found distinct species of herbivores, parasitoids, and hyperparasitoids distributed within four trophic levels in our source food web (Fig. 2).
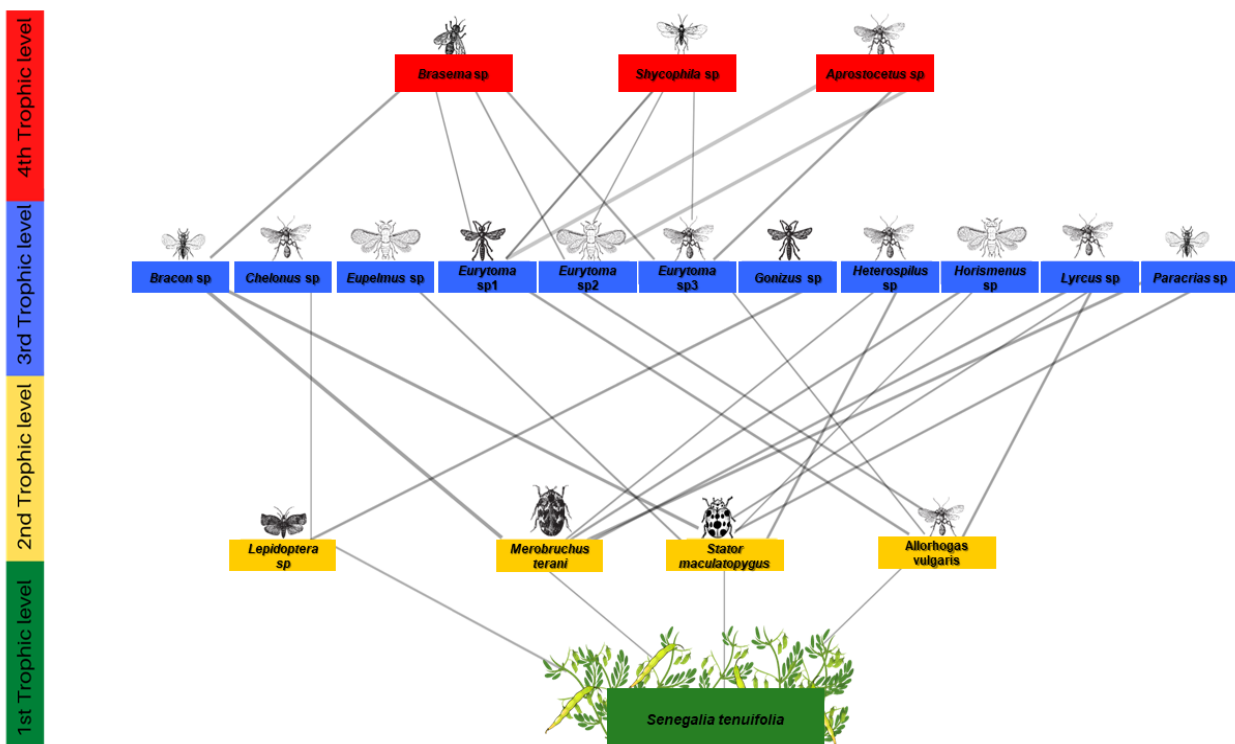
Fig. 2: Source food web. The first trophy level is represented by *Senegalia tenuifolia* resources. The second trophic level is quantified in four different species of herbivores, (*Lepidoptera* sp; *Allorhogas vulgaris*; *Merobruchus terani*, and *Stator maculatopygus*). The third trophic level is represented by primary parasitoids species, (*Bracon* sp; *Chelonus* sp; *Eupelmus* sp; *Eurytoma* sp1; *Eurytoma* sp2; *Eurytoma* sp3; *Gonizus* sp; *Heterosilu*s sp; *Horismenu*s sp; *Lyrcus* sp, and *Paracrias* sp). The fourth trophic level was composed of the hyperparasitoids (*Brasema* sp, S*ycophila* sp, and *Aprostocetu*s sp). The arrows represent interactions between all trophic levels.

The frequency of the species contained in the seeds remained the same pattern of previous studies designed by Maia et al., (2018). The first level was represented by *Senegalia tenuifolia* resources, which were sampled 1937 fruits and 17669 seeds for five years Among them, about 3563 (20.16%) seeds were consumed by herbivores (Table 1).

Table 1: *Senegalia tenuifolia*. Quantity of fruits and seeds as well the number of seeds consumed by herbivores and attacked by parasitoids for five years in different sites.

Site	*S. tenuifolia* fruits spots collection	Fruits		Seeds			
		Total fruit	Presence of parasitoid	Total seed	Consumed	Not consumed	Aborted
A	A1	50	14	327	81	201	45
	A2	50	13	359	50	276	33
	A3	50	14	335	100	203	32
	A4	NA	NA	NA	NA	NA	NA
B	B1	50	10	409	86	322	1
	B2	49	10	409	130	244	35
C	C1	50	4	210	72	107	31
	C2	50	5	430	170	248	12
	C3	50	14	430	262	140	28

Senegalia tenuifolia - 2012

Site	*S. tenuifolia* fruits spots collection	Fruits		Seeds			
		Total fruit	Presence of parasitoid	Total seed	Consumed	Not consumed	Aborted
A	A1	75	10	761	82	624	55
	A2	75	4	803	8	728	67
	A3	75	12	695	61	585	49
	A4	75	5	850	38	741	71
B	B1	76	10	788	67	685	36
	B2	NA	NA	NA	NA	NA	NA
C	C1	NA	NA	NA	NA	NA	NA
	C2	75	6	684	41	607	36
	C3	74	6	738	129	561	48

To be continued...

Site	*S. tenuifolia* fruits spots collection	Fruits		Seeds			
		Total fruit	Presence of parasitoid	Total seed	Consumed	Not consumed	Aborted
A	A1	50	31	472	148	205	119
	A2	50	11	502	70	186	246
	A3	50	14	511	95	290	126
	A4	50	2	430	32	340	58
B	B1	50	26	491	147	284	60
	B2	NA	NA	NA	NA	NA	NA
C	C1	50	5	478	86	334	58
	C2	49	4	313	39	204	70
	C3	25	3	184	4	151	29

Senegalia tenuifolia - 2013

Site	*S. tenuifolia* fruits spots collection	Fruits		Seeds			
		Total fruit	Presence of parasitoid	Total seed	Consumed	Not consumed	Aborted
A	A1	50	31	480	192	250	38
	A2	50	6	532	26	305	201
	A3	49	28	565	124	373	68
	A4	50	22	505	113	286	106
B	B1	50	22	522	218	227	77
	B2	NA	NA	NA	NA	NA	NA
C	C1	NA	NA	NA	NA	NA	NA
	C2	50	23	504	179	263	62
	C3	50	23	305	129	86	90

Senegalia tenuifolia - 2014

To be continued...

Senegalia tenuifolia - 2017							
Site	**S. tenuifolia fruits spots collection**	**Fruits**		**Seeds**			
		Total fruit	**Presence of parasitoid**	**Total seed**	**Consumed**	**Not consumed**	**Aborted**
A	A1	50	22	484	122	362	0
	A2	50	20	454	104	344	6
	A3	50	11	398	53	345	0
	A4	50	28	478	86	385	8
B	B1	40	7	407	98	295	14
	B2	NA	NA	NA	NA	NA	NA
C	C1	50	11	426	112	303	11
	C2	NA	NA	NA	NA	NA	NA
	C3	NA	NA	NA	NA	NA	NA

The second trophic level was quantified in four different species of herbivores, (*Lepidoptera* sp; *Allorhogas vulgaris*; *Merobruchus terani*, and *Stator maculatopygus*) that was divided into three orders (Lepidoptera, Hymenoptera, and Coleoptera). In this level were sampled, 3006 individuals consuming the seed. *Merobruchus terani* was the most abundant insect herbivore, totaling 1747 individuals sampled during five years of study. The total abundance of herbivores varied temporally (763, 164, 352, 1368, and 359 herbivores from 2011 through 2017, respectively), (Table 2).

Table 2. Species of herbivores associated with the food web supported by fruits of *Senegalia tenuifolia*. Abundance, and relative frequency (RF%) of herbivores insects at the collection sites of *S. tenuifoli*a fruits during the five years of study.

Herbivores	Year	**2011**			**2012**			**2013**			**2014**			**2017**		
	Site	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**
Lepidoptera sp	Abundance	5	0	1	3	0	3	13	0	6	2	0	2	14	11	1
	RF%	3,03	0	0,23	5,35	0	4	7,83	0	8,21	0,35	0	0,34	53,8	42,3	3,8
	Year	**2011**			**2012**			**2013**			**2014**			**2017**		
	Site	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**
Allorhogas vulgaris	Abundance	14	37	3	26	4	26	104	40	1	169	132	11	46	5	0
	RF%	8,48	21,38	0,70	46,42	12,12	34,66	62,65	24,09	1,36	29,96	58,92	1,89	90,1	9,80	0
	Year	**2011**			**2012**			**2013**			**2014**			**2017**		
	Site	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**
Merobruchus terani	Abundance	134	123	370	26	27	46	46	49	69	198	56	358	151	17	77
	RF%	81,21	71,09	87,05	46,42	81,81	61,33	27,71	46,22	84,93	35,10	25	61,72	70,89	58,62	65,81
	Year	**2011**			**2012**			**2013**			**2014**			**2017**		
	Site	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**	**A**	**B**	**C**
Stator macutalopygus	Abundance	12	13	51	1	2	0	3	17	4	195	36	209	23	7	5
	RF%	7,26	7,51	12	1,78	6,06	0	1,80	16,03	5,47	34,57	16,07	36,03	10,79	24,13	4,27

The third trophic level was represented by primary parasitoids species, totaling 14 genres of the herbivores parasitoids (*Bracon* sp; *Chelonus* sp; *Eudecatoma* sp; *Eulophinae* sp; *Eupelmu*s sp; *Eurytoma* sp1; *Eurytoma* sp2; *Eurytoma* sp3; *Gonizus* sp; *Heterospillus* sp; *Horismenus* sp; *Lyrcus* sp; *Paracrias* sp; *Pteromalinae* sp), all of the Hymenoptera order. The genre *Paracrias* sp that is a gregarious parasitoid was quantified as the most abundant parasitoid, totaling 386 individuals, followed by the parasitoid *Horismenus* sp with 354 individuals sampled during years of study (Table 3). The parasitoid abundance varied temporally (99, 60, 126, 223, and 305 parasitoids from 2011 through 2017, respectively), (Table 3). The fourth trophic level was composed of the hyperparasitoids all belonging to the Hymenoptera order and classified into three taxonomic genres (*Aprostocetus* sp, *Brasema* sp, and *Sycophila* sp) were highlight *Brasema* sp with 75 specimens, that is hyperparasitoid most abundant in all system (Table 4). The hyperparasitoid abundance varied temporally (9, 0, 0, 63, and 4 hyperparasitoids from 2011 through 2017, respectively) (Table 3).

Table 3. Species of Hymenoptera associated with herbivores in the food web supported by fruits of *Senegalia tenuifolia* (*1: Aprostocetus* sp*; 2: *Bracon* sp; 3: *Brasema* sp*; 4: *Chelonus* sp; 5: *Eudecatoma* sp; 6: *Eulophinae* sp; 7: *Eupelmu*s sp; 8: *Eurytoma* sp1; 9: *Eurytoma* sp2; 10: *Eurytoma* sp3; 11: *Gonizus* sp; 12: *Heterospillus* sp; 13: *Horismenus* sp; 14: *Lyrcus* sp; 15: *Paracrias* sp; 16: *Pteromalinae* sp; 17: *Sycophila* sp*). Abundance and relative frequency (%) of parasitoids and hyperparasitoids at the collection sites of *S. tenuifoli*a fruits during the five years of study. Asterisk corresponds to hyperparasitoid species.

Site	Spots	*Senegalia tenuifolia* fruit- 2011																
		Hymenoptera species richness, abundance and relative frequence (%)																
		1*	2	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17*
A	A1	0	0	0	0	0	0	0	3	0	1	0	0	17	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	3.70%	0%	1.23%	0%	0%	20.98%	0%	0%	0%	0%
	A2	1	0	0	0	0	0	0	1	0	0	0	2	11	0	0	0	0
		2%	0%	0%	0%	0%	0%	0%	2%	0%	0%	0%	4%	22%	0%	0%	0%	0%
	A3	0	0	2	0	0	0	1	3	0	0	0	0	14	0	0	0	0
		0%	0%	2%	0%	0%	0%	7.1%	1%	0%	0%	0%	0%	14%	0%	0%	0%	0%
	A4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
B	B1	0	0	3	0	0	0	0	2	1	1	0	2	13	0	0	0	0
		0%	0%	3.48%	0%	0%	0%	0%	2.32%	1.16%	1.16%	0%	2.32%	15.11%	0%	0%	0%	0%
	B2	0	0	3	0	0	0	0	10	0	0	0	0	1	0	0	0	0
		0%	0%	2.30%	0%	0%	0%	0%	7.69%	0%	0%	0%	0%	0.76%	0%	0%	0%	0%
C	C1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2.77%	0%	0%	2.77%	0%
	C2	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	1.17%	0%	0%	1.17%	0%
	C3	0	0	0	0	0	0	0	0	1	0	0	0	18	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0.38%	0%	0%	0%	6.87%	0%	0%	0%	0%

To be continued...

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Site	Spots	Senegalia tenuifolia fruit- 2012																
		Hymenoptera species richness, abundance and relative frequence (%)																
		1*	2	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17*
A	A1	0	0	0	1	0	0	1	6	1	2	0	0	3	0	0	0	0
		0%	0%	0%	1.21%	0%	0%	1.21%	7.31%	1.21%	0%	0%	0%	3.65%	0%	0%	0%	0%
	A2	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	50%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	A3	0	0	0	0	0	0	0	0	1	1	0	0	12	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	1.63%	1.63%	0%	0%	19.67%	0%	0%	0%	0%
	A4	0	0	0	0	0	0	0	1	1	0	0	0	4	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	2.36%	2.63%	0%	0%	0%	10.52%	0%	0%	0%	0%
B	B1	0	0	0	0	0	0	0	1	0	0	0	0	9	0	16	0	0
		0%	0%	0%	0%	0%	0%	0%	1.49%	0	0	0	0	13.43%	0	23.88%	0	0
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	C1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	2.43%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C3	0	0	0	0	0	0	1	0	0	0	3	0	5	0	0	0	0
		0%	0%	0%	0%	0%	0%	0.77%	0%	0%	0%	2.32%	0%	3.87%	0%	0%	0%	0%

To be continued...

Site	Spots	*Senegalia tenuifolia* fruit- 2013																
		Hymenoptera species richness, abundance and relative frequence (%)																
		1*	2	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17*
A	A1	0	0	0	0	3	0	0	78	4	2	0	0	14	0	0	0	0
		0%	0%	0%	0%	2.02%	0%	0%	52.70%	2.70%	1.35%	0%	0%	9.45%	0%	0%	0%	0%
	A2	0	0	0	0	2	0	0	12	0	1	0	0	4	4	0	0	0
		0%	0%	0%	0%	2.85%	0%	0%	17.14%	0%	1.42%	0%	0%	5.71%	5.71%	0%	0%	0%
	A3	0	0	0	0	0	0	0	13	3	3	0	0	6	1	0	0	0
		0%	0%	0%	0%	0%	0%	0%	13.68%	3.15%	3.15%	0%	0%	6.31%	1.05%	0%	0%	0%
	A4	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	12.5%	0%	0%	0%	0%
B	B1	0	0	0	0	0	0	5	0	0	0	0	0	28	0	0	0	0
		0%	0%	0%	0%	0%	0%	3.40%	0%	0%	0%	0%	0%	19.04%	0%	0%	0%	0%
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	C1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2.32%	0%	0%	0%	0%
	C2	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
		0%	0%	0%	2.56%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2.56%	0%	0%	0%
	C3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	25%	0%	0%	0%

To be continued...

