Universidade de São Paulo
Instituto de Biociências
Programa de Pós-Graduação em Ecologia

Camila Celestino Hohlenwerger

Efeito da estrutura da paisagem sobre a provisão dos serviços de polinização e controle de pragas

(Foto de Latin American Lifestyle and Art - LALA, Roatán: "Coffee Plantation" by the artist Angelina Quic [1])

São Paulo
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[1] *Imagem disponível em: https://www.tripadvisor.co/LocationPhotoDirectLink-g944573-d4471264-i70823377-Latin_American_Lifestyle_and_Art_LALA-West_Bay_Roatan_Bay_Islands.htm

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Efeito da estrutura da paisagem sobre a provisão dos serviços de polinização e controle de pragas

Landscape structural effects on the provision of pollination and natural pest control services

Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para obtenção do Título de Doutor em Ciências, na Área de Ecologia

Orientador: Jean Paul Walter Metzger
Co-orientador: Leandro Reverberi Tambosi

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Dedication

Para minha avó e minha mãe, Sônia Silva e Kátia Quadros, duas fontes infinitas e eternas de amor, dedicação e bondade.

Epigraph

“Toda as vossas coisas sejam feitas com amor“

1 Coríntios 16:14

Agradecimentos

Esse momento chegou! E que jornada que foi esse doutorado! Quem me conhece sabe o quanto eu vim ansiando por esse momento, por concluir essa etapa, por dar continuidade na caminhada. Mas não se engane, esse ansiar pelo “movimento” não tem nada haver com não ter aproveitado e adorado os caminhos que trilhei nessa jornada, pelo contrário, tem haver com ter passado um tempo lindo e intenso cultivando as “asas”, e eu posso provar! rs

Começo agradecendo ao Programa de Pós Graduação em Ecologia-USP não só por ter sido minha casa ao longo desses 9 anos entre mestrado e doutorado, mas principalmente por ter feito eu me sentir em casa. Eu estou para conhecer ambiente de trabalho e ensino mais acolhedor que esse PPG, me sinto privilegiada de ter podido crescer tanto dentro desse ambiente. Queria então agradecer a todas as Comissões de Pós Graduação (CCP) por fazerem desse ambiente de trabalho tão acolhedor e pró-alune. Agradeço em especial a CCP de 2019 que fez eu e Duda nos sentirmos pertencentes e aptos a contribuir. Aqui, queria agradecer muito ao Paulo Inácio Prado, ao Glauco Machado e ao Alexandre Adalardo por tamanho aprendizado, paciência e dedicação com e por nós alunes. É impressionante o carinho e dedicação que vocês nos dedicaram, muito obrigada. É óbvio que dentro desse time eu não poderia deixar de reservar um lugar mais que especial para a querida Vera Lima. Vera que é absurdamente competente, Vera que é altamente atenciosa, Vera que é a “chefia”, e como se tudo isso não fosse bastante, Vera que é como se fosse mãe das(os) alunas(os) de tão carinhosa, amável e dedicada que é. Vera, não existem palavras para definir a sua importância nessa jornada. Sempre que penso nesse percurso, sua atenção e cuidado sempre aparecem ali no top 10, gratidão viu?! Agradeço também à Erika e Shirlene que sempre estão prontas para nos ajudar!

Eu tenho muita sorte com orientação, você vai ver quando eu começar a agradecer ao Jean e ao Le, rs. Mas eu tenho tanta sorte que ela se expande para além da orientação formal e chega no que as pessoas chamam formalmente de “mentores”. E olha que até nisso eu tenho sorte, porque dessa formalidade, não precisei. Começo então agradecendo a ela, “Rainha” como sempre muito orgulhoso diz Peu Rocha: Renata Pardini. Rê, eu não tenho como agradecer pelo tanto que aprendi ao seu lado. Entre a incrível experiência da monitoria em VertSul (que disciplina, que privilégio!), a paciência e o crescimento gigantesco no IB Mulheres, e claro, entre uma pizza e outra na sua casa, eu te digo com todas as letras que você foi parte importantíssima dessa jornada. Serei sempre muito grata por ter tido o mega privilégio de conviver tanto com você e ter aprendido e ensinado do seu lado (que ousadia, não? Tenho sorte! Já disse isso? rs). Agradeço muito também ao Paulo Roberto

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John Uribe (Hola amor!!!). Vocês são raio de sol em dias de chuva, são a minha Bahia em São Paulo, são a certeza de um encontro gostoso e de uma amizade pra vida. Los quiero mucho! Agradeço muito à Dudurududa por ter sido a melhor parceira que eu podia ter durante a representação discente, por ter vivido comigo uma das melhores viagens que eu já fiz, e por ser uma fonte de boas vibrações, de bons desejos, de amizade e carinho. Obrigada demais, Dudurududa! Agradeço tb à turma dos "coroas" da Eco: Dri maravilhosa, poço de bondade e fofura; Li Carneiro e Will Sabino, meninos de ouro, garantia de boa comida e diversão; Ari, tão querido e prestativo! Só vem coisa boa da convivência com esse menino, incrível!; Di Bertuol, Morma, Natcho, Rodolfex (meu primeiro "orientando") e Lu Caires, obrigada por serem tão carinhosos e fazerem da Eco (literalmente, essa gente construiu partes lindas desse PPG!) um ambiente tão gostoso. Aos meus queridos da Costa Rica, Rosinha, Andresito, e Dieguito: Obrigada por ampliar meus horizontes e por serem tão, mais tão queridos! Andresito, tenho um carinho enorme por você, obrigada por todas brejas, por cuidar com carinho do meu campo (Obrigada tb Bru!!), e por ter feito dos dias dessa jornada mais cheios de vida e de happy hours hahaha. Dieguito, você é pura alegria, impossível olhar pra você e não sorrir, obrigada pelo carinho, guapo lindo! Agradeço à Pam Santana por ser sempre tão fofa e querida, obrigada por todo estímulo e amizade! Erika e Paulo Marques, vocês são incríveis, uma explosão de energia boa e diversão, obrigada por serem tão lindos e queridos! Julia Assis (Ju), obrigada por ser tão divertida e por estar sempre me impulsionando! Ao povo maravilhoso do Interface e do Lepac (e aqui vou listar pq, ainda bem, somos muitos: Lu Teixeira, Carito, Doug, Artur, Karla, Naty, Mari Eiko, MaFê, Ju, Clari, Rafa, Chico, Adrian (e Maria maravilhosa), Bolinho, Pa Prist: vocês são incríveis e tornam o nosso lab, o trabalho e a vivência muito mais especiais! Bolinho, um agradecimento especial à você pelos trezentos churrascos, feijucas, macarronadas, pizzadas e tudo mais que nós do lab e da Eco vivemos graças em muito à Andrés e a você, com seu jeito leve e agregador! Agradeço em especial também a Isa, que foi muito importante em momentos de alegria e de tristeza, e que sem dúvidas tornou muitos dos dias dessa jornada mais carinhosos e gostosos. Agradeço demais à Lari, com quem eu aprendi (e aprendo) muito! Obrigada por ser essa potência, amar tanto o que faz e nos ensinar tanto! Por fim, agradeço imensamente à Paty, ô mulher querida, Jesus! Paty, você é uma força e uma inspiração, obrigada por ser tão amiga, tão atenciosa e cuidadosa. Nossa, quanto que eu aprendo com você! Tenho um carinho sem tamanho por você! Ao povo da Eco, vocês são tão sensacionais! Agradeço em especial JP, Bru França, Luís Felipe: obrigada por serem lindos, pela amizade gostosa e por terem feito o possível e impossível em só um ano de representação discente.

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Índice

Capítulo 1:
"*Forest cover and proximity to forest affect predation by natural enemies in pasture and coffee plantations differently*"

Capítulo 2:
"Determining the effects of landscape structure on coffee pollination using provision networks"

Capítulo 3:
"*Pollination and pest control are mainly driven by flow-related landscape attributes: the need to account for multiple scales and disservices"*

Resumo

Compreender os processos que determinam os benefícios ou bens que as pessoas obtêm da natureza (i.e., os *serviços ecossistêmicos*) é essencial para que possamos desenhar paisagens multifuncionais. Como produto da relação entre a *demanda* (e.g., sociedade) e a *oferta* (e.g., natureza), a provisão dos serviços ecossistêmicos depende de *relações socioecológicas* que acontecem no espaço. Tais relações conectam, portanto, a oferta à demanda através do *fluxo* de pessoas, matéria ou organismos, e estão sujeitas aos *efeitos da configuração e composição da paisagem*. Assim, entender como características da paisagem modulam as interações entre estes componentes da *cadeia de provisão* (i.e., *oferta, demanda e fluxo*) é essencial para que possamos criar e adequar estratégias de manejo que garantam uma provisão intensa e duradoura de múltiplos serviços ecossistêmicos. Nesta tese, nós buscamos entender como a paisagem afeta a provisão dos serviços de *polinização e controle de pragas* em *cafezais*, considerando os efeitos sobre a oferta, demanda e fluxos de serviços. O Brasil é o maior produtor de café do mundo, produzindo em torno de 3 milhões de toneladas anualmente. O serviço de polinização é capaz de aumentar a produtividade de café em 30%, enquanto o serviço de controle de pragas pode reduzir as atuais perdas em até 40%, dependendo da configuração e composição da paisagem. Dada tamanha relevância econômica, essa tese buscou entender melhor como se dão esses benefícios no espaço. No primeiro capítulo, nós usamos experimentos de predação para investigar se matrizes com diferentes graus de similaridade estrutural às florestas nativas (i.e., matrizes de pastagem e de cafezal) modulam os efeitos de cobertura florestal e proximidade à floresta sobre as taxas de predação por diferentes inimigos naturais. Nossos resultados mostram que *as duas matrizes estudadas favorecem a provisão do serviço de controle de pragas por diferentes inimigos naturais*. Enquanto artrópodes contribuem para taxas de predação em ambas matrizes e independentemente da distância à borda da floresta, aves tendem a atuar quase que exclusivamente em matrizes de café e mais proximamente à interface matriz-floresta. Já no segundo capítulo, nós avaliamos como se dá o serviço de polinização do café através de uma abordagem de *rede de interações socioecológicas*. Nesta rede, a oferta de organismos polinizadores, providos essencialmente por fragmentos florestais, e a demanda pelos serviços nas áreas dos cafezais são conectadas através dos fluxos de polinizadores entre essas áreas. Nós mostramos que atributos dos nós de demanda associados à quantidade e intensidade das interações com os nós de oferta afetam a produção de café, e que, portanto, *o serviço de polinização responde a características estruturais e funcionais da paisagem*. No terceiro capítulo, nós utilizamos dados sobre os serviços de polinização e controle de pragas por formigas, aves e morcegos para investigar a existência de sinergias ou demandas conflitantes entre estes serviços. Nós mostramos que atributos espaciais associados a uma *maior heterogeneidade da paisagem aumentam a provisão de ambos os serviços*, mas que *o planejamento da paisagem precisa considerar o efeito de múltiplas escalas espaciais, além de eventuais desserviços* na produção de café. Nossos trabalhos mostram, portanto, que a avaliação da provisão de múltiplos serviços ecossistêmicos precisa *i) considerar atributos da paisagem associados aos três componentes da cadeia de provisão*, *ii) ter uma detalhada caracterização dos fluxos que conectam a oferta à demanda*, *iii) considerar o efeitos de diferentes matrizes e da heterogeneidade da paisagem do entorno*, e *iv) utilizar abordagens multiescalares que considerem a provisão de serviços e desserviços*. Por fim, nossos resultados mostram o *potencial da análise de redes socioecológicas* para avançar no entendimento de como a paisagem modula a provisão de serviços ecossistêmicos. Finalmente, nós utilizamos estes resultados para reforçar a importância do *manejo da paisagem que combine estratégias locais e regionais* e que permita, portanto, considerar os efeitos das diferentes escalas na provisão dos serviços de polinização e controle de pragas em cafezais. Nós sugerimos que *o desenho de paisagens florestais agrícolas que vise as sinergias entre estes serviços* deve considerar *práticas de manejo que garantam níveis médios de cobertura florestal (~30-40%)*, promover uma maior permeabilidade e *heterogeneidade da matriz*, além de aumentar *a proximidade e os contatos entre matriz e floresta*.

Palavras-chave: Serviços ecossistêmicos; Estrutura da paisagem; Controle de pragas; Polinização; Mata Atlântica; Cadeia de provisão; Redes socioecológicas.

Abstract

Understanding the processes that determine the benefits that people obtain from nature (i.e., *ecosystem services*) is crucial for us to be able to design multifunctional landscapes. As a product of the relationship between *demand* (e.g., society) and *supply* (e.g., nature), ecosystem service provision relies on *social-ecological relationships* that take place in space. Such relationships connect the supply to demand through the *flow* of people, matter or organisms, and are thus subject to *landscape configuration and composition effects*. Therefore, understanding how landscape features modulate the interactions between the components of the *provision chain* (i.e., supply, demand and flow) is essential to creating and adapting management strategies that guarantee an intense and lasting provision of multiple ecosystem services. In this thesis, we seek to understand how the landscape affects the provision of *pollination and pest control services in coffee plantations*, considering the effects on service supply, demand, and flows. Brazil is the largest coffee producer in the world, producing around 3 million tons annually. The pollination service can increase coffee productivity by 30%, while pest control service can reduce current losses by up to 40%, depending on landscape configuration and composition. Given such economic relevance, this thesis sought to better understand how these benefits occur in space. In the first chapter, we used predation experiments to investigate whether matrices with different degrees of structural similarity to native forests (i.e., pastures and coffee plantations) modulate the effects of forest cover and forest proximity on predation rates by natural enemies. Our results show that *the two studied matrices favor the provision of pest control services by different natural enemies*. While arthropods contribute to predation rates in both matrices and irrespective of the distance from the forest edge, birds tend to act almost exclusively on coffee matrices and closer to the matrix-forest interface. In the second chapter, we evaluate the provision of coffee pollination through a *network approach of social-ecological interactions*. In this network, the supply of pollinating organisms, provided essentially by forest fragments, and the demand for provision in coffee plantation areas are connected through the flow of pollinators between these areas. We show that attributes of demand nodes associated with the amount and intensity of interactions with supply nodes affect coffee production, and that, therefore, *pollination responds to structural and functional features of the landscape*. In the third chapter, we use data already collected on pollination and pest control services by ants, birds and bats to investigate the existence of synergies or conflicting demands between these services. We show that spatial attributes associated with *greater landscape heterogeneity increase the provision of both services*, but that *landscape planning needs to consider the effect of multiple spatial scales, in addition to eventual disservices*, on coffee production. Our work shows, therefore, that the assessment of the provision of multiple ecosystem services needs to *i) consider landscape attributes associated with the three components of the provision chain*, ii) *have a detailed characterization of the flows that connect supply to demand*, iii) *consider the effects of different matrices and of the heterogeneity of the surrounding landscape*, and iv) *use multi-scale approaches that consider the provision of services and disservices*. Finally, our results show the *potential of approaches such as the analysis of social-ecological networks* to advance the understanding of how the landscape modulates the provision of ecosystem services. Finally, we use these results to reinforce the importance of *landscape management that combines local and regional strategies* and that allows, therefore, to address the effects of different scales in the provision of pollination and pest control services in coffee plantations. We suggest that *the design of agricultural forest landscapes that aims at synergies between these services* should consider *management practices that guarantee average levels of forest cover (~30-40%), promote landscape heterogeneity and matrix permeability, and increase proximity and contacts between matrix and forest*.

Keywords: *Ecosystem services; Landscape structure; Pest control; Pollination; Atlantic Forest; Provision chain; Social-ecological networks*.

Introdução geral

Serviços ecossistêmicos são bens ou benefícios à sociedade que são providos pelos ecossistemas por meio de funções ou processos ecológicos (MEA 2005; IPBES 2019). Como bens ou benefícios que ligam o meio ambiente ao ser humano, sua provisão depende de relações socioecológicas que conectam a *oferta* à *demanda* através de *fluxos* de pessoas, organismos ou matéria (Fisher et al. 2009; Mitchell et al. 2015). Tais relações acontecem no espaço e são, portanto, sujeitas aos efeitos de configuração e composição da paisagem (Metzger et al. 2021a). Embora essencial ao bem-estar humano, a provisão de serviços ecossistêmicos vem globalmente diminuindo devido à conversão de ambientes naturais (Kubiszewski et al. 2020). Esse é o caso da expansão agrícola, que substitui áreas de vegetação nativa, apesar do potencial dessas áreas em prover serviços ecossistêmicos essenciais ao bem-estar humano, como a polinização e o controle de pragas (Tscharntke et al. 2005). O serviço de polinização contribui para cerca de 75% da produção agrícola mundial, enquanto o serviço de controle de pragas pode reduzir as atuais perdas agrícolas em até 30-80%, a depender do tipo de cultivo (BPBES/REBIPP 2019; IPBES 2019). Dada a importância destes serviços, entender como características da paisagem afetam as interações entre os componentes da *cadeia de provisão* (i.e., *oferta*, *demanda* e *fluxo*) é essencial para que possamos criar e adequar estratégias de gestão que garantam uma provisão intensa e duradoura de serviços ecossistêmicos (Boesing et al. 2020). Dentro desse contexto teórico e ao longo do desenvolvimento desta tese, nós buscamos contribuir para o entendimento de como integrar os efeitos da paisagem nas avaliações de serviços ecossistêmicos, considerando: i) a oferta, demanda e fluxo dos serviços; ii) as dinâmicas espaço-temporais destes três componentes; e iii) como diferentes tipos de governança afetam a cadeia de provisão através de mudanças na paisagem. Para isso, nós construímos os três capítulos dessa tese buscando avançar, em mais detalhe, no entendimento do item i), e produzimos três artigos onde apresentamos diferentes abordagens que permitem integrar os itens i), ii) e iii) nas avaliações de serviços ecossistêmicos.

A paisagem pode afetar a provisão de serviços alterando a quantidade e intensidade das interações entre os componentes da cadeia de provisão (Metzger et al. 2021a). Em um contexto de paisagens agrícolas com remanescentes florestais, a oferta de serviços pode ser representada pelas áreas de vegetação nativa que sustentam a biodiversidade que provém serviços, como os de polinização e controle de pragas. Em contrapartida, a demanda pode ser representada pelas áreas de plantio agrícola que requerem tais serviços. Dado que a efetividade do fluxo de serviços depende de características da oferta e da demanda e da paisagem que existe entre essas áreas (Baró et al. 2017), é esperado que a paisagem também afete a intensidade dos fluxos e, portanto, a provisão de serviços. Por exemplo, é esperado que a proporção e arranjo de vegetação nativa em relação às áreas produtivas na paisagem afetem a provisão dos serviços de controle de pragas através dos seus efeitos positivos na diversidade e *spillover* de espécies de pássaros (Boesing et al. 2018). Ainda, é esperado que o tamanho e proximidade dos fragmentos florestais às áreas de plantio beneficiem a provisão dos serviços de controle de pragas e polinização através do aumento do fluxo de espécies entre a oferta e a demanda (González-Chaves et al. 2020). Por fim, é esperado que essas relações variem com os diferentes tipos de uso da terra. Matrizes agrícolas estruturalmente mais parecidas com o habitat natural das espécies provedoras de serviços ecossistêmicos devem oferecer menos resistência ao movimento destas espécies, aumentando a chance de provisão de serviços ecossistêmicos, como o controle de pragas (Hohlenwerger et al. 2022). Uma maior diversidade de matrizes na paisagem pode também resultar numa maior oferta de serviços devido ao potencial dessas áreas em oferecer recursos e espécies complementares aos oferecidos pelas áreas de vegetação nativa (Prevedello and Vieira, 2010; Blitzer et al., 2012).

Avançar na compreensão de como o espaço modula a interação entre a oferta, demanda e fluxo é essencial para entender como diferentes dinâmicas espaciais e temporais desses componentes afetam a provisão do serviço ao longo do tempo. Apenas quando essas dinâmicas são consideradas, é que conseguimos desenvolver estratégias de manejo desenhadas para aumentar o fluxo entre a oferta e demanda, bem como reduzir o risco de perda da provisão ao longo do tempo (Boesing et al. 2020). Ainda, apenas quando integramos os efeitos da paisagem na cadeia de provisão é que podemos identificar como diferentes tipos de governança podem agir na oferta, demanda e fluxo de modo a garantir ou intensificar a provisão de serviços ecossistêmicos. Assim, paralelamente à construção desta tese, nós investimos em desenvolver três abordagens que permitissem: i) integrar processos ecológicos no nível da paisagem (e.g., perda de habitat e conectividade) na avaliação da provisão de serviços ecossistêmicos que considerem todos os componentes da cadeia de provisão (Metzger et al 2021a); ii) identificar quais padrões espaciais geram tendências temporais de ameaça à provisão de serviços ecossistêmicos ao longo do tempo (Boesing et al. 2020); e iii) identificar como diferentes governanças podem modificar a estrutura da paisagem e, portanto, afetar a provisão de serviços ecossistêmicos (Metzger et al. 2021b).

Em *Metzger et al. (2021a; Considering landscape-level processes in ecosystem service assessments)*, nós discutimos como a configuração e composição da paisagem afetam a provisão de serviços ecossistêmicos através de diversos processos no nível da paisagem, como a perda de habitat e a conectividade. Estes processos agem, portanto, sobre áreas de oferta e demanda dos serviços ecossistêmicos, bem como no fluxo entre essas áreas. Dessa maneira, nós reforçamos não só a necessidade de se considerar os distintos efeitos da estrutura da paisagem nos diferentes componentes da provisão, como apresentamos como esses processos e efeitos podem ser incorporados nas avaliações da provisão de serviços ecossistêmicos. Em suma, nós mostramos através de simulações espacialmente explícitas que é possível estimar corretamente a provisão de serviços ecossistêmicos quando se incorporam os efeitos da paisagem sobre cada um dos três componentes da cadeia de provisão.

Entendendo a importância de se considerar os processos no nível da paisagem nas avaliações de serviços ecossistêmicos, em *Boesing et al. (2020; Ecosystem services at risk: integrating spatiotemporal dynamics of supply and demand to promote long-term provision)*, nós propomos uma abordagem que integra dinâmicas espaço-temporais das áreas de oferta e de demanda para prever tendências temporais de provisão de serviços ecossistêmicos. Nós mostramos que algumas dinâmicas espaço-temporais da oferta e demanda resultam em riscos para provisão de serviços no longo prazo. Por exemplo, nós mostramos que para dinâmicas espaço-temporais nas quais a oferta é reduzida e a demanda ultrapassa essa oferta, a provisão dos serviços ecossistêmicos assume uma tendência negativa que leva à interrupção da provisão ao longo do tempo. Por fim, nós mostramos que uma vez que as dinâmicas de oferta e demanda, bem como as tendências de provisão são identificadas, é possível manejar a paisagem de forma a aumentar o fluxo entre a oferta e a demanda e assim reduzir o risco de perda do serviço no futuro.

Por fim, procuramos entender como diferentes tipos de governança, ou seja, de formas de gestão dos serviços ecossistêmicos, podem atuar sobre a oferta, demanda e fluxo destes serviços. Em *Metzger et al. (2021b; Connecting governance interventions to ecosystem services provision: a social-ecological network approach),* nós usamos uma abordagem socioecológica de redes para mostrar que modelos de governança hierárquica (como a criação de áreas protegidas), de mercado (por exemplo, pagamentos por serviços ambientais), e baseadas em comunidades (i.e., que fortalecem conexões entre as partes sociais interessadas) regulam diferentemente os componentes da cadeia de provisão na paisagem. Através da abordagem apresentada, nós mostramos que é possível identificar o tipo de intervenção de governança ideal para lidar com situações em que diferentes componentes da cadeira de provisão estão limitando o serviço ecossistêmico. Nós mostramos que conectar governança e serviços ecossistêmicos através das suas relações socioecológicas é essencial para se alcançar a provisão sustentável de serviços ecossistêmicos.

Dentro deste contexto mais amplo, no âmbito desta tese de doutorado, nós buscamos entender como a paisagem afeta a provisão dos serviços de polinização e controle de pragas em cafezais. Mais especificamente, nós buscamos avaliar como estes serviços são afetados por atributos da paisagem associados à oferta, demanda e aos fluxos. A produção de café é uma das principais atividades de importância econômica e cultural para o Brasil, o maior produtor e exportador de café do mundo (Conab 2018). Para esse cultivo, os serviços de polinização e controle de pragas podem representar um aumento de 20 a 40% na produtividade (Saturni et al. 2016; Aristizábal and Metzger, 2019). Assim, visto a importância do espaço em modular a provisão de serviços ecossistêmicos, nós buscamos responder três grandes perguntas:

Como diferentes matrizes antrópicas modulam os efeitos da estrutura da paisagem na provisão do serviço de controle de pragas?

Para responder essa pergunta, nós usamos experimentos de predação para investigar se matrizes com diferentes graus de similaridade estrutural às florestas nativas (i.e., matrizes de pastagem e de cafezal) modulam os efeitos de cobertura florestal e proximidade à floresta sobre as taxas de predação por diferentes inimigos naturais. Nós mostramos que os efeitos da paisagem nas taxas de predação variam com a resposta dos diferentes inimigos naturais (i.e., artrópodes e aves) aos tipos de matriz. Os resultados deste capítulo estão publicados na revista *Agriculture, Ecosystem and Environment* com coautoria de Leandro R. Tambosi e Jean Paul Metzger.

Como a estrutura da paisagem afeta o serviço de polinização em cafezais através dos seus efeitos na quantidade e intensidade das conexões entre áreas de oferta e demanda?

Para responder essa pergunta, nós utilizamos dados sobre a produção de café, o fluxo de polinização, e a configuração e composição de áreas de oferta (i.e., fragmentos florestais) e demanda (i.e., cafezais). Com isso, nós avaliamos como se dá o serviço de polinização na paisagem através de uma abordagem de rede de interações socioecológicas, onde a oferta e a demanda são conectadas através do fluxo de polinização. Nós mostramos que atributos dos nós de demanda associados à quantidade e intensidade das interações com os nós de oferta afetam a produção de café. Esse capítulo foi pré-selecionado para ser submetido à edição especial da revista *People and Nature: Understanding land-use driven biodiversity change: frontiers in linking ecological and socio-economic data and models*. Neste capítulo, nós (Camila Hohlenwerger, Leandro R. Tambosi e Jean Paul Metzger) contamos com a colaboração de um grupo internacional de coautores: Laura J. Graham, Jonathan R. Rhodes, Marie-Josée Fortin, Matthew G. E. Mitchell, Barbara Schröter, Felix Eigenbrod, Anna Cord, Mariana M. Vidal, Claudia Sattler, Luis Roman Carrasco e Pedro Fieldman.

Em que escalas e como a estrutura da paisagem atua como motores comuns dos serviços de polinização e controle biológico de pragas em plantações de café?

Neste capítulo, nós utilizamos dados já coletados sobre os serviços de polinização, controle de pragas por formigas, aves e morcegos para investigar a existência de sinergias ou demandas conflitantes entre estes serviços. Nós mostramos que atributos espaciais associados a uma maior heterogeneidade da paisagem aumentam a provisão de ambos os serviços, mas que o planejamento de paisagem precisa considerar o efeito de múltiplas escalas espaciais, além de desserviços na produção de café. Esse capítulo foi pré-selecionado para a edição especial da revista *Landscape Ecology: Understanding relationships between biodiversity and ecosystem services in real landscapes*. Neste capítulo, nós (Camila Hohlenwerger, Leandro R. Tambosi e Jean Paul Metzger) tivemos a contribuição dos seguintes coautores: Rebecca Spake, Natália Aristizábal, Adrian González-Chaves, Felipe Librán-Embid, Fernanda Saturni e Felix Eigenbrod.

Referências:

Aristizabal, N., & Metzger, J. P. (2019). Landscape structure regulates pest control provided by ants in sun coffee farms. Journal of Applied Ecology, 56(1), 21-30.

Baró, F., Gómez-Baggethun, E., & Haase, D. (2017). Ecosystem service bundles along the urban-rural gradient: Insights for landscape planning and management. Ecosystem Services, 24, 147-159.

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A. M., Rand, T. A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. Agriculture, Ecosystems & Environment, 146(1), 34-43.

Boesing, A. L., Nichols, E., & Metzger, J. P. (2018). Land use type, forest cover and forest edges modulate avian cross-habitat spillover. Journal of Applied Ecology, 55(3), 1252-1264.

Boesing, A. L., Prist, P. R., Barreto, J., Hohlenwerger, C., Maron, M., Rhodes, J. R., ... & Metzger, J. P. (2020). Ecosystem services at risk: integrating spatiotemporal dynamics of supply and demand to promote long-term provision. One Earth, 3(6), 704-713.

BPBES/REBIPP (2019): Relatório temático sobre Polinização, Polinizadores e Produção de Alimentos no Brasil. Marina Wolowski et al. (Orgs.). 1ª edição, São Carlos, SP: Editora Cubo. 184 pg.

Conab (2018) Levantamento da companhia nacional de abastecimento de café.http://www.conab.gov.br/OlalaCMS/uploads/arquivos.

Fisher, B., Turner, R. K., & Morling, P. (2009). Defining and classifying ecosystem services for 831 decision making. Ecological Economics, 68(3), 643–653.

González-Chaves, A., Jaffé, R., Metzger, J. P., & de MP Kleinert, A. (2020). Forest proximity rather than local forest cover affects bee diversity and coffee pollination services. Landscape Ecology, 35(8), 1841-1855.

Hohlenwerger, C., Tambosi, L. R., & Metzger, J. P. (2022). Forest cover and proximity to forest affect predation by natural enemies in pasture and coffee plantations differently. Agriculture, Ecosystems & Environment, 333, 107958.

IPBES. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. (C. N. Z. S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S.

M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A, Ed.). Bonn, Germany.

Kubiszewski, I., Costanza, R., Anderson, S., & Sutton, P. (2020). The future value of ecosystem services: Global scenarios and national implications. In Environmental Assessments. Edward Elgar Publishing.

MEA (Millennium Ecosystem Assessment) (2005). Ecosystems and human well-being: wetlands and water. World resources institute.

Metzger, J. P., Villarreal-Rosas, J., Suárez-Castro, A. F., López-Cubillos, S., González-Chaves, A., Runting, R. K., Holenwerger, C. & Rhodes, J. R. (2021a). Considering landscape-level processes in ecosystem service assessments. Science of The Total Environment, 796, 149028.

Metzger, J. P., Fidelman, P., Sattler, C., Schroter, B., Maron, M., Eigenbrod, F., Hohlenwerger, C. & Rhodes, J. R. (2021b). Connecting governance interventions to ecosystem services provision: A social-ecological network approach. People and Nature.

Mitchell, M. G., Suarez-Castro, A. F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K. J., ... & Rhodes, J. R. (2015). Reframing landscape fragmentation's effects on ecosystem services. Trends in ecology & evolution, 30(4), 190-198.

Prevedello, J. A., & Vieira, M. V. (2010). Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation, 19(5), 1205-1223.

Saturni, F. T., Jaffe, R., & Metzger, J. P. (2016). Landscape structure influences bee community and coffee pollination at different spatial scales. Agriculture, Ecosystems & Environment, 235, 1-12.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan‐Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecology Letters, 8(8), 857-874

Chapter 1

Forest cover and proximity to forest affect predation by natural enemies in pasture and coffee plantations differently

Camila Hohlenwerger, Leandro R. Tambosi, Jean Paul Metzger

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(“Morrogacho” de autoria do artista plástico Juan Carlos Suarez[2])

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Forest cover and proximity to forest affect predation by natural enemies in pasture and coffee plantations differently

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Abstract

Biological pest control is one of the key services from which agricultural production benefits. Despite being a well-studied ecosystem service, the potential of different matrices in shaping natural enemy contributions to pest predation is not yet clear. We used an experimental approach with predation experiments to investigate whether matrices with different degrees of structural similarity to the native forest (coffee and pasture) modulated the effects of forest cover and forest proximity on predation rate from different natural enemies. The effects of landscape structure on predation rates varied with natural enemy response to matrix type. Predation rates by arthropods (the main natural enemy acting in both matrices) were higher in coffee plantations and were positively and negatively affected by landscape and local forest cover, respectively. Predation rates by birds were higher near the forest in both matrices and two times higher in coffee plantations than in pastures. Regardless of natural enemy identity, predation rates inside agricultural matrices were higher in low-contrasting matrices, and increase with forest cover and proximity to forest. Given the clear importance of matrix type in modulating the effects of forest cover and forest proximity on predation rates, we recommend that agricultural management consider reducing habitat-matrix contrasts while increasing contact and habitat cover in the landscape to improve biological pest control. Among matrix management strategies, we recommend within-farm actions that would lead to greater matrix heterogeneity and permeability, along with an increase in landscape habitat cover,

such as more sustainable and wildlife-friendly agricultural systems and the restoration of protected areas within farms.

Keywords: Agricultural landscapes, Arthropods, Biological pest control, Birds, Ecosystem services, Matrix quality

1. Introduction

Agricultural expansion has modified and replaced areas of natural habitat (Curtis et al., 2018), disregarding the roles such areas play in providing ecosystem services as biological pest control, which can benefit agricultural production (Mitchell et al., 2015). However, those benefits tend to occur only in specific landscape conditions (Karp et al., 2018). Indeed, native forests, which usually act as habitats for natural enemy species, can be more or less effective in supplying biological pest control according to their spatial arrangement and landscape context (Karp et al., 2018; Haan et al., 2020). This variation can be due to the different sensitivities of natural enemies to native vegetation (e.g., native forest) or matrix (e.g., crop areas) attributes, which affect their spillover movements, i.e., movement of organisms from their habitat patch (e.g., fragments of native forest) to the matrix, which may result in ecological processes occurring within the matrix and thus the services they provide (Blitzer et al., 2012; Boesing et al., 2017, 2018b). Therefore, to ensure biological pest control in agricultural landscapes, we need to better understand how landscape structure differently affects pest predation rates provided by natural enemies that respond differently to agricultural matrices (Rusch et al., 2016).

Matrix type can be a key landscape feature modulating these landscape structural effects on pest control (Driscoll et al., 2013; Arroyo-Rodríguez et al., 2020). The degree of structural similarity of different agricultural fields (i.e., matrix types) to native vegetation (i.e., native forests) affects matrix permeability and, therefore, shapes species movement by facilitating or hindering the access of animals to different habitat patches across the matrix (Rand et al., 2006). Matrices that are more structurally similar to native habitats are less resistant to species movement and therefore favor cross-habitat spillover (Boesing et al., 2018b), which may increase predation inside agricultural matrices (Boesing et al., 2018a). Additionally, agricultural matrices can offer complementary resources for the forest community (Prevedello and Vieira, 2010; Blitzer et al., 2012), which encourages natural enemies to cross native forest edges to benefit from these resources (Fahrig, 2007).

However, foraging outside native vegetation may alter the balance between potential benefits and risks, as natural enemies could be more exposed to their predators (Brown, 1999; Hernández and Laundré, 2005; Biz et al., 2017). This increase in natural enemy vulnerability inside agricultural fields can make pest control more intense near forest edges (Tremblay et al., 2001). Thus, the effect of proximity to habitat (i.e., the negative effect of distancing from the forest interior and moving into the matrix) on pest predation is expected to vary with matrix type and natural enemy identity due to varying degrees of spillover. In forested agricultural landscapes, an increase in forest cover across spatial scales promotes changes in individual fitness (Foley et al., 2005), altering the community and increasing species diversity, including that of natural enemies (Hendrickx et al., 2007; Boesing et al., 2018a; Medeiros et al., 2019). An increase in species densities inside habitat patches can foster predation outside the habitat through cross-habitat spillovers (Brudvig et al., 2009), which should be enhanced by matrix permeability.

Despite these generally observed patterns between habitat or crop attributes and biological pest control in agricultural landscapes, the roles of different matrices in shaping natural enemy contributions to pest predation have been poorly explored (Karp et al., 2018). Here, we used predation experiments to investigate whether matrix type affects pest predation rate by modulating different natural enemy responses to forest cover and proximity to forest. More specifically, we tested the following hypotheses: (1) an increase in landscape forest cover increases predation rates inside focal agricultural matrices (pasture and coffee plantation); (2) predation rates should be higher near forest-agricultural edges than in the matrix interior; and (3) the hypothesized effects of landscape forest cover (1) and distance from the forest (2) should vary between natural enemies and agricultural matrices with different degrees of structural similarity to native habitat, having stronger effects on a low-contrasting matrix (i.e., coffee plantations) than on a high-contrasting matrix (i.e., pastures). To test our hypotheses, we studied landscapes within the Brazilian Atlantic forest region with two contrasting agricultural matrices: cattle pastures and sun-coffee plantations, the second and fifth main produced and exported agricultural commodities of Brazil, respectively (COMEX-STAT, 2019).

2. Methods

2.1. Study region

Field data were collected in one of the most important coffee regions of Brazil between the states of São Paulo and Minas Gerais (Fig. 1a). This region alone is responsible for almost 25% of the total coffee production in the country (Conab, 2018) and is characterized by a subtropical climate with mean temperatures between 13.6 and 20.4 °C, dry winters, rainy summers (Pompeu et al., 2009), and hilly relief with elevations varying between 700 and 1300 m.a.s.l. Landscapes in the region are composed of Atlantic Forest fragments mainly comprising secondary forests as a result of forest regeneration after an intense dynamic of land-use conversion in the mid-nineteenth century towards the beginning of the twentieth century (Carlucci et al. 2021, Rosa et al. 2021). These forest fragments are immersed primarily in a matrix of coffee crops and pastures and secondarily with eucalyptus and sugarcane plantations, followed by other land uses such as human settlements and rivers. Coffee crops in the studied region are sun-grown coffee plantations cultivated mostly in small- to medium-sized properties (20 to 65 ha), and they are managed mainly by local producers from traditional coffee-producing families in the region. The coffee production expansion, especially at the beginning of the twentieth century, was one of the main drivers of deforestation, transforming regions originally covered with Atlantic Forest into agricultural landscapes (Joly et al., 2014). The Atlantic Forest is one of the most diverse regions in the world, but due to anthropogenic pressures, it is also one of the most threatened (Myers et al., 2000; Ribeiro et al., 2009). Forest cover has reduced to only 26% (Rezende et al., 2018) and has been intensively fragmented, with most fragments having less than 50 ha, most of which are in early or medium successional stages (Ribeiro et al., 2009).

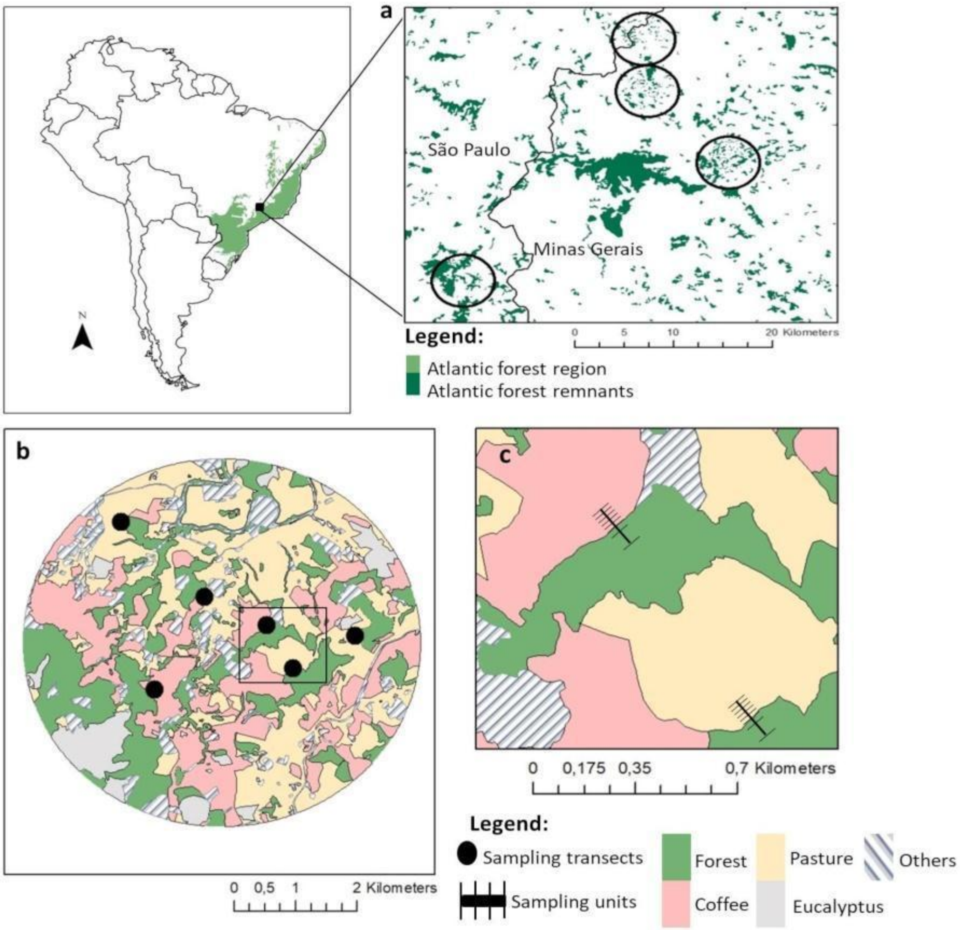

Figure 1: Geographical location of the four experimental landscapes in the Brazilian Atlantic Forest region (a). Distribution of the six sampling transects in one landscape (b), and a zoom into two sampling transect locations inserted in coffee and pasture matrix (c). Each transect has six sampling units inside the matrix and two inside the adjacent forest fragment (modified from Boesing et al 2018).

2.2. Pest control systems

Extensive cattle ranching and coffee plantations in Brazil are affected by three main pests: "grass-feeding spittlebugs" (Deois flavopicta) (Valério and Oliveira, 2005) in cattle pastures and "coffee leaf miner" (CLM; Leucoptera coffeella) (Pierre, 2011) and "coffee berry borer" in coffee plantations (CBB; Hypothenemus hampei) (Vega et al., 2009). Grass-feeding spittlebugs introduce toxins into pasture plants, making them unpalatable and reducing the amount of food resources available to cattle (Valério and Nakano, 1988). In the Neotropics, this pest can cause economic losses in the range of US$ 40–143 million per year depending on the infestation level (Holmann and Peck, 2002). Only in Brazil are pasture forage losses estimated to be approximately 15% of total cattle meat production (Nilakhe et al., 1985). CBB and CLM are also economically important, causing yield losses of 12-30% (Oliveira et al.,

2013) and 9-50% (Pierre, 2011; Librán-Embid et al., 2017), respectively. While CBB attacks the berries, destroying them or reducing bean weight (Oliveira et al., 2013), CLM attacks the leaves, reducing photosynthetic area or provoking leaf loss (Pierre, 2011). Together, these pests cause economic losses of more than US$ 358 million per year in Brazil, the major coffee producer and exporter in the world (ICO, 2019). Bird and arthropod species may represent possible allies to farmers and coffee producers by offering the service of biological pest control (Aristizábal and Metzger, 2019; Librán-Embid et al. 2017; Boesing et al 2018; Medeiros, 2019). Most natural enemies are expected to be habitat-generalist (species with higher plasticity of habitat use) and forest-dependent species (species that are mostly dependent on forests for breeding and foraging) from forest fragments, with lower contributions of the latter, especially in locations far from forest edges (Prata-Gonçalves, 2016; Boesing et al. 2018; 2021; Medeiros et al. 2019).

2.3. Landscape selection and metrics

Field data collection occurred between March and April 2018 at 24 sites distributed in four agricultural landscapes and inside two matrices with different degrees of structural similarity to the native forest (coffee and cattle pasture). The four independent landscapes were chosen to represent a gradient of forest cover (see Saturni et al., 2016; Boesing et al., 2018b for landscape selection details). Land use and land cover were mapped using high-resolution images (ArcGIS 10.3 base map imagery, DigitalGlobe satellites 2010–2011, 0.5–1 m resolution, 1:5,000 visualization scale. Mapping accuracy was extensively validated in the field in 2014 and 2018, and all interpretation errors or landscape changes between 2014 and 2018 were edited. For each landscape, we calculated native forest cover at several scales and the distance from each sample unit to the forest edge. Our sample allowed a wide range of landscape and local forest covers (composition metric; 13% to 48% at 3km and 8% to 67% at 500 m) and distance (configuration metric; 100 m inside the forest and 100 m inside each matrix). All landscape metrics were calculated using ArcGIS 10.4. To represent the scale of movement of potential natural enemies of invertebrates in agricultural matrices, we considered forest cover at a wide range of scales (500, 1000, 1500, 3000 m). Landscape-level scales such as 3 km are justified by previous studies that have shown that ecological processes related to potential natural enemies such as birds and ants are particularly important at broad scales (Boesing et al. 2017; Prata-Gonçalves, 2016). In addition, forest cover at landscape and local scales are especially related to the provision of biological pest control by birds, bats and ants in the study region (Aristizábal and Metzger, 2019; Librán-Embid et al. 2017). We then selected the most significant “scale of effect” (i.e., the scale at which an ecological response or process is best predicted by landscape metrics - Jackson and Fahrig 2015) for each dataset based on the Akaike information criterion corrected for small sample sizes (AICc) (Table A1).

2.4. Study sites and experimental design

To evaluate the effect of matrix type, forest cover and distance from forest on predation rates, we sampled six sites in each of the four studied landscapes and divided by matrix type (three for each type) (Fig. 1b). Each site consisted of a transect allocated at the interface of forest fragments with pasture or coffee matrices. Transects were allocated perpendicularly to forest edges and were 200 m long, with 100 m established in the matrix (6 sampling units 20 m apart from each other) and 100 m inside the forest (two sampling units, at 20 and 100 m from the edge) (Fig. 1c). To have an even distribution of forest fragment sizes between pasture and coffee transects, site selection assured that forest fragments adjacent to each matrix had similar sizes between them (i.e., forest fragments’ size difference lower than 10%). Coffee matrices were sun-coffee plantations with manual harvest covered with Coffee arabica, while pastures were mostly composed of exotic Brachiaria grasses (Urochloa spp).

Building upon previous studies that have shown species spillover from the forest and into pastures and coffee matrices in the region (Prata-Gonçalves, 2016; Boesing et al 2018; Boesing et al 2021; Medeiros, 2019), we were interested in understanding forest species’ abilities to act as natural enemies within agricultural matrices. Sampling units inside the forest had the objective of assessing the predation capacity of these organisms within their habitat but surrounded by each matrix, creating a continuum of predation rates into the matrix. To encompass possible edge effects in forest-dependent natural enemies and on their predation contribution, we selected two distances for the forest sampling units (20 m and 100 m from the edge). In each of the 8 sampling units (six inside the matrix and two inside the adjacent forest fragment; Fig. 1c), a dummy caterpillar predation experiment was conducted for 96 hours (e.g., Howe et al., 2009). Dummy caterpillar experiments are widely used in predation experiments, allowing predator identification through their predation marks (Howe et al., 2009; Low et al 2014). Because this is a well-established method and has the advantage of allowing predator identification (Meyer et al 2015), it is particularly useful for comparative predation studies in which the exact prey or pest representation is logistically unworkable (Pierre et al. 2011; Vega et al. 2009; Valério and Oliveira, 2005). In addition, dummy models may not represent the exact form of main prey or pests of the studied system; however, they are part of the diet of many natural enemies, such as birds and ants, making them useful subjects for predation assessments within forest fragments and agricultural matrices (Milligan et al. 2016; Perfecto et al. 2004). Nevertheless, as this method alone does not allow the full identification of the attacking species (Low et al 2014), inferences about service provision using this method should be made with caution. In this matter, additional information regarding the study system (e.g., knowledge about the community of natural enemies in the region) or supplementary methods that allow further identification of the attacking species (e.g., camera traps) may strengthen inferences about service provision (Schwab et al 2021). Finally, although this method cannot reveal true pest removal rates, it can provide measurements of predation in relation to matrix type, forest cover and distances from forest by distinct potential natural enemies.

In each sampling unit, we provided 24 identical models simulating real caterpillars and following literature suggestions regarding color and size (Howe et al. 2009; Low et al 2014; Meyer et al 2015). Dummy caterpillars were made of green nontoxic plasticine clay due to its usefulness for comparative studies such as this one (Howe et al. 2009), and with lengths of 40 mm and diameters of 4 mm, which is the approximate size of dummy caterpillars used in the tropics (Leles et al 2017; Maas et al 2015; Molleman et al. 2016; Nurdiansyah et al 2016a, 2016b; Roselin et al 2017; Schwab et al. 2021; Seifert et al. 2015; Seifert et al 2016; Zvereva et al. 2019); additionally, this clay allows predation marks from predators with different bite forces (Low et al. 2014). Dummy caterpillars were spaced one meter from each other and placed in a way that optimized the link between predation rates and potential natural pest control. Therefore, subjects were fixed with superglue at the top of coffee and pasture leaves, which are areas usually used by some of the main pests in both systems (“coffee leaf miner” - Leucoptera coffeella - in coffee plantations and “grass-feeding spittlebugs” - Deois flavopicta - in pastures). None of the materials used had any overpowering odor that could attract, repel or present any danger to attacking predators. The 24 dummy caterpillars were initially exposed for 48 hours. After this period, to record variations in the dummy models available, we checked for predation marks and counted dummy caterpillars that were not found and were thus considered lost. If there were predation marks, to avoid underestimating the final predation rate, the model was identified as preyed upon and removed without replacement (Howe et al., 2009). The remaining models were exposed for another 48 hours, totaling 96 hours of exposure. At the end of 96 hours, all dummy caterpillars were taken and checked for predation marks. All dummy caterpillars with predation marks in both 48 and 96 hours had their marks identified at a broad taxonomic level (mammal, bird or arthropod) according to standard identification keys (Low et al., 2014).

2.5. Data analysis

The relationships between landscape attributes (forest cover, distance from forest and matrix type) and predation rates were evaluated by generalized linear mixed models with a binomial distribution (Zuur et al., 2009). The predation rate was calculated as the total number of dummy caterpillars preyed upon at both 48 and 96 hours, divided by the number of dummy caterpillars initially provided (24) minus the total number of dummy caterpillars not found at either 48 or 96 hours (Fig. A1). Although we cannot know if every lost model was preyed upon or not, most missing dummy caterpillars tend to be a result of uncontrollable factors, such as weather disturbances, and not predation. This is due to attacking predators commonly recognizing the dummies as not being food and, thus, not trying to remove a dummy after tasting it (Schwab et al. 2021). Therefore, we followed literature practices in this matter (see Ferrante et al. 2014; Molleman et al. 2016; Roselin et al 2017; Sam et al. 2016; Schwab et al. 2021; Seifert et al. 2015; Zvereva et al. 2019) and removed missing dummy caterpillars from the predation rate measurement. However, to account for the possible effect of lost models on the predation probability (Figs. A2 and A3), we included the number of lost models in each sampling unit as an additive fixed effect in all statistical models.

To evaluate whether the effect of landscape attributes varied between natural enemies, we divided the main data set into the broad taxonomic group of each natural enemy. For this analysis, a predation rate was calculated for each natural enemy. The predation rate was calculated as the number of dummy caterpillars preyed on by one group (e.g., by birds), divided by the number of dummy caterpillars not preyed on, plus the number of dummy caterpillars preyed on by another group (e.g., by arthropods). Dummy caterpillars preyed on by more than one natural enemy were considered as preyed on in each taxonomic predation rate.

Landscape and transect identifications were included in the analysis as nested random factors (Zuur et al., 2009). All landscape attributes were included in the models as fixed effects along with the additive effect of lost models. All continuous explanatory variables were centered and scaled to a mean of zero and one standard deviation. To account for overdispersion, an observational-level random effect was included in all models (Harrison, 2015). Model goodness-of-fit was tested by residual analysis using the DHarma package (Hartig, 2019). The Akaike information criterion corrected for small sample sizes was used to select which of the models (Table A2) explained the predation rate better (ΔAICc < 2). All models with ΔAICc < 2 were considered equally possible after comparison (Burnham and Anderson 2002). Analyses were performed using R and the ‘lme4’ package in R (R Development Core Team, 2014; Bates et al., 2015).

3. Results

Of the 4,608 exposed dummy caterpillars, 1,168 (25%) had predation marks. Most of the marks were from arthropods (n = 813; 70%), followed by birds (n = 294; 25%). Mammal marks were rare (n = 11; 1%) and were therefore not analyzed separately. Due to the incertitude of the natural enemy, 50 predation marks (4%) could not be identified and were removed from the taxonomic analysis. Arthropod and bird predation marks were found in both matrices, but bird marks were two times higher in transects of coffee (69%) than in pastures (31%). Differences between matrices were less pronounced for arthropod predation marks (58% in coffee and 42% in pastures). Predation by birds and arthropods represented 28 and 66% of predation attacks in coffee, respectively, and 20 and 76% of predation attacks in pastures, respectively. Regardless of natural enemy identity, predation rates inside agricultural matrices were higher in coffee matrices and increased with forest cover and proximity to the forest interior.

Table 1: Summary of the selected relationships (∆AICc < 2; Table 2) between landscape structure attributes and predation rate by matrix type and for each group of natural enemies. See Fig. A4 for the uncertainty and magnitude of the effects of each variable.

Landscape structure attributes		**Natural Enemies**		
		Bird	***Arthropod***	***Community***
Low-contrasting matrix 	***Distance***	Negative; Flatter	—	Negative; Higher
	Landscape Forest cover	—	Positive; Higher	Positive; Higher
	Local Forest cover	—	Negative; Higher	—
High-contrasting matrix 	***Distance***	Negative; Steeper	—	Negative; Lower
	Landscape Forest cover	—	Positive; Lower	Positive; Lower
	Local Forest cover	—	Negative; Lower	—

Note: The comparative terms (higher, lower, steeper, flatter) refer to the comparison between matrices.

The results from the selected best models (∆AICc < 2) show that the effects of distance from forest and forest cover on predation rates were modulated by matrix type and varied among natural enemies and across scales (see Table 1 and Table 2 for a qualitative and statistical summary of the results, respectively, and Fig. A4 for the magnitude of the effects of the variables). We found an effect of distance from forest ($p < 0.001$) and matrix type ($p < 0.001$) on predation rates by birds (Fig. 2; Fig. A4C). Although distance effects on predation by birds were negative in both matrices, this effect was steeper in pastures. Predation rates by arthropods were higher in coffee matrices than in pastures ($p < 0.001$) and increased with landscape forest cover ($p > 0.05$) while decreasing with local forest cover ($p > 0.05$) (Fig. 3; Fig. A4D-G). Regardless of natural enemy identity, we found an effect of all landscape attributes on the predation rate (Fig. 4; Fig. A4A). Predation rates were higher in coffee matrices ($p < 0.001$) and, increase with landscape forest cover ($p < 0.05$) and proximity to the forest interior ($p < 0.001$).

Table 2: GLMM selection via AICc to test the effect of landscape structure attributes on predation rates (for the community, birds and arthropods). Only models with ∆AICc<2 shown out of the total models for each dataset. df = Degrees of freedom.

Response variable	Models	Fixed effects	df	AICc	delta	weight
Predation rate by the community	A	Lost models + Landscape forest cover + Distance from forest + Matrix type	8	971.6	0.0	0.44
	B	Lost models + Distance from forest + Matrix type	7	972.2	0.6	0.32
Predation by birds	C	Lost models + Distance from forest * Matrix type	8	574.5	0.0	0.98
Predation by arthropods	D	Lost models + Matrix type	6	872.7	0.0	0.19
	E	Lost models + Landscape forest cover + Matrix type	7	873.1	0.4	0.15
	F	Lost models + Local forest cover + Matrix type	7	873.7	1.0	0.11
	G	Lost models + Landscape forest cover	6	874.2	1.5	0.09

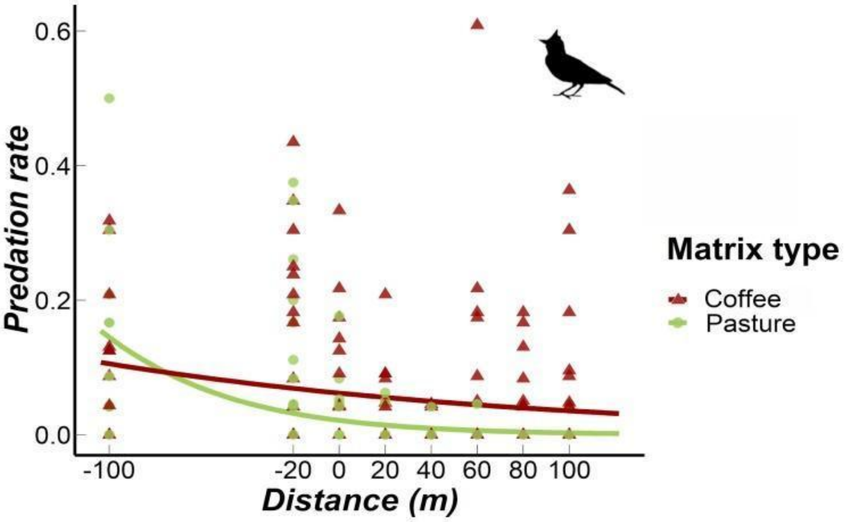

Figure 2: Relationships between distance from forest and matrix type (red triangles: coffee plantations; green circles: pastures) on predation rates by birds. Both relationships were significant ($p < 0.001$) and the magnitude of the effects of each variable is shown in Fig. A4.