Site	Spots	Senegalia tenuifolia fruit- 2014																
		Hymenoptera species richness, abundance and relative frequence (%)																
		1*	2	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17*
A	A1	0	0	8	0	6	1	0	25	0	0	0	0	27	2	0	0	0
		0%	0%	4.16%	0%	3.12%	0.52%	0%	13.02%	0%	0%	0%	0%	14.06%	1.04%	0%	0%	0%
	A2	0	0	0	0	3	0	1	4	0	0	0	0	0	1	0	0	0
		0%	0%	0%	0%	11.53%	0%	3.84%	15.38%	0%	0%	0%	0%	0%	3.84%	0%	0%	0%
	A3	0	0	32	0	0	0	0	7	1	0	0	0	14	0	0	0	0
		0%	0%	25.80	0%	0%	0%	0%	5.64%	0.80%	0%	0%	0%	11.29%	0%	0%	0%	0%
	A4	0	0	8	0	1	0	0	7	0	0	0	0	26	0	0	0	0
		0%	0%	7.07%	0%	0.88	0%	0%	6.19%	0%	0%	0%	0%	23%	0%	0%	0%	0%
B	B1	0	0	4	0	12	0	0	12	0	0	0	0	13	0	2	0	0
		0%	0%	1.83%	0%	5.50%	0%	0%	5.50%	0%	0%	0%	0%	5.96%	0%	0.91%	0%	0%
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	C1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C2	0	0	5	0	0	0	0	0	0	0	0	0	29	0	0	0	0
		0%	0%	2.79%	0%	0%	0%	0%	0%	0%	0%	0%	0%	16.20%	0%	0%	0%	0%
	C3	0	26	11	0	0	0	1	1	0	0	0	0	2	1	32	0	0
		0%	20.15%	8.52%	0%	0%	0%	0.77%	0.77%	0%	0%	0%	0%	1.55%	0.77%	24.80%	0%	0%

To be continued...

Site	Spots	*Senegalia tenuifolia* fruit- 2017																
		Hymenoptera species richness, abundance and relative frequence (%)																
		1*	2	3*	4	5	6	7	8	9	10	11	12	13	14	15	16	17*
A	A1	0	0	0	0	0	0	0	0	0	0	0	0	25	0	71	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	20.49%	0%	58.19%	0%	0%
	A2	0	0	3	0	0	0	0	11	1	4	0	2	14	0	28	0	1
		0%	0%	2.88%	0%	0%	0%	0%	10.57%	0.96%	3.84%	0%	1.92%	13.46%	0%	26.92%	0%	0.96%
	A3	0	0	0	0	0	0	0	2	0	0	0	1	13	0	1	0	0
		0%	0%	0%	0%	0%	0%	0%	3.77%	0%	0%	0%	1.88%	24.52%	0%	1.88%	0%	0%
	A4	0	0	0	0	0	0	0	2	0	1	0	0	17	0	235	0	0
		0%	0%	0%	0%	0%	0%	0%	2.32%	0%	1.16%	0%	0%	19.76%	0%	273.25%	0%	0%
B	B1	0	0	0	0	0	0	0	1	0	0	0	0	9	0	7	0	0
		0%	0%	0%	0%	0%	0%	0%	1.02%	0%	0%	0%	0%	9.18%	0%	7.14%	0%	0%
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	C1	0	0	0	10	0	0	0	0	0	0	0	0	6	0	8	0	0
		0%	0%	0%	8.92%	0%	0%	0%	0%	0%	0%	0%	0%	5.35%	0%	7.14%	0%	0%
	C2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%

Figure 3: *Senegalia tenufolia* food web. Difference between the complexities of the food web in relation to the year and site of fruit collecting. (a) Complex food web located on-site A (Municipality of Luminárias-MG-Brazil) – 2014. (b) Not complex web food located on-site B (Municipality of Lavras-MG-Brazil) -2013.

Furthermore, the quantitative metrics of the food web varied considerably over the five years of study, except fraction top-level had constant values with few changes (Table 4). Connectance obtained the largest metrics in 2014, which the food web that reached greater complexity located on-site A (Municipality of Luminárias-MG-Brazil) (Table 4, Fig. 3 (a)) contrasting with the food web dated in the year 2013 on-site B (Municipality of Lavras-MG-Brazil) (Table 4, Fig. 3 (b)). The other food web of the years 2011, 2012, and 2017 can be found in the supplementary material.

Table 4: Quatitatives metrics of the *Senegalia tenuifolia* food web. The quantitative metrics represent the food web structure.

Metrics	2011			2012			2013			2014			2017		
	A	B	C	A	B	C	A	B	C	A	B	C	A	B	C
Fraction top level	0.5455	0.4444	0.4286	0.5455	0.5000	0.4444	0.4545	0.3333	0.5000	0.5000	0.3636	0.5000	0.6000	0.5000	0.4286
Fraction intermediate	0.3636	0.4444	0.4286	0.3636	0.3750	0.4444	0.3636	0.5000	0.1250	0.4286	0.5455	0.4167	0.3333	0.3750	0.4286
Fraction basal	0.0909	0.1111	0.1429	0.0909	0.1250	0.1111	0.1818	0.1667	0.3750	0.0714	0.0909	0.0833	0.0667	0.1250	0.1429
Ratio resources consumers	0.5000	0.6250	0.6667	0.5000	0.5714	0.6250	0.6667	0.8000	0.5714	0.5385	0.7000	0.5455	0.4286	0.5714	0.6667
Link density	1.0000	1.0000	1.0000	1.0000	1.1250	0.8889	1.0000	1.0000	1.0000	1.2143	1.0909	1.0833	1.0667	1.1250	1.1429
Connectance	0.0909	0.1111	0.1429	0.0909	0.1406	0.0988	0.0909	0.1667	0.1250	0.0867	0.0992	0.0903	0.0711	0.1406	0.1633
Fraction links top intermediate	0.5455	0.4444	0.5714	0.6364	0.6667	0.5000	0.4545	0.5000	0.5000	0.5294	0.5000	0.5385	0.6250	0.5556	0.6250
Fraction links top basal	0.0909	0.1111	0.0000	0.0000	0.0000	0.0000	0.0909	0.0000	0.1250	0.0588	0.0000	0.0769	0.0625	0.1111	0.0000
Fraction links intermediate	0.0909	0.1111	0.0000	0.0000	0.0000	0.0000	0.0909	0.0000	0.0000	0.2353	0.2500	0.1538	0.1250	0.0000	0.0000
Fraction links intermediate basal	0.2727	0.3333	0.4286	0.3636	0.3333	0.5000	0.3636	0.5000	0.3750	0.1765	0.2500	0.2308	0.1875	0.3333	0.3750
Generality	1.1000	1.1250	1.1667	1.1000	1.2857	1.0000	1.2222	1.2000	1.1429	1.3077	1.2000	1.1818	1.1429	1.2857	1.3333
Vulnerability	2.2000	1.8000	1.7500	2.2000	2.2500	1.6000	1.8333	1.5000	2.0000	2.4286	1.7143	2.1667	2.6667	2.2500	2.0000

The quantitative properties of food web descriptors

The variabilities in the total function of herbivores, parasitoids, and hyperparasitoids were correlated to the metrics of the *Senegalia tenuifolia* food web (Fig.4).
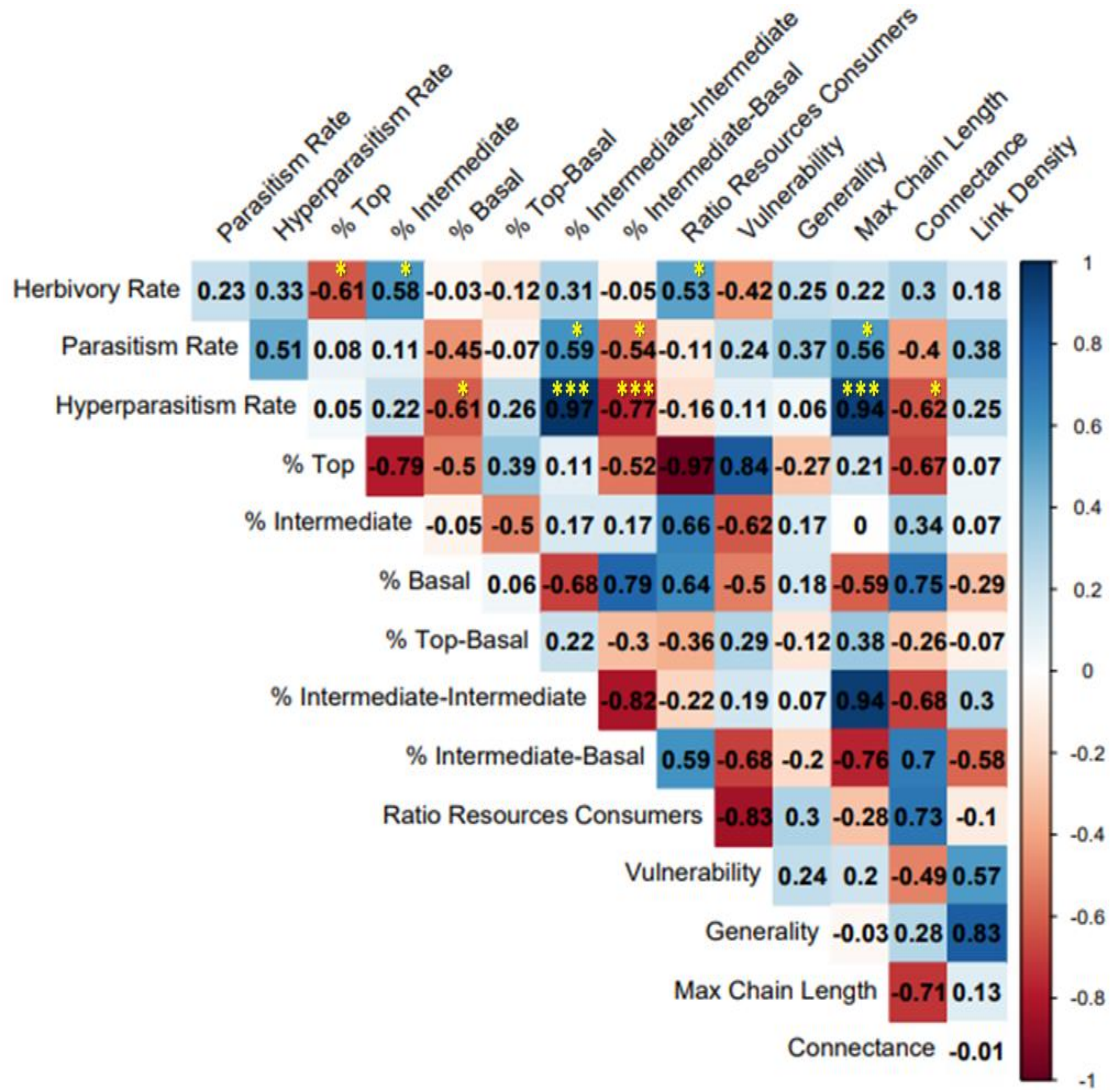
Fig. 4*: Correlation matrix between trophic level functionality (herbivory, parasitism, and hyperparasitism rates) and metrics of the *Senegalia tenuifolia* food web. The yellow asterisk indicates the significance - (Significance of codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1)

For the herbivory rate the quantitative metrics of the food web were the following correlations: fraction top (%Top), (p= 0.0149, r= -0.6139666); fraction intermediate (%Intermediate), (p= 0.02453, r= 0.57631), and ratio consumer-resource (p= 0.04046, r= 0.5337033), (Fig.5)
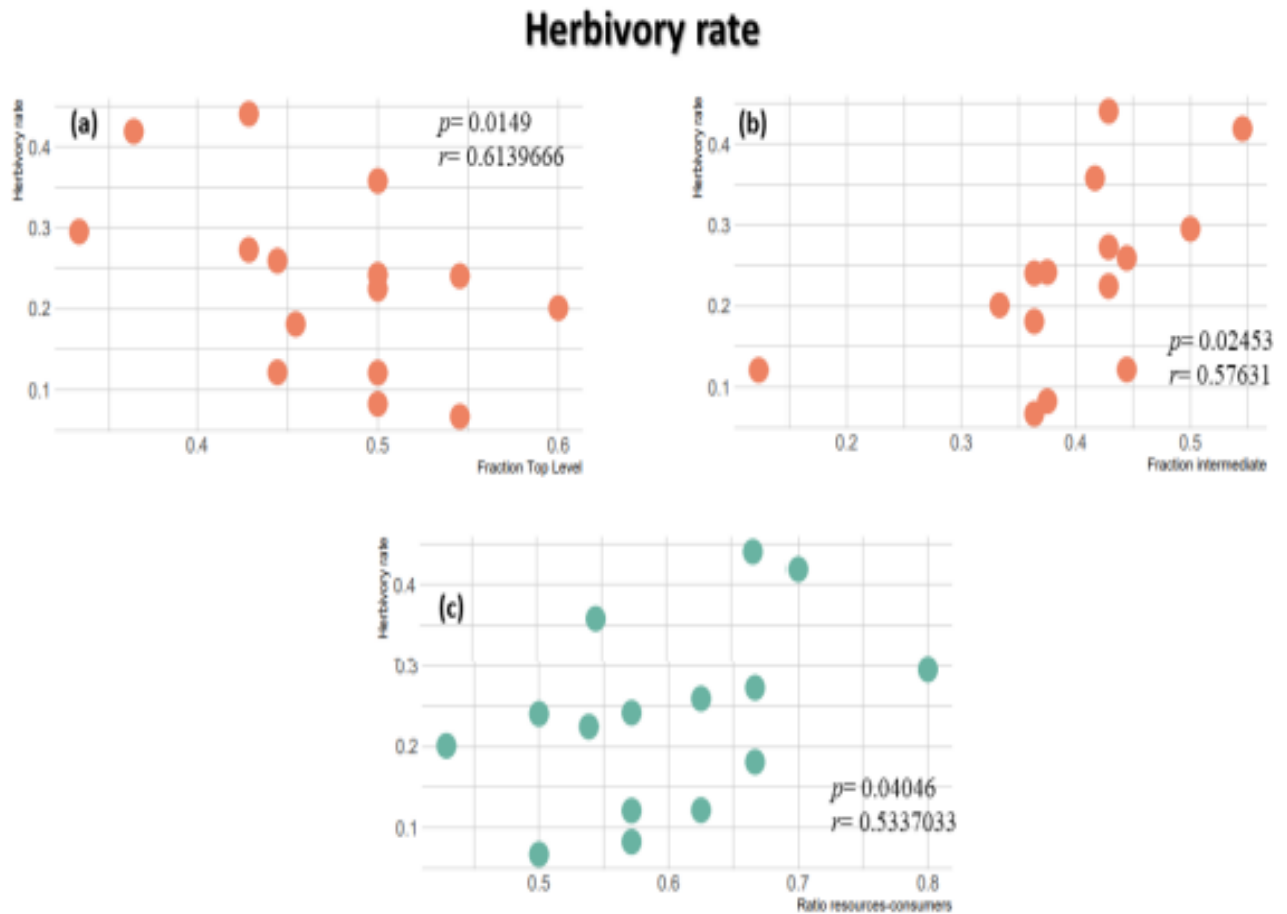
Fig. 5: Relationships between the herbivory rate and metrics of *Senegalia tenuifolia* food web. (a) The fraction top-level (%Top). (b) Fraction intermediate (%Intermediate). (c) Ratio resources-consumers.

Parasitism rate was associated to: fraction links intermediate-intermediate (%Intermediate-Intermediate), (p= 0.01973, r= 0.5933086); fraction links intermediate-basal (%Intermediate-Basal), (p= 0.03966, r= -0.5355003), and max chain length (p= 0.03111, r= 0.5567306), (Fig. 6).
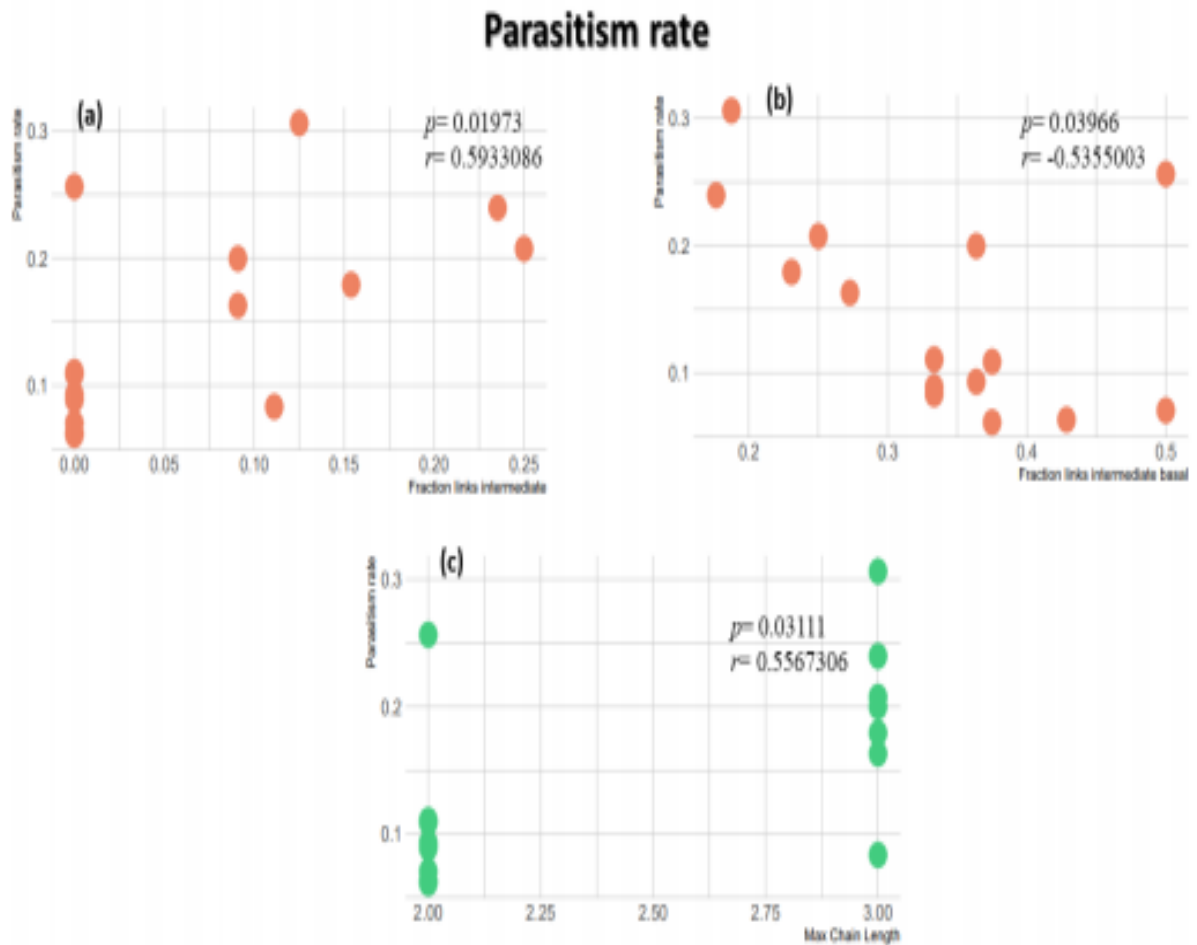
Fig. 6: Relationships between the parasitism rate and metrics of *Senegalia tenuifolia* food web. (a) Fraction links intermediate (%Intermediate-Intermediate). (b) Fraction links intermediate-basal (%Intermediate-Basal). (c) Max chain length.

Finally, hyperparasitism rate were associated to: fraction basal (%Basal) (p= 0.01585, r= -0.6095172); fraction links intermediate-intermediate (%Intermediate-Intermediate) (p= 9.871e-10, r= 0.9737124); fraction links intermediate-basal (%Intermediate-Basal) (p= 0.0008482, r= -0.7669706); max chain length (p= 2.083e-07, r= 0.9393364), and connectance (p= 0.01355, r= -0.6206414), (Fig. 7).
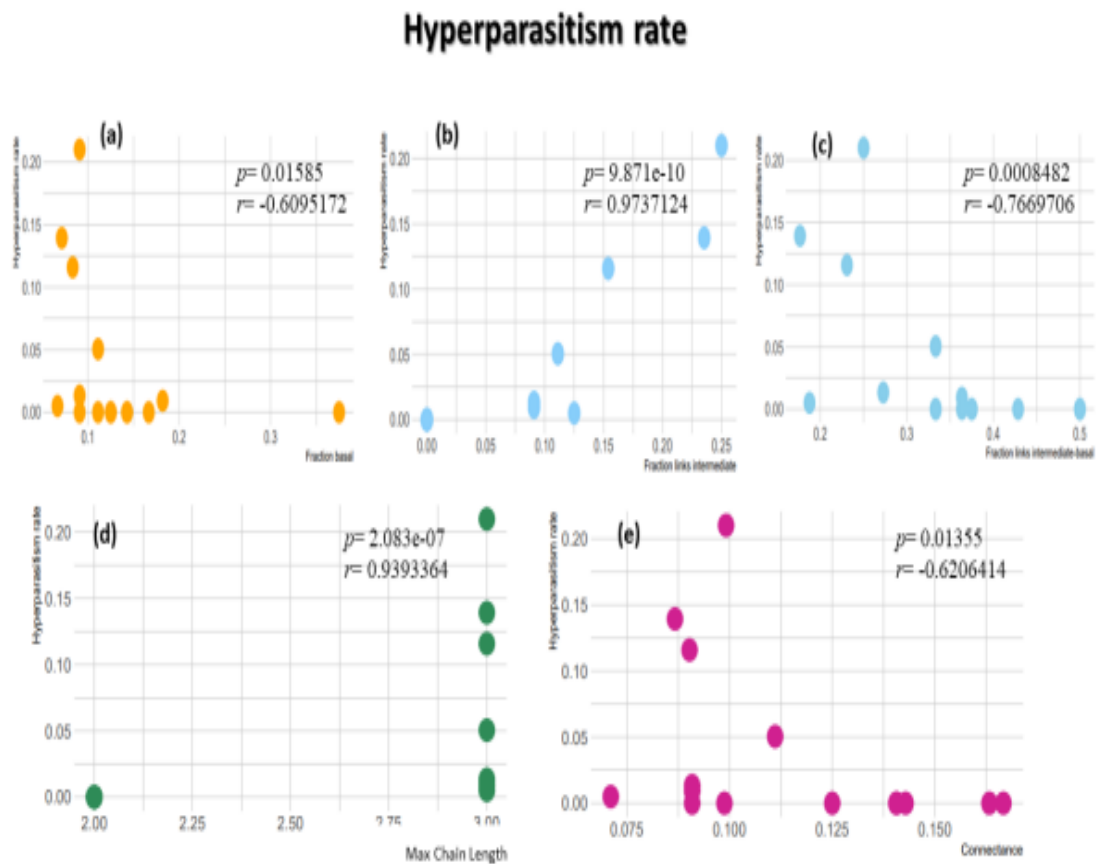
Fig. 7: Relationships between the hyperparasitism rate and metrics of *Senegalia tenuifolia* food web. (a) Fraction basal (%Basal). (b) Fraction links intermediate (%Intermediate-Intermediate). (c) Fraction intermediate-basal (%Intermediate-Basal). (d) Max chain length. (e) Connectance

Discussion

We found clues of the relationship among herbivory, parasitism, and hyperparasitism rates and metrics of the food web, suggesting that function, structure, and complexity of the food web are correlated. Our results showed that the herbivory rate is negatively associated with fractions of the top (% Top) and positively associated with intermediate (% Intermediate) and ratio consumer-resource. This indicates that the herbivory rate increases as the number of herbivores increases (i.e.% Intermediate) since the plant is host to a great richness of herbivore species (Tuller et al., 2015, Maia et al., 2018). The results of this correlation also can be attributed to the fact that the relationship between species at different trophic levels are on a dependent scale, that is, the fractions of intermediate species increase while the top and basal species decrease (Martinez & Lawton, 1995, Martinez, 1994) therefore, the functionality that species played for dynamic scale dependencies is necessary because it allows determining

if some communities have unusual properties of the food web to support more species than their size allows (Martinez & Lawton, 1995). According to, Bukovinszky et al. (2008), the changes in the food web are dependent on both trait- and density-mediated interactions among species.

The parasitism rate is negatively correlated to the fractions links intermediate-basal (%Intermediate-Basal) and positively correlated to links intermediate-intermediate (%Intermediate-Intermediate), and also the max chain length. When correlating the parasitism rate to metrics of the food web, we can evidence the efficiency of the parasitoid in performing its role through its relationship between the fractions of link (i.e. % Intermediate-Basal and %Intermediate-Intermediate). Despite the correlation coefficient (*r*) having a low significance to %Intermedite-Basal, we can evidence the parasitoid's ability that is highlighted with negative *r*, which decreasing links of the intermediate-basal, being a natural enemy in controlling herbivores and minimizing pressure on seeds. The negative value of this correlation gives us the idea that the links between the intermediate-basal species decrease as the parasitism rate increases. The low correlation was already expected because, the parasitoids here in question are mostly generalists and have complementarity resource use (Hooper &Vitousek, 1997, Maia et al., 2018), it could occur in space, because of differences in host-searching ability in different sites in which the host is (Rodríguez & Hawkins, 2000).

However, the positive correlation between %Intermediate-Intermedite may be related to the fact that the richness of herbivores can support different kinds of parasitoid species that attack that host species, and all parasitoids attack similar host stages and at the season of fruit ripening (Tuller et al., 2015, Maia et al, 2018). The theory of consumer-resource interactions provides an alternative way to view the relationship between the function of species and the structure of the food web for understanding interspecific interactions (Murdoch et al. 2003; Turchin 2003). This classic hypothesis predicts that with increasing the availability and sensitivities of resources to consumers, the length of the food chain should increase and, therefore, increase its complexity by adding more species and trophic levels (Matsuda et al., 1996; Post et al., 2000, Byers et al., 2017), which the probability species coexistence emerge through changes in parameter values of consumer-resource interactions (Holland & DeAngelis, 2009). According to Kondoh and Ninomya (2009), food-chain length responds to changes in resource availability in which are influenced by species richness. A community complexity, measured by the number of local food webs and their connectedness, elicits a self-regulating, negative-feedback mechanism and thus stabilizes food-web dynamics (Mougi & Kondoh, 2016). This finding corroborates with our positive correlation in which the

parasitism rate increases as the length of the chain also increases, due to the wide richness of genera of primary parasitoids sampled and also temporal variation both in the abundance of the host and their parasitoids. This is true and explained through the qualitative description of the food web of *S. tenuifolia*, where we find the food web more complex than another, differing to the year and site, where could have a growing concordance between habitat connectivity on food webs (LeCraw et al., 2014).

On the other hand, when the fourth trophic level is present the correlation shows a positive result between hyperparasitism rate and max chain length demonstrate that food-chain length is influenced by the foraging of the order Hymenoptera in response to the availability of resources and is determined by the number of links among species (Eveleigh et al., 2007; Kondoh & Ninomiya, 2009). According to Eveleigh et al (2007), in a complex food web, the interaction between herbivores and their natural enemies displays significant architectural flexibility over a large fluctuation in the natural abundance of the main herbivore. Sustained by food-web theory that involves evaluating species trophic interactions to depict the mechanisms by which natural communities maintain stability (De Angelis 1975; McCann et al., 1998; Stouffer & Bascompte 2011).

We discuss that the hyperparasitism rate is responsible to ensure the structure and stability of the food web through the high mobility and generality of the hyperparasitoid (i.e. topology of the food web) to the abundance of the host in which the flexibility of the food web is conditioned by the change in choice of them (Eveleigh et al., 2007). Our results also show that hyperparasitism rate is negatively correlated to fraction basal (%Basal), and fractions of links between intermediate and basal (%Intermediate-Basal), thusly we argue that the functional composition of the top-level (i.e. hyperparasitoid) has a direct effect on the food web through the effects of species traits and an indirect effect through its impact on the structure of the food web (Gravel et al., 2016), and seems that the food-web topology and population stability combine to produce a single conceptual framework (Rooney & McCann 2012; Borrelli et al. 2015), in which the topology may be consequences of dynamic relationships between species (Tunney et al. 2012), likewise the population stability promote food-web topology (Monteiro & Faria, 2017), that regulate population outbreaks and prevent a total system destabilization (Elton 1927; McCann 2000; Dunne et al. 2005). This occurs because hyperparasitoids develop at the expense of primary parasitoids and are, thus, likely to limit the control of herbivores hosts by the following parasitoid generation (Rosenheim, 1998; Sullivan & Völkl, 1999). These consumer-resource relationships in nature could be due to their intrinsic dynamical properties (Allesina & Tang, 2012).

Further, our results also demonstrated a negative correlation to connectance (i.e. complexity) conditioned by hyperparasitism rate, it could scale up to produce network-level topology patterns, such as lower modularity and a higher degree of generality (Monteiro & Faria, 2017). The negative effect of the number of species and connectance on population stability has long been known (May 1972). However, there is a controversial duality about stability and complexity. On the one hand, in the case of population dynamics, the destabilizing effect is compensated by dynamic stability, through the blend between weak and strong interaction strengths (McCann, Hastings & Huxel 1998). On the other hand, species-level topologies could dampen the strong negative effect of connectance on stability; and that weak interaction strengths could be either stabilizing or destabilizing, depending on the species-level topology (Allesina & Pascual 2008; Allesina & Tang 2015; Allesina et al. 2015), suggesting that topologies are better able to maintain stability, in which all species could coexist (Borrelli et al., 2015).

In summary, our results demonstrated that the trophic level functionality is correlated with food web metrics, where the structure of the food web can modulate by the functionality of the dynamic interaction between species. However, the complexity of the food web could be matching the connectivity of the habitat over the pattern of the food web through the level topology, represented by the hyperparasitoid and its functional rate, it is suggested that the topologies are responsible for maintaining stability that could be conditioned to the high level of generality (i.e. generalist species) of the top-level