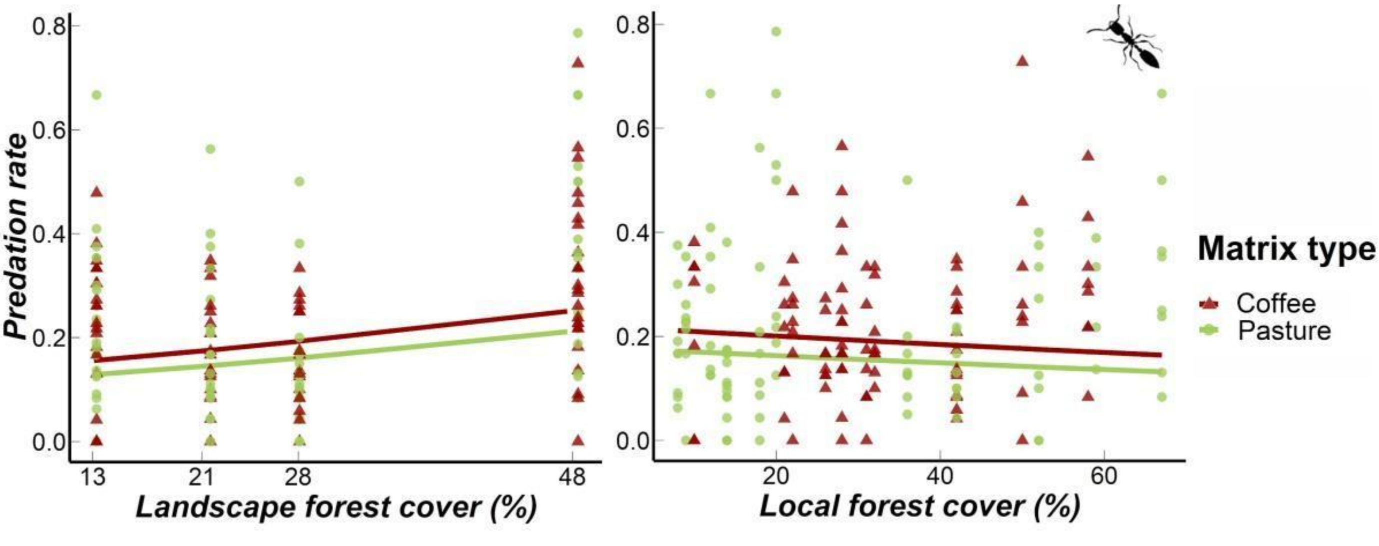

Figure 3: Relationships between landscape and local forest cover and matrix type (red triangles: coffee plantations; green circles: pastures) on predation rates by arthropods. The effect of matrix type was significant ($p < 0.001$) and the magnitude of the effects of each variable is shown in Fig. A4.

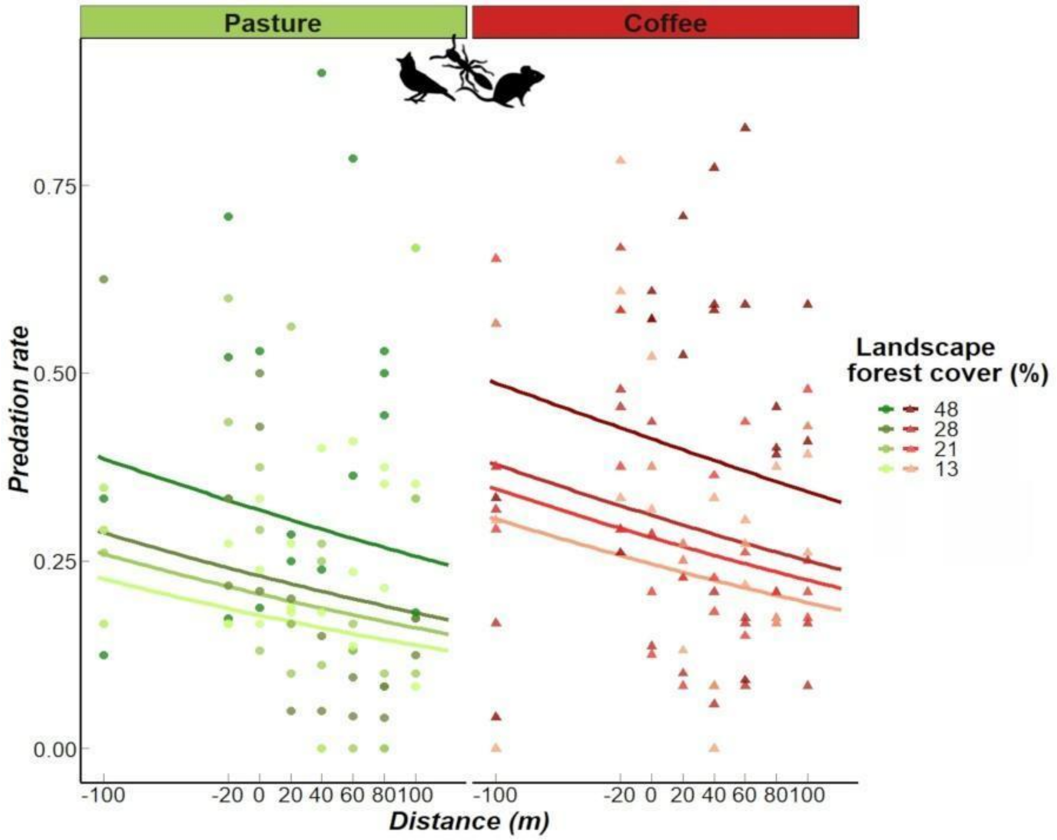

Figure 4: Relationships between distance from forest, matrix type (red triangles: coffee plantations; green circles: pastures) and landscape forest cover on predation rates by the natural enemy community. All three relationships were significant ($p < 0.05$) and the magnitude of the effects of each variable is shown in Fig. A4.

4. Discussion

We present evidence that agricultural matrices modulate the effects of forest cover and distance from forest on predation rates. Furthermore, this response varied with natural enemy's group. While arthropods were affected by forest cover and matrix type, birds responded to the interaction of distance from forest with matrix type. Overall, regardless of natural enemy identity, predation rates were positively affected by matrix structural similarity to habitat, landscape forest cover and proximity to forest interior. These results suggest that predation rates by natural enemies can be the product of landscape structure effects on predation rates of each natural enemy group. As these processes are strongly regulated by matrix type, exploring natural enemies' sensitivities to matrix type can increase knowledge on the underlying mechanisms of such landscape structure effects. Finally, these results suggest that further investigating pest predation by different bird and arthropod species could widen our understanding of how the contribution to biological pest control is distributed within species of these two groups of natural enemies.

4.1. Matrix type modulates bird and arthropod contributions to pest predation risk

The spillover of natural enemies and the service provided in anthropogenic matrices can be constrained by their vulnerability to predation inside the matrix (Brown, 1999). The homogeneity and low hospitality of some matrices, such as pastures, may increase predation risk for bird species due to higher exposure to predators (Biz et al., 2017), reducing the spillover and services provided by these species (Boesing et al., 2018b). Likewise, we found that predation by birds was two times lower in the high-contrasting matrix than in the low-contrasting matrix, indicating that the degree of structural similarity of the matrix to native habitat is an important driver of pest control by this group. However, compared to the forest interior, predation rates were lower in both matrices, indicating that birds' contributions to biological control were constrained inside agricultural areas (Boesing et al., 2018b). An increase in matrix heterogeneity and complexity could improve pest control in agricultural areas (Chisholm et al., 2014). For instance, shaded coffee plantations and agroforests are known to maintain higher bird diversity inside agricultural matrices (Faria et al., 2006) and improve predation rates (Philpott et al., 2008).

4.2. Forest cover effects across matrix types

Landscape forest cover is likely to increase pest predation rates by arthropods through its effect on the arthropod community (Prata-Gonçalves, 2016; Gonzalez et al., 2017; Medeiros et al 2019). At high landscape forest cover, invertebrate richness and abundance tend to increase (Hendrickx et al., 2007; Tscharntke et al., 2008). This increase in abundance may lead to more species spillover into agricultural matrices due to the higher species density inside forest patches (Brudvig et al., 2009). Pest predation rates by arthropods could also benefit from forest cover through its effect in non-forest-dependent species. Higher amounts of forest may represent an increase in alternative food sources and temporary shelter for non-forest-dependent predatory arthropods acting in these matrices, bolstering this community and altering service provision (Tscharntke et al., 2007; Grass et al., 2019). However, at more local scales, an increment in forest cover could lead to an increase in predation pressure upon predatory arthropods via intraguild predation by flying vertebrates (Martin et al 2013). This antagonistic interaction between natural enemies could in turn reduce the contribution of arthropods to predation rates. Indeed, past studies in the region have shown that at higher local forest cover, the presence of birds and bats reduces the provision of biological pest control. This effect is expected to occur due to the release of predation pressure on agricultural pests via intraguild predation of birds on predatory arthropods (Libran-Embid et al 2017). Therefore, although forest cover may have an important role in fostering predation rates via higher arthropod richness and abundance, depending on the scale, it may also be responsible for boosting antagonistic interactions between natural enemies, and thus constraining predation rates at local scales. Finally, further studies are needed to assess if the reduction in predation rates by arthropods at local forest covers represents significant reductions in the provision of the service of biological pest control.

Although an increase in forest cover could potentially also lead to an increase in agricultural pests (Tscharntke et al 2016), previous studies have shown a positive effect of forest cover in increasing biological pest control (Aristizábal and Metzger, 2019; Librán-Embid et al. 2017) and reducing pest abundance (Avelino et al. 2012; Medeiros et al. 2019). In addition, because the main pests of both pastures and coffee plantations are very specialized in these systems (Sujii, 1998; Pierre et al. 2011; Vega et al. 2009; Valério and Oliveira, 2005), it would be very unlikely that an increase in forest cover would lead to a higher abundance of these organisms inside the forest. Furthermore, although landscape forest cover increased predation in both matrices, low-contrasting matrices had higher predation rates. Matrices that are structurally more complex may present more refuge and food opportunities (Gaigher et al., 2016), fostering spillover and within-field diversity (Philpott et al., 2008; Boesing et al., 2018a). Although higher arthropod diversity may result in higher pest predation by improving spillover and ecological redundancy (Tscharntke et al., 2008), the link between species diversity and pest control still needs to be better explored (Landis et al., 2000). To improve biological pest control in agricultural landscapes, it is necessary to identify not only how landscape structure affects species diversity but also what are the key ecological aspects of diversity that affect service provision (Landis et al., 2000).

The lack of a forest cover effect on predation rates by birds may indicate that the positive effect of forest cover on bird richness reported in the literature (Banks-Leite et al., 2014; Boesing et al., 2018a) does not necessarily translate into higher pest predation rates by this group. This result is probably due to the high sensitivity of forest-dependent birds to agricultural matrices. Previous studies in the same region have found that the majority of forest-dependent bird species do not spillover from forest to pasture or, to a lesser extent, from forest to coffee (only 24% of the forest-dependent species pool - Boesing et al., 2018b). Additionally, our results showed higher predation rates in the forest interior than in both matrices, which may suggest that i) forest-dependent species indeed do not spill over into agricultural areas, mainly contributing to predation inside the forest; ii) non-forest-dependent species, which may be less sensitive to agricultural matrices and thus more prone to spillover to these matrices (Boesing et al., 2018b), have little contribution to pest predation inside these matrices; or iii) both. Indeed, mismatches between patterns of species diversity and pest regulation or yield have also been found for other taxonomic groups (Mitchell et al., 2014). Therefore, our results may indicate that an increase in species diversity should not be directly converted into an increase in service provision by this group. We then highlight the importance of further understanding relationships between landscape structure, species diversity and the ecosystem services they provide, as these outputs may be influenced by species composition and their ability to use agricultural matrices (Landis et al., 2000).

4.3. Distance effects across matrix types

Distance effects on predation rate are also likely to vary with matrix type due to natural enemies' abilities to use agricultural matrices. Proximity to forest enhanced predation rates by birds in pasture and coffee sites, suggesting that both matrices may act as a barrier to longer spillovers (Boesing et al., 2018b). This movement constraint is probably due to the lower tolerance of most forest birds to anthropogenic matrices (Biz et al., 2017; Boesing et al., 2018a). However, the absence of predation beyond 60 m into high-contrasting matrices indicates that matrix type also plays a role in modulating the distance effects on predation rates by this group. This difference in predation rates between matrices may be a consequence of higher movement constraints in high-contrasting matrices than in low-contrasting matrices, thus restricting the contribution of birds to pest control (Boesing et al., 2018b).

Although foraging outside habitat boundaries imposes a higher predation risk to natural enemies (Brown, 1999), the benefit and risk balance of spilling over into the matrix, i.e., their sensitivity to nonhabitats, may vary with natural enemies (Brown, 1999; Fahrig, 2007). The lack of distance effects on predation rates by arthropods may suggest that the spillover by this group is not entirely constrained in agricultural matrices. In fact, other studies reported an absence of distance effects on predation rates due to forest-dependent arthropods spilling over into anthropogenic matrices (Lacasella et al., 2015). Another possible explanation is that species from both forests and matrices contribute to predation (Lacasella et al., 2015; González et al., 2017). Indeed, proximity to the forest edge has been reported to have no effect on pest control due to the contribution of non-forest-dependent arthropods to predation (González et al., 2017; Haan et al., 2020). Furthermore, regardless of distance effects, our results showed that predation rates by birds and arthropods were higher in low-contrasting matrices than in high-contrasting matrices. This result suggests that regardless of the mechanism (either matrix resistance or higher contribution of non-forest-dependent species), coffee plantations are more suitable for pest control than are pastures.

4.4. Implications for ecosystem service provision and landscape management

Given the importance of matrix type in shaping and accentuating the effects of proximity to forest and forest cover on predation rate, we highlight the need to consider matrix management, along with the management of natural or seminatural habitats, to improve pest control provision. This study shows that matrices that are structurally more similar to habitat hold higher predation rates by arthropods and birds while allowing longer provision by birds across a distance gradient from habitat interior. Low-contrast matrices hold higher heterogeneity (Driscoll et al., 2013), increasing refuge and food sources for forest and non-forest species (Gaigher et al., 2016). Additionally, low-contrast matrices encourage and facilitate animal movement (Boesing et al., 2018b) by decreasing edge contrasts and mortality rates outside habitats (Pinto et al., 2010; Arroyo-Rodríguez et al., 2020). Therefore, matrix management actions that focus more on sustainable agriculture techniques, such as agriculture consortium and agroforestry systems (e.g., silvopastoral and agrosilvicultural systems) (FAO, 2019) should benefit from higher pest control

(Kremen and Merenlender, 2018) through the increase in within-field heterogeneity and decrease in habitat-matrix contrast. Indeed, while wildlife-friendly systems such as polycultures and rustic production tend to increase biological pest regulation (Isaacs et al., 2009; Jha et al., 2014), monocultures hold simplified plant and animal communities, reducing the functional diversity associated with service provision (Martin et al., 2016; Landis, 2017). This is particularly the case for shaded coffee production, which, compared to sun-coffee plantations, may harbor a higher diversity of birds and arthropods and thus increase the potential for the provision of pest control (Borkhataria et al. 2012; Buechley et al. 2016).

Furthermore, our results suggest that to increase the likelihood of pest control provision, matrix management should focus on increasing habitat-matrix spatial interspersion. Since forest fragments can act as sources of natural enemies (Karp et al., 2018), higher contact between habitat and agricultural areas can improve pest control by increasing overall spillover into the matrix (Boesing et al., 2018b; Grass et al., 2019). Additionally, crop areas with higher forest-agricultural edges should benefit from proximity to forest via an increase in natural enemies even if most natural enemies (e.g., forest birds) are sensitive to distance effects (Boesing et al., 2018a). Configuration effects on pest predation can be especially important when planning land-sparing systems. Since this system focuses on a less interspersed landscape, particular spatial arrangements of agricultural and natural areas may drastically reduce forest-agricultural contact (Phalan, 2018).

Along with managing matrix quality and spatial arrangement, our results suggest that landscape management that fosters higher landscape forest cover could also result in higher pest control, especially from arthropods. This increase in forest cover within agricultural landscapes could be achieved by restoring natural protected areas within farms, such as the “Legal Reserves” in Brazil (Metzger et al., 2019). Legal Reserves represent the fixed amount of native vegetation land owners are obliged to maintain inside their property. The size of the Legal Reserve is a proportion of the total property, varying between 20 and 80% depending on the ecological region (Metzger et al., 2019). Restoring Legal Reserves could benefit both biodiversity, by protecting native vegetation remnants inside private lands (Sparovek et al., 2012), and people, by increasing ecosystem services that benefit from the increase in landscape forest cover or proximity, such as pest control (Librán-Embid et al., 2017; Medeiros et al. 2019) and pollination (Saturni et al., 2016;

González-Chaves et al., 2020). Finally, the spatial arrangement of Legal Reserves across farms within the landscape should also be considered during landscape management (Metzger et al 2019). A well-planned spatial arrangement of such set-aside areas may improve service provision through higher landscape connectivity and forest cover (Balmford et al 2012; Tambosi et al 2014) and higher forest-matrix contact, while controlling for possible negative effects of local forest cover (in general, avoiding excessive fragmentation in the spatial arrangement of forest areas).

Seminatural habitats such as floral strips, living fences or sparse trees in the matrix also play roles in benefiting biodiversity and service provision (Albrecht et al., 2020; Arroyo-Rodríguez et al., 2020). These features can be easily managed within farms (Kremen and Merenlender, 2018) and increase matrix quality, attracting animals through an increase in structural and biological resources within the matrix, even if scattered or inside highly contrasting matrices such as pastures (Harvey et al., 2005; Arroyo-Rodríguez et al., 2020).

5. Conclusion:

To our knowledge, this is the first study to quantify the role of structurally contrasting matrices through a paired experimental design and modulating predation rates of distinct natural enemies. Our results suggest that matrices that are more similar to habitat increase the predation rates by both birds and arthropods while modulating their responses to forest proximity and forest cover. Therefore, to improve pest control provision by different natural enemies, we recommend actions designed to improve matrix quality and increase forest-matrix interspersion and landscape forest cover. This can often be achieved through management decisions made by landowners, potentially creating landscapes that benefit both people and nature. Furthermore, we highlight the need to further investigate the partial contributions of each species of natural enemies and identify the scales that most significantly represent the relationship between them and the service they provide. We believe these studies will build on our results on the importance of matrix type in shaping predation rates in agricultural areas and may allow even more targeted local management suggestions.

Declaration of Competing Interest:

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References:

Albrecht, M., Kleijn, D., Williams, N., Tschumi, M., Blaauw, B., Bommarco, R., Campbell, A., Dainese, M., Drummond, F., Entling, M., et al., 2020. Global synthesis of the effectiveness of flower strips and hedgerows on pest control, pollination services and crop yield. Ecol Lett. https://doi.org/10.22541/au.158618502.29242370.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P., et al., 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecol Lett. https://doi.org/10.1111/ele.13535.

Balmford, A., Green, R., Phalan, B., 2012. What conservationists need to know about farming. Proc R Soc Lond [Biol], 279(1739), 2714-2724.https://doi.org/10.1098/rspb.2012.0515

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., et al., 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science 345, 1041–1045. https://doi.org/10.1126/science.1255768.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Grothendieck, G., Eigen, C., Rcpp, L., 2015. Package ‘lme4’. Convergence 12.

Biz, M., Cornelius, C., Metzger, J.P.W., 2017. Matrix type affects movement behavior of a neotropical understory forest bird. PECON 15, 10–17. https://doi.org/10.1016/j.pecon.2017.03.001.

Blitzer, E.J., Dormann, C.F., Holzschuh, A., Klein, A.M., Rand, T.A., Tscharntke, T., 2012. Spillover of functionally important organisms between managed and natural habitats. Agricult Ecosys Environ 146, 34–43. https://doi.org/10.1016/j.agee.2011.09.005.

Boesing, A.L., Nichols, E., Metzger, J.P., 2017. Effects of landscape structure on avian-mediated insect pest control services: a review. Landsc. Ecol. 32, 931–944. https://doi.org/10.1007/s10980-017-0503-1.

Boesing, A.L., Nichols, E., Metzger, J.P., 2018a. Biodiversity extinction thresholds are modulated by matrix type. Ecography 41, 1520–1533. https://doi.org/10.1111/ecog.03365.

Boesing, A.L., Nichols, E., Metzger, J.P., 2018b. Land use type, forest cover and forest edges modulate avian cross-habitat spillover. J Appl Ecol 55, 1252–1264. https://doi.org/10.1111/1365-2664.13032.

Boesing, A. L., Marques, T. S., Martinelli, L. A., Nichols, E., Siqueira, P. R., Beier, C., de Camargo, P.B., Metzger, J. P., 2021. Conservation implications of a limited avian cross-habitat spillover in pasture lands. Biol Cons, 253, 108898. https://doi.org/10.1016/j.biocon.2020.108898

Borkhataria, R. R., Collazo, J. A., & Groom, M. J., 2012. Species abundance and potential biological control services in shade vs. sun coffee in Puerto Rico. Agricult Ecosys Environ, 151, 1-5. https://doi.org/10.1016/j.agee.2012.01.025

Brown, J.S., 1999. Vigilance, patch use and habitat selection: foraging under predation risk. Evol. Ecol. Res. 1, 49–71.

Brudvig, L.A., Damschen, E.I., Tewksbury, J.J., Haddad, N.M., Levey, D.J., 2009. Landscape connectivity promotes plant biodiversity spillover into non-target habitats. PNAS 106, 9328–9332. https://doi.org/10.1073/pnas.0809658106.

Buechley, E. R., Şekercioğlu, Ç. H., Atickem, A., Gebremichael, G., Ndungu, J. K., Mahamued, B. A., Beyene, T., Lens, L., 2015. Importance of Ethiopian shade coffee farms for forest bird conservation. Biol Cons, 188, 50-60. https://doi.org/10.1016/j.biocon.2015.01.011

Carlucci, M. B., Marcilio-Silva, V., Torezan, J. M., 2021. The southern Atlantic Forest: use, degradation, and perspectives for conservation. In The Atlantic Forest (pp. 91-111). Springer, Cham. DOI: 10.1007/978-3-030-55322-7_5

Chisholm, P.J., Gardiner, M.M., Moon, E.G., Crowder, D.W., 2014. Tools and techniques for investigating impacts of habitat complexity on biological control. Biol Control 75, 48–57. https://doi.org/10.1016/j.biocontrol.2014.02.003.

COMEX-STAT, 2019. Comexstat – comércio exterior do brasil – consórcio pesquisa café. http://comexstat.mdic.gov.br/pt/geral/14539 Accessed in June 2020.

Conab, 2018. Levantamento da companhia nacional de abastecimento de café. http://www.conab.gov.br/OlalaCMS/uploads/arquivos Accessed in August 2018.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361, 1108–1111. https://doi.org/10.1126/science.aau3445.

Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., Smith, A.L., 2013. Conceptual domain of the matrix in fragmented landscapes. Trends Ecol Evolut 28, 605–613. https://doi.org/10.1016/j.tree.2013.06.010.

Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes Funct Ecol 21, 1003–1015. https://doi.org/10.1111/j.1365- 2435.2007.01326.x.

FAO, 2019. Food and agriculture organization of the United Nations, Rome. http://www.fao.org/statistics/en/ Accessed in June 2020.

Faria, D., Laps, R.R., Baumgarten, J., Cetra, M., 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the atlantic forest of southern Bahia, Brazil. Biodivers. Conserv. 15, 587–612. https://doi.org/10.1007/s10531-005-2089-1.

Ferrante, M., Lo Cacciato, A. L., Lövei, G. L., 2014. Quantifying predation pressure along an urbanisation gradient in Denmark using artificial caterpillars. Eur. J. Entomol., 111(5), 649. https://doi.org/10.14411/eje.2014.082

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., et al., 2005. Global consequences of land use. Science 309, 570–574. https://doi.org/10.1126/science.111177.

Gaigher, R., Pryke, J., Samways, M., 2016. Old fields increase habitat heterogeneity for arthropod natural enemies in an agricultural mosaic. Agricult Ecosys Environ 230, 242–250. https://doi.org/10.1016/j.agee.2016.06.014.

González, E., Salvo, A., Valladares, G., 2017. Arthropod communities and biological control in soybean fields: forest cover at landscape scale is more influential than forest proximity. Agricult Ecosys Environ 239, 359–367. https://doi.org/10.1016/j.agee.2017.02.002.

González-Chaves, A., Jaff´e, R., Metzger, J.P., de MP Kleinert, A., 2020. Forest proximity rather than local forest cover affects bee diversity and coffee pollination services. Landsc. Ecol., 1–15. https://doi.org/10.1007/s10980-020-01061-1.

Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa, J., Tiede, J., et al., 2019. Land-sharing/sparing connectivity landscapes for ecosystem services and biodiversity conservation. People and Nature 1, 262–272. https://doi.org/10.1002/pan3.21.

Haan, N.L., Zhang, Y., Landis, D.A., 2020. Predicting landscape configuration effects on agricultural pest suppression. Trends Ecol Evolut 35, 175–186. https://doi.org/10.1016/j.tree.2019.10.003.

Hanski, I., Pöyry, J., 2007. Insect populations in fragmented habitats. Insect Conserv

Biol, 175–202.

Harrison, X.A., 2015. A comparison of observation-level random effect and beta-binomial models for modelling overdispersion in binomial data in ecology & evolution. PeerJ 3, e1114. https://doi.org/10.7717/peerj.1114.

Hartig, F., 2019. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.4.

Harvey, C.A., Villanueva, C., Villacís, J., Chacón, M., Muñoz, D., López, M., Ibrahim, M., Gómez, R., Taylor, R., Martinez, J., et al., 2005. Contribution of live fences to the ecological integrity of agricultural landscapes. Agricult Ecosys Environ 111, 200–230. https://doi.org/10.1016/j.agee.2005.06.011.

Hendrickx, F., Maelfait, J.P., Van Wingerden, W., Schweiger, O., Speel- mans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., et al., 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. J Appl Ecol 44, 340–351. https://doi.org/10.1111/j.1365- 2664.2006.01270.x.

Hernández, L., Laundré, J.W., 2005. Foraging in the ‘landscape of fear’ and its implications for habitat use and diet quality of elk cervus elaphus and bison bison bison. Wildlife Biol 11, 215–220. https://doi.org/10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2.

Holmann, F., Peck, D.C., 2002. Economic damage caused by spittlebugs (Homoptera: Cercopidae) in Colombia: a first approximation of impact on animal production in Brachiaria decumbens pastures. Neotrop. Entomol. 31, 275–284. https://doi.org/10.1590/S1519-566X2002000200016.

Howe, A., Lövei, G.L., Nachman, G., 2009. Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. Entomol. Exp. Appl. 131, 325–329. https://doi.org/10.1111/j.1570-7458.2009.00860.x.

ICO, 2019. Coffee Market Report. Technical Report. International Coffee Organization. www.ico.org. Accessed in June 2020

Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., Landis, D., 2009. Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Front Ecol Environ 7, 196–203. https://doi.org/10.1890/080035.

Jackson, H.B., Fahrig, L., 2015. Are ecologists conducting research at the optimal scale? Glob. Ecol. Biogeogr. 24, 52–63. https://doi.org/10.1111/geb.12233.

Jha, S., Bacon, C.M., Philpott, S.M., Ernesto Mendez, V., Läderach, P., Rice, R.A., 2014. Shade coffee: update on a disappearing refuge for biodiversity. BioScience 64, 416–428. https://doi.org/10.1093/biosci/biu038.

Joly, C.A., Metzger, J.P., Tabarelli, M., 2014. Experiences from the brazilian atlantic forest: ecological findings and conservation initiatives. New Phytol. 204, 459–473. https://doi.org/10.1111/nph.12989.

Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., et al., 2018. Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. PNAS, 201800042. https://doi.org/10.1073/pnas.1800042115.

Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. Science 362. https://doi.org/10.1126/science.aau6020.

Lacasella, F., Gratton, C., De Felici, S., Isaia, M., Zapparoli, M., Marta, S., Sbordoni, V., 2015. Asymmetrical responses of forest and “beyond edge” arthropod communities across a forest–grassland ecotone. Biodivers. Conserv. 24, 447–465. https://doi.org/10.1007/s10531-014-0825-0.

Landis, D.A., 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. BAAE 18, 1–12. https://doi.org/10.1016/j.baae.2016.07.005.

Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu. Rev. Entomol. 45, 175–201. https://doi.org/10.1146/annurev.ento.45.1.175.

Leles, B., Xiao, X., Pasion, B. O., Nakamura, A., Tomlinson, K. W., 2017. Does plant diversity increase top-down control of herbivorous insects in tropical forest? Oikos, 126(8), 1142–1149. https://doi. org/10.1111/oik.03562

Librán-Embid, F., De Coster, G., Metzger, J.P., 2017. Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. Landsc. Ecol. 32, 1907–1920. https://doi.org/10.1007/s10980-017-0555-2.

Low, P.A., Sam, K., McArthur, C., Posa, M.R.C., Hochuli, D.F., 2014. Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. Entomol. Exp. Appl. 152, 120–126. https://doi.org/10.1111/eea.12207.

Maas, B., Tscharntke, T., Saleh, S., Dwi Putra, D., Clough, Y., & Siriwardena, G., 2015. Avian species identity drives predation success in tropical cacao agroforestry. J Appl Ecol, 52(3), 735–743. https://doi.org/10.1111/1365-2664.12409

Martin EA, Reineking B, Seo B, Steffan-Dewenter I (2013) Natural enemy interactions constrain pest control in complex agricultural landscapes. PNAS USA 110(14):5534–5539. https://doi.org/10.1073/pnas.1215725110

Martin, E.A., Seo, B., Park, C.R., Reineking, B., Steffan-Dewenter, I., 2016. Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. Ecol Appl 26, 448– 462. https://doi.org/10.1890/15-0856.

Medeiros, H. R., 2019. The effects of landscape structure and crop management on insect community and associated ecosystem services and disservices within coffee plantation. Tese de Doutorado, Ecologia de Agroecossistemas, Universidade de São Paulo, Piracicaba. doi:10.11606/T.91.2019.tde-27032019-175059. Accessed in May 2021 from www.teses.usp.br

Medeiros, H.R., Martello, F., Almeida, E.A., Mengual, X., Harper, K.A., Grandinete, Y.C., Metzger, J.P., Righi, C.A., Ribeiro, M.C., 2019. Landscape structure shapes the diversity of beneficial insects in coffee producing landscapes. Biol Cons 238, 108193. https://doi.org/10.1016/j.biocon.2019.07.038.

Metzger, J.P., Bustamante, M.M., Ferreira, J., Fernandes, G.W., Librán-Embid, F., Pillar, V.D., Prist, P.R., Rodrigues, R.R., Vieira, I.C.G., Overbeck, G.E., 2019. Why brazil needs its legal reserves. PECON 17, 91–103.

https://doi.org/10.1016/j.pecon.2019.07.002.

Meyer, S. T., Koch, C., & Weisser, W. W., 2015. Towards a standardized rapid ecosystem function assessment (REFA). Trends Ecol Evolut, 30(7), 390-397. https://doi.org/10.1016/j.tree.2015.04.006

Milligan, M. C., Johnson, M. D., Garfinkel, M., Smith, C. J., Njoroge, P., 2016. Quantifying pest control services by birds and ants in Kenyan coffee farms. Biol Cons, 194, 58-65. https://doi.org/10.1016/j.biocon.2015.11.028

Mitchell, M.G., Bennett, E.M., Gonzalez, A., 2014. Agricultural landscape structure affects arthropod diversity and arthropod-derived ecosystem services. Agricult Ecosys Environ 192, 144–151. https://doi.org/10.1016/j.agee.2014.04.015.

Mitchell, M.G., Suarez-Castro, A.F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K.J., Johansen, K., Rhodes, J.R., 2015. Reframing landscape fragmentation's effects on ecosystem services. Trends Ecol Evolut 30, 190–198. https://doi.org/10.1016/j.tree.2015.01.011.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853. https://doi.org/10.1038/35002501.

Molleman, F., Remmel, T., Sam, K., 2016. Phenology of predation on insects in a tropical forest: temporal variation in attack rate on dummy caterpillars. Biotropica, 48(2), 229–236. https://doi.org/10.1111/btp. 12268

Nilakhe, S., Paschoal, G., Savidan, Y., 1985. Survival and fecundity of spittle-bugs on different grasses, in: Proceedings International Grassland Congress, 791–793.

Nurdiansyah, F., Clough, Y., Wiegand, K., & Tscharntke, T. (2016a). Local and landscape management effects on pests, diseases, weeds and biocontrol in oil palm plantations – A review. University of Goettingen.

Nurdiansyah, F., Denmead, L. H., Clough, Y., Wiegand, K., & Tscharntke, T. (2016b). Biological control in Indonesian oil palm potentially enhanced by landscape context. Agricult Ecosys Environ, 232, 141–149. https://doi.org/10.1016/j.agee.2016.08.006

Oliveira, C., Auad, A., Mendes, S., Frizzas, M., 2013. Economic impact of exotic insect pests in brazilian agriculture. J Appl Entomol 137, 1–15. https://doi.org/10.1111/jen.12018.

Perfecto, I., Vandermeer, J. H., Bautista, G. L., Nunñez, G. I., Greenberg, R., Bichier, P., & Langridge, S. (2004). Greater predation in shaded coffee farms: the role of resident neotropical birds. Ecology, 85(10), 2677-2681. https://doi.org/10.1890/03-3145

Phalan, B.T., 2018. What have we learned from the land sparing-sharing model? Sustainability 10, 1760. https://doi.org/10.3390/su10061760.

Philpott, S.M., Arendt, W.J., Armbrecht, I., Bichier, P., Diestch, T.V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-Santos, R., Soto-Pinto, L., et al., 2008. Biodiversity loss in Latin american coffee landscapes: review of the evidence on ants, birds, and trees. Conserv. Biol. 22, 1093–1105. https://doi.org/10.1111/j.1523-1739.2008.01029.x.

Pierre, L.S.R., 2011. Níveis populacionais de Leucoptera coffeella (Lepidoptera:

Lyonetiidae) e Hypothenemus hampei (Coleoptera: Scolytidae) e a ocorrência de seus parasitoides em sistemas de produção de café orgânico e convencional. Ph.D. thesis. Escola Superior de Agricultura Luiz de Queiroz.

Pinto, S.R., Mendes, G., Santos, A.M., Dantas, M., Tabarelli, M., Melo, F.P., 2010. Landscape attributes drive complex spatial microclimate configuration of brazilian atlantic forest fragments. Trop. Conserv. Sci. 3, 389–402. https://doi.org/10.1016/j.tree.2013.06.010.

Pompeu, P., Costa, M., Fontes, M., Carvalho, L., Pereira, J., Pellicciottii, A., Gomes, D., Cipriani, H., Martins, M., 2009. Classificação e apresentação dos parâmetros climáticos de poços de caldas-mg, in: III Congresso Latino Americano de Ecologia, São Lourenço-MG

Prata-Gonçalves, G., 2016. Influência da cobertura florestal sobre a composição de espécies de formigas em agroecossistemas de café. Trabalho de Conclusão de Curso (Graduação em Ciências Biológicas) – Universidade Federal de São Paulo – Campus Diadema.

Prevedello, J.A., Vieira, M.V., 2010. Does the type of matrix matter? a quantitative review of the evidence. Biodivers. Conserv. 19, 1205–1223. https://doi.org/10.1007/s10531-009-9750-z.

R Development Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0.

Rand, T.A., Tylianakis, J.M., Tscharntke, T., 2006. Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. Ecol Lett 9, 603–614. https://doi.org/10.1111/j.1461- 0248.2006.00911.x.

Rezende, C., Scarano, F., Assad, E., Joly, C., Metzger, J., Strassburg, B., Tabarelli, M., Fonseca, G., Mittermeier, R., 2018. From hotspot to hopespot: An opportunity for the brazilian atlantic forest. PECON 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The brazilian atlantic forest: How much is left, and how is the remaining forest distributed? implications for conservation. Biol Cons 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021.

Rosa, M. R., Brancalion, P. H., Crouzeilles, R., Tambosi, L. R., Piffer, P. R., Lenti, F. E., Hirota, M., Santiami, E., Metzger, J. P., 2021. Hidden destruction of older forests threatens Brazil’s Atlantic Forest and challenges restoration programs. Sci. Adv., 7(4), eabc4547. https://doi.org/10.1126/sciadv.abc4547

Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., Barrio, I. C., Basset, Y., Boesing, A. L., Bonebrake, T. C., Cameron, E. K., Dáttilo, W., Donoso, D. A., Drozd, P., Gray, C. L., Hik, D. S., Hill, S. J., Hopkins, T., Huang, S., Koanne, B., Laird-Hopkins, B., Laukkanen, L., Lewis, O. T., Milne, S., Mwesige, I., Nakamura, A., Nell, C. S., Nichols, E., Prokurat, A., Sam, K., Schmidt, N. M., Slade, A., Slade, V., Suchanková, A., Teder, T., van Nouhuys, S., Vandik, V., Weissflog, A., Zhukovich, V., Slade, E. M, 2017. Higher predation risk for insect prey at low latitudes and elevations. Science, 356(6339), 742–744. https://doi.org/10.1126/science. aaj1631

Rusch, A., Chaplin-Kramer, R., Gardiner, M.M., Hawro, V., Holland, J., Landis, D., Thies, C., Tscharntke, T., Weisser, W.W., Winqvist, C., et al., 2016. Agricultural landscape simplification reduces natural pest control: a quantitative synthesis. Agricult Ecosys Environ 221, 198–204. https://doi.org/10.1016/j.agee.2016.01.039.

Sam, K., Remmel, T., Molleman, F., 2015. Material affects attack rates on dummy caterpillars in tropical forest where arthropod predators dominate: an experiment using clay and dough dummies with green colourants on various plant species. Entomol. Exp. Appl., 157(3), 317-324. https://doi.org/10.1111/eea.12367

Saturni, F.T., Jaffé, R., Metzger, J.P., 2016. Landscape structure influences bee community and coffee pollination at different spatial scales. Agricult Ecosys Environ 235, 1–12. https://doi.org/10.1016/j.agee.2016.10.008.

Schwab, D., Wurz, A., Grass, I., Rakotomalala, A. A., Osen, K., Soazafy, M. R., Martin, D. A., Tscharntke, T., 2021. Decreasing predation rates and shifting predator compositions along a land-use gradient in Madagascar's vanilla landscapes. J Appl Ecol, 58(2), 360-371. https://doi.org/10.1111/1365-2664.13766

Seifert, C. L., Lehner, L., Adams, M.-O., Fiedler, K., 2015. Predation on artificial caterpillars is higher in countryside than near-natural forest habitat in lowland south-western Costa Rica. J. Trop. Ecol., 31(3), 281–284. https://doi.org/10.1017/S0266467415000012

Seifert, C. L., Schulze, C. H., Dreschke, T. C. T., Frötscher, H., Fiedler, K., 2016. Day vs. night predation on artificial caterpillars in primary rainforest habitats – An experimental approach. Entomol. Exp. Appl., 158(1), 54–59. https://doi.org/10.1111/ eea.12379

Sparovek, G., Berndes, G., Barretto, A.G.D.O.P., Klug, I.L.F., 2012. The revision of the Brazilian forest act: increased deforestation or a historic step towards balancing agricultural development and nature conservation? Environ Sci Policy 16, 65–72. https://doi.org/10.1016/j.envsci.2011.10.008.

Tambosi, L. R., Martensen, A. C., Ribeiro, M. C., Metzger, J. P., 2014. A framework to optimize biodiversity restoration efforts based on habitat amount and landscape connectivity. Restor. Ecol., 22(2), 169-177. https://doi.org/10.1111/rec.12049

Tremblay, A., Mineau, P., Stewart, R., 2001. Effects of bird predation on some pest insect populations in corn. Agricult Ecosys Environ 83, 143–152. https://doi.org/10.1016/S0167-8809(00)00247-4.

Tscharntke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P., Tylianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89, 944–951. https://doi.org/10.1890/07-0455.1.

Tscharntke, T., Tylianakis, J.M., Wade, M.R., Wratten, S.D., Bengtsson, J., Kleijn, D., 2007. Insect conservation in agricultural landscapes. Insect Conserv. Biol. 16, 383–404.

Valério, J.R., Nakano, O., 1988. Danos causados pelo adulto da cigarrinha zulia entreriana na produ¸c˜ao e qualidade de brachiaria decumbens. Pesquisa Agropecuária Brasileira 23, 447–453.

Valério, J.R., Oliveira, M.C., 2005. Parasitismo de ovos de cigarrinhas-das-pastagens (Homoptera: Cercopidae) pelo microhimenóptero anagrus urichi pickles (Hymenoptera: Mymaridae) na região de campo grande, ms. Neotrop. Entomol. 34, 137–138.

Vega, F.E., Infante, F., Castillo, A., Jaramillo, J., 2009. The coffee berry borer, Hypothenemus hampei (Ferrari) (Coleoptera: Curculionidae): a short review, with recent findings and future research directions. Terr. Arthropod Rev. 2, 129. https://doi.org/10.1163/187498209X12525675906031.

Zvereva, E. L., Castagneyrol, B., Cornelissen, T., Forsman, A., Hernández-Agüero, J. A., Klemola, T., Paolucci, L., Polo, V., Salinas, N., Theron, K. J., Xu, G., Zverev, V., Kozlov, M. V., 2019. Opposite latitudinal patterns for bird and arthropod predation revealed in experiments with differently colored artificial prey. Ecol. Evol., 9(24), 14273-14285. https://doi.org/10.1002/ece3.5862

Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G., 2009. Mixed-effects models and extensions in ecology with R. Springer Science & Business Media.

Appendix A: Supplementary material

Lost dummy caterpillars

Of the total of 4,608 dummy caterpillars exposed across the 24 experiment sites, only 336 dummy models were not found at the end of the experiment. The number of lost dummies did not vary much between the four landscapes with increasing forest cover (88; 83; 86 and 79 respectively), type of matrix (155 in coffee and 181 in pastures) or sampling distance units from forest interior to matrix interior (37; 43; 48; 46; 40; 38; 40 and 44 respectively).

Exploratory analyses of lost dummy caterpillars

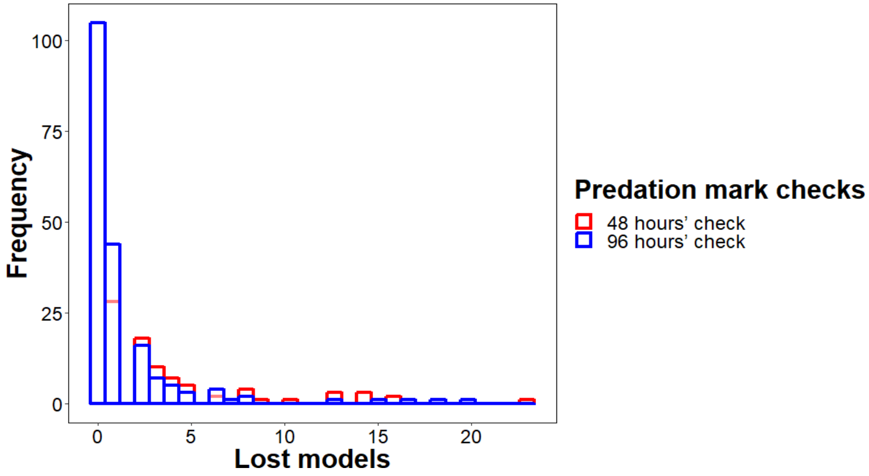

Figure A1: Histogram of lost dummy caterpillars during the first set of 48 hours (red) and the second set of 48 hours (blue).

To test if dummy caterpillars lost rate was homogeneous through time, we divided the total number of dummy caterpillars lost into two data sets: dummy caterpillars lost in the first set of 48 hours (from experiment installation until the checking time), and dummy caterpillars lost in the second set of 48 hours (from the checking time until the end of the experiment). We then tested model lost rate homogeneity through an ANOVA. The difference between the number of dummy caterpillars lost in the first and second set of 48 hours was not significant (p= 0.108), meaning that the model lost rate was homogeneous through the experiment time (Fig. A2).

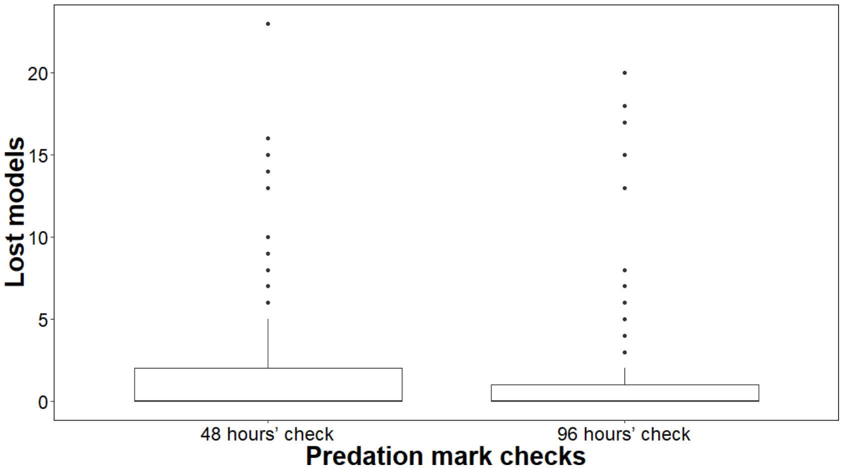

Figure A2: Number of dummy caterpillars lost through experiment time. There were no significant differences between dummy caterpillars lost in the first (IQR= 0-2) and second set.

Effect of lost dummy caterpillars through time

To estimate the effect of dummy caterpillars lost on predation probability, we divided our entire data into the same two intervals used to test lost rate homogeneity, the first and the second set of 48 hours. The total number of dummy caterpillars in the first set of 48 hours is higher than in the second set of 48 hours because the total of dummy caterpillars in the second set is the number of dummy caterpillars left after the first set of 48 hours. To compare these two data sets we evened out the number of dummy caterpillars by sampling in the first data set the same number of dummy caterpillars as at the second data set. We then compared the difference between means with an ANOVA. Predation probability increases with lost dummy caterpillars, meaning that the reduction in dummy caterpillars availability increases the chance of a model to be preyed (Figure A3).

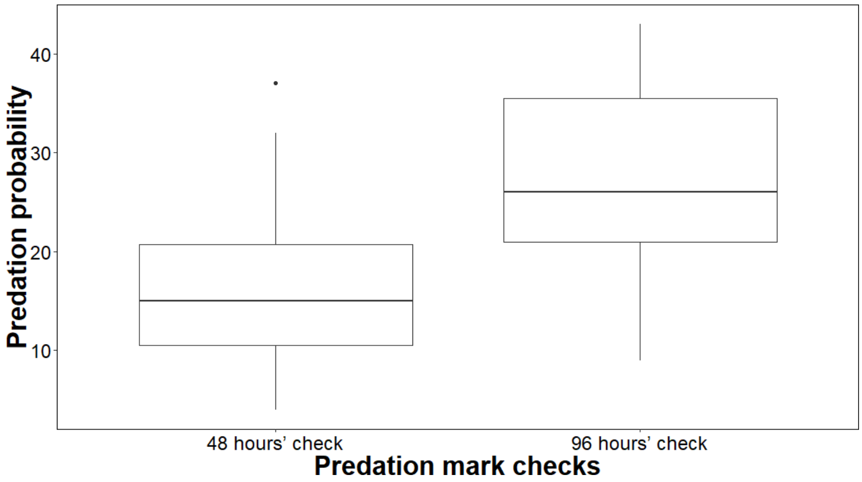

Figure A3: Increase in predation probability through time due to an increase in the number of dummy caterpillars lost. (p= 0.000125, F value= 15.55, Df= 46).

Statistical Analysis

Table A 1: GLMM selection of the "scale of effect" of the effects of forest cover on predation rates by birds, arthropods and the community via AICc. Showing the selected most significant scales (ΔAICc<2) for the effects of forest cover on predation rates after considering several scales (500, 1000, 1500 and 3000m).

Response variable	Selected scales	df	AICc	delta	weight
Predation rate by the community	3 km	6	982.5	0.00	0.53
Predation by birds	1.5 km	6	610.0	0.0	0.53
	3 km	6	611.4	1.45	0.25
Predation by arthropods	3 km	6	874.2	0.0	0.42
	500m	7	875.7	1.44	0.20

Table A 2: Set of models used in the model selection for all three analyses: predation rates by the community of natural enemies (regardless of natural enemy identity; 11 models), predation rates by birds (17 models) and predation rates by arthropods (17 models).

Predation rate by the community
Lost models + Landscape forest cover (3 km)
Lost models + Distance from forest
Lost models + Matrix type
Lost models + Landscape forest cover (3 km) + Distance from forest
Lost models + Landscape forest cover (3 km) + Matrix type
Lost models + Matrix type + Distance from forest
Lost models + Landscape forest cover (3 km) * Distance from forest
Lost models + Landscape forest cover (3 km) * Matrix type
Lost models + Matrix type * Distance from forest
Lost models + Landscape forest cover (3 km) + Distance from forest +Matrix type
Null
Predation rate by birds
Lost models + Landscape forest cover (3 km)
Lost models + Local forest cover (1.5 km)
Lost models + Distance from forest
Lost models + Matrix type
Lost models + Landscape forest cover (3 km) + Distance from forest
Lost models + Landscape forest cover (3 km) + Matrix type
Lost models + Local forest cover (1.5 km) + Distance from forest
Lost models + Local forest cover (1.5 km) + Matrix type
Lost models + Landscape forest cover (3 km) + Local forest cover (1.5 km)
Lost models + Matrix type + Distance from forest
Lost models + Landscape forest cover (3 km) * Distance from forest
Lost models + Landscape forest cover (3 km) * Matrix type
Lost models + Local forest cover (1.5 km) * Distance from forest
Lost models + Local forest cover (1.5 km) * Matrix type
Lost models + Landscape forest cover (3 km) * Local forest cover (1.5 km)
Lost models + Matrix type * Distance from forest
Lost models + Landscape forest cover (3 km) + Local forest cover (1.5 km) + Distance from forest +Matrix type
Null

Predation rate by arthropods

Lost models + Landscape forest cover (3 km)
Lost models + Local forest cover (500 m)
Lost models + Distance from forest
Lost models + Matrix type
Lost models + Landscape forest cover (3 km) + Distance from forest
Lost models + Landscape forest cover (3 km) + Matrix type
Lost models + Local forest cover (500 m) + Distance from forest
Lost models + Local forest cover (500 m) + Matrix type
Lost models + Landscape forest cover (3 km) + Local forest cover (500 m)
Lost models + Matrix type + Distance from forest
Lost models + Landscape forest cover (3 km) * Distance from forest
Lost models + Landscape forest cover (3 km) * Matrix type
Lost models + Local forest cover (500 m) * Distance from forest
Lost models + Local forest cover (500 m) * Matrix type
Lost models + Landscape forest cover (3 km) * Local forest cover (500 m)
Lost models + Matrix type * Distance from forest
Lost models + Landscape forest cover (3 km) + Local forest cover (500 m) + Distance from forest +Matrix type
Null

Chapter 2

Determining the effects of landscape structure on coffee pollination using provision networks

Camila Hohlenwerger, Leandro R. Tambosi, Laura J. Graham, Jonathan Rhodes, Anna Cord, Felix Eigenbrod, Pedro Fieldman, Marie-Josée Fortin, Matthew G. E. Mitchell, Luis Roman Carrasco, Claudia Sattler, Barbara Schröter, Mariana M. Vidal, and Jean Paul Metzger.

(To be submitted to *People and Nature: “Understanding land-use driven biodiversity change' in People and Nature”*)

("Colhedores de Café” de autoria do artista plástico Nerival Rodrigues[3])

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[3] Imagem disponível em: http://naifjunioartesnobrasil.blogspot.com/2014/08/nerival-rodrigues-tema-colhedores-de.html

Determining the effects of landscape structure on coffee pollination using provision networks

(To be submitted to People and Nature: “Understanding land-use driven biodiversity change' in People and Nature”)

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Abstract:

The provision of ecosystem services depends on social-ecological relationships, in particular on links connecting areas of service demand to supply areas or natural capital. These links include ecological or human flows, which occur through space and are affected by landscape structure. Here, we developed a network approach to evaluate how landscape structure affects the number and strength (i.e. intensity) of pollination flows in coffee production, a globally important agricultural system. We used data on coffee yield, pollination flows and the spatial configuration and composition of native forests (here considered as supply areas of pollination services) and coffee farms (as demand areas) from the Mogiana region, one of the most important coffee producing regions in Brazil. We investigated if attributes related to i) supply-demand links, ii) to the capacity of the supply node, iii) to its supply-supply links, and iv) to its links with all demand nodes in the network were affecting coffee yield in demand nodes. We show that node-level attributes (e.g. number and strength of links) related to pollination flows originating from supply areas indeed affect coffee yield. Particularly, the number and strength of supply-demand links and the capacity of supply nodes positively affect yield. In contrast, competition for supply (i.e., the effects of how many demand nodes are sharing the same supply) negatively affects yield. These results suggest that increases in coffee productivity can be attributed, at least partially, to an increase in pollination flows, which are affected by the spatial arrangement of supply and demand nodes, thus shaping their connections. Our study also provides evidence that social-ecological networks can be an extending approach to assess service provision as different interactions (e.g. supply-demand and supply-supply) and functional attributes of provision (e.g. competition for supply and supply capacity) of the pollination provision network were clearly related to coffee yield. The network analysis allowed us to outline which types of links are most relevant for pollination provision (e.g., supply-demand over supply-supply links) and which landscape parameters affect those links most (e.g., supply and demand interspersion). Understanding and quantifying the structure of pollination networks will allow more targeted management of landscapes to increase pollination provision and crop yield. For coffee landscapes, productivity can be improved by promoting more wildlife-friendly agricultural practices to increase within farms forest cover and interspersion, as well as matrix permeability to pollinators.

Keywords: Ecosystem services; demand; supply; flow; tropical forest; coffee production; social-ecological networks

1. Introduction:

Ecosystem services (ES), understood as the benefits people receive from nature, are driven by the links between ecological and social systems (Wang et al 2022). Service provision relies on connections between service supply areas (i.e. ecosystems capable of producing a service based on their processes or functions, such as natural ecosystems providing habitat to bees; see Table 1 for definitions) and demand areas (i.e. land uses that represent people's needs, such as crop areas demanding pollination service; see Table 1 for definitions) (Fisher et al. 2009). The interactions between the demand and supply of ES are shaped by the flow of organisms, people, or matter between the supply and demand areas (Mitchell et al. 2015; Metzger et al. 2021a). Characteristics of the interactions between supply, demand and flow (hereafter referred to as the “provision chain” - Fisher et al. 2009; see Table 1 for definitions) will then define the amount and intensity of provision and the benefits generated. For example, more contact between supply and demand areas should increase agricultural production due to higher pollination and pest control flow from supply to demand areas (Hohloenwerger et al. *In prep*.).

The inherently social-ecological and spatial nature of spatial-explicit network analysis makes it a powerful tool to connect ecosystem functions to society’s interests (Metzger et al. 2021b; Felipe-Lucia et al. 2022). This is mostly due to the ability of network analysis to explicitly account for the complex interactions between network components while considering dependencies and intrinsic characteristics related to the identity of each node in the network (Felipe-Lucia et al. 2022). However, the use of this approach in a spatially explicit manner to evaluate how the spatial context shapes ES provision by altering the links between supply areas (i.e., supply nodes in a network; see Table 2 for definitions) and demand (i.e., demand nodes in a network) is still in its infancy (Dee et al 2017; Firkowski et al., 2021; Felipe-Lucia et al. 2022).