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SUPPORTING INFORMATION

Supplementary Material

Food web for years 2011,2012, 2013, 2014, and 2017.
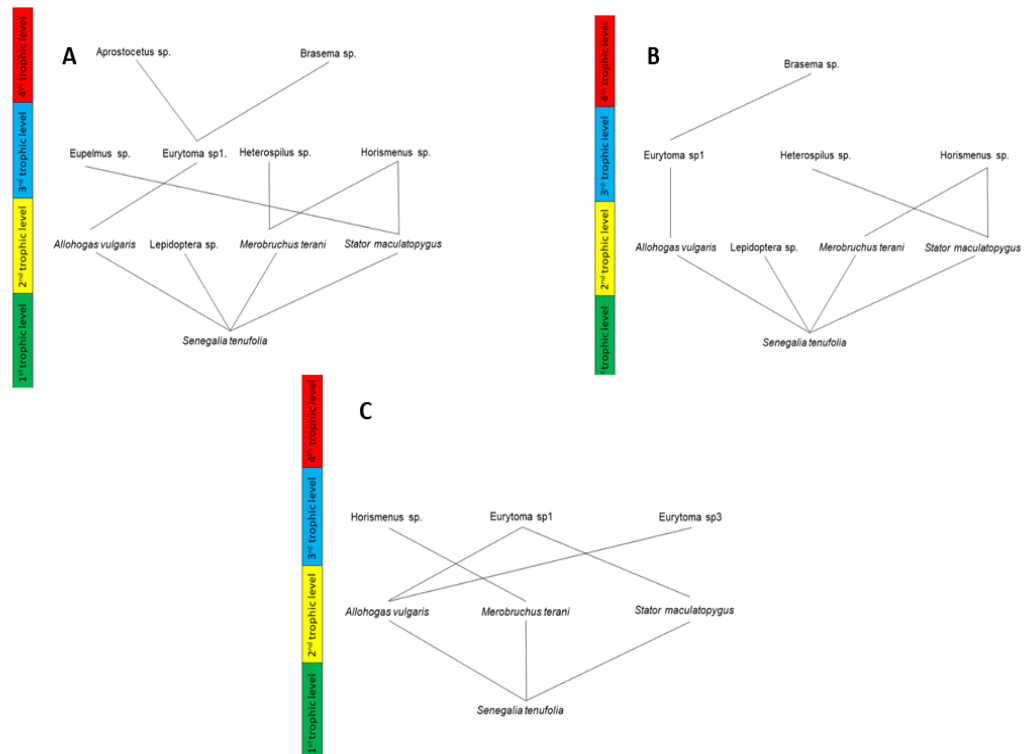
Fig. 1: *Senegalia tenuifolia* food web in the year 2011. A- *S. tenuifolia* fruits collection spots located in Luminárias municipality. B and C- *S. tenuifolia* fruits collection different spots located in Lavras municipality.
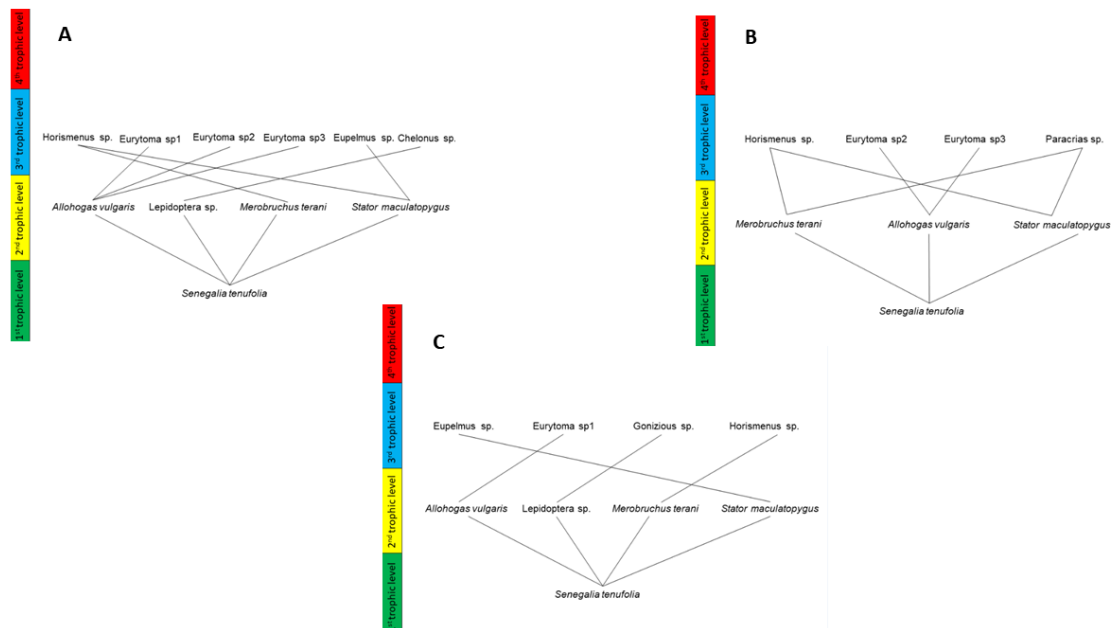
Fig. 2: *Senegalia tenuifolia* food web in the year 2012. A- *S. tenuifolia* fruits collection spots located in Luminárias municipality. B and C- *S. tenuifolia* fruits collection different spots located in Lavras municipality.
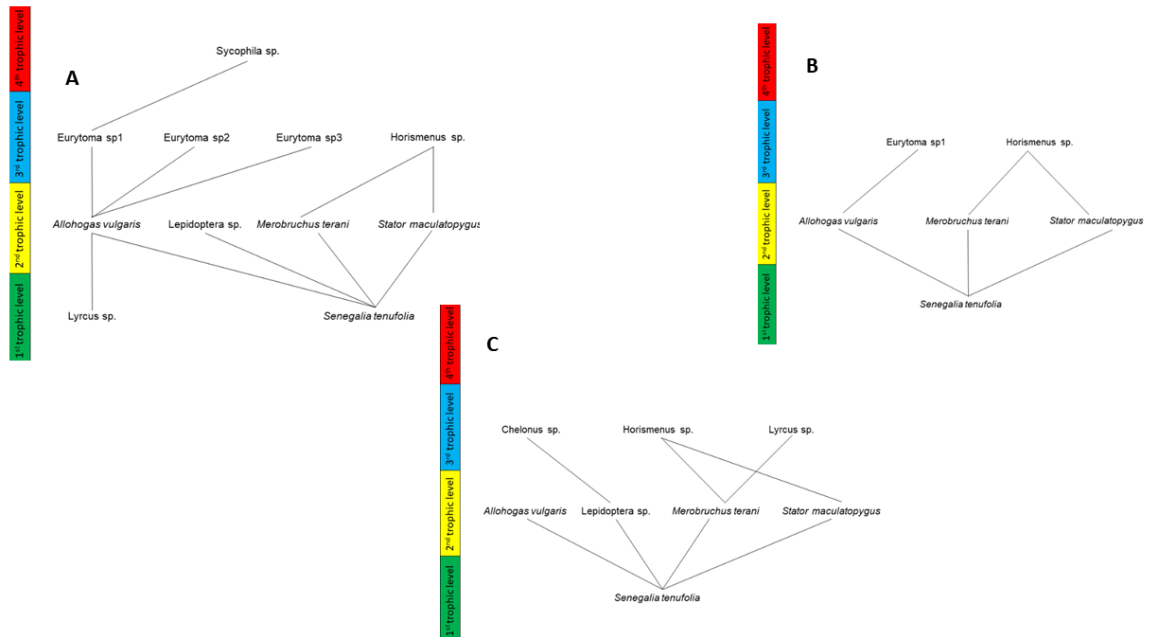
Fig. 3: Senegalia tenuifolia food web in the year 2013. A- *S. tenuifolia* fruits collection spots located in Lumínárias municipality. B and C- *S. tenuifolia* fruits collection different spots located in Lavras municipality.
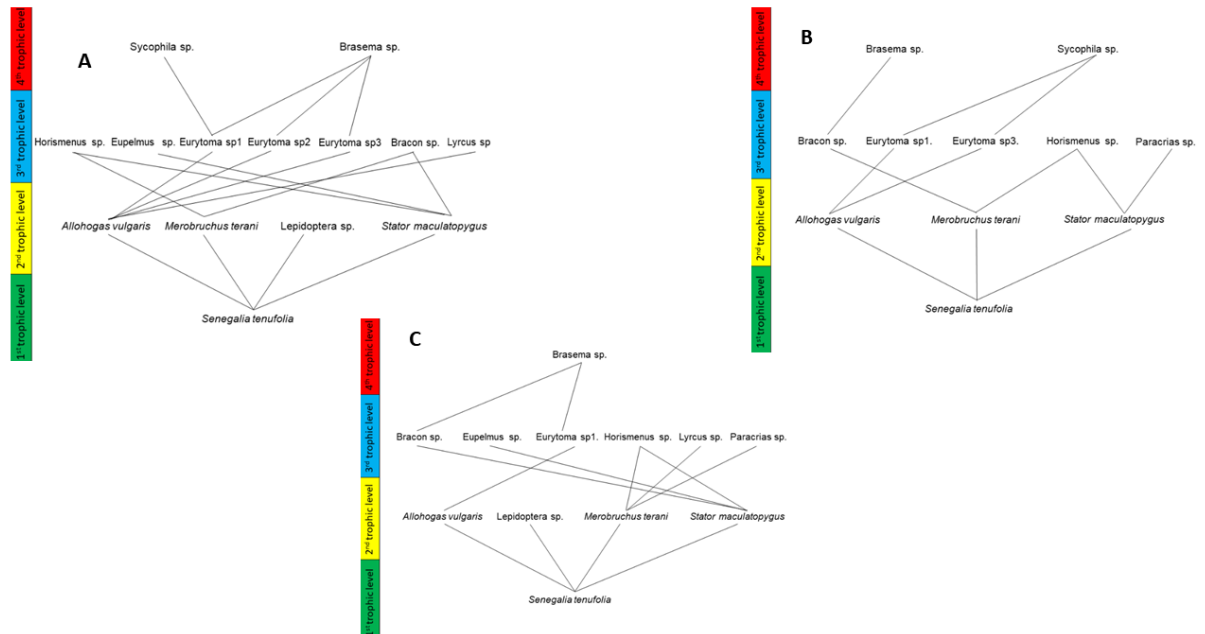
Fig. 4: Senegalia tenuifolia food web in the year 2014. A- *S. tenuifolia* fruits collection spots located in Lumínárias municipality. B and C- *S. tenuifolia* fruits collection different spots located in Lavras municipality.
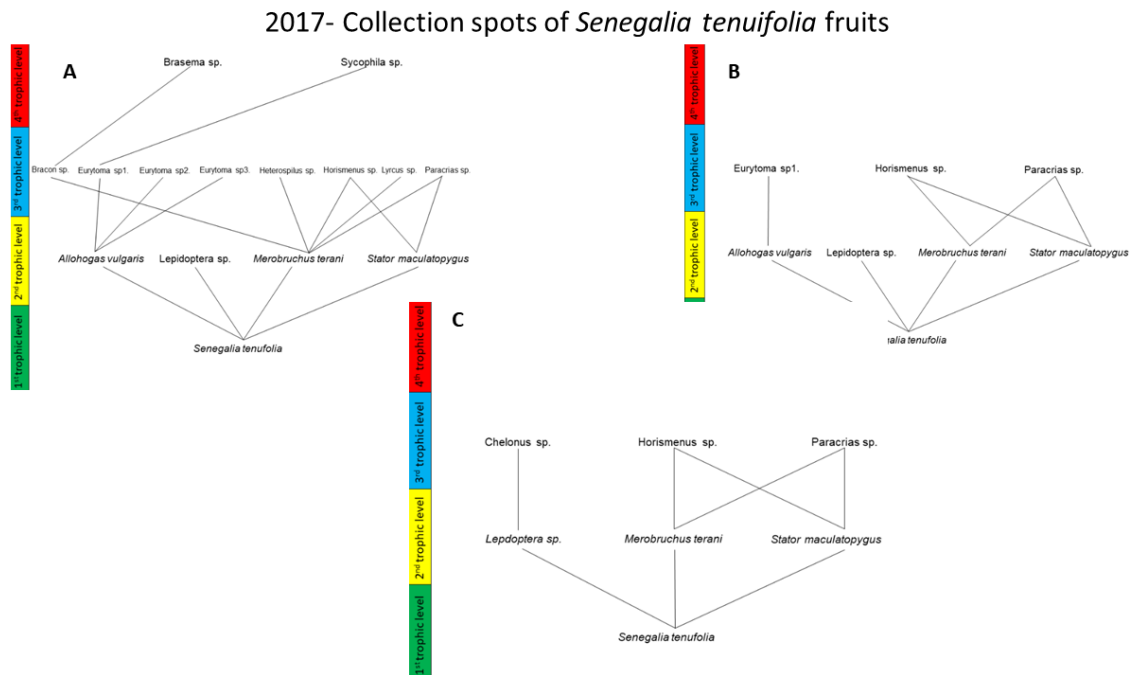
Fig. 4: *Senegalia tenuifolia* food web in the year 2017. A- *S. tenuifolia* fruits collection spots located in Luminárias municipality. B and C- *S. tenuifolia* fruits collection different spots located in Lavras municipality

Artigo 2: Backstage of the functional multitrophic host-parasitoid food web: a picture of the environmental effects on herbivory and parasitism rates in the long term

"Este artigo está formatado nas normas do periódico Ecological Entomology (versão preliminar)"
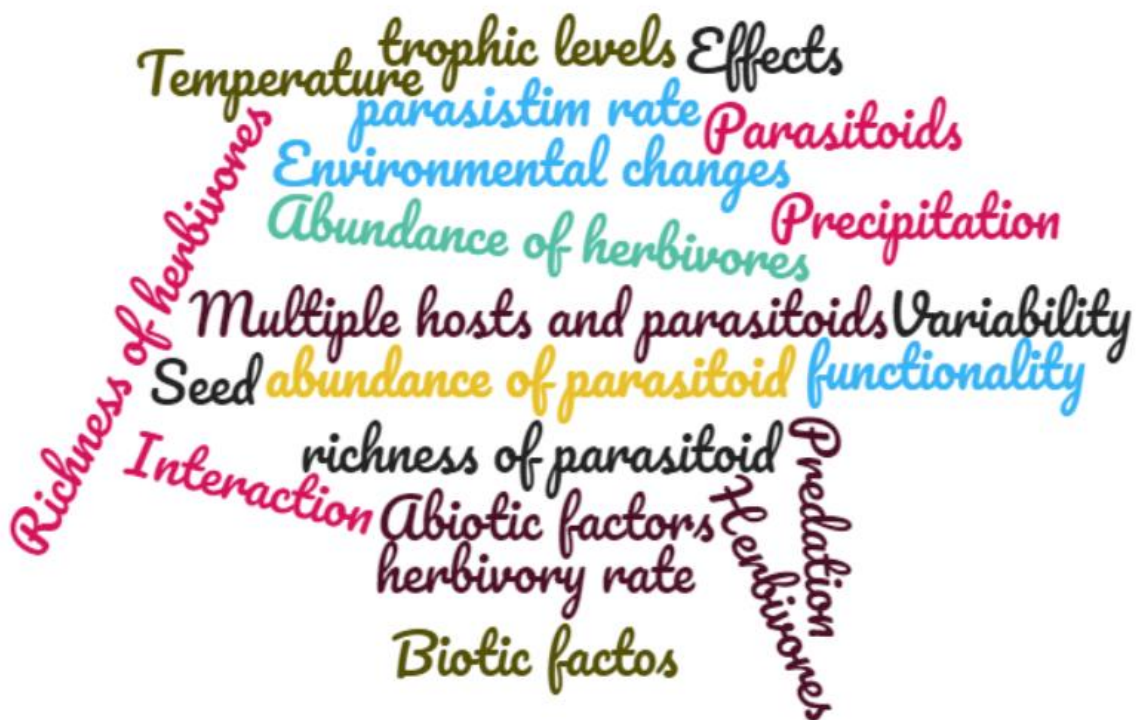
Acknowledgments

Graphical Abstracts
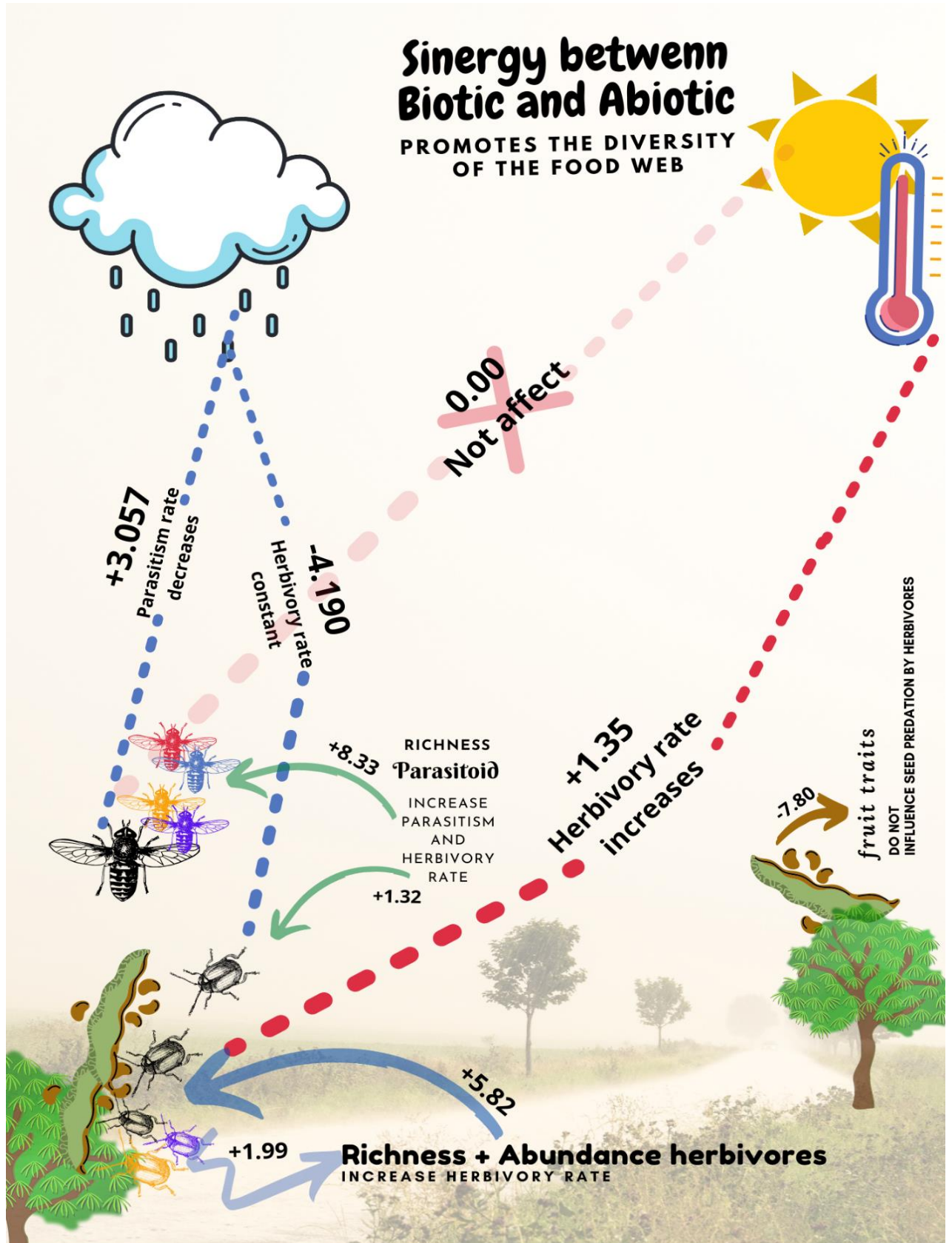
Introduction

In natural communities, multiple hosts and parasitoids are linked to form a complex food web of interactions. Understanding how each species respond to variations in the environment driven by biotic and abiotic factors in the long term is relevant for studying the diversity function of species in the ecosystem. The relationship between species diversity and primary productivity may be highly dynamic-changing over time (Rodriguez & Hawkins, 2000; Cardinale *et al.*, 2006; Parmesan, 2006; Thierry *et al.*, 2019).