Landscape structure can define both the structure of a provision network (e.g. type of nodes and number and strength of links; see Table 1 for definitions), as well as the functional relationships that emerge from the different interactions (e.g. supply-demand and supply-supply; see Table 2 for definitions) within this network (Metzger et al. 2021b; Felipe-Lucia et al. 2022). For instance, the spatial location of supply relative to demand nodes may allow a better distribution of supply across the network, thus reducing competition for supply by demand nodes (i.e., negative effects that emerge from having many demand nodes sharing the same supply). This effect is likely to be particularly important for rival services (see Table 1 for definition), for which links of a demand node to a supply node may reduce the amount of supply available for other demand nodes (Fisher et al 2009).

Furthermore, proximity between supply and demand areas plays a key role in enhancing the number of functional links as well as the strength of those links (i.e., species flows from forest to crop areas) (Hipólito et al., 2018; González-Chaves et al. 2020; Metzger et al. 2021; Hohlenwerger et al. 2022). Finally, the intensity of supply-demand links can also be shaped by spatial and functional characteristics of the components of the network (Metzger et al. 2021). For example, large and well-connected supply areas (i.e., with many supply-supply links) may result in high species flow to demand areas due to the positive effects of area and connectivity on the diversity of species in these patches (Krishnan et al. 2012; Boreux et al. 2013). On the other hand, this increase in connectivity between supply areas may reduce the number of species spilling over to demand areas due to higher in-patch resources (Seltmann et al. 2007; Rosa García e Minarro 2014).

Social-ecological network analysis (SENA) allows consideration and balancing of these functional and structural relationships between landscape structure and supply, demand areas and flow. In addition, SENA also allows the assessment of the effect of each individual node and its connection in relation to the amount of service delivered by the whole network (Dee et al., 2017; Felipe-Lucia et al., 2022). As a consequence, SENA may allow an assessment of the key components of the network, i.e. the ones most relevant to ensure sustainable and long-term ES provision, or conversely, components that are hindering ES flows in the landscape (Boesing et al. 2020; Metzger et al. 2021b). Finally, because flow has a key role in defining the number and strength of the interactions between demand and supply areas, this approach is a direct and robust way to assess ES provision in the landscape without the need for more complex spatially explicit models (Metzger et al. 2021b).

Here, we explore the potential of SENA by examining how landscape structure affects pollination flows between native forests (here considered as supply nodes in the network) and coffee farms (demand nodes in the network). Higher pollinator diversity is linked to higher pollination provision, which can increase coffee production by up to 30-50% (Ricketts et al. 2004; Garibaldi et al. 2016; Saturni et al. 2016), reinforcing its relevance to this intensively traded commodity (Ricketts et al. 2004; Moreaux et al. 2022). As a biodiversity mediated service, landscape structure should affect coffee pollination in demand areas through its effects on the presence, absence and intensity of pollinators flow between supply and demand areas (González-Chaves et al. 2020).

Using SENA we test how increases in yield in demand nodes are affected by: (i) the strength of supply links per demand node; (ii) the amount of supply-supply links (i.e. forest-forest links) of supply nodes connected to demand nodes; (iii) the number of extra demand nodes sharing each of the connected supply nodes in the network; and (iv) the amount of supply capacity of each supply node connected to a demand node. Our hypotheses are that coffee yield increases as the amount and strength of supply links per demand node increases (H1: *supply-demand hypothesis*). Also, we expected coffee yield to be higher in demand nodes connected to supplies of higher capacity (H2: *supply capacity hypothesis*) and which had fewer links with other demand nodes (H3: *competition for supply hypothesis*). Finally, we hypothesise that the number of supply-supply links has contrasting effects on coffee yield (H4: *supply-supply hypothesis*) as more supply-supply links may end up fostering or hindering pollinating species flows.

Table 1: Glossary of the main definitions used in this study.

	Definitions
Provision chain	Interaction of a chain of components (supply areas connected to demand areas through biotic or abiotic flows; Fisher et al. 2009; Metzger et al. 2021b). Sometimes also defined as “supply chain” (see Tallis et al. 2012 for differences).

Components of the ecosystem service provision chain	Supply	The potential of a given ecosystem to produce a service based on its processes or functions (Burkhard et al. 2012).
	Demand	The amount of a service required or desired by society (Villamagna et al., 2013). Demand areas can be linked to land uses that represent people's needs, such as crops “demanding” pollination services (Fisher et al. 2009).
	Flow	Processes that actually connect supply and demand (flows of people, organisms or matter in space), within the concept of the “service provision chain” (Fisher et al. 2009; Mitchell et al. 2015).
	Provision	The realized service or benefit of an ecosystem service, i.e. when supply meets demand (Metzger et al. 2021b).
Provision network		A social-ecological network that represents the specific interactions between supply and demand through flows (i.e., the provision chain).
Pollination flow		The movement of bees (in number of individuals and/or species) between supply and demand areas, and between supply and supply areas (Saturni et al., 2016; González-Chaves et al. 2020; Vidal & Metzger, 2018).
Rival services		Ecosystem services for which the use of these services makes it unavailable or less available for another user (i.e., finite resource; Fisher et al. 2009)
Non-rival services		Ecosystem services for which the use of these services does not reduce the amount available for others (i.e., not subject to physical consumption; Fisher et al. 2009).

2. Methods:

2.1 Study area:

Our study took place in one of the most important and traditional coffee-producing regions in Brazil, in the southeastern region of the country, between São Paulo and Minas Gerais states (Figure 1a). This region alone is responsible for almost 25% of the country’s production (Conab, 2018). Coffee crops in the region are sun-grown coffee plantations mainly covered with *Coffea arabica* and cultivated by family farmers. The Brazilian Atlantic Forest, the original biome of the region and one of the most diverse and threatened biomes in the world (Myers et al., 2000; Ribeiro et al., 2009), has been drastically reduced due to generalised agricultural expansion at the beginning of the 20th century (Joly et al 2014). It has a subtropical climate with mean temperatures between 13.6 and 20.4°C, dry winter and rainy summers (Pompeu et al., 2009), and hilly terrain with elevations varying between 700 to 1300 m.a.s.l., making this region ideal for coffee production. In fact, coffee expansion has been one of the main drivers of deforestation of the Atlantic Forest (Carlucci et al. 2021, Rosa et al. 2021). Nowadays, landscapes in the region are composed of Atlantic Forest remnants immersed primarily in a matrix of coffee crops and pastures, and secondarily by eucalyptus and sugarcane plantations (Fig 1b).

In this region, five independent experimental landscapes with a 3 km radius (Figure 1b) were chosen to encompass a variation in forest cover (13-45%) and controlled for soil type and altitude (for selection details, see Saturni et al., 2016; Boesing et al 2018). Landscape centroids were at least six kilometres apart from each other. Land use and land cover were manually mapped using high-resolution images (ArcGIS 10.3 base map imagery, DigitalGlobe satellites 2010–2011, 0.5–1 m resolution, 1:5,000 visualisation scale (see Boesing et al., 2018 for mapping details). Mapping was extensively validated in the field in 2013 and 2015, and all interpretation errors or landscape changes between 2010 and 2015 were edited.

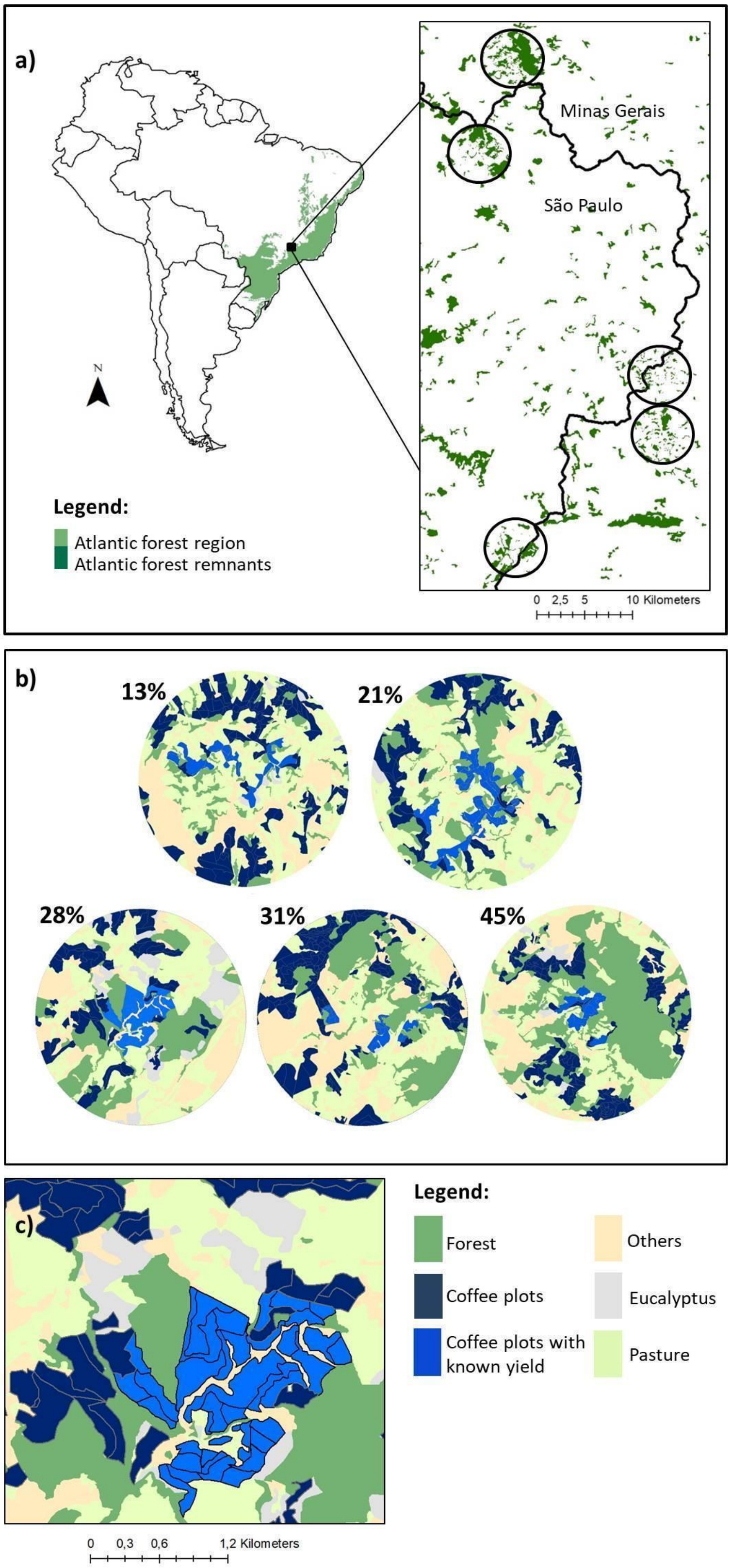

Figure 1: Geographical location of the five landscapes in the Brazilian Atlantic Forest region (a). Forest cover of each of the five landscapes (b) and a zoom into one of the landscapes showing the limits of coffee plots (outlined dark and light blue polygons) within coffee plantation areas (c).

To assess pollination provision, we interviewed farm owners and managers to collect data on coffee yield (number of 60 kg bags) per coffee plot (management divisions of the productive areas within a coffee farm) from ten coffee farms across the five landscapes (Figure 1b). As coffee farms were selected based on farmers' willingness to participate in the study, we were not able to have access to coffee yield data from all farms within the five landscapes. Nevertheless, we mapped all coffee plots in each landscape (Figures 1b and c). All coffee plots were considered as demand nodes for the calculation of the node-level metrics of interest, and were mapped in ArcGIS 10.3 using the land use and land cover validated maps of the landscapes. Finally, the studied coffee plots were only composed of sub-varieties of *Coffea arabica* which are physiologically similar, such as Catuaí and Catucaí, or Catuaí and Mundo Novo (Dias and Souza 2015).

Table 2: Glossary of network metrics and attributes applied to this study.

Network metric or attribute	Definition	Social-ecological meaning
Node	Each element in the network. Here: supply (i.e., native forest fragments) and demand (i.e., coffee plots) areas.	Different components of the social-ecological system that interact and eventually affect ecosystem services provision (Felipe-Lucia et al. 2020 and 2022)
Link	A connection between two nodes. Here, parameterized by pollination flows.	The connection between supply and demand nodes, and between supply and supply nodes. Here, this connection is defined as the flow (i.e., spillover of bee species) from native forest fragments to coffee areas, and among native forest fragments.
Link weight	Strength of the connections between two nodes. Here, defined by a distance decay function applied for the Euclidean distances between supply and demand areas, and supply and supply areas.	The intensity of the connections between supply and demand nodes, and between supply and supply nodes. Here, defined as the intensity of pollination flows (i.e., the amount of bee species richness and abundance) from native forest fragments to coffee areas, and from native forest fragments to native forest fragments. Flow intensity will be defined by the spatial arrangement of supply and demand areas due to its effect on the diversity of bees (Saturni et al., 2016; González-Chaves et al. 2020). Coffee areas and native forest

		fragments, as well as native forests closer to each other will have higher flow intensity, compared to arrangements where those areas are far apart.
Supply-demand link	A connection between supply and demand nodes and its respective weight. Here, defined by a distance decay function.	The connection between supply and demand nodes through pollination flows. Those are the links essentially needed for ES provision within the concept of provision used here (i.e., the demand from coffee areas being met by native forest flows).
Supply-supply link	A connection between supply and supply nodes and its respective weight. Here, defined by a distance decay function.	The connection between supply and supply nodes through pollination flows. Here, supply and supply links are used to indicate the connections between native forest fragments in the landscape.
Degree	Total number or weight of links of a node in the network. Here, the total weight (i.e., sum) of links of demand nodes with supply nodes (i.e., supply-demand links), and the total weight (i.e, sum) of links of supply nodes with supply nodes (i.e., supply-supply links)	The total intensity (i.e., sum) of the flows a demand or supply node has in the network. For example, the degree of a demand node tells how much ecosystem service is arriving at that focal demand node from all supply nodes connected to it.
Provision matrix	Resulted matrix of the interactions (i.e., links) between demand and supply nodes.	A matrix of the interactions between demand and supply nodes that defines which nodes are connected and to whom they are connected, as well as the amount of flows leaving the supply and arriving at the demand through that connection.
Supply-supply matrix	Resulted matrix of the interactions (i.e., links) between supply and supply nodes.	A matrix of the interactions between supply and supply nodes that defines which nodes are connected and to whom they are connected, as well as the amount of flows leaving the supply and arriving at other supply nodes through that connection.

2.2 From landscape structure to pollination social-ecological networks:

For each of the five landscapes, we established a social-ecological network (Figures 2) related to the pollination service, called hereafter “pollination provision network”. This network was composed of native forest fragments represented as *supply nodes*, and coffee plots represented as *demand nodes* (González-Chaves et al., 2020; Saturni et al., 2016; Martínez-Salinas et al., 2022; see Table 4 for the description of the provision networks from the five landscapes). The pollination service was then conceptualised as an output of the interactions of this provision network (Metzger et al., 2021b; see Table 1 and 2 for definitions), hypothesised to affect the coffee yield produced at each coffee plot (i.e., each demand node). To account for the positive effects found for the relationships between proximity to forest, bee diversity and community integrity (Vidal & Metzger, 2018.), the *link between supply and demand nodes*, i.e., the *pollination flow*, was defined by a distance decay function pollinator data (bee diversity across distances from the forest from Vidal & Metzger, 2018; Figure S1). This decay function also defined the *strength of the link* (see section S1 of the Appendix for details). Therefore, demand nodes closer to supply nodes will have a stronger link (i.e., more flow). In addition, following the same decay function, the strength of this link starts to get weaker after 43 m from forest edge, and keeps reducing as the distance from forest edge increases until a point where two nodes are not linked due to a lack of pollination flow (Vidal & Metzger, 2018; see section 1 of Appendix for details). The distance between nodes was measured as the smallest Euclidean distance between coffee plots and native forest fragments (i.e., demand and supply nodes), and among native forest patches (i.e., supply and supply nodes). All distances were calculated in ArcGIS 10.4. Afterwards, the distance between nodes was converted into the strength of the link or the absence of a link between those focal nodes through the distance decay function (Figure S1). The same distance decay function was then used to determine *links between supply and supply nodes* (i.e. forest patches), as a way to account for forest connectivity while considering the effects of agricultural matrix resistance on species diversity (i.e., variation in the strength of supply-supply links) (Prevedello and Vieira, 2010). Finally, we considered forest patches with different sizes as proxies of variations in *supply capacity* (Metzger et al., 2021b), due to the potential of larger patches to support richer and more abundant pollinator communities (García & Minarro 2014). We thus obtained the values of fragment size (with ArcGIS 10.4.) and centred and scaled them by deducting the mean size and dividing by the standard deviation so it could have an equal range to the other independent variables in this study (see section 2.3 and 2.4 for metric and data analysis detail). These values were then used as a proxy of supply capacity.

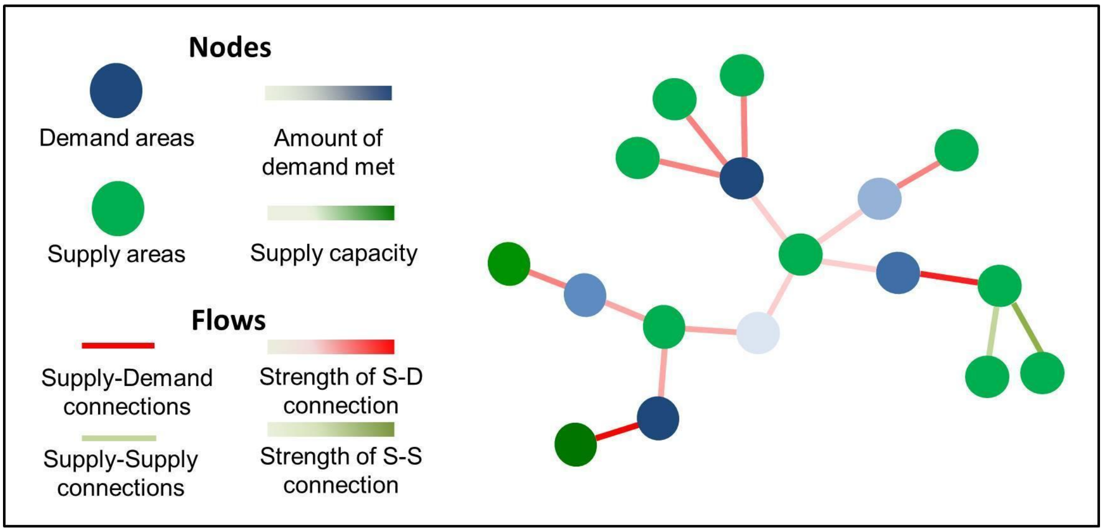

Figure 2. Schematic representation of a social-ecological network composed of links between supply and demand, and supply and supply. Supply and demand links vary in strength according to the spatial distance between supply and demand nodes, the amount of supply capacity and supply-supply links of each supply node, and the number of demand nodes connected to a single supply node. The amount of demand met will then be a result of the strength of the links between demand and supply nodes.

Demand-demand links may play a role in shaping provision through dilution processes (i.e. meaning that there is more demand for pollinators than they can actually meet; Vanbergen 2013), or even through other types of competition between demand nodes (Metzger et al. 2021a). However, given the uncertainties of the nature of these interactions (i.e., flow between demand and demand) and their influence on coffee productivity, we did not evaluate this connection. Despite these limiting factors for the estimation of demand-demand links, we understand the importance of assessing and controlling for the potential effects of higher demand and increased pollination dilution in the network. Therefore, the size of the demand node and if it was part of the same coffee farm was taken into account as a random effect in all models when assessing pollination provision (see details section 3 of the main text). Furthermore, the network approach allows us to evaluate how different interactions between a specific pair of nodes may affect other links those nodes may have (Guimarães 2020). Therefore, we evaluated if different pairs of supply-demand links would result in different amounts of service provision if the connected supply node had many other links to demand nodes, i.e. if the supply was shared with many demand nodes (see details in sections 2.3.2 of the main text and 2.3 of the Appendix).

2.3 Node-level metrics:

To assess the effect of the spatial network structure on pollination provision, we evaluated how different links (i.e. supply-demand and supply-supply) and the strength of those links potentially affected yields in each of the demand nodes in the network. This assessment focused on demand nodes, where the provision of pollination service occurs and is demanded. Therefore, by evaluating the characteristics of the links of a focal demand node (see Figure 3), we are able to relate those with the amount of service (indirectly evaluated through coffee yield) provided at the demand node level (i.e. coffee plot level). This approach allows us to understand which landscape attributes shape the type and strength of the links and therefore, affect the delivery of the service to each node. It is complementary to a network-level analysis, which would allow an understanding of which social and spatial patterns of the supply and demand layout shape the overall distribution of the service across the entire network (Felipe-Lucia et al. 2022).

For each demand node of the five landscapes, we calculated four node-level metrics, each associated with one of our hypotheses: *H1*: *supply-demand hypothesis* (Figure 3a and Table 3); *H3*: *competition for supply hypothesis* (Figure 3b and Table 3); *H2*: *supply capacity hypothesis* (Figure 3c and Table 3); and *H4*: *supply-supply hypothesis* (Figure 3d and Table 3).

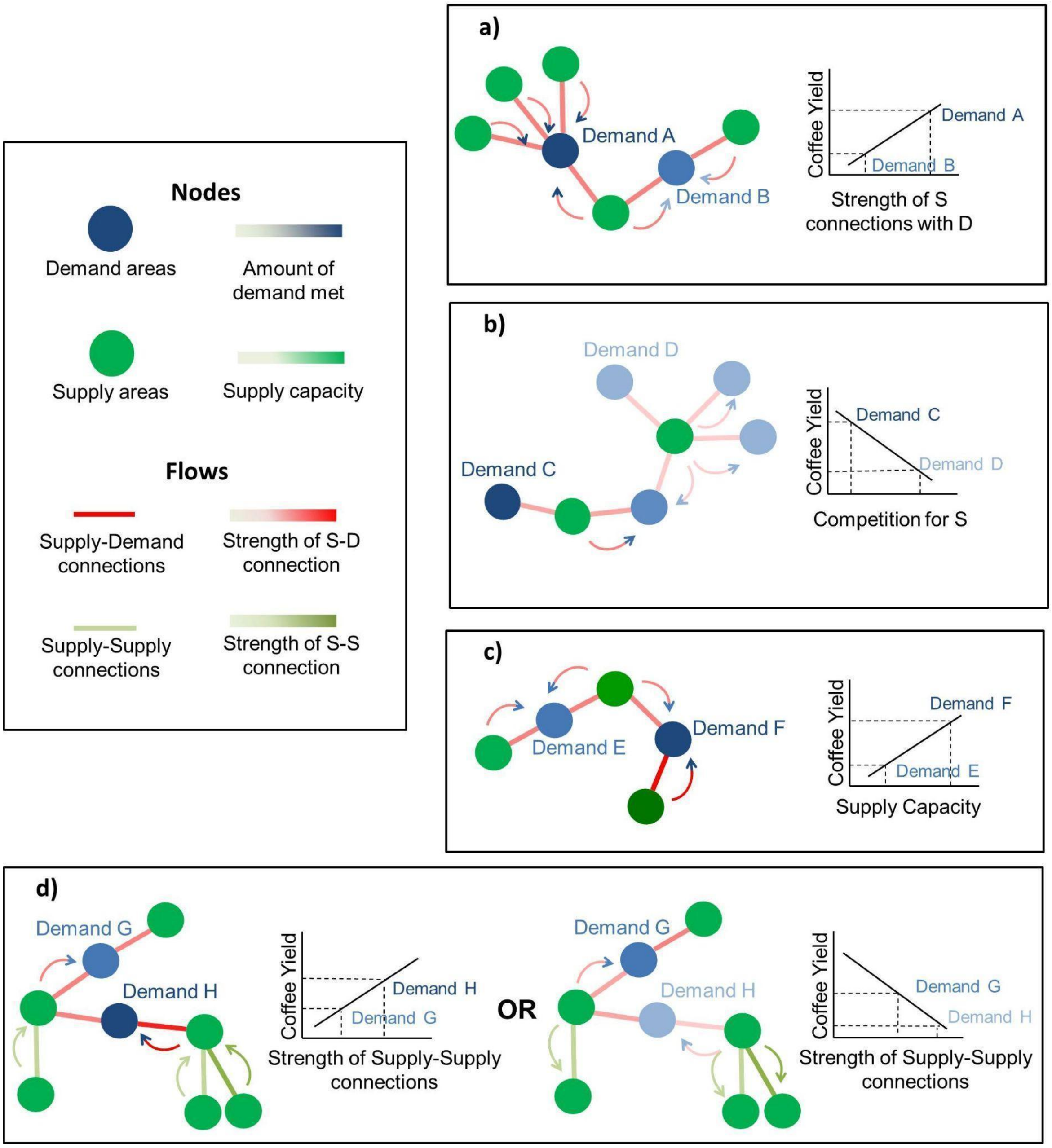

Figure 3: Schematic representation of the four hypothesised relationships for each of the node-level metrics evaluated. Coffee yield is expected to vary with the provision of pollination services (controlling for the effect of other environmental and farm management variables). Coffee yield is thus expected to be higher in demand nodes with more and stronger links to supply nodes (a). Conversely, demand nodes connected to supply nodes with many other demand links should have lower coffee yield (b). Furthermore, demand nodes connected to supply nodes with higher capacity are expected to have high yields (d). Finally, demand nodes connected to supply nodes with supply links should have either more or lower coffee yield depending on the effects of this supply connectivity on the flows from supply to demand (d).

Table 3: Glossary of node-level metrics and their social-ecological meaning applied to this study

Node-level metrics	Definition	Calculation logic	Social-ecological meaning
Strength of supply-demand links	A degree metric to assess the total strength of supply-demand links per focal demand node.	The total weight (i.e., sum) of all links with supply nodes calculated per demand node (Figure 3a). See section S2.1 for a detailed description of how they are computed.	*Motivation:* Investigate if the number and strength of supply-demand links would affect coffee yield. Strength of the connections between supply and demand nodes defined by the amount of flows originating from the supply (i.e., bees spillover from forest fragments) and arriving at the demand.
Supply capacity	A degree metric to assess the potential of a supply node to provide the service.	This metric depends on the size (ha) of the supply node and the weight of the links between this focal supply node with demand nodes (defined by the distance decay function; Figure 3c, S1 and S6) This metric is calculated per demand as the interaction between the weight of its supply-demand connections and the size of each of those connected supply nodes. See section S2.3 for a detailed description of the supply node.	*Motivation:* Investigate if variations in supply capacities would affect coffee yield. Potential of the supply node (e.g., diversity of bees) to provide the service of pollination through its effects on the amount of flows that originates from it.

Competition for supply	A degree metric to assess the effect of having several demand nodes sharing the same supply nodes.	This metric is calculated per demand node as the interaction between the weight of its supply-demand connections and the sum of all supply-demand connections of each focal supply node (Figure S1 and S5). See section S2.2 for a detailed description of how they are computed.	*Motivation:* Investigate if demand nodes were competing with each other for supply. Importance of having several demand nodes sharing (i.e., connected) the same supply node. High sharing levels may result in lower flows from the focal supply to all demand nodes connected to it.
Strength of supply-supply links	A degree metric to assess the effect of having demand nodes connected to supply nodes that have supply-supply connections.	This metric depends on the number and strength of the supply-supply connections of each supply node in the provision network. This metric is calculated per demand node as the interaction between the weight of its supply-demand connections and the total strength (i.e., sum) of all supply-supply connections of each supply node in the provision network (Figure 3d, S1 and S7). See section S2.4 for a detailed description of how they are computed.	Motivation: Investigate if supply-supply links would affect coffee yield in connected demand nodes. Potential of supply-supply connections to enhance or hinder service provision through their effect on the amount of supply (i.e., species diversity) and on flows (i.e., species spillover).