Temperature and precipitation - i.e., abiotic factors - appear to combine with resource traits, abundance, and richness of species - i.e., biotic factors - to determine the dynamics of interactions and complexity of the food web (Micheli *et al.*, 1999). Excessive precipitation can hurt arthropods by impairing survival and increasing their development time, interrupting the flight process, and even reducing the foraging efficiency of herbivores and parasitoids. Regarding temperature, increasing it can raise metabolism for insect herbivorous and mortality for parasitoid species (Bale *et al.*, 2002; Stireman *et al.*, 2005). Because each insect population responds idiosyncratically to environmental variations, it can directly or indirectly impact growth, developmental rates, and interaction (Davis *et al.*, 1998, Bale *et al.*, 2002). Therefore, environmental variation alters the taxa's absolute and relative abundances (Cardinale *et al.*, 2006). The climatic variation affects primary productivity, and resource traits cause a positive relationship between plant and functional-group (Micheli *et al.*, 1999, Loreau, 1998). In this sense, large fruits may be more attractive to insects' colonization (Cope & Fox, 2003; de Sousa-Lopes *et al.*, 2019).

Food webs are more than the sum of their component species and can respond to environmental changes in ways that are unpredictable and not adequately reflected by changes in the abundance and diversity of their component species (Tylianakis *et al.*, 2007). Abundance and richness of herbivores and parasitoid species affect interaction among them, promoting disturbances and accentuating intra and interspecific competition in natural communities (Denno et al.,1995; Ribeiro-Costa, 1998). According to Bird *et al.* (2019), competition between herbivorous insects increases with population density and tends to be stronger between than within feeding guilds. According to Denno *et al.*, (1995) increased parasitoid attack on the inferior herbivore competitor may hasten its reduction. Likewise, through indirect effects of the parasitoid, when two or more herbivore species share the same parasitoid, this can increase the pressure of natural enemies to attack a particular herbivorous species more susceptible to parasitism, which is reflected in the decrease of seed consumption

(Denno *et al.*, 1995; Abrams & Matsuda, 1996; Abrams *et al.*, 1998; Thierry *et al.*, 2019). This scenario can be attributed to the fact that parasitism modulates competition among herbivores by modifying the interaction strength and species richness in the food web structure. (Eveleigh et al.,2007; Thierry et al., 2019).

A closely related question that intrigues the scientific community is whether the diversity of communities is also related to ecosystem function (Huston, 1997; Grime, 1998; Rodríguez & Hawkins, 2000; van der Plas, 2019), which include the presence or relative abundance a top species, a combination of species, beyond variation in functional composition (van der Plas, 2019). The host-parasitoid interactions provide interesting case studies for biotic and abiotic factors because the time lag between the host and the parasitoid will determine the observed pattern of community variability and their functionality (Micheli *et al.*, 1999b; Hughes, 2000; Thierry *et al.*, 2019)

Multitrophic host-parasitoid food web supported by *Senegalia tenuifolia* (L.) BRITTON & ROSE (Fabaceae: Mimosoideae) is assumed as a model to explore the herbivory and parasitism behavior to the abiotic and biotic environment in the long term. The plant species is a host of several herbivorous insect species consuming fruits and seed, such as Lepidoptera, Coleoptera, and Hymenoptera. In extension, third and fourth parasitoid trophic levels depict different parasitoids (Tuller *et al.*, 2015; Maia *et al.*, 2017, 2018). In this study, we investigated the effects of the biotic and abiotic factors on herbivory and parasitism rates in a multitrophic host-parasitoid food web over the years. We raise two questions: (*i*) do temperature and precipitation affect herbivory and parasitism rates?; (*ii*) how do fruit traits, abundance, and richness of herbivore and parasitoid species act on herbivory and parasitism rates.

Material e Methods

Field description

We carried out this study at the municipalities of Lavras and Luminarias in fragments of Brazilian cerrado (savanna) in the south of Minas Gerais state, southeastern Brazil. The study was divided into three main areas (i. e. sites) as a unit of logistic reachability, called A (located in the municipality of Luminárias-MG), B and C (located in the municipality of Lavrass-MG). Across these three sites, nine collection spots which are our true replica, were established which were at least 400 m from each other (**A1:** 21∘31′ 1.36″S, 044∘53′ 1.78″W;

A2: 21∘31′ 5.13″S, 044∘52′ 6.32″W; **A3:** 21∘31′ 5.31″S, 044∘52′ 3.84″W; **A4:** 21° 31'32.3" S, 044° 52'24.3" W; **B1:** 21∘18′ 3.46″S, 044∘58′ 0.53″W; **B2:** 21∘19′ 4.85″S, 044∘57′ 8.66″W; **C1:** 21∘14′ 4.57″S, 044∘57′ 6.38″W; **C2:** 21∘14′ 5.71″S, 044∘57′ 8.66″W; **C3:** 21∘14′ 7.87″S, 044∘58′ 0.06″W), (Fig. 1). According to the Köppen-Geiger climate classification, this region's climate is classified as Cwa and Cwb, being defined by a subtropical altitude climate with dry winter and mild summer (Köppen, 1900.; Kottek et al., 2006; Reboita et al., 2015). The average temperature of 19.4°C, and the annual average rainfall of 1529.5mm - Brazilian National Institute of Meteorology (INMET) (BRAZIL, 1992).

Fig. 1. A- Map of Brazil, highlighting the state of Minas Gerais.
B - Map of Minas Gerais, highlighting the municipalities of Lavras and Luminárias.
C-Location of the sampling sites from where we collected Senegalia tenuifolia fruits.
Extracted from Maia et al., 2017. **A1, A2, A3, A4** correspond to spots the municipality of Luminárias-MG. **B1, B2, C1, C2** and **C3** correspond to spots the municipality of Lavras

Temperature and precipitation (Satellite data)

Land surface temperature (LST) has an essential role in understanding the energy exchange between land and atmosphere, urban climatology, and environment change (Sobrino *et al.*, 2003, Weng *et al.*, 2014). The MODIS LST products are generated as a sequence of products beginning with a swath (scene) and progressing, through spatial and temporal transformations, to daily, eight-day, and monthly global gridded products with different spatial resolutions (Wan, 2007). This study selected MODIS Land Surface and Emiss -V6

products (MOD11A1V6) at daily data and 1-km spatial resolution for the years 2011, 2012, 2013, 2014, and 2017 in the municipalities Lavras and Luminárias/ MG – Brazil. All the datasets were downloaded from the website of NASA's Earth Observing System Data and Information System (https://earthexplorer.usgs.gov/). Daily temperature values were extracted by the QGIS software and converted to °C using the scale factor 0.02 (Wan, 2007), then the average monthly temperature was calculated for all the years studied. The rainfall distribution is one of the most critical parameters in the hydrological cycle (Kummerow *et al.*, 2000). Moreover, the frequency and intensity of precipitation are directly linked to the local temperature (Trenberth *et al.*, 2020). Therefore, we estimated the precipitation in the study region through The Tropical Rainfall Measuring Mission (TRMM). TRMM's precipitation radar is specifically for rainfall monitoring (Kummerow *et al.*, 2000), including the minimum measurable rain rate of 0.5 mm/h and a swath width of 200km or more (Kozu *et al.*, 2001). We used the satellite TRMM 3B43 v7 and opted to extract the precipitation data by month/milliliters. The datasets were also downloaded from NASA's Earth Webinar Series website: Giovanni (https://giovanni.gsfc.nasa.gov/giovanni/).

Multitrophic host-parasitoid food web

   Senegalia tenuifolia is known from almost all states of Brazil and several phytogeographic domains (Barros & Morim, 2014). However, in the Atlantic Domain, its altitudinal gradient varies between 250–847m. It has a wide distribution in the Americas (Rico-Arce 2007). The species has branches terete, with exfoliating bark and prickles recurved. The species is characterized principally by the scandent or liane habit, within fruits straight and margins sinuous (Barros & Morim, 2014). The plant also has therapeutic potential in the use of rheumatic pain and column (Ribeiro, 2014). *Senegalia tenuifolia* is the host of the different taxonomic groups of insects, predominant to order Coleoptera and Hymenoptera (Tuller *et al.*, 2015; Maia *et al.*, 2017, 2018). Among them, *Merobruchus terani* Kingsolver, 1980, *Stator maculatopygus* (Pic, 1930) (Chrysomelidae: Bruchinae) and *Allorhogas vulgaris* Zaldívar-Riverón & Martinez, 2018 (Hymenoptera: Braconidae: Doryctinae) are commonly associated with the predation of *S. tenuifolia* seeds, where *M. terani* is the most representative and abundant species. According to Dan Johnson & Romero (2004), Bruchinae has different oviposition guilds, *M. terani* belongs to "Mature Fruit Guild (A)", who glue their eggs to the outside of the fruit, oviposit in crevices in the fruit wall and their larvae burrow through the fruit wall into seeds, while *S. maculatopygus* belongs to

"Mature Fruit Guild (C)", who feed in seeds from dehiscent or partially dehiscent fruits and are not known to feed in seeds from indehiscent fruits.

Traits fruits and seeds and interactions

Senegalia tenuifolia fruits were collected between July and August, during five years (2011, 2012, 2013, 2014, and 2017). The months are corresponding to the season of greater development and ripening of fruits. We collected 25 fruits per spot each month, totaling 1896 fruits (Table 2). As *S. tenuifolia* is a liana, we could not distinguish the number of different plants at each site, so we opted to collect the fruits randomly in each spot (Maia *et al.*, 2017, 2018). For the removal of fruits, we used pruning shears with a long stem. In the field, fruits were stored in paper packages properly identified by plant and later moved to the Laboratory. Each fruit was individually stored in labeled PVC tubes, and sealed at both ends with voile fabric, fixed by rubber, in order to allow the entry of oxygen and balance moisture, which prevents the proliferation of fungi and permits the development of organisms contained in fruits and their containment after emergence. Fruits were stored for three months to allow insects inside the seeds to complete their development and emerge as adults.

To determine the interactions between beetles and parasitoids, we dissected the seeds and examined the cephalic capsule and the host remnants (Maia *et al.*, 2018; Morales-Silva *et al.*, 2018). We established the interactions involving the seed-feeding species using information from previous works (Tuller *et al.*, 2015; Maia *et al.*, 2018; Zaldívar-Riverón *et al.*, 2018). After it, seeds were separated into the general categories: not predated, predated, with the presence or not of the parasitoid, and aborted seeds were disregarded. We gathered information on fruits after the emergence of adult insects. We estimated the width and the length of each fruit and seeds using a digital caliper. Each fruit had its width measured in three places, measuring each end's region and a measure in the central region of the fruit to calculate the average area. The emerged insects of each fruit were identified to the lowest taxonomical level possible and deposited in the Entomological Collection of the Laboratory of Ecology and Complexity at the Federal University of Lavras, Minas Gerais, Brazil.

Data analysis

We assumed herbivory and parasitism rates as functional multitrophic host-parasitoid dynamics processes closely influenced by concepts abiotic and biotic. We considered abiotic factors the monthly average precipitation and temperature of all the sites. In contrast, fruits area, abundance, and richness of herbivores and parasitoids were considered biotic factors.

Seed numbers consumed by herbivores (*SC*) in total seeds (*TS*) expressed the herbivory rates (*HR*), as follow:

$$HR = (SC)/(TS) \qquad\qquad \text{eqn 1}$$

The parasitism rates (*PR*) was determined by herbivores abundance (*HA*) and parasitoids abundance (*PA*), as follows:

$$PR = (PA)/(PA) + (HA) \qquad\qquad \text{eqn 2}$$

We employing generalized additive models for location, scale and number of shape (GAMLSS) employing *gamlss* package (Stasinopoulos & Rigby, 2007) to unfold the effects abiotic factors and biotic factors have on herbivory and parasitism rates in the long term. We built models using the rate of herbivory and parasitism as variable responses while the monthly mean temperature and precipitation, and fruit area, richness, and abundance of herbivores and parasitoids as explanatory variables. The year and site we considered as random. Within the framework the function of the response variable is left general, with no explicit distribution-specific (Stasinopoulos & Rigby, 2007), employing *fitDist* function (Stasinopoulos & Rigby, 2007) to fit the best distribution of each model – i.e., herbivory and parasitism rates.

Distribution family depends on response variable, so we used *realplus* argument to explore parasitism and herbivory rates distribution. The next step was to select the best model according to the Generalized Akaike Information criterion (GAIC) (Stasinopoulos & Rigby, 2007). For the diagnostic test, we used the worm plots proposed by Buuren & Fredriks, 2001 to verify intervals of explanatory variable that the model is not fit adequately. This checks non-overlapping for residual difference ranges by default (Stasinopoulos & Rigby, 2007).

RESULTS

Biotic and abiotic factors

The average temperature recorded during the years 2011 and 2017 varied widely between July and August, which correspond to the season of greater development and ripening of *S. tenuifolia* fruits. The minimum temperature observed during the five years of study was 21.86°C in 2012, and the year 2017 was the year warmer with the maximum

temperature reaching 32.37°C (Table 1, Fig. 2). The average precipitation fluctuated between 0 and 55.23170 mm per month (Table 1). The year 2017 was considered the year with the highest precipitation rates, with values ranging from 8.6 to 55.2317 mm/m. While the year 2011 was registered as the driest year with maximum precipitation of 0.0095239 mm/m (Table 1, Figure 2). We also noticed that although the site is very close to each other, there is a slight shift in temperature (+ 1ºC) (Table 1).
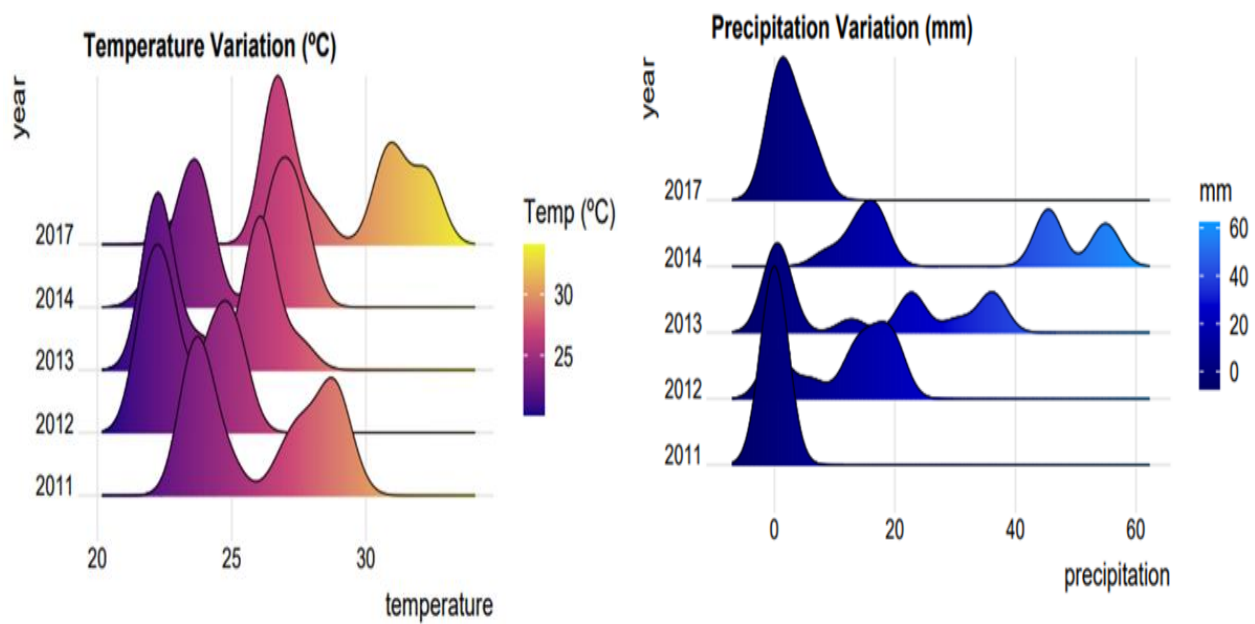
Fig. 2. Temperature and precipitation variation in the collection spots of *Senegalia tenuifolia* fruits during five years of study

Table 1. Climatic variation and variation of fruits and seeds indicating seeds consumed and not consumed by insect herbivores in addition to the presence of the parasitoid during five years (2011; 2012; 2013, 2014, and 2017) of collections in different sites and spots.