2.4 Data analysis:

We quantified the effects of *the four node-metrics* on coffee yield in 2015 using a linear mixed-effects model (LMM; Zuur et al 2019). Although all coffee plots were considered as demand nodes for node metrics calculations, only demand nodes with known coffee yield and their respective node metrics were modelled as response and predictor variables, respectively. All four node-level metrics were centred and scaled to a mean of zero and standard deviation of one and included in all models as fixed effects. To account for the fact that some demand nodes (i.e. coffee plots) belong to the same farm, and thus are subjected to similar management practices that could influence yield, and that some demand and supply nodes belong to the same landscape, the coffee farm and landscape identification were included in all models as random crossed intercepts. To account for the variation in demand sizes, the area (ha) of each coffee plot was included as an offset in all models. The final set of models was then built considering the interaction and the additive effects of the four predictor variables (Supply capacity; Supply-demand links; Competition for supply; Supply-Supply links) considering the correlation levels (Pearson correlation levels) between them (Table S1). Model goodness-of-fit was tested by residual analysis using the DHarma package (Hartig, 2019). The Akaike information criterion, corrected for small sample sizes (AICc) was used to select which of the models better explained coffee yield (ΔAICc < 2) (Table S2). All models with ΔAICc < 2 were considered equally possible after comparison (Burnham and Anderson 2002). Analyses were performed using R and the 'lme4′ package.

3. Results:

The results from the selected best models (ΔAICc < 2) show that coffee yield in our five landscapes (Figure 4) is modulated by the strength of supply-demand links (*H1* hypothesis), supply capacity (*H2* hypothesis) and competition for supply nodes (*H3* hypothesis) (Table 5). In particular, of the three selected models, supply capacity was the only node-level metric to be present in all models.

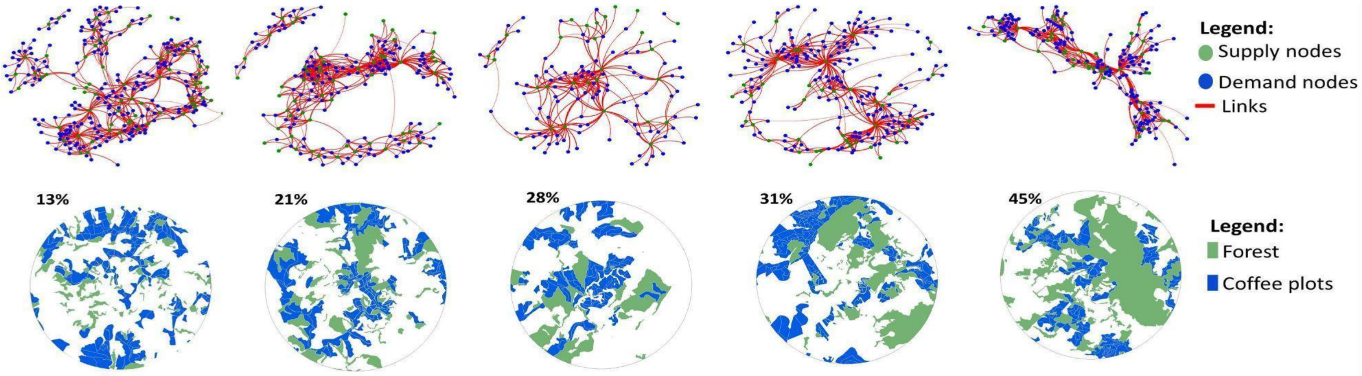

Figure 4: Resulting provision network of the links between supply nodes (i.e. forest fragments) and demand nodes (i.e. coffee plots) across the five landscapes.

Table 4: Description of the main provision network of the links between supply (S) and demand (D) defined by the distance decay function for each of the five landscapes.

Landscape forest cover	Number of D nodes	Number of S nodes	Total number of S-D links	Mean number of S links with D	Maximum number of S links with D	Mean strength of S links with D	Maximum strength of S links with D
13%	205	69	677	3	10	3.31	10.44
21%	145	58	586	4	9	4.21	12.61
28%	99	28	257	2	7	2.67	9.83
31%	181	41	465	2	6	2.60	8.26
45%	155	42	476	3	10	3.15	13.41

Table 5: Model selection via AICc to test the effect of node metrics on coffee yield. Only models with ΔAICc< 2 shown out of the total models. df = Model's degrees of freedom.

Response variable	Models	Fixed effects	Coefficient	df	ΔAICc	delta	weight
Coffee yield ~ (number of 60 kg bags)	A	Supply capacity	16.360	4	1130.4	0.00	0.211
	B	Supply capacity + Supply-demand links	13.768 10.282	5	1131.3	0.90	0.135
	C	Supply capacity + Supply-demand links + Competition for supply	17.003 19.349 -15.517	6	1131.6	1.14	0.119

As the strength of supply links with demand nodes increases, so does coffee yield (Figure 4a). Furthermore, coffee yield is higher in demand nodes connected to supply nodes with higher capacity (Figure 4b). Finally, demand nodes connected to supply nodes which have many other demand connections have lower coffee yield, suggesting a competition for supply between the connected demand nodes (Figure 4c).

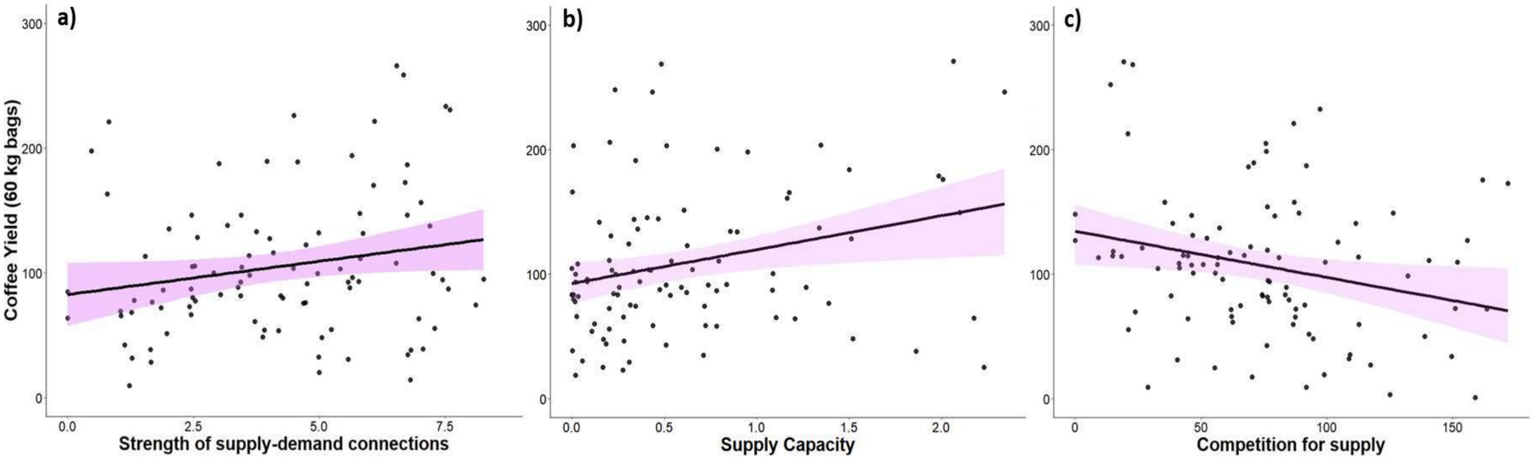

Figure 4: Predicted relationships between coffee yield on connected demand nodes and the strength of its supply-demand connections (a), supply capacity of connected supply nodes (b), and competition for supply (c).

4. Discussion:

Through network analysis, we present new evidence that node-level characteristics related to supply-demand links, supply capacity and demand competition affect coffee yield. In other words, the spatial arrangement of supply and demand nodes, and intrinsic characteristics of each supply and its links with several demand nodes in the network affect service provision. The network approach revealed relationships that go beyond the understanding of landscape composition effects, allowing functional assessment of the importance of interspersion among supply and demand areas, as well as supply capacity, and competition between demand areas for increasing ecosystem service benefits for coffee production.

The network approach allowed us to combine attributes of supply related to both configuration and composition into a single metric, the *strength of supply-demand links* (Figure 3a). This metric was then able to account for the effects of different quantities and arrangements of supply areas in the landscape on flow. By doing so, we were able to simultaneously assess how the resulting output of these effects affects service provision. In this setting, our results on the positive effects of the *strength of supply-demand links* on yield reinforce the importance of targeting together the proportion and interspersion of supply and demand nodes to increase coffee yield. Landscapes with intermediate habitat cover can maintain biodiversity and community integrity in working landscapes (Banks-Leite et al. 2014; Mitchell et al. 2015; Boesing et al. 2018), while maintaining a high level of interspersion and number of patches (Villard and Metzger, 2014), which should enhance pollination. Indeed, other studies have shown the potential of managing coffee field configuration within landscapes of intermediate forest cover to increase coffee yield (González-Chaves et al. 2022).

Besides favouring the *strength of supply-demand links*, increasing interspersion while maintaining intermediate levels of habitat cover should also benefit pollination by reducing the negative effects of isolation (Metzger et al. 2021b). The closer demand areas are to supply, the higher the intensity of flow from species spilling over to the matrix (González-Chaves et al. 2020; Vidal & Metzger, 2018). Proximity effects are also known to have positive effects on coffee yield through higher biological control (Librán-Embid et al., 2017; Aristizábal & Metzger, 2019; Medeiros et al., 2019). Therefore, although our network was set by pollinator data through the distance decay function (i.e., the pollination flow), tackling interspersion as a way to increase pollination could also result in higher yields derived from other ES which are also favoured by this supply-demand proximity (Hohlenwerger et al. 2022). As coffee plantations in the Atlantic Forest are located on average <200 m from forest patches in landscapes with more than 20% of forest cover (González-Chaves et al., 2022), these coffee-producing landscapes should thus especially benefit from proximity effects, resulting thus in higher provision of pollination and pest control services.

Moreover, because the network approach accounts for characteristics related to the identity of the network's nodes, we were able to assess how differences in *supply capacity* shape flow intensity and thus service provision. Our network analysis revealed the importance of maintaining large forests and close patches to ensure high yield in coffee fields. Larger forest patches should be enhancing flow intensity and service provision due to their positive effects on species abundance and richness (Krishnan et al. 2012). Furthermore, as larger forest patches tend to hold higher diversity of nesting sites and floral resources (Boreux et al. 2013), they should be particularly important for services such as coffee pollination. This is particularly relevant due to the ephemeral characteristics of coffee blooming that only provide floral resources to bees for a very short period of time and at most twice a year (Morais et al. 2008). Long-term service provision should also benefit from larger patches through their positive effects on the persistence of species, especially in highly dynamic landscapes (Rosa et al. 2021).

Finally, the network approach also allowed us to identify novel functional and spatial relationships between the landscape and service provision as is the case for the effects of *competition for supply by demand nodes*. Our result shows that supply nodes connected to many other demand nodes result in overall less yield in each of those connected demands. This reduction in the strength of the flow is probably due to the negative effects of biological dilution on service provision (Vanbergen 2013). As a rival service, it is expected that there exists a limit on the number of flowers for which the diversity of pollinators supplied by each supply node are able to pollinate within their spillover range (Fisher et al. 2009; Jha and Vandermeer, 2009). Therefore, a reduction in the number of demand nodes connected to the same supply node should lessen these negative effects not only on pollination provision but also on pest control, which should also be affected by biological dilution (Hohlenwerger et al. 2022). Finally, this result also suggests that landscape management actions focused on increasing coffee yield should prioritise landscape designs which balance the relative proportion of demand and supply areas. These forested agricultural landscapes should then benefit from a better distribution of supply across connected demand nodes throughout the landscape, and thus along with the whole provision network.

4.1. Implications for landscape management:

The importance of the *strength of supply-demand links* and *supply capacity* to high coffee yield revealed in this study has direct implications for two types of protection instruments on private land in Brazil. These are: (i) Legal Forest Reserves and (ii) Areas of Permanent Protection (Metzger et al. 2019). Established under Brazilian Forest Code, these instruments provide opportunities to increase pollination provision in coffee-producing landscapes. Legal Forest Reserves refer to a proportion of the native vegetation area relative to the area of a rural property that landowners must keep within their property - in the case of the study, the Legal Reserve must be at least 20% of the total property area (Metzger et al. 2019). Areas of Permanent Protection (APPs) are areas meant to protect riparian corridors and steep slopes (Metzger et al. 2019). Combined, they can provide good opportunities for in-farm management actions in search of the best spatial arrangements of native vegetation areas to better benefit service provision. Different arrangements of Legal Reserves in relation to APPs can thus be designed to locally increase the number of links of demand with many supply areas, while encouraging the conservation and connection of larger and possibly older forest patches (Rosa et al. 2021), thus ensuring higher supply capacity at the landscape level.

Given the potential of restoring Legal Reserves within farms to increase coffee productivity, we support previous studies which advocate in favour of in-farm restoration and against forest compensations out-farm (see Brancalion et al., 2019; Metzger et al., 2019; de Mello et al., 2021a.b; González-Chaves et al., 2022). Forest compensations outside farm boundaries may result in an unbalanced distribution of supply and demand across regions (Metzger et al., 2019; de Mello et al., 2021a), and therefore hinder the potential of demand areas to benefit from ecosystem service provision (González-Chaves et al., 2022).

In addition to promoting forest protection and restoration, another possibility to increase service provision may be to optimise land management of agricultural areas adjacent to coffee plots. Coffee plantations could be changed in order to increase their habitat value for bees (e.g. by establishing flower strips) in order to create additional supply nodes within coffee plots. This could be supported by suitable governance instruments such as offering payments for ecosystem services, including agri-environmental and climate measures, to the respective land managers (Cong et al. 2014, Bethwell et al. 2022).

Furthermore, our results suggest that to increase coffee yield, matrix management should focus on avoiding the negative effects of competition for supply. In that sense, larger and homogenous coffee farms with only a few habitat patches should suffer from reduced pollination due to an increase in the number of supply nodes connected to many demand nodes, as well as to the decrease in the overall supply and demand links, and overdemand at the landscape level. Indeed, larger coffee fields have been reported to receive fewer benefits from pollination compared to smaller ones (Garibaldi et al. 2016). Therefore, we suggest that long and homogenous extensions of monocultures should be avoided. Instead, coffee producers should prioritise landscapes with higher spatial heterogeneity, where habitat-matrix interspersion can enhance farmers' revenue from pollination and pest control benefits to yield.

4.2. Network approach for ecosystem services: benefits and challenges:

In the face of the high demand for ES, especially those related to food security and sustainable agricultural development, it is essential to disentangle how landscape-level processes affect the complex interactions between supply and demand through its effect on the flow of services (Garibaldi et al. 2016; Metzger et al., 2021b). Here, we use existing models that assume ecosystem service as the output of interactions between supply and demand through flows (Fisher et al., 2009; Mitchell et al., 2015; Metzger et al., 2021a), to move forward on the understanding of how the spatial context shapes coffee pollination provision through the use of a network approach. Provision was inferred from provision matrices of supply and demand links defined by flow properties under the effect of landscape-level processes. Therefore, assessing pollination as a social-ecological network was a useful approach to explore the connection between landscape context and ES as it allowed the combination of functional and spatial mechanisms related to service provision across the space to be represented (Metzger et al. 2020; 2021; Felipe-Lucia et al. 2022). Furthermore, this approach also allowed us to simultaneously assess the resulting output of supply compositional and configurational effects on service provision. These results then reinforced the importance of a balance between high supply and demand interspersion, along with a sufficient amount of supply nodes to assure many and strong supply-demand links.

Despite its clear advantages, the network approach also presents some challenges that need to be overcome to ensure its development and use, particularly guiding management practices focused on improving provision (Metzger et al., 2021a). First, it is important to have a clear identification and quantification of supply and demand areas in order to properly estimate which and how the social and spatial characteristics of these components may affect provision. Additionally, given the key role that characteristics of the links play in defining supply and demand interactions, it is important to notice that social-ecological approaches are particularly useful to the study of ES for which the spatial or social relationships of flow are known or can be estimated. Here, flow properties were parameterised using results from a well-established negative relationship between distance to forest edges and bee diversity and community integrity (Vidal & Metzger, 2018; González-Chaves et al., 2020), and its known effect on pollination provision and coffee yield (Garibaldi et al., 2016). However, other types of flow such as the ones that connect demand-demand links are still poorly known and, therefore, are a limiting factor in our provision system. Hence, we understand that identifying and measuring flow properties are two of the main constraints in ES assessments, with studies often recurring to proxies, indicators or using other components of the provision chain as indistinguishable replacements (Eigenbrod et al., 2010, Spake et al., 2017; Schirpke et al., 2019)

Also, diving deeper into the specifics of the social network component might be worthwhile (e.g. Tindall and Robinson 2017) to analyse how collaboration among potential users (e.g. farmers coordinating pollinator-friendly land management measures with each other, at the landscape scale) might influence ecosystem services flows in the network. Here social capital might play a vital role, encouraging collective action and reciprocal behaviour (e.g. Auer et al. 2020, Yoder and Chowdhury 2018).

Finally, combining the analytical potential of network theory with ecological models that connect landscape structural effects on the supply, flow and demand of services reveals new opportunities to further explore the diverse layers of complexity that encompass the relationships between space and service provision (Metzger et al. 2021b; Felipe-Lucia et al. 2022). Next steps in exploring these complexity layers could include: (i) Investigating the role of other land uses as different nodes in the provision network to explore their effect in modulating service provision, as well as to investigate whether different land uses would act as supply or demand components in the provision chain; (ii) Evaluating more than one ecosystem service as meta-networks to assess how landscape structure affects the interaction of potential common drivers associated to the supply, flow and demand of services; (iii) Identify which of the three components are related to synergies or trade-offs between services when accounting for indirect and direct effects between them (Metzger et al., 2020; Felipe-Lucia et al. 2022); and (iv) Examining if and how supply and demand links change when non-rival services are considered, and how this affects the ecosystem service network structure and service provision.

5. Conclusion:

Our results provide new empirical evidence on the importance of interspersion among supply and demand areas, as well as supply capacity, and less competition between demand areas for increasing ecosystem service benefits, such as pollination for coffee production. Furthermore, we show that this ecosystem service assessment benefited from the potential of the spatial-explicit network approach in evaluating the effects of different node-specific links, strengths and characteristics on service provision. We emphasise that assessing service provision through a social-ecological network approach presents new opportunities to integrate structural spatial and functional relationships to disentangle landscape's structural effects on the interactions of the components of the provision chain.

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References:

Aristizabal, N., & Metzger, J. P. (2019). Landscape structure regulates pest control provided by ants in sun coffee farms. Journal of Applied Ecology, 56(1), 21-30.

Auer, A., Von Below, J., Nahuelhual, L., Mastrángelo, M., Gonzalez, A., Gluch, M., ... & Paruelo, J. (2020). The role of social capital and collective actions in natural capital conservation and management. Environmental Science & Policy, 107, 168-178.

Banks-Leite, C., Pardini, R., Tambosi, L. R., Pearse, W. D., Bueno, A. A., Bruscagin, R. T., ... & Metzger, J. P. (2014). Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science, 345(6200), 1041-1045.

Bethwell, C., Sattler, C., & Stachow, U. (2022). An analytical framework to link governance, agricultural production practices, and the provision of ecosystem services in agricultural landscapes. Ecosystem Services, 53, 101402.

Boesing, A. L., Nichols, E., & Metzger, J. P. (2018). Land use type, forest cover and forest edges modulate avian cross‐habitat spillover. Journal of Applied Ecology, 55(3), 1252-1264.

Boesing, A. L., Prist, P. R., Barreto, J., Hohlenwerger, C., Maron, M., Rhodes, J. R., ... & Metzger, J. P. (2020). Ecosystem services at risk: integrating spatiotemporal dynamics of supply and demand to promote long-term provision. One Earth, 3(6), 704-713.

Boreux, V., Kushalappa, C. G., Vaast, P., & Ghazoul, J. (2013). Interactive effects among ecosystem services and management practices on crop production: pollination in coffee agroforestry systems. Proceedings of the National Academy of Sciences, 110(21), 8387-8392.

Brancalion, P. H., Niamir, A., Broadbent, E., Crouzeilles, R., Barros, F. S., Almeyda Zambrano, A. M., ... & Chazdon, R. L. (2019). Global restoration opportunities in tropical rainforest landscapes. Science advances, 5(7), eaav3223.

Burnham, K. P., & Anderson, D. R. (2002). A practical information-theoretic approach. Model selection and multimodel inference, 2, 70-71.

Carlucci, M. B., Marcilio-Silva, V., & Torezan, J. M. (2021). The southern Atlantic Forest: use, degradation, and perspectives for conservation. In The Atlantic Forest (pp. 91-111). Springer, Cham.

Conab (2018) Levantamento da companhia nacional de abastecimento de café. (http://www.conab.gov.br/OlalaCMS/uploads/arquivos) Accessed in August 2018.

Cong, R. G., Smith, H. G., Olsson, O., & Brady, M. (2014). Managing ecosystem services for agriculture: Will landscape-scale management pay?. Ecological Economics, 99, 53-62.

Dee, L. E., Allesina, S., Bonn, A., Eklöf, A., Gaines, S. D., Hines, J., Jacob, U., McDonald-Madden, E., Possingham, H., Schröter, M., & Thompson, R. M. (2017). Operationalizing network theory for ecosystem service assessments. Trends in Ecology & Evolution, 32(2), 118–130. https://doi.org/10.1016/j.tree.2016.10.011

de Mello, K., Fendrich, A. N., Sparovek, G., Simmonds, J. S., Maron, M., Tavares, P. A., ... & Metzger, J. P. (2021a). Achieving private conservation targets in Brazil through restoration and compensation schemes without impairing productive lands. Environmental Science & Policy, 120, 1-10.

de Mello, K., Fendrich, A. N., Borges-Matos, C., Brites, A. D., Tavares, P. A., da Rocha, G. C., ... & Metzger, J. P. (2021b). Integrating ecological equivalence for native vegetation compensation: A methodological approach. Land Use Policy, 108, 105568.

Dias FP, Souza CAS (2015) Caracterização de progênies do cafeeiro (Coffea arabica L.) selecionadas em Minas Gerais: II-caracteres relacionados à produção. Ceres 52(299).

Eigenbrod, F., Armsworth, P. R., Anderson, B. J., Heinemeyer, A., Gillings, S., Roy, D. B., Thomas, C. D., & Gaston, K. J. (2010). The impact of proxy-based methods on mapping the distribution of ecosystem services. Journal of Applied Ecology, 47(2), 377–385.

Felipe-Lucia, M. R., Soliveres, S., Penone, C., Fischer, M., Ammer, C., Boch, S., ... & Allan, E. (2020). Land-use intensity alters networks between biodiversity, ecosystem functions, and services. Proceedings of the National Academy of Sciences, 117(45), 28140-28149.

Felipe-Lucia, M. R., Guerrero, A. M., Alexander, S. M., Ashander, J., Baggio, J. A., Barnes, M. L., ... & Dee, L. E. (2022). Conceptualizing ecosystem services using social–ecological networks. Trends in ecology & evolution.

Firkowski, C. R., Schwantes, A. M., Fortin, M. J., & Gonzalez, A. (2021). Monitoring social–ecological networks for biodiversity and ecosystem services in human-dominated landscapes. Facets, 6(1), 1670-1692.

Fisher, B., Turner, R. K., & Morling, P. (2009). Defining and classifying ecosystem services for decision making. Ecological economics, 68(3), 643-653.

García, R. R., & Minarro, M. (2014). Role of floral resources in the conservation of pollinator communities in cider-apple orchards. Agriculture, Ecosystems & Environment, 183, 118-126.

Garibaldi, L. A., Carvalheiro, L. G., Vaissière, B. E., Gemmill-Herren, B., Hipólito, J., Freitas, B. M., ... & Zhang, H. (2016). Mutually beneficial pollinator diversity and crop yield outcomes in small and large farms. Science, 351(6271), 388-391.

González-Chaves, A., Jaffé, R., Metzger, J. P., & de MP Kleinert, A. (2020). Forest proximity rather than local forest cover affects bee diversity and coffee pollination services. Landscape Ecology, 35(8), 1841-1855.

González‐Chaves, A., Carvalheiro, L. G., Garibaldi, L. A., & Metzger, J. P. (2022). Positive forest cover effects on coffee yields are consistent across regions. Journal of Applied Ecology, 59(1), 330-341.

Guimarães Jr, P. R. (2020). The structure of ecological networks across levels of organization. Annual Review of Ecology, Evolution, and Systematics, 51, 433-460.

Hartig, F. (2019) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.2.4.

Hipólito, J., Boscolo, D., & Viana, B. F. (2018). Landscape and crop management strategies to conserve pollination services and increase yields in tropical coffee farms. Agriculture, Ecosystems & Environment, 256, 218-225.

Hohlenwerger, C., Tambosi, L. R., & Metzger, J. P. (2022). Forest cover and proximity to forest affect predation by natural enemies in pasture and coffee plantations differently. Agriculture, Ecosystems & Environment, 333, 107958.

Jha, C.M. Bacon, S.M. Philpott, V. Ernesto Mendez, P. Läderach, R.A. Rice Shade coffee: update on a disappearing refuge for biodiversity BioScience, 64 (2014), pp. 416-428, 10.1093/biosci/biu038

Joly C.A. Joly, J.P. Metzger, M. Tabarelli (2014)Experiences from the brazilian atlantic forest: ecological findings and conservation initiatives. N. Phytol., 204 (2014), pp. 459-473, 10.1111/nph.12989

Krishnan, S., Kushalappa, C. G., Shaanker, R. U., & Ghazoul, J. (2012). Status of pollinators and their efficiency in coffee fruit set in a fragmented landscape mosaic in South India. Basic and Applied Ecology, 13(3), 277-285.

Librán-Embid, F., De Coster, G., & Metzger, J. P. (2017). Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. Landscape Ecology, 32(9), 1907-1920.

Martínez-Salinas, A., Chain-Guadarrama, A., Aristizábal, N., Vilchez-Mendoza, S., Cerda, R., & Ricketts, T. H. (2022). Interacting pest control and pollination services in coffee systems. Proceedings of the National Academy of Sciences, 119(15), e2119959119.

Medeiros, H. R., Grandinete, Y. C., Manning, P., Harper, K. A., Cutler, G. C., Tyedmers, P., ... & Ribeiro, M. C. (2019). Forest cover enhances natural enemy diversity and biological control services in Brazilian sun coffee plantations. Agronomy for Sustainable Development, 39(6), 1-9.

Metzger, J. P., Bustamante, M. M., Ferreira, J., Fernandes, G. W., Librán-Embid, F., Pillar, V. D., ... & Overbeck, G. E. (2019). Why Brazil needs its legal reserves. Perspectives in Ecology and Conservation, 17(3), 91-103.

Metzger, J. P., Fidelman, P., Sattler, C., Schroter, B., Maron, M., Eigenbrod, F., ... & Rhodes, J. R. (2021a). Connecting governance interventions to ecosystem services provision: A social-ecological network approach. People and Nature.

Metzger, J. P., Villarreal-Rosas, J., Suárez-Castro, A. F., López-Cubillos, S., González-Chaves, A., Runting, R. K., ... & Rhodes, J. R. (2021b). Considering landscape-level processes in ecosystem service assessments. Science of The Total Environment, 796, 149028.

Mitchell, M. G., Suarez-Castro, A. F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K. J., ... & Rhodes, J. R. (2015). Reframing landscape fragmentation's effects on ecosystem services. Trends in ecology & evolution, 30(4), 190-198.

Morais, H., Caramori, P.H., Koguishi, M.S. & Ribeiro, A.M. de A. (2008). Escala fenológica detalhada da fase reprodutiva de Cooffea arabica. Bragantia, 67, 257–260.

Moreaux, C., Meireles, D. A., Sonne, J., Badano, E. I., Classen, A., González-Chaves, A., ... & Dalsgaard, B. (2022). The value of biotic pollination and dense forest for fruit set of Arabica coffee: A global assessment. Agriculture, Ecosystems & Environment, 323, 107680.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), 853-858.

Prevedello, J. A., & Vieira, M. V. (2010). Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation, 19(5), 1205-1223.

Pompeu, P., Costa, M., Fontes, M., Carvalho, L., Pereira, J., Pellicciottii, A., Gomes, D., Cipriani, H., Martins, M., (2009). Classificação e apresentação dos parâmetros climáticos de poços de caldas-mg, in: III Congresso Latino Americano de Ecologia, São Lourenço-MG.

R Development Core Team (2014), R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3–900051-07–0.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J., & Hirota, M. M. (2009). The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological conservation, 142(6), 1141-1153.

Ricketts, T. H., Daily, G. C., Ehrlich, P. R., & Michener, C. D. (2004). Economic value of tropical forest to coffee production. Proceedings of the National Academy of Sciences, 101(34), 12579-12582.