2011										
Climate Variability						**Fruits**		**Seeds**		
Site	Temperature (°C) ☀ 29.35 (Max) 23.44222 (Min)		Precipitation ☁ (*mm/m*) 0.0095239 (Max) 0 (Min)			Total fruit	Parasitoid Abundance	Total seed	Consumed	Not-consumed
	Spot	July	August	July	August					
A	A1	23.99	28.32	0	0.008	50	14	327	81	201
	A2	24.97	29.35	0	0.009	50	13	359	50	276
	A3	24.02	27.56	0	0.009	50	14	335	100	203
	A4	24.02	27.56	0	0.009	NA	NA	NA	NA	NA
B	B1	24.02	27.56	0	0.009	50	10	409	86	322
	B2	24.02	27.56	0	0.009	49	10	409	130	244
C	C1	23.44	28.79	0	0.005	50	4	210	72	107
	C2	23.44	28.79	0	0.005	50	5	430	170	248
	C3	23.44	28.79	0	0.005	50	14	430	262	140
2012										
Climate Variability						**Fruits**		**Seeds**		
Site	Temperature (°C) ☀ 29.35 (Max) 23.44222 (Min)		Precipitation ☁ (*mm/m*) 0.0095239 (Max) 0 (Min)			Total fruit	Parasitoid Abundance	Total seed	Consumed	Not-consumed
	Spot	July	August	July	August					
A	A1	21.87	23.9	16.19	0	75	10	761	82	624
	A2	22.7	25.2	19.55	0	75	4	803	8	728
	A3	21.8	24.2	19.55	6.04	75	12	695	61	585
	A4	21.8	24.2	19.55	6.04	75	5	850	38	741
B	B1	24.6	25.19	16	0.4	76	10	788	67	685
	B2	24.6	25.19	16	0.4	NA	NA	NA	NA	NA
C	C1	22.56	25.12	13.14	0	NA	NA	NA	NA	NA
	C2	22.56	25.12	13.14	0	75	6	684	41	607
	C3	22.56	25.12	13.14	0	74	6	738	129	561

To be continued...

2013										
Climate Variability					**Fruits**		**Seeds**			
Site		Temperature (°C) ☀ 29.35 (Max) 23.44222 (Min)		Precipitation 🌧 (*mm/m*) 0.0095239 (Max) 0 (Min)		Total fruit	Parasitoid Abundance	Total seed	Consumed	Not-consumed
	Spot	July	August	July	August					
A	A1	21.91	25.55	30.31	0.40	50	31	472	148	205
	A2	22.85	27.54	36.16	0.39	50	11	502	70	186
	A3	22.20	26.19	36.16	0.39	50	14	511	95	290
	A4	22.20	26.19	36.16	0.39	50	2	430	32	340
B	B1	23.95	26.14	12.8	1.9	50	26	491	147	284
	B2	23.95	26.14	12.8	1.9	NA	NA	NA	NA	NA
C	C1	22.25	26.04	22.74	0.07	50	5	478	86	334
	C2	22.25	26.04	22.74	0.07	49	4	313	39	204
	C3	22.25	26.04	22.74	0.07	25	3	184	4	151
2014										
Climate Variability					**Fruits**		**Seeds**			
Site		Temperature (°C) ☀ 29.35 (Max) 23.44222 (Min)		Precipitation 🌧 (*mm/m*) 0.0095239 (Max) 0 (Min)		Total fruit	Parasitoid Abundance	Total seed	Consumed	Not-consumed
	Spot	July	August	July	August					
A	A1	22.07	26.70	54.35	15.46	50	31	480	192	250
	A2	23.86	27.65	45.49	17.16	50	6	532	26	305
	A3	23.13	26.47	45.49	17.16	49	28	565	124	373
	A4	23.13	26.47	45.49	17.16	50	22	505	113	286
B	B1	23.50	26.93	45.3	8.6	50	22	522	218	227
	B2	23.50	26.93	45.3	8.6	NA	NA	NA	NA	NA
C	C1	23.95	27.44	55.23	13.44	NA	NA	NA	NA	NA
	C2	23.95	27.44	55.23	13.44	50	23	504	179	263
	C3	23.95	27.44	55.23	13.44	50	23	305	129	86

To be continued…

		Climate Variability				Fruits		Seeds		
2017										
Site		Temperature (°C) ☀ 29.35 (Max) 23.44222 (Min)		Precipitation ☁ (*mm/m*) 0.0095239 (Max) 0 (Min)		Total fruit	Parasitoid Abundance	Total seed	Consumed	Not-consumed
	Spot	July	August	July	August					
A	A1	26.92	31.23	1.016	3.188	50	22	484	122	362
	A2	28.13	32.36	1.025	6.043	50	20	454	104	344
	A3	26.59	30.75	1.025	6.043	50	11	398	53	345
	A4	26.59	30.75	1.025	6.043	50	28	478	86	385
B	B1	23.08	26.51	0	0	40	7	407	98	295
	B2	23.08	26.51	0	0	NA	NA	NA	NA	NA
C	C1	26.84	32.25	0.96	2.39	50	11	426	112	303
	C2	26.84	32.25	0.96	2.39	NA	NA	NA	NA	NA
	C3	26.84	32.25	0.96	2.39	NA	NA	NA	NA	NA

Furthermore, the precipitation was correlated to temperature (r= -0.42, p= 0.0001477); abundance and richness of herbivores (r= -0,06; p= 0.005359 and r= -0.09; p= 0.0002168, respectively), abundance and richness of parasitoids (r=0,1; p= 1.138e-05 and r= 0.1; p= 1.587e-05, respectively). While temperature was correlated to fruit area (r= -0.09, p= 0.0001477); abundance and richness of herbivores (r= 0.31; p= < 2.2e-16 and r= 0.31; p= < 2.2e-16, respectively), abundance and richness of parasitoids (r=0,17; p= 3.941e-13 and r= 0.17; p= 5.511e-12, respectively), (Fig. 3).
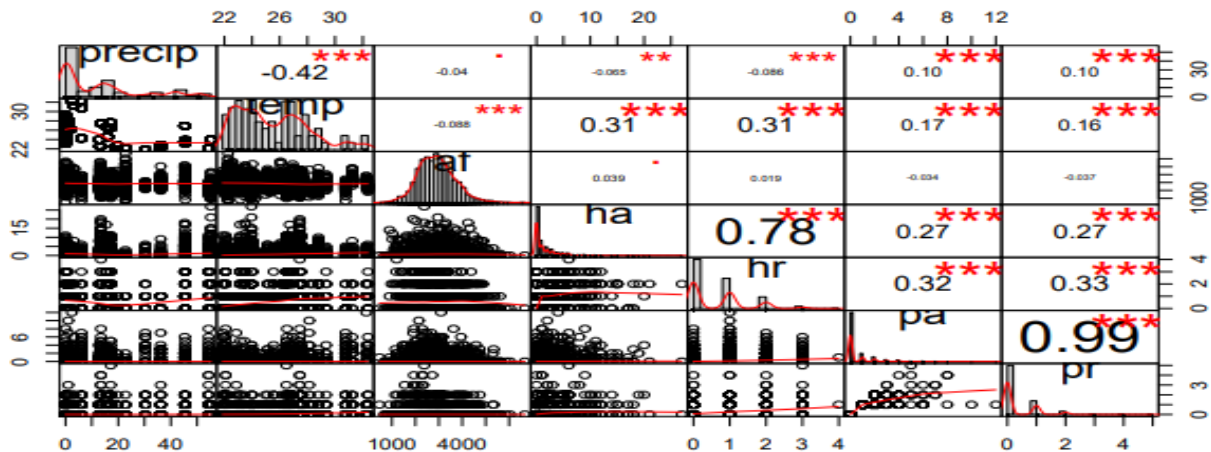
Fig. 3. Spearman rank correlation. The relationship among all explanatory variables - i.e, biotic (af: fruit area; ha: abundance of herbivores; hr: richness of herbivores; pa: abundance of parasitoids and pr: richness of parasitoids) and abiotic (precip: precipitation; temp: temperature) factors, during five years of study.

Herbivory rate

We sampled 1937 fruits and 17669 seeds of *S. tenuifolia* for five years. All fruits had their seeds categorized as consumed and not consumed by herbivores. About 3563 (20.16%) seeds were consumed by seed feeders (Table 1). *Merobruchus terani* was the most abundant insect herbivore, totaling 1747 individuals sampled during five years of study (Table 2).

Table 2. Species of insects herbivores and parasitoids associated with the food web supported by fruits of *Senegalia tenuifolia*. Abundance and relative frequency (%) of herbivores and parasitoids at the collection sites of *S. tenuifoli*a fruits during the five years of study. Species of herbivores (1: *Allorhogas vulgaris*; 2: *Lepidoptera* sp; 3: *Merobruchus terani*; 4: *Stator maculatopygu*s. Species of Hymenoptera (*5: Aprostocetus* sp; 6: *Bracon* sp; 7: *Brasema* sp; 8: *Chelonus* sp; 9: *Eudecatoma* sp; 10: *Eulophinae* sp; 11: *Eupelmu*s sp; 12: *Eurytoma* sp1; 13: *Eurytoma* sp2; 14: *Eurytoma* sp3; 15: *Gonizus* sp; 16: *Heterospillus* sp; 17: *Horismenus* sp; 18: *Lyrcus* sp; 19: *Paracrias* sp; 20: *Pteromalinae* sp; 21: *Sycophila* sp).

		Senegalia tenuifolia **fruit- 2011**																			
Site	**Spots**	Herbivores Species richness, abundance and relative frequency (%)				Hymenoptera Species richness, abundance and relative frequency (%)																
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**
A	A1	5	0	51	1	0	0	0	0	0	0	0	3	0	1	0	0	17	0	0	0	0
		6.1%	0%	62.9%	1.2%	0%	0%	0%	0%	0%	0%	0%	3.7%	0%	1.2%	0%	0%	20.9%	0%	0%	0%	0%
	A2	1	2	22	6	1	0	0	0	0	0	0	1	0	0	0	2	11	0	0	0	0
		1.6%	3.3%	37.2%	10.1%	2%	0%	0%	0%	0%	0%	0%	2%	0%	0%	0%	4%	22%	0%	0%	0%	0%
	A3	8	3	61	5	0	0	2	0	0	0	1	3	0	0	0	0	14	0	0	0	0
		8%	3%	61.6%	5%	0%	0%	2%	0%	0%	0%	1%	3%	0%	0%	0%	0%	14%	0%	0%	0%	0%
	A4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
B	B1	2	0	57	4	0	0	3	0	0	0	0	2	1	1	0	2	13	0	0	0	0
		2.3%	0%	66.2%	4.6%	0%	0%	3.4%	0%	0%	0%	0%	2.3%	1.1%	1.1%	0%	2.3%	15.1%	0%	0%	0%	0%
	B2	35	0	66	9	0	0	3	0	0	0	0	10	0	0	0	0	1	0	0	0	0
		26.9%	0%	50.7%	6.9%	0%	0%	2.30%	0%	0%	0%	0%	7.69%	0%	0%	0%	0%	0.76%	0%	0%	0%	0%
C	C1	0	1	51	6	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0
		0%	1.3%	70.8%	8.8%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2.77%	0%	0%	2.77%	0%
	C2	3	0	119	22	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2	0
		1.76%	0%	70%	12.9%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	1.17%	0%	0%	1.17%	0%
	C3	0	0	200	23	0	0	0	0	0	0	0	0	1	0	0	0	18	0	0	0	0
		0%	0%	76.3%	8.7%	0%	0%	0%	0%	0%	0%	0%	0%	0.38%	0%	0%	0%	6.87%	0%	0%	0%	0%

To be continued...

Site	Spots	Herbivores Species richness, abundance and relative frequency (%)				Hymenoptera Species richness, abundance and relative frequency (%)																
		1	**2**	**3**	**4**	**5***	**6**	**7***	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21***
A	A1	22	2	10	0	0	0	0	1	0	0	1	6	1	2	0	0	3	0	0	0	0
		26.8%	2.4%	12.1%	0%	0%	0%	0%	1.2%	0%	0%	1.2%	7.3%	1.2%	2.4%	0%	0%	3.6%	0%	0%	0%	0%
	A2	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	50%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	A3	0	1	13	1	0	0	0	0	0	0	0	0	1	1	0	0	12	0	0	0	0
		0%	1.6%	21.3%	1.6%	0%	0%	0%	0%	0%	0%	0%	0%	1.6%	1.6%	0%	0%	19.6%	0%	0%	0%	0%
	A4	4	0	3	0	0	0	0	0	0	0	0	1	1	0	0	0	4	0	0	0	0
		7.8%	0%	10.5%	0%	0%	0%	0%	0%	0%	0%	0%	2.3%	2.63%	0%	0%	0%	10.5%	0%	0%	0%	0%
B	B1	4	0	21	2	0	0	0	0	0	0	0	1	0	0	0	0	9	0	16	0	0
		5.9%	0%	31.3%	2.9%	0%	0%	0%	0%	0%	0%	0%	1.4%	0	0	0	0	13.4%	0	23.8%	0	0
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	C1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C2	7	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
		17%	2.4%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2.4%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C3	19	2	46	0	0	0	0	0	0	0	1	0	0	0	3	0	5	0	0	0	0
		14.7%	1.5%	35.6%	0%	0%	0%	0%	0%	0%	0%	0.7%	0%	0%	0%	2.3%	0%	3.8%	0%	0%	0%	0%

Table title: *Senegalia tenuifolia* fruit- 2012

To be continued...

		Senegalia tenuifolia fruit- 2013																				
Site	Spots	Herbivores Species richness, abundance and relative frequency (%)				Hymenoptera Species richness, abundance and relative frequency (%)																
		1	2	3	4	5*	6	7*	8	9	10	11	12	13	14	15	16	17	18	19	20	21*
A	A1	55	7	23	0	0	0	0	0	3	0	0	78	4	2	0	0	14	0	0	0	0
		37.1%	4.7%	15.5%	0%	0%	0%	0%	0%	2.0%	0%	0%	52.7%	2.7%	1.3%	0%	0%	9.4%	0%	0%	0%	0%
	A2	11	1	3	0	0	0	0	0	2	0	0	12	0	1	0	0	4	4	0	0	0
		15.7%	1.4%	4.2%	0%	0%	0%	0%	0%	2.8%	0%	0%	17.1%	0%	1.4%	0%	0%	5.7%	5.7%	0%	0%	0%
	A3	38	5	6	3	0	0	0	0	0	0	0	13	3	3	0	0	6	1	0	0	0
		40%	5.2%	6.3%	3.1%	0%	0%	0%	0%	0%	0%	0%	13.6%	3.1%	3.1%	0%	0%	6.3%	1%	0%	0%	0%
	A4	0	0	14	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
		0%	0%	43.7%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	12.5%	0%	0%	0%	0%
B	B1	40	0	49	17	0	0	0	0	0	0	5	0	0	0	0	0	28	0	0	0	0
		27.2%	0%	33.3%	11.5%	0%	0%	0%	0%	0%	0%	3.4%	0%	0%	0%	0%	0%	19%	0%	0%	0%	0%
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	C1	0	0	48	4	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
		0%	0%	55.8%	4.6%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2.32%	0%	0%	0%	0%
	C2	1	2	14	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0
		1.1%	2.3%	16.2%	0%	0%	0%	0%	2.5%	0%	0%	0%	0%	0%	0%	0%	0%	0%	2.5%	0%	0%	0%
	C3	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
		0%	100%	0	0	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	25%	0%	0%	0%

To be continued...