Rosa, M. R., Brancalion, P. H., Crouzeilles, R., Tambosi, L. R., Piffer, P. R., Lenti, F. E., ... & Metzger, J. P. (2021). Hidden destruction of older forests threatens Brazil’s Atlantic Forest and challenges restoration programs. Science advances, 7(4), eabc4547.

Saturni, F. T., Jaffe, R., & Metzger, J. P. (2016). Landscape structure influences bee community and coffee pollination at different spatial scales. Agriculture, Ecosystems & Environment, 235, 1-12.

Spake, R., Lasseur, R., Crouzat, E., Bullock, J. M., Lavorel, S., Parks, K. E., Schaafsma, M., Bennett, E. M., Maes, J., Mulligan, M., Mouchet, M., Peterson, G. D., Schulp, C. J. E., Thuiller, W., Turner, M. G., Verburg, P. H., & Eigenbrod, F. (2017). Unpacking ecosystem service bundles: Towards predictive mapping of synergies and trade-offs between ecosystem services. Global Environmental Change, 47, 37–50. https://doi.org/10.1016/j.gloenvcha.2017.08.004

Seltmann, P., Renison, D., Cocucci, A., Hensen, I., & Jung, K. (2007). Fragment size, pollination efficiency and reproductive success in natural populations of wind-pollinated Polylepis australis (Rosaceae) trees. Flora-Morphology, Distribution, Functional Ecology of Plants, 202(7), 547-554.

Tallis, H., Mooney, H., Andelman, S., Balvanera, P., Cramer, W., Karp, D., ... & Walz, A. (2012). A global system for monitoring ecosystem service change. Bioscience, 62(11), 977-986.

Tindall, D. B., & Robinson, J. L. (2017). Collective action to save the ancient temperate rainforest: social networks and environmental activism in Clayoquot Sound. Ecology and Society, 22(1).

Vanbergen, A. J., & Initiative, T. I. P. (2013). Threats to an ecosystem service: pressures on pollinators. Frontiers in Ecology and the Environment, 11(5), 251-259.

Vidal M. M. & Metzger, J.P. (2018). A influência da estrutura da paisagem sobre a organização de sistemas de polinização e dispersão de sementes.

Villamagna, A. M., Angermeier, P. L., & Bennett, E. M. (2013). Capacity, pressure, demand, and flow: A conceptual framework for analyzing ecosystem service provision and delivery. Ecological Complexity, 15, 114-121.

Villard, M. A., & Metzger, J. P. (2014). Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. Journal of Applied Ecology, 51(2), 309-318.

Wang, X., Peng, J., Luo, Y., Qiu, S., Dong, J., Zhang, Z., ... & Meersmans, J. (2022). Exploring social-ecological impacts on trade-offs and synergies among ecosystem services. Ecological Economics, 197, 107438.

Yoder, L., & Chowdhury, R. R. (2018). Tracing social capital: How stakeholder group interactions shape agricultural water quality restoration in the Florida Everglades. Land Use Policy, 77, 354-361.

Zuur, E. Ieno, N. Walker, A. Saveliev, G. (2009) Smith Mixed-effects Models and Extensions in Ecology with R Springer Science & Business Media

Appendix: Supplementary material

1. *Distance decay function:*

The distance decay function (Figure S1) was built based on the results found for the relationships between bee diversity and distance to forest (m), as well as community nestedness (NODF) and distance to forest (m) (Vidal & Metzger, 2018- see Appendix 2)). These results show that as distance to forest cover increases, the diversity of bees decreases - (Figure S2). Furthermore, they show that at distances greater than 43 meters from the forest edge, the community of bees becomes subsets of the full community (Figure S3).

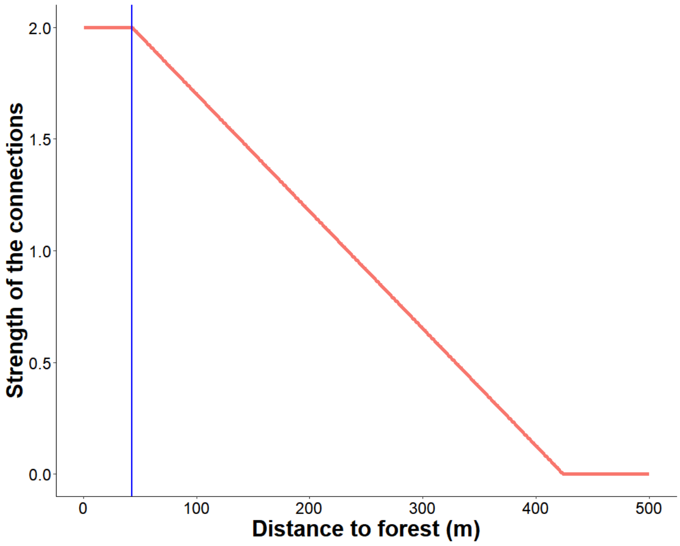


Figure S1: Output of the distance decay function (red line) defining the strength of the links between supply and demand, and supply and supply, while considering the positive effect of proximities closer than 43 m on bee's community integrity (blue line).

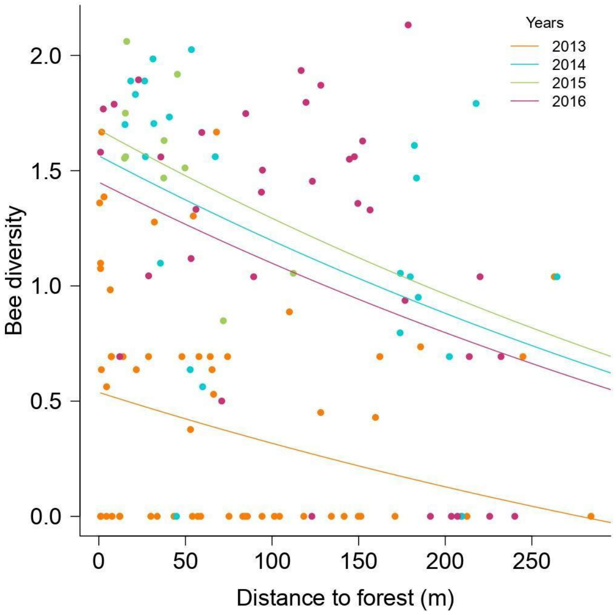


Figure S2: Relationships between distance to forest and bee diversity for different sampled years from Vidal & Metzger, 2018.

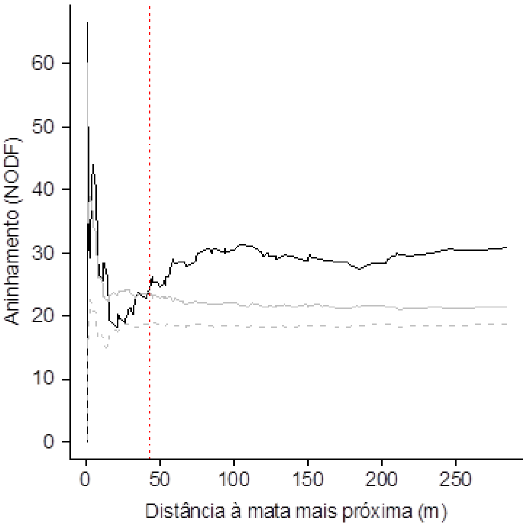
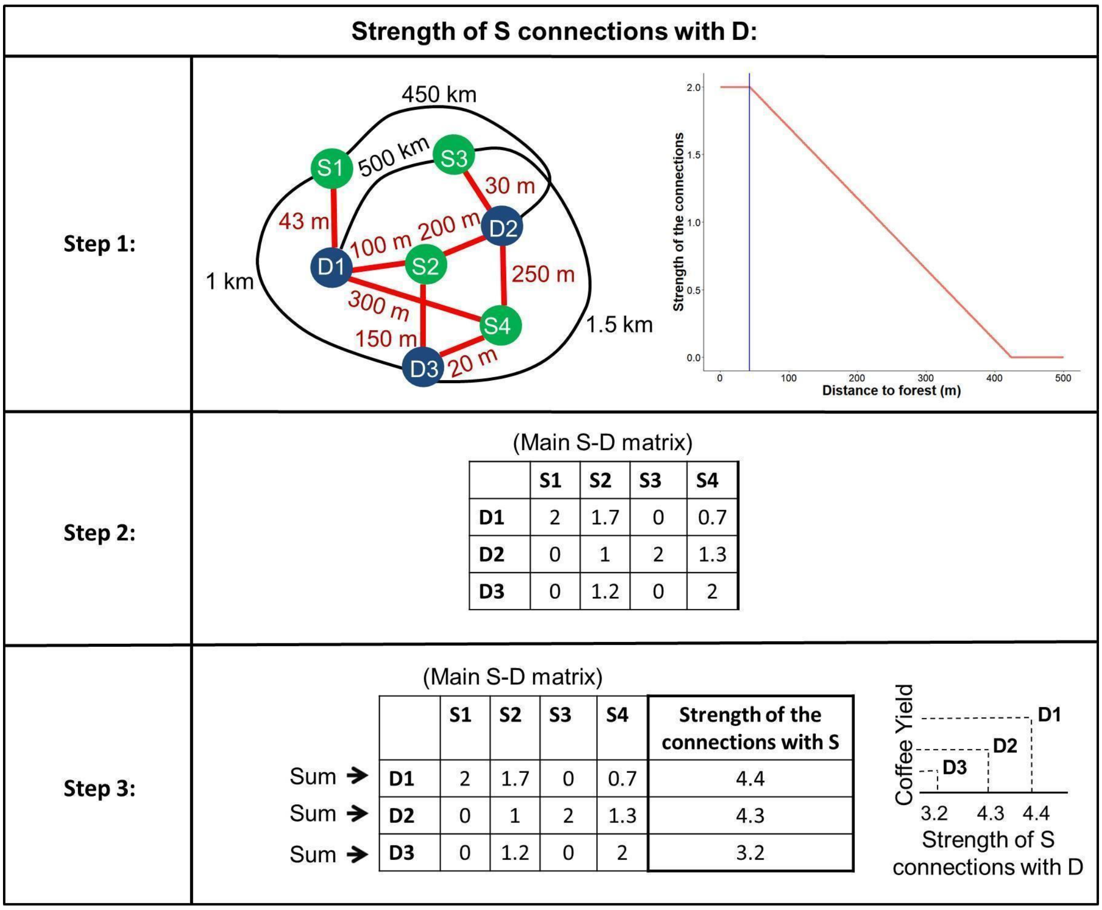


Figure S3: Nestedness (NODF - y-axis) between sampling points located at different distances from the forest (x-axis) found by Vidal & Metzger, 2018. The black line represents nestedness as the matrix of occurrences is reduced to ever shorter distances from the forest (from right to left on the graph). Grey lines delimit the percentiles of 50% (tracked line) and 95% (solid line) of nestedness obtained from null matrices. Null matrices are capable of predicting the observed degree of nestedness when the maximum distance from the forest is reduced to 43 m (red dashed line).

2. Node-level metrics:

2.1: Strength of supply-demand links:

For this node-level metric, calculations took two steps. First, the smallest Euclidean distance between nodes was converted into the strength of the connection between supply and demand through the distance decay function (Figure S4-Step 1). This first step then generates an adjacent provision matrix for which, for each demand node and each supply node in the network, not only do we know if they are connected (red links between supply and demand in Figure S4-Step 1) or not (black links between supply and demand in Figure S3-Step 1), but also the strength of their connection (Figure S4-Step 2). Afterwards, this main supply-demand matrix was used to calculate the final values of this metric by summing all supply links per demand node in the network (Figure S4-Step 3).



(Main S-D matrix)

	S1	S2	S3	S4
D1	2	1.7	0	0.7
D2	0	1	2	1.3
D3	0	1.2	0	2

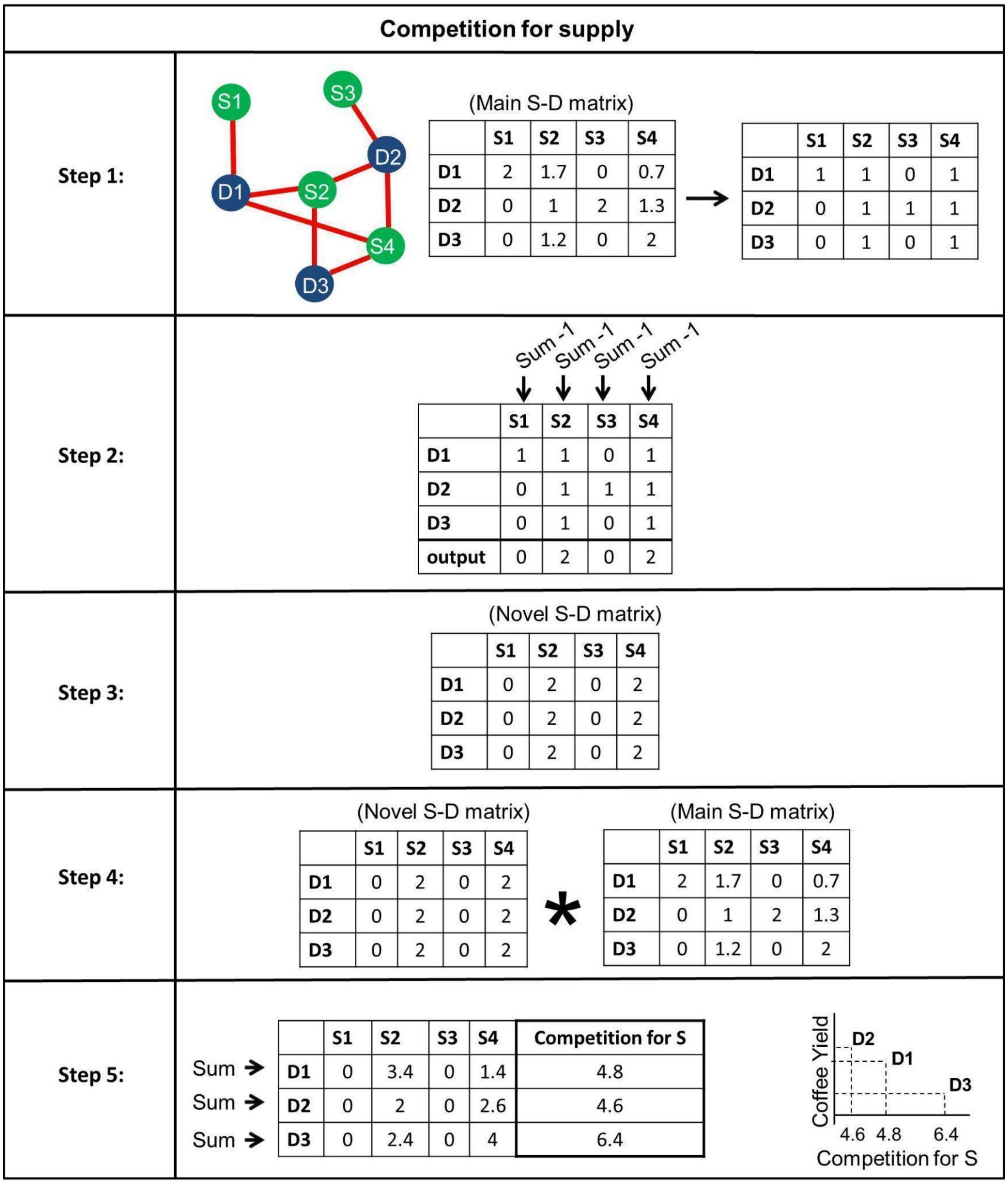
(Main S-D matrix)

	S1	S2	S3	S4	Strength of the connections with S
D1	2	1.7	0	0.7	4.4
D2	0	1	2	1.3	4.3
D3	0	1.2	0	2	3.2

Figure S4: Schematic representation of the two steps required to calculate the strength of supply links with D. First, the main supply-demand matrix is generated based on the relationships between the distance among supply and demand nodes and the distance decay function (a and b). Afterwards, by summing all supply links per demand node, we obtain the final values of this node-level metric (c).

2.2: Competition for supply

For this metric, calculations took five steps. First, the adjacent and weighted main supply-demand matrix generated above was transformed into a binary matrix (Figure S5-Step 1). Then, for each supply node in the network, we calculated the sum of all links it has with demand nodes and subtracted this sum by one (Figure S5-Step 2). This subtraction occurs so that for each demand node in the network, we can have the number of all other links with demand each of its connected supply nodes has besides the one with each focal demand node. This procedure occurs because we were interested in the potential effect of competition for supply between demand nodes, and not on the total number of links each supply node has with demand nodes. Therefore, this second step then generates a novel supply-demand matrix for which each cell of the supply and demand links contains the number of other demand links each of these supplies in the network has (Figure S5-Step 3). To account for the effects of the strength particular to each supply-demand connection, this novel supply-demand matrix is then multiplied by the main supply-demand matrix originated from the distance decay function (Figure S5-Step 4). Finally, using the resulting matrix from the previous step, the node-level metric is then calculated as the sum of all supply links per demand node in the network (Figure S5-Step 5).



Competition for supply

Step 1:

(Main S-D matrix)

	S1	S2	S3	S4
D1	2	1.7	0	0.7
D2	0	1	2	1.3
D3	0	1.2	0	2

→

	S1	S2	S3	S4
D1	1	1	0	1
D2	0	1	1	1
D3	0	1	0	1

Step 2:

	S1	S2	S3	S4
D1	1	1	0	1
D2	0	1	1	1
D3	0	1	0	1
output	0	2	0	2

Step 3:

(Novel S-D matrix)

	S1	S2	S3	S4
D1	0	2	0	2
D2	0	2	0	2
D3	0	2	0	2

Step 4:

(Novel S-D matrix)

	S1	S2	S3	S4
D1	0	2	0	2
D2	0	2	0	2
D3	0	2	0	2

(Main S-D matrix)

	S1	S2	S3	S4
D1	2	1.7	0	0.7
D2	0	1	2	1.3
D3	0	1.2	0	2

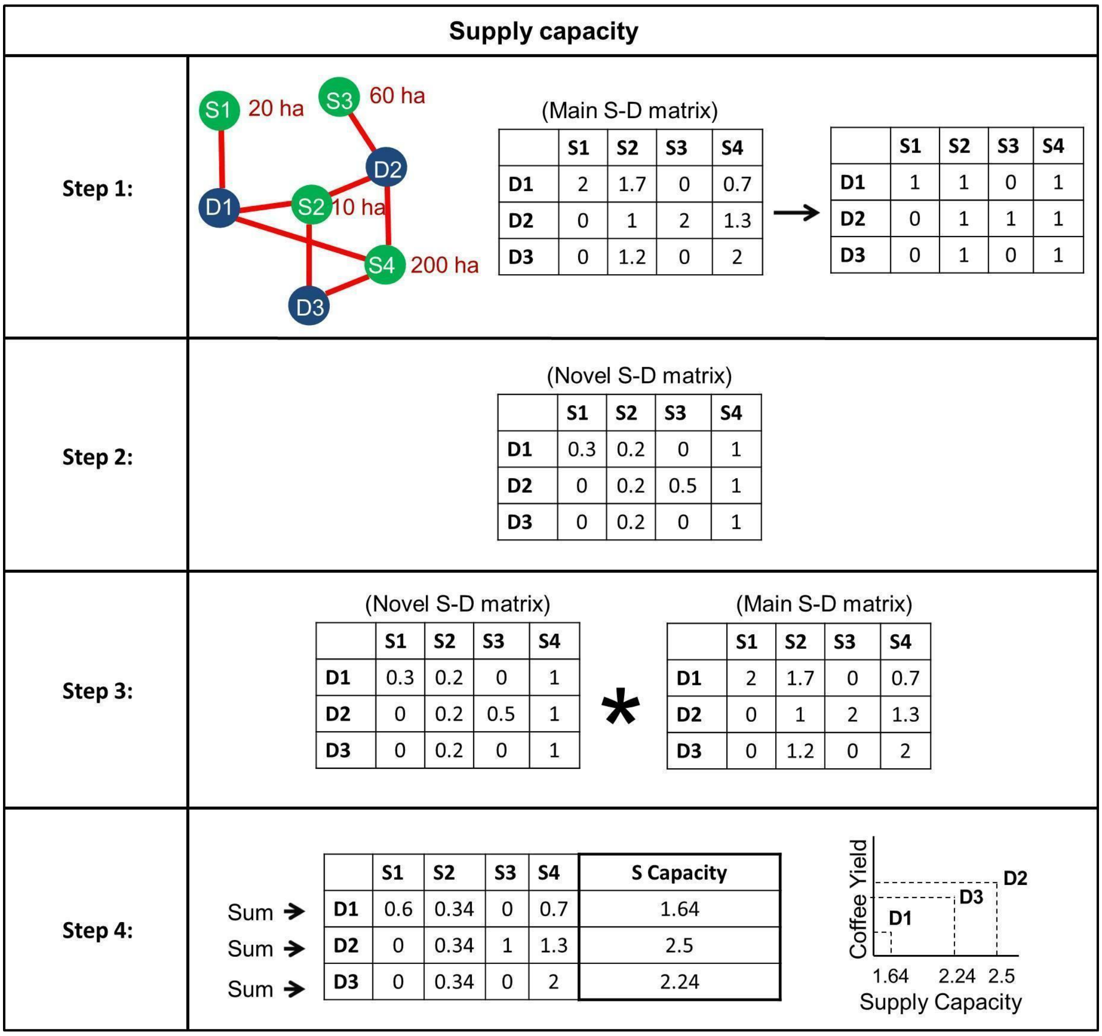
Step 5:

	S1	S2	S3	S4	Competition for S
D1	0	3.4	0	1.4	4.8
D2	0	2	0	2.6	4.6
D3	0	2.4	0	4	6.4

Figure S5: Schematic representation of the five steps required to calculate the node-level metric related to the competition between demand nodes for supply. First, the main supply-demand matrix is transformed into a binary matrix and used to calculate the number of other demand links each supply node in the network has (a and b). Afterwards, a novel supply-demand matrix is generated containing the resulting value of the previous step for each of the supply and demand links (c). This novel matrix is then multiplied by the main supply-demand matrix (d). Finally, by using the resulting matrix, we obtain the final values of this node-level metric by summing all supply links per demand node (e).

2.3: Supply capacity

For this metric, calculations took four steps. Again, we start by transforming the adjacent and weighted main supply-demand matrix into a binary matrix (Figure S6-Step 1). Then, each of the cells which represents a supply and demand connection is filled with the size of each of the connected supply nodes (Figure S6-Step 2). Afterwards, to account for the effects of the strength particular to each supply-demand connection, this novel supply-demand matrix is then multiplied by the main supply-demand matrix originated from the distance decay function (Figure S6-Step 3). Finally, using the resulting matrix from the previous step, the node-level metric is then calculated as the sum of all supply links per demand node in the network (Figure S6-Step 4).



Step 1: (Main S-D matrix)

	S1	S2	S3	S4
D1	2	1.7	0	0.7
D2	0	1	2	1.3
D3	0	1.2	0	2

→

	S1	S2	S3	S4
D1	1	1	0	1
D2	0	1	1	1
D3	0	1	0	1

Step 2: (Novel S-D matrix)

	S1	S2	S3	S4
D1	0.3	0.2	0	1
D2	0	0.2	0.5	1
D3	0	0.2	0	1

Step 3: (Novel S-D matrix)

	S1	S2	S3	S4
D1	0.3	0.2	0	1
D2	0	0.2	0.5	1
D3	0	0.2	0	1

*

(Main S-D matrix)

	S1	S2	S3	S4
D1	2	1.7	0	0.7
D2	0	1	2	1.3
D3	0	1.2	0	2

Step 4:

	S1	S2	S3	S4	S Capacity
D1	0.6	0.34	0	0.7	1.64
D2	0	0.34	1	1.3	2.5
D3	0	0.34	0	2	2.24

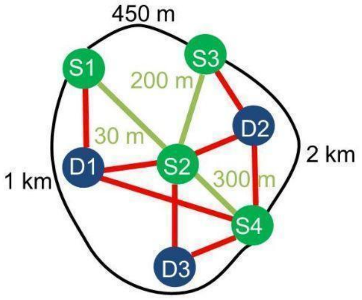
Figure S6: Schematic representation of the four steps required to calculate the node-level metric related to supply capacity. First, the main supply-demand matrix is transformed into a binary matrix and each of the cells which represent supply-demand links is filled with the respective size value of each supply node (a and b). This novel matrix is then multiplied by the main supply-demand matrix (c). Finally, by using the resulting matrix, we obtain the final values of this node-level metric by summing all supply links per demand node (d).

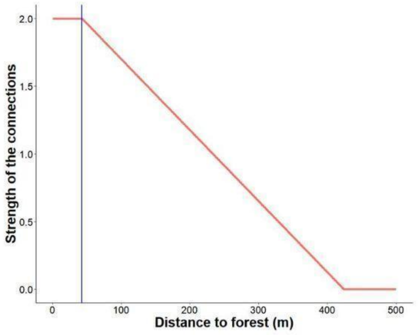
2.4: Supply-supply links

For this node-level metric, calculations took six steps. First, the smallest Euclidean distance between supply and supply nodes was converted into the strength of the connection between supply and demand through the distance decay function (Figure S7-Step 1). This first step then generates an adjacent provision matrix for which, for each supply node in the network, not only do we know if they are connected with other supply nodes (green links between supply and demand in Figure S7a) or not (black links between supply and demand in Figure S7a), but also the strength of their connection (Figure S7-Step 2). Afterwards, this adjacent supply-supply matrix was used to calculate the total amount of supply-supply links by summing all supply links per supply node in the network (Figure S7-Step 3). Then, by using the main supply-demand matrix to identify all cells which represent supply and demand links, we replaced each of the values related to the strength of the supply and demand connection with the respective value of the total number of supply-supply links each of those connected supply nodes (Figure S7-Step 4). Afterwards, to account for the effects of the strength particular to each supply-demand connection, this novel supply-demand matrix is then multiplied by the main supply-demand matrix originated from the distance decay function (Figure S7e). Finally, using the resulting matrix from the previous step, the node-level metric is then calculated as the sum of all supply links per demand node in the network (Figure S7f).

Supply connectivity

Step 1:





Step 2:

	S1	S2	S3	S4
S1	-	2	0	0
S2	0	-	1	0.5
S3	0	1	-	0
S4	0	0.5	0	-

Step 3:

	S1	S2	S3	S4	output	
S1	-	2	0	0	2	← Sum
S2	0	-	1	0.5	3.5	← Sum
S3	0	1	-	0	1	← Sum
S4	0	0.5	0	-	0.5	← Sum

Step 4:

(Novel S-D matrix)

	S1	S2	S3	S4
D1	2	3.5	0	0.5
D2	0	3.5	1	0.5
D3	0	3.5	0	0.5

Step 5:

(Novel S-D matrix)

	S1	S2	S3	S4
D1	2	3.5	0	0.5
D2	0	3.5	1	0.5
D3	0	3.5	0	0.5

*

(Main S-D matrix)

	S1	S2	S3	S4
D1	2	1.7	0	0.7
D2	0	1	2	1.3
D3	0	1.2	0	2

Step 6:

		S1	S2	S3	S4	Strength of S-S connections
Sum →	D1	4	5.95	0	0.35	6.3
Sum →	D2	0	3.5	2	0.65	4.15
Sum →	D3	0	4.2	0	1	5.2

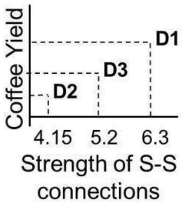


Figure S7: Schematic representation of the six steps required to calculate the node-level metric related to the strength of supply-supply links. First, a supply-supply adjacent matrix is generated by using the distance between supply nodes and the distance decay function (a and b). Afterwards, this supply-supply matrix is used to calculate the sum of all supply links per supply node in the network (c). Then, by using the main supply-demand connection of the network, each of the cells which represent supply-demand links is filled with the respective number of supply-supply links of each supply node (d). This novel matrix is then multiplied by the main supply-demand matrix (e). Finally, by using the resulting matrix, we obtain the final values of this node-level metric by summing all supply links per demand node (f).

3. *Data analysis:*

Table S1: Set of all 17 models used in the model selection. Supply capacity; Supply-demand links: Number of supply links per demand; Competition for supply: Number of other demand links per connected supply; Supply-Supply links: Number of supply-supply links.