		Herbivores Species richness, abundance and relative frequency (%)				Hymenoptera Species richness, abundance and relative frequency (%)																
Site	**Spots**	**1**	**2**	**3**	**4**	**5***	**6**	**7**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17***
A	**A1**	75	0	72	52	0	0	8	0	6	1	0	25	0	0	0	0	27	2	0	0	0
		39%	0%	37.5%	27%	0%	0%	4.1%	0%	3.1%	0.5%	0%	13%	0%	0%	0%	0%	14%	1%	0%	0%	0%
	A2	21	0	2	1	0	0	0	0	3	0	1	4	0	0	0	0	0	1	0	0	0
		80%	0%	7.6%	3.8%	0%	0%	0%	0%	11.5%	0%	3.8%	15.3%	0%	0%	0%	0%	0%	3.8%	0%	0%	0%
	A3	52	2	53	89	0	0	32	0	0	0	0	7	1	0	0	0	14	0	0	0	0
		46%	1.7%	46%	71%	0%	0%	25.8%	0%	0%	0%	0%	5.6%	0.8%	0%	0%	0%	11%	0%	0%	0%	0%
	A4	21	0	74	53	0	0	8	0	1	0	0	7	0	0	0	0	26	0	0	0	0
		18.5%	0%	65%	46%	0%	0%	7%	0%	0.8%	0%	0%	6.1%	0%	0%	0%	0%	23%	0%	0%	0%	0%
B	**B1**	132	0	56	36	0	0	4	0	12	0	0	12	0	0	0	0	13	0	2	0	0
		60%	0%	25%	16%	0%	0%	1.8%	0%	5.5%	0%	0%	5.5%	0%	0%	0%	0%	5.9%	0%	0.9%	0%	0%
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	**C1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C2	0	1	240	129	0	0	5	0	0	0	0	0	0	0	0	0	29	0	0	0	0
		0%	0.5%	134%	72%	0%	0%	2.7%	0%	0%	0%	0%	0%	0%	0%	0%	0%	16.2%	0%	0%	0%	0%
	C3	11	1	118	80	0	26	11	0	0	0	1	1	0	0	0	0	2	1	32	0	0
		8.5%	0.7%	91.4%	62%	0%	20.1%	8.5%	0%	0%	0%	0.7%	0.77%	0%	0%	0%	0%	1.5%	0.7%	24.8%	0%	0%

Senegalia tenuifolia **fruit- 2014**

To be continued

…

| Site | Spots | Herbivores | | | | Hymenoptera | | | | | | | | | | | | | | | | |
		Species richness, abundance and relative frequency (%)				Species richness, abundance and relative frequency (%)																
		1	2	3	4	5*	6	7*	8	9	10	11	12	13	14	15	16	17	18	19	20	21*
A	A1	3	0	66	13	0	0	0	0	0	0	0	0	0	0	0	0	25	0	71	0	0
		2.4%	0%	54%	10.6%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	20.4%	0%	58.1%	0%	0%
	A2	25	0	30	2	0	0	3	0	0	0	0	11	1	4	0	2	14	0	28	0	1
		24%	0%	28.8%	1.9%	0%	0%	2.8%	0%	0%	0%	0%	10.5%	0.9%	3.8%	0%	1.9%	13.4%	0%	26.9%	0%	0.9%
	A3	5	0	31	5	0	0	0	0	0	0	0	2	0	0	0	1	13	0	1	0	0
		9.4%	0%	58.4%	9.4%	0%	0%	0%	0%	0%	0%	0%	3.7%	0%	0%	0%	1.8%	24.5%	0%	1.8%	0%	0%
	A4	6	0	24	3	0	0	0	0	0	0	0	2	0	1	0	0	17	0	235	0	0
		6.9%	0%	27.9%	3.4%	0%	0%	0%	0%	0%	0%	0%	2.3%	0%	1.1%	0%	0%	19.7%	0%	273.2%	0%	0%
B	B1	5	0	17	7	0	0	0	0	0	0	0	1	0	0	0	0	9	0	7	0	0
		5.1%	0%	17.3%	7.14%	0%	0%	0%	0%	0%	0%	0%	1%	0%	0%	0%	0%	9.1%	0%	7.1%	0%	0%
	B2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
C	C1	0	0	77	5	0	0	0	10	0	0	0	0	0	0	0	0	6	0	8	0	0
		0%	0%	68.7%	5.1%	0%	0%	0%	8.92%	0%	0%	0%	0%	0%	0%	0%	0%	5.35%	0%	7.14%	0%	0%
	C2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
	C3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%

Through the Generalised Akaike Information criterion (GAIC), the best distribution was Box-Cox Power Exponential-orig (BCPEo) – (please, for information about worm plot of the residuals see Fig.1 -Supplementary Material). We showed that the climatic variable (i. e. abiotic factors) is an important condition for herbivory rates' success. Temperature positively affects the herbivory rate ($p < 0.05$, Table 3), as the temperature increases, the herbivory rate also increases (Fig. 4 (a)). The same effect was observed for precipitation ($p < 0.001$, Table 3). However, the herbivory rate remains constant at high precipitation values observed (Fig. 4 (b)).

Table 3. Generalized additive models for location, scale, and shape (GAMLSS) using Box-Cox Power Exponential-orig (BCPEo) distribution in gamlss family performed on the factors that influenced the herbivory rates.

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	-1.801e+00	1.919e-01	-9.386	< 2e-16 ***
Precipitation (mm)	-4.190e-03	1.135e-03	1.135e-03	0.000231 ***
Temperature (°C)	1.357e-02	6.720e-03	2.019	0.043729 *
Fruit area	-7.804e-05	2.032e-05	-3.841	0.000129 ***
Herbivore abundance	5.828e-02	6.587e-03	8.848	< 2e-16 ***
Herbivore richness	1.994e-01	2.303e-02	8.661	< 2e-16 ***
Parasitoid abundance	2.141e-02	2.272e-02	0.942	0.346250
Parasitoid richness	1.032e-01	4.433e-02	2.329	0.020026 *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Relationship between herbivory rate and climatic variations
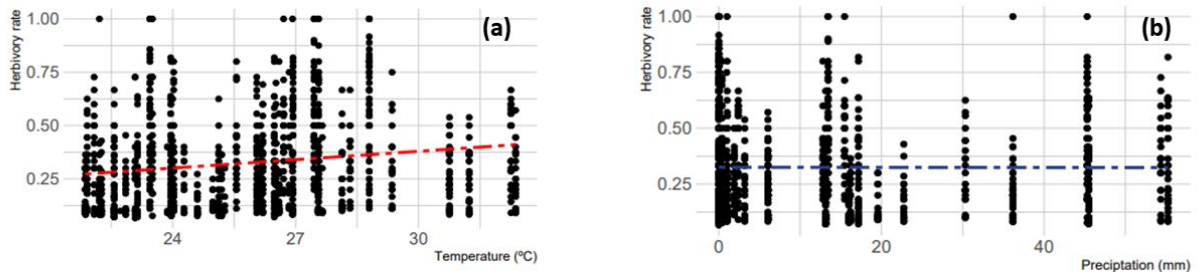
Fig. 4. Generalized additive models for location, scale, and shape (GAMLSS) using Box-Cox Power Exponential-orig (BCPEo) distribution in gamlss family. Scatterplot Smother with linear regression fit for the positive relationship between (a) herbivory rate and monthly average temperature and (b) negative relationship precipitation.

The abundance and richness of herbivores positively influence the herbivory rate ($p < 0.001$; Table 3, Fig. 5 (a) and (b), respectively) however, larger fruit areas harmed the herbivory rate ($p < 0.001$; Table 3, Figure 5 (c)). Furthermore, we observed that parasitoids' richness also positively influences the herbivory rate ($p < 0.05$, Table 3, Fig. 5 (d)).

Herbivory rate
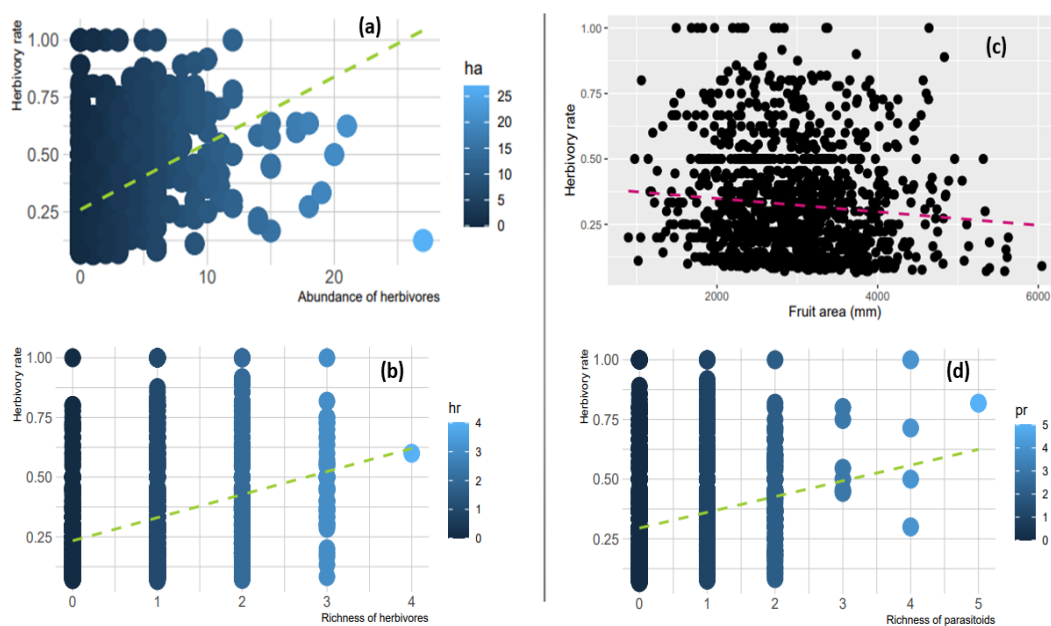
Fig. 5. Relationship among herbivory rate and abundance of herbivores (a), richness of herbivores (b), fruit area (c), and richness of parasitoid species (d).

Parasitism rate

Regarding the total of fruits of *S. tenuifolia*, whose 3563 seeds were consumed by herbivores, approximately 25.19% of them showed some sign of parasitoid attack (Table 1). This study cataloged seventeen species of parasitoid active in *S. tenuifolia* fruits, which gregarious parasitoid *Paracrias* sp was quantified as the most abundant parasitoid, totaling 386 individuals, followed by the parasitoid *Horismenus* sp with 354 individuals sampled during five years of study (Table 2).

Through the Generalised Akaike Information criterion (GAIC), the best distribution was Box-Cox-t-orig (BCTo) – (please, for information about worm plot of the residuals, see Fig. 2 -Supplementary Material). We noticed that precipitation harms the parasitism rate (p < 0.001; Table 4, Fig. 6 (a)). The abundance of herbivore (p < 0.001) keeps the parasitism rate constant, while parasitoid richness (p < 0.01) positively influence the parasitism rate (Table 4, Fig. 6 (b) and (c)). We also observed that neither the abundance and richness of parasitoid could promote an increase in the rate of parasitism (p < 0.001; Table 4, Fig. 6 (d) and (e)) in the *S. tenuifolia* fruits.

Table 4: Generalised additive models for location, scale, and shape (GAMLSS) using Box-Cox Power Exponential-orig (BCPEo) distribution in gamlss family performed on the factors that influenced the herbivory.

	Estimate	Std. Error	t-value	Pr(>|t|)
Intercept	-6.374e-01	1.403e-01	-4.544	7.03e-06 ***
Precipitation	3.057e-03	8.923e-04	3.426	0.000665 ***
Temperature	8.418e-03	4.674e-03	1.801	0.072334 ·
Fruit area	-1.101e-05	1.577e-05	-0.698	0.485257
Abundance of herbivores	-1.987e-01	7.630e-03	-26.042	< 2e-16 ***
Richness of herbivores	-1.510e-01	1.948e-02	-7.751	5.65e-14 ***
Abundance of parasitoids	1.149e-01	9.953e-03	11.549	< 2e-16 ***
Richness of parasitoids	8.333e-02	2.685e-02	3.104	0.002027 **
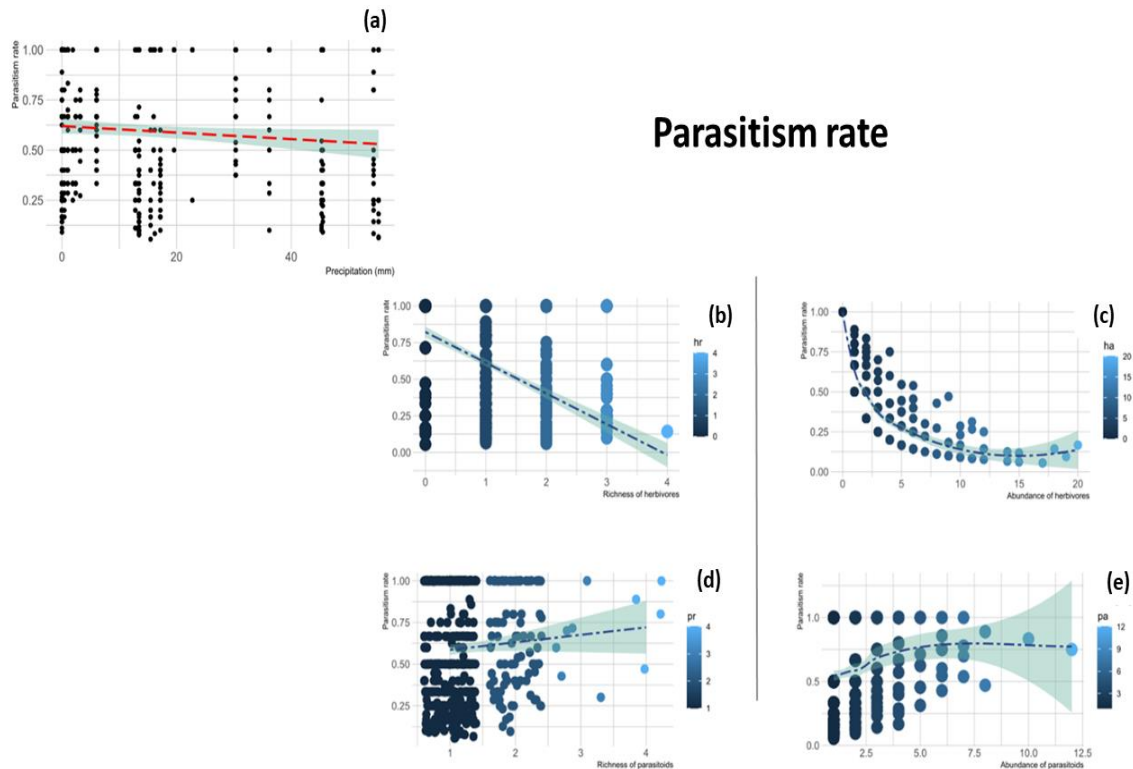
Fig. 6: Generalised additive models for location, scale and shape (GAMLSS) using Box-Cox-t-orig (BCTo) distribution in gamlss family. Scartterplot Smother with linear regression fit for the positive relationship among parasitism rate and (a) precipitation, (b) richness of herbivores, (c) abundance of parasitoid, (d) richness of parasitoid and (e) abundance of parasitoid.