Response variable	Models	Fixed effects
Coffee yield ~ (60 kg bags)	1	Supply capacity
	2	Supply-demand links
	3	Competition for supply
	4	Supply-Supply links
	5	Supply capacity + Supply-Supply links
	6	Supply capacity + Competition for supply
	7	Supply capacity + Supply-Supply links
	8	Supply-Supply links + Competition for supply
	9	Supply-demand links + Competition for supply
	10	Supply capacity * Supply-demand links
	11	Supply capacity * Competition for supply
	12	Supply capacity * Supply-Supply links
	13	Supply-Supply links * Competition for supply
	14	Supply-demand links * Competition for supply
	15	Supply capacity + Supply-demand links + Competition for supply
	16	Supply capacity + Supply-Supply links + Competition for supply
	17	Null

Appendix 2:

Vidal M. M. & Metzger, J.P. (2018). A influência da estrutura da paisagem sobre a organização de sistemas de polinização e dispersão de sementes.

Combining bee diversity data collected over four years (2013 to 2016) and across nine 3-km-radius landscapes across the same study region as this study, Vidal & Metzger (2018) sought to identify a possible critical distance to the forest, from which the bee community would become dramatically impoverished. In addition, they used their interannual database to assess the effect of distance to the forest on bee diversity. Vidal & Metzger (2018)'s dataset encompassed 1323 bee individuals distributed across 27 species. Their best model to explain bee diversity patterns was composed of the effects of distance to forest and sampled years. Differences between years were argued to be mainly due to climatic differences and sampling teams among sampled years. Nevertheless, for all sampled years, distance to forest has a negative effect on the diversity of bees (Figure S2). Furthermore, their results show that the degree of nesting between the columns of their bee occurrence matrix was significant (NODF=30.80, $p<0.001$), indicating that areas far from forest edges present subsets of the species found in areas closer to the forest. By progressively removing the most distant points of the forest, they also observed a significantly nested pattern until about 43 m from the forest (Figure S3). Thus, at distances smaller than 43 m, the composition of bees is similar between the sampling points.

Chapter 3

Pollination and pest control are mainly driven by flow-related landscape attributes: the need to account for multiple scales and disservices

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(To be submitted to *Landscape Ecology: Understanding relationships between biodiversity and ecosystem services in real landscapes*)

(“Paisaje Cultural Cafetero” de autoria do artista plástico Juan Carlos Suarez[4])

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[4] Imagem disponível em: https://www.flickr.com/photos/94037592@N06/8553471557

Pollination and pest control are mainly driven by flow-related landscape attributes: the need to account for multiple scales and disservices

(To be submitted to *Landscape Ecology: Understanding relationships between biodiversity and ecosystem services in real landscapes*)

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Abstract:

Context: Managing landscapes to increase the provision of multiple ecosystem services can be a consistent alternative to agricultural intensification in search of higher agricultural yield. Nonetheless, the relative importance of landscape management and the scale of its effect are yet to be understood.

Objectives: Focused on synergies and trade-offs in real-world landscapes, we investigated how and at which scales landscape structure acts as a common driver of pollination and biological pest control in coffee plantations.

Methods: Considering landscapes located in an important and traditional coffee-producing region in Brazil, we tested the multiscale effects of forest and coffee cover, distance to forest, forest-coffee edge density, and edge diversity on pollination by non specified pollinators and pest control by birds, bats and ants. Services were quantified through exclusion experiments.

Results: Edge diversity was the main driver of pollination and pest control and was most relevant at local scales (up to 300 m). Both services were differently affected by landscape structure and the scale of effect of each landscape structural component varied between services. Furthermore, the relationships for pest control encompassed the provision of both ecosystem services and disservices.

Conclusions: Edge diversity enhance and modulate pollination and biological pest control, suggesting that heterogeneous landscapes around coffee crops may favour provision of these ecosystem services. Furthermore, the small scale of effect of these relationships suggests that edge diversity effects are modulated by local flows, such as cross-habitat spillovers. The variety of scales of effect and the complexity of pest control provision reinforces the need to combine local and regional actions when planning multiple service provision.

Keywords: Ecosystem service drivers; Trade-off and synergies; Ecosystem service supply, demand, and flow; Crop diversity; Scale of effect; Ecosystem disservices

1. Introduction

Agricultural intensification has successfully increased yield across homogenous agricultural landscapes (Winqvist et al. 2012). However, these productivity gains have been at the expense of native species and ecosystem service provision (Tscharntke et al. 2005; Bommarco et al. 2013). To face the high demand for agricultural goods and more sustainable agricultural practices, landscape management that maximises the provision of multiple ecosystem services can be an important alternative to intensive agriculture (Qiu et al. 2021). Nonetheless, despite advances in multiple ecosystem services assessments (see Garibaldi et al., 2018 and Martínez-Salinas et al., 2022), the relative importance of landscape structure and the scale of its effect on multiple services provision remains a key challenge to landscape management (Bommarco et al. 2013; Chain-Guadarrama et al, 2019; Gagic et al. 2019; Qiu et al. 2021).

Pollination and biological pest control are two of the most important ecosystem services associated with crop yield (Power 2010; Dainese et al. 2019). These services are particularly relevant for economically and culturally important agricultural goods such as coffee, one of the most traded commodities in the world (Conab 2018). Pollinators and natural pest controllers can increase coffee yield up to 40% (Saturni et al. 2016; Aristizábal and Metzger, 2019; Moreaux et al. 2022). The influence of landscape properties on pollination and pest control services is well-studied (Librán-Embid et al 2017; Aristizábal and Metzger, 2019; Gagic et al. 2019; González-Chaves et al 2020). However, potential synergies and trade-offs between those services that arise from landscape modification, and their consequences for agricultural production is still poorly understood (Chain-Guadarrama et al, 2019; Qiu et al. 2021). Both pollination and biological pest control are biodiversity-mediated services that rely on the flow of species that connect areas of service 'supply' (i.e. ecosystems that support key processes or functions, such as natural land cover) to areas of 'demand' (i.e. cropland where the service is required). Furthermore, both services tend to be positively affected by the amount and proximity to supply, while being negatively affected by increases in demand (Saturni et al. 2016; Aristizábal and Metzger, 2019). Pollination and pest control services have thus similar spatial relationships with the three components of the "provision chain" (supply, demand and flow; Fisher et al 2019, Metzger et al. 2021). Due to these relationships, it is expected that the composition and configuration of supply and demand areas at landscape-scales are important drivers of pollination and pest control, by influencing the flow properties between these components.

Although pollination and pest control may be similarly linked to the provision chain, the scale at which landscape characteristics affect these services may differ. Indeed this 'scale of effect' sensu Holland et al. (2004) may differ with service, yield parameter and landscape attribute investigated (Martin 2018). The scale of effect is also expected to vary with characteristics of species that mediate provision (e.g. movement range and body size), and with the ecological processes involved in service provision (e.g. species spillover and pollination efficiency) (Moraga et al., 2019). For example, on one hand, services that rely on species that have large habitat requirements, such as pest control by birds and bats, may be affected by landscape composition at broad scales (Librán-Embid et al 2017). While ecological processes that occur at more local scales, such as species spillover between land uses, may be influenced by landscape components at smaller scales (Saturni et al. 2016; González-Chaves et al 2020). Moreover, services that involve multiple species, with different biological characteristics, will be affected by multiple scales (Metzger et al. 2021). The identification of pertinent scales of effect for different services can be used to inform landscape planning for multiple service provisions (Chain-Guadarrama et al. 2019; Qiu et al. 2021). General management recommendations that fail to account for the complex relationships between landscape structure and multiple provisions at different scales may not succeed in creating synergies and avoiding trade-offs between services (Garibaldi et al. 2018; Metzger et al. 2021).

Here, we combined a landscape ecological approach with exclusion experiments to investigate how and at what scales landscape structure simultaneously affects pollination and pest control by ants, birds and bats in coffee plantations. Specifically, we tested whether configuration and compositional aspects of the landscape linked to the supply, demand and flow of pollination and pest control could similarly modulate the provision of both services and the resulting synergies and trade-offs between them. We used a multiscaled approach to investigate whether the distance to forest fragments (related to *flow*), the amount of forest (*supply*) and coffee cover (*demand*), the density of edges between forest and coffee patches (*flow*), and the diversity of land uses in contact with coffee patches (*supply* and *flow*) similarly modulated the provision pollination and pest control.

We predicted pollination and pest control to increase with forest cover, proximity and the density of forest-coffee edge habitats, and to decrease with increasing distance from forest edges and landscape-level coffee cover. We expected these services to increase with the diversity of land uses in contact with coffee patches, given the greater potential of heterogeneous landscapes to maintain a diversity of species acting on pollination and pest control. Furthermore, we expected the scale of effect to vary with species and service, with pollination and pest control by ants affected by landscape structure at smaller scales, while pest control by birds and bats affected at broader scales. Finally, we also expected that landscape attributes associated with the flow of species between supply and demand patches, such as the distance to forest edges, the density of forest and coffee edges and the diversity of land uses in contact with coffee patches, would have a more local effect on both pollination and pest control provision.

2. Methods

2.1 Study area

Our study took place in one of the most important and traditional coffee-producing regions in Brazil, in the southeastern region of the country, between São Paulo and Minas Gerais states (Figure 1a). This region alone is responsible for almost 25% of the country's production (Conab, 2018), with Brazil being the main exporter and accounting on average for 30-35% of the total coffee production worldwide (FAO, 2019). Coffee crops in the region are sun-grown coffee plantations (sun-exposed coffee trees with no canopy cover planted on previously cleared land; Muschler, 1997), mainly *Coffea arabica* cultivated by family farmers. The Brazilian Atlantic Forest, the original biome of the region and one of the most diverse but also threatened biomes in the world (Myers et al., 2000; Ribeiro et al., 2009), has been drastically reduced due to generalised agricultural expansion at the beginning of the 20th century (Joly et al 2014). A subtropical climate with mean temperatures between 13.6 and 20.4°C, dry winter and rainy summers (Pompeu et al., 2009) and a hilly terrain with elevation varying between 700 to 1300 m.a.s.l., make this region ideal for coffee production. In fact, coffee expansion has been one of the main drivers of deforestation of the Atlantic Forest (Carlucci et al. 2021, Rosa et al. 2021). Nowadays, landscapes in the region are composed of Atlantic Forest remnants immersed primarily in a matrix of coffee crops and pastures, and secondarily by eucalyptus and sugarcane plantations (Fig 1).

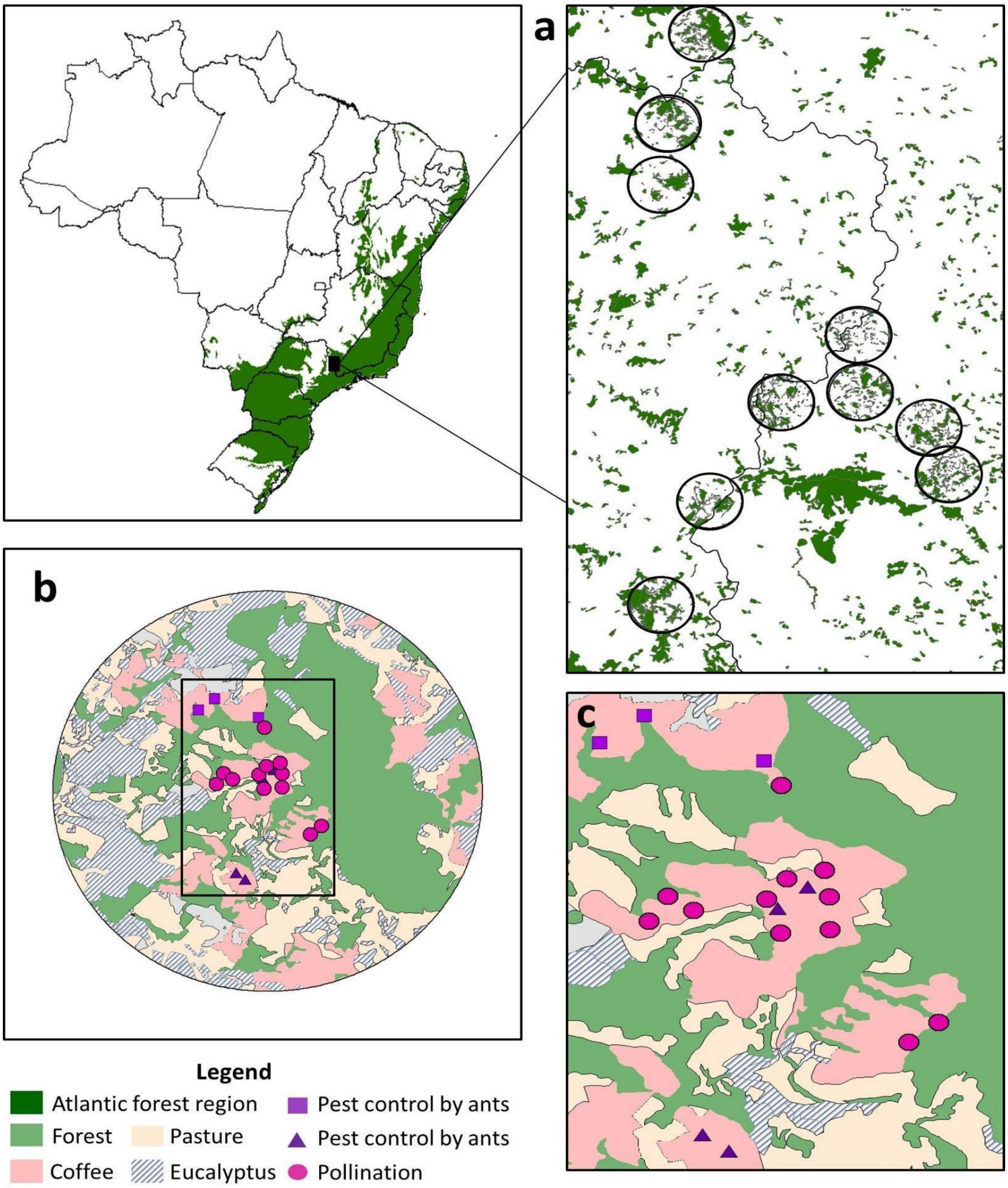


Fig. 1: Geographical location of the ten landscapes in the Brazilian Atlantic Forest region, between São Paulo and Minas Gerais states (a). Distribution of experimental sites in one of the landscapes (b), and a zoom into pollination, pest control by ants and pest control by birds and bats sampling sites in coffee plantations (c).

Field data collection occurred between 2013 and 2015 and across 10 independent experimental landscapes with a 3 km radius (Figure 1a). Landscapes were selected to encompass a gradient of landscape forest cover (13% to 48%), but controlling for soil type and altitude (for selection details, see Boesing et al 2018). Landscape centroids were at least six kilometres apart from each other. Land use and land cover were mapped using high-resolution images (ArcGIS 10.3 base map imagery, DigitalGlobe satellites 2010–2011, 0.5–1 m resolution, 1:5,000 visualisation scale). Mapping was extensively validated in the field in 2013 and 2015, and all interpretation errors or landscape changes between 2010 and 2015 were edited.

To assess the contribution of pollinators and pest controllers to pollination and biological pest control, respectively, each landscape had multiple experimental sites with exclusion experiments, totalling 292 experimental sites across the 10 landscapes (Figure 1a). All experimental sites were separated by at least 100 m to ensure independence among samples while encompassing a wide variation of landscape attributes, such as local forest and coffee cover and distance to forest edge (for more details, see Saturni et al. 2016, Librán-Embid et al. 2017, Aristizábal and Metzger, 2018 and González-Chaves et al. 2020). In addition, the studied sub-varieties of *Coffea arabica* were controlled , with sites only composed of varieties that are physiologically similar, such as Catuaí and Catucaí, or Catuaí and Mundo Novo (Dias and Souza 2015, but see Saturni et al 2016).

2.2 Landscape metrics

For all ten experimental landscapes, we calculated five landscape metrics associated with one or more components of the provision chain. *Forest cover* and *edge diversity* were selected as potential supply measures, acting as likely sources of pollinators and natural pest controllers, and thus potentially affecting both the abundance and diversity of those species. However, as agricultural matrices may often offer movement resistance to the species, *edge diversity*, similar to *forest-coffee edge density* and *distance to forest edge*, could also act as an indication of flow, meaning that land uses in contact with coffee patches could facilitate the flow of species between supply and demand. Finally, coffee cover was used as an indication of areas demanding the diversity of pollinators and natural pest controllers being supplied by the forest or other land uses.

Forest and *coffee cover* (%), *forest-coffee edge density* (m/m^2) and *edge diversity* (number of land uses in contact with coffee areas) were calculated at the selected “scale of effect” (i.e. the scale at which an ecological response or process is best predicted by landscape metrics - Jackson and Fahrig 2015; Table SI1), using circular buffers around each of the 292 experimental sites. The *distance to forest edge* (m) was calculated as the Euclidean distance of each experimental site to the nearest forest patch. For all four scale-dependent metrics, we first considered a wide variety of scales (30, 50, 100 up to 500 with 100 m intervals, 1000, 2000 and 3000 m) around each experimental site to encompass spatial dimensions for a variety of ecological traits of possible pollinators and pest controllers (Kremen et al, 2004; Ribeiro et al. 2008; Boscolo and Metzger 2009; Bichara et al. 2010; Jackson and Fahrig 2015; Boesing et al 2018). Afterwards, we selected the appropriate 'scale of effect' of each landscape metric based on the Akaike Information Criterion corrected for small sample sizes (AICc) using the "multifit" function in R (R Development Core Team, 2014; Huais, 2018) (Table S1). Experimental sites encompassed a wide overall range of forest cover (0-61%), coffee cover (4-100%), forest-coffee edge density (0-0.00842 m/m^2), edge diversity (1 to 8 neighbour land uses) and distance to the forest (0-324 m). All five landscape metrics were calculated in R (R Development Core Team, 2014).

2.3 Exclusion experiments

2.3.1. Pollination

To quantify the service of coffee pollination, 159 pollination-exclusion experiments were placed across the experimental sites in nine landscapes (Figure 1b and 1c). Each experiment encompassed exclusion branches (i.e. branches in which the presence of pollinators was experimentally prevented) paired with control branches (i.e. branches in which the flowers were opened and accessible to pollinators). Paired branches from both treatments were randomly selected across different coffee bushes at the experimental sites. To exclude pollinators but still allow airflow, a thin mesh bag (3 mm) was placed around each exclusion branch. After approximately a week of the flowering period, exclusion branches were marked and all mesh bags removed to avoid any effects on fruit development. Altogether, pollination-exclusion experiments totalled an effort of 765 branches per treatment. Finally, for each branch on both treatments, the number of flowers at the blooming period (September and October 2013, and October 2015) and the number of coffee berries at the harvest period (May 2013 and 2015) were counted (see Appendix S2, Saturni et al. 2016 and González-Chaves et al. 2020 for detailed information on sampling design and procedures detail).

2.3.2. *Pest control*

To quantify the service of pest control, we investigated the potential of natural control of two of the main pests of coffee plantations: the Coffee Leaf Miner *(*CLM - *Leucoptera coffeella)* and the Coffee Berry Bore*r (*CBB - *Hypothenemus hampei)*. Like the pollination service, natural pest control-exclusion experiments were placed across the experimental sites in ten landscapes (Figure 1b).

For CLM, we considered the control by birds and bats, and used data from 24 exclusion experiments placed across six landscapes. Exclusion experiments were composed of four coffee bushes in which birds and bats were excluded (i.e. exclusion units), paired with another four adjacent coffee bushes that were accessible to all potential pest controllers (i.e. control units), resulting in 576 branches per treatment. To exclude birds and bats while still allowing arthropods to enter, a nylon monofilament mesh was used to cover all four exclusion bushes. Each coffee bush, regardless of the treatment, then had randomly marked branches from which randomly selected leaves and coffee berries were marked and counted (see Appendix S2 and Librán-Embid et al. 2017 for detailed information on sampling design and exclusion experiments).

For CBB, we considered control by ants, and used data on 29 ant-exclusion experiments placed across 10 landscapes right before the main flowering to ensure CBB absence (see Appendix S2). At each of the 10 coffee bushes per experimental site, exclusion experiments encompassed one randomly selected branch in which ants were excluded paired to another randomly selected neighbouring branch that was accessible to ants. Altogether, pest control-exclusion experiments totalled an effort of 300 branches per treatment. For each experimental branch, regardless of the treatment, the number of berries produced and berries bored was counted, and all coffee berries were collected right before farmers' harvest time. Care was taken to ensure a similar number of flowers, height, and position to all experimental branches (see Appendix S2 and Aristizábal and Metzger for detailed information on sampling design and procedure details).

2.4 Quantification of pollination and pest control service

We considered five response variables, or indicators of pollination and pest control by birds, bats and ants, to test how landscape structure could be affecting drivers associated with the supply, demand and flows of these services. Therefore, we used *Fruit set* as a measure of fruit production and an indication of pollination service. Since CLM affects leaves' persistence in coffee bushes which in turn affects fruit production due to photosynthesis reduction (Pierre 2011), we also used *Fruit set*, along with *Leaf loss*, as indications of natural coffee leaf miner control by birds and bats. Finally, for CBB control by ants, we used *CBB presence*, *CBB infestation's level*, and *CBB bean damage* to consider the ecological interactions between ants and CBB at the three different stages of pest control. For pollination, as well as for CLM control by birds and bats, *Fruit set* was calculated as the proportion of berries out of the total of flowers per branch during the blooming period. *Leaf loss* was calculated as the proportion of fallen leaves out of the total leaves initially marked per branch. The *presence of CBB* was considered when there was at least one bored coffee berry on a branch, while CBB absence was considered when none of the coffee berries on a branch had CBB. *CBB infestation* was calculated as the proportion of coffee berries with CBB out of the total of berries produced per branch. Finally, for each bored coffee berry, *CBB damage* was calculated as the proportion of damage to each coffee bean out of the total size of the coffee bean inside the bored berry (see Aristizábal and Metzger, 2018 for damage measurement details).

2.5 Data analysis

We quantified the effects of *forest cover*, *coffee cover*, *distance to forest edge*, *forest-coffee edge density* and *edge diversity* on all three services using generalised linear mixed models (GLMMs; Zuur et al 2009). All three response variables for pest control by ants (*CBB presence*, *CBB infestation* and *CBB damage*), and the response variable for pollination (*Fruit set*) were modelled using a binomial distribution and a logit-link function ("lme4" package; Bates et al. 2015). The two response variables for pest control by birds and bats (*Fruit set* and *Leaf loss*) were modelled using a beta-binomial distribution ("glmmTMB" package; Magnusson et al 2017) to account for overdispersion (Harrison 2015). As the total number of flowers, leaves and berries differed between branches, response variables were calculated inside the models as a two-vector response variable (e.g., number of coffee berries from the total number of flowers per branch) using the "cbind" function (R Development Core Team, 2014). All five landscape attributes were centred and scaled to mean zero and one standard deviation and included as fixed effects in the full model.

To account for the fact that our pollination measurement (*Fruit set*) was collected in different years (2013 and 2014), the measurement year was included as a fixed effect in all models with this service (Bolker et al 2013). For each service, we created ‘full models’ that included the variables: *forest cover*, *coffee cover*, *distance to forest edge*, *forest-coffee edge density* and *edge diversity*. The full model included the interaction of the animal exclusion experiments (presence and absence of animals in branches or flowers), all landscape metrics (each at their final ‘scale of effect’) (Table S1), and random effects. The scale-dependent landscapes metrics were specified at the appropriate “scale of effect” (further details in section 2.3 and in Appendix S1). To account for potential non-independence of multiple sampling transects within each landscape, a landscape identifier was specified as a random intercept (Zuur et al, 2009). As experimental units usually had more than one experimental coffee bush, and each bush had more than one experimental branch, both the experimental unit and bush identifications were also included as nested random effects in all models (Zuur et al 2009). In addition, to account for overdispersion, an observation-level random effect was included in all pollination models (Harrison 2015).

For each response variable, we separately performed ‘all subsets’ model selection procedure for each full model using the “dredge” function (“MuMin” package; Barton and Barton 2015) with the full model for each service and the Akaike Information Criterion corrected for small sample sizes (AICc). Substantially supported models (ΔAICc < 2) were averaged, and final models were built using significant relationships for each service (Table S2). Models’ goodness-of-fit was tested by residual analysis using “DHarma” package (Hartig, 2020), and multicollinearity was measured using a generalised variance-inflation factor (“car” package - Fox et al 2007). All analyses were conducted in R (R Development Core Team, 2014).

3. Results:

Pollinators and natural pest controllers increased coffee productivity by affecting the amount of fruit, leaf and pest levels on coffee plants. While the presence of pollinators always resulted in service provision (i.e., higher fruit set), the presence of birds, bats and ants resulted in both service and disservice (i.e., positively and negatively affecting fruit set, leaf loss, and CBB presence, infestation and damage).

Landscape structure exerted different effects on each of the services. The number of land uses in contact with coffee (*edge diversity*) was the main driver (i.e., most common driver) of both pollination and pest control by ants, and pest control by birds and bats (Table 1). Furthermore, for both services, the effect of *edge diversity* on provision was consistently local (30, 100, 200 and 300 m). Finally, apart from *edge diversity*, the 'scale of effect' of all other scale-dependent landscape structure components (*forest cover*, *coffee cover* and *forest-coffee edge density*) varied greatly between services (Table 1).

Pollination

The positive effect of bees to fruit set (orange areas in Figure 3) decreased as *coffee cover* (within 1 km, Fig. 3a) and *distance from the forest edge* increased (Fig. 3b). Increases in *edge diversity* within 100 m were associated with stronger effects of bees on fruit set (shaded areas width in Fig 3c). See Table 1 and S2 for model's details.

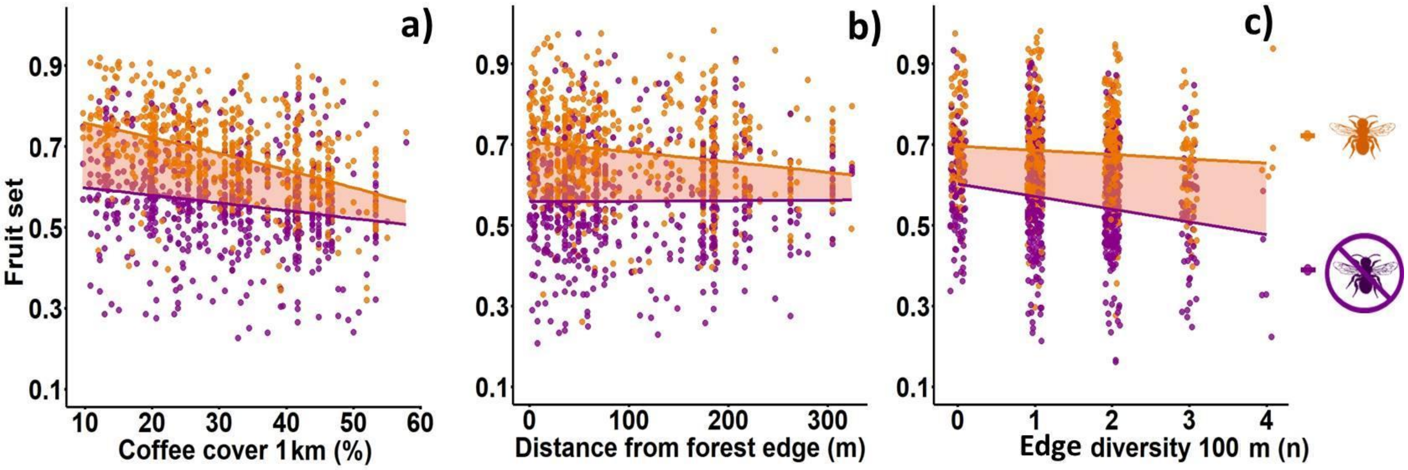


Figure 3. Partial effects of the relationships between the proportion of *fruit set* with and without bees' contribution to pollination and (a) *coffee cover* (%), (b) *edge diversity* (n) and (c) *distance to forest edge* (m). Shaded areas between curves show the interaction between exclusion experiments (bees presence/absence) and the intensity of provision (width of the shaded area along the gradient of the predictor variable). Shaded areas in orange represent where bees had positive effects (i.e., service).

Coffee leaf miner (CLM) control

Model comparisons suggested that the effects of bird and bat exclusion on the fruit set were influenced by *forest-coffee edge density* and *edge diversity,* measured within 300-m (Table S2). For both landscape attributes, birds and bats' contributions to *the Fruit set* (as shown respectively by orange and purple areas in Fig. 4) varied with these landscape metrics, thus providing both service (i.e., a positive effect of the presence of birds and bats) and disservice (i.e., a negative effect of the presence of birds and bats) to