Discussion

We described some biotic and abiotic mechanisms behind the herbivory and parasitism rates that can affect the host-parasitoid multitrophic food web. Indeed, each biotic and abiotic factor influences the host-parasitoid interaction in the food web differently.

Temperature is the primary abiotic factor affecting insect development, reproduction, foraging behavior, distribution range, and the timing of their activities (Angilletta, 2009; Sánchez-Guillén *et al.*, 2016; Abram *et al.*, 2017; Córdoba-Aguilar *et al.,* 2018). In the multitrophic food web supported by *S. tenuifolia*, the temperature can induce the first trophic level behavior for a higher seed consumption, thereby increasing herbivory rates in higher temperatures. An increase in temperature can faster metabolic reactions of insects that result in the momentum of higher feeding and immature development, whose more resistant to increase of the temperature than insects adults (Ma *et al.*, 2020). However, our results demonstrated that temperature does not affect parasitism rates, whose species of the order Hymenoptera tend to be more resistant to thermal variations (Hance *et al.*, 2007).

Nevertheless, Zhang *et al*. (2019) demonstrated that 34°C is the most stressful for parasitoids. This may suggest why the temperature was insignificant for the parasitism rate since the maximum temperature recorded in our study was 32°C.

Our results also demonstrated that precipitation can also affect both herbivory and parasitism rates. According to Andrade *et al.* (2020), herbivory damage is more concentrated in drier areas. When insects are more exposed to plants, the direct effect of rain tends to harm survival and increase their development time, compromising herbivory efficiency (Chen *et al.*, 2019). However, at least in this system that includes the multitrophic food web of *S. tenuifolia*, precipitation is an inherent abiotic factor since the larval phase is protected by the seed and fruit coat, which keeps the herbivory rate constant. On other the hand, the average increases in precipitation may negatively impact arthropods by disrupting a flight, reducing foraging efficiency (Peng *et al*., 1992; Drake, 1994; Kasper *et al.,* 2008), which negatively affects the functionality of the parasitoid that is sensitive to precipitation (Speight et al., 2008). During rain, the parasitoid ceases all foraging activities (Weisser *et al.*, 1997). Besides, the chemical communication between them is compromised, chemical clues are essential for the parasitoid to find its host (Dicke 2016). Thus, the female's reproductive success is greatly reduced in seasonal rain (Weisser *et al.*, 1997). The same was verified by Rand *et al.* (2020), that when manipulating the level of precipitation in different treatments on tri-trophic interactions observed a lower in the parasitism in precipitations.

In this study, we also observed that the relationship between parasitism rate and abundance of herbivores cannot be described by linear regression, being, therefore, a non-linear regression with decreasing exponential function that indicates a decrease in the parasitism rate in the presence of great herbivore abundance. The same is observed for herbivore richness, however, it is explained by linear regression. Parasitism involves a sequence of processes that enables parasitoids to locate, select the host, parasitize, and alter host physiology to allow the development of their offspring in the selected host (Vet & Dicke, 1992, Godfray, 1994). During this sequence, several mechanisms can result in a variety of outcomes that affect parasitoid efficiency (Abram et al., 2019). However, the parasitism also non-reproductive effects that negatively affect their hosts without their offspring successfully developing or directly feeding on them, such unsuccessful parasitism, nonreproductive killing, hypersensitivity of the parasitoid, could result from unsuccessful attacks that hosts survive (Abram et al., 2019). It could be attributed to hosts defense mechanisms against parasitoids, such as hemocyte encapsulation of parasitoid eggs and larvae or also defensive strategies when the host can detect the presence of parasitoids, which can occur before

parasitoids insert their ovipositor into the host (Carton et al., 2008; Abram et al., 2019, Thierry et al., 2019). Furthermore, as shown in the results above, impacts within this system may be driven by a number of underlying mechanisms, such as direct effects of increased precipitation on parasitoid performance. A reduced infestation of the parasitoid in wet years is thought to result from adult females laying fewer eggs and moving less that result in the decrease parasitism rate.

Our results also demonstrated that the relationship between parasitism rate and abundance of parasitoid can not be described by linear regression, being, therefore, a non-linear regression with a logarithmic function that indicates a constant action of the parasitoid on herbivore host. We observed also that the parasitism rate increases slightly when the parasitoid richness increases, which in turn was demonstrated by a linear regression line. The increase in the parasitism rate even if subtle in the presence of richness of parasitoid species indicated evidence of a link between parasitoid diversity and their ability to inflict mortality of herbivore, since that it insert their ovipositor in the host for ensuring their progenies.

Thus greater parasitoid species richness potentially allows access to a greater proportion of available host, leading to an increasing total parasitism rate, stressing that diversity and function of the top-level are not independent. Cardinale et al., (2002), showed that increasing the topographic complexity, that is, increasing the species diversity of a functional group induces facilitative interactions where the fluxes of energy and matter can be influenced by the biophysical complexity of species and generate positive interactions that enhance ecosystem functioning. Within the same line of research, Eveleigh *et al.* (2007) found greater action by herbivore–natural enemy in heterogeneous forests in which the increase in the density of the host corresponds to a cascade of increasing diversity and complexity of the food web.

In the long term, the herbivory rates had a positive effect on both the abundance and richness of herbivores. We observed the direct relationship between herbivory rate and abundance and richness of herbivores, whereas the abundance and richness of herbivore increase it is also possible to notice an increase in herbivory rate. However, the data showed that despite an increase in the rate of herbivory to the two explanatory variables, the rate increase is limited to an abundance of twenty individuals and richness of four herbivores. This limitation in the herbivory rate is most likely associated with a variety of herbivorous species in the fruits and how their relative abundance is also impacted by competitive interactions (Denno *et al.*, 1995, Kaplan & Denno, 2007). According to Bird *et al.* (2019), competition between herbivorous insects increases with population density and tends to be

stronger between than within feeding guilds. Cannibalism among larvae is common in the Bruchinae (Ribeiro-Costa, 1998; Richardson et al., 2010). According to Messina (2004) and Guedes et al. (2007), the mortality of Bruchine larvae in competition for seed resources is inevitable, especially when the larvae develop within a single seed since the larvae are unable to avoid competition among themselves. Host plant-related defense, physical factors, such as temperature, and precipitation, and natural enemies also could limit the action of herbivores (Denno et al., 1995). However, here we observed that the number of parasitoid species in the food web positively affects the herbivory rates that increase as the parasitoid richness increases. In this case, the presence of natural enemies may alter the outcome of competition between two herbivores species. According to Denno et al. (1995), increased parasitoid attack on the inferior herbivore competitor may hasten its reduction.

Likewise, through indirect effects of the parasitoid, when two or more herbivore species share the same parasitoid, this can increase the pressure of natural enemies to attack a particular herbivorous species more susceptible to parasitism, which is reflected in the decrease of seed consumption (Abrams & Matsuda, 1996; Abrams et al., 1998, Denno et al., 1995, Thierry et al., 2019). In addition, the fruit area was associated only with the herbivory rate. Although the resource traits influence the oviposition behavior of Bruchinae, where fruits with larger areas are more attractive for females laid more eggs (Morales-Silva *et al.*, 2018; de Sousa-Lopes *et al.*, 2019), here we found that the herbivory rate tends to decrease as the area of the fruit increases. The same result was found by Modena *et al*. (2012), who found that fruit traits do not influence seed predation by Bruchinae.

In summary, our results proved to be complex and relevant to the functionality of the trophic level that makes up the multitrophic host-parasitoid food web in the long term. With our first question, we verified that each functional composition is impacted differently by temperature and precipitation. In the second question, we observed that the fruits traits, abundance, and richness of herbivore and parasitoid species also have different effects in relation to herbivory and parasitism rates. Temperature does not hurt the parasitism rate, but it increases the consumption of seeds, which herbivory rate increases as the temperature increases. Precipitation affects only the parasitism rate, it manages to keep the herbivory rate constant. However, fruit traits do not influence seed predation by herbivores. In high precipitation, the parasitism rate decreases but on the other hand, it increases with the richness of parasitoid species. Parasitoid richness also leads to an increase in the herbivory rate, in which the herbivore community is controlled by an abundance of the parasitoid that ensures that the parasitism rate remains constant. Therefore, we conclude that the synergy between

biotic and abiotic factors promotes the diversity of the food web that is dependent on functionality rates, mainly of the diversity top-level trophic.

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SUPPORTING INFORMATION

Supplementary Material

Worm plot: diagnostic of residuals for GAMLSS
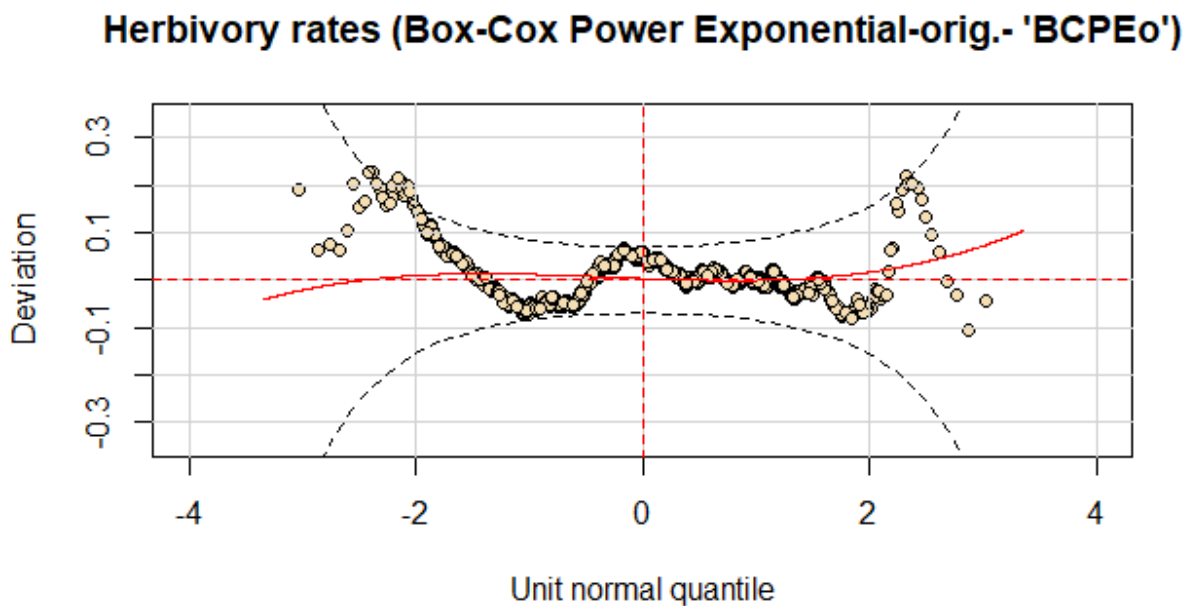
Fig. 2: Worm plot for gamlss distribution family (BCPEo) fitted of herbivory rate. The points show how far the residuals are from their expected values represented in the figure by the horizontal red dotted. The point-wise 95% confidence regions are given by the two elliptic curves in the middle of

the figure. If the model is correct we would expect approximately 95% of the points to be between the two elliptic curves and 5% outside. A higher percentage of points outside the two elliptic curves indicates that the fitted distribution of the model is inadequate to explain the response variable.
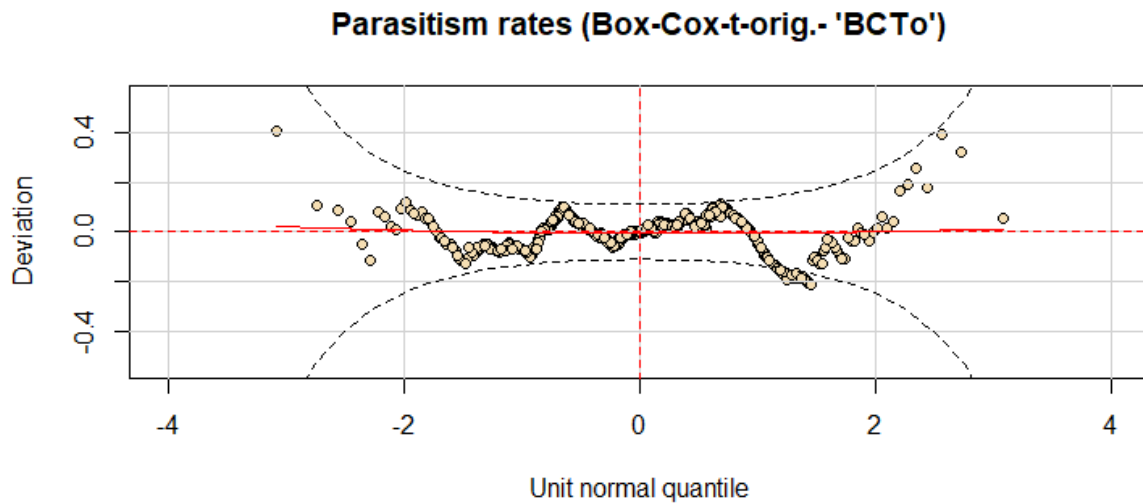
Fig. 2: Worm plot for gamlss distribution family (BCTo) fitted of parasitism rate. The points show how far the residuals are from their expected values represented in the figure by the horizontal red dotted. The point-wise 95% confidence regions are given by the two elliptic curves in the middle of the figure. If the model is correct we would expect approximately 95% of the points to be between the two elliptic curves and 5% outside. A higher percentage of points outside the two elliptic curves indicates that the fitted distribution of the model is inadequate to explain the response variable.

CONCLUSÃO GERAL

- A complexidade da rede trófica suportada por *Senegalia tenuifolia* altera de um ano para o outro, bem como de um local de coleta para outro**.**

- A composição funcional das espécies dos diferentes níveis tróficos estão correlacionados com as métricas da rede trófica que remetem à estrutura, complexidade e estabilidade.

- A taxa de herbivoria foi correlacionada negativamente com as espécies do topo e positivamente correlacionada com as espécies intermediárias, demonstrando que há uma escala dependente entre os níveis tróficos, enquanto um diminui o outro aumenta.

- A taxa de parasitismo foi correlacionada positivamente com o link entre as espécies intermediária-intermediária e com o comprimento máximo da cadeia. Foi também correlacionado negativamente com o link entre as espécies intermediária-basal, demonstrando que o parasitoide primário desempenha a sua função em controlar a comunidade de herbívoros e diminuir a pressão nas sementes.

- A taxa de hiperparasitismo foi correlacionado negativamente com a fração basal, fração de link entre espécies intermediário-basal e conectância. Enquanto que, o comprimento máximo da cadeia e link entre as espécies intermediária-intermediária foram correlacionadas positivamente.

- Precipitação afeta tanto a taxa de herbivoria como parasitismo.

- Temperatura afeta somente as taxas de herbivoria.

- A taxa de herbivoria aumenta com a riqueza e abundância de herbívoros e diminui a medida que a área do fruto aumenta.

- Riqueza de parasitoide contribui para um aumento na taxa de herbivoria.

- A taxa de parasitismo diminui em decorrência da abundância e riqueza de herbívoros.

- A taxa de parasitismo se mantém constante com a abundância de parasitoide e aumenta com a riqueza de parasitoides.

- fatores bióticos e abióticos impulsionam a dinâmica da rede trófica através da funcionalidade da espécie.

Os achados do primeiro capitulo, impulsionou para a teoria da interação entre consumidor e recurso, na qual a probabilidade das espécies coexistirem pode estar ligada à mudanças nos parâmetros alimentar das espécies de topo, ou seja generalidade em se alimentar dos mais diferentes recursos disponíveis. Dessa forma, a complexidade da rede alimentar poderia estar combinado com a conectividade do habitat sobre o padrão da rede trófica através da topologia de nível, representada pelo hiperparasitóide e sua taxa funcional, evidenciando que as topologias são responsáveis pela manutenção da estabilidade que poderia ser condicionado ao alto nível de generalidade (ou seja, espécies generalistas) do nível superior.

No segundo capitulo, os resultados mostraram-se complexos e relevantes para o nível trófico que compõem a rede trófica hospedeiro-parasitoide. A composição da rede trófica reage de maneira diferenciada pra os fatores bióticos e abióticos. Sinergismo entre os fatores bióticos e abióticos promovem a diversidade da rede trófica, na qual é impulsionada pela variabilidade funcional do último nível trófico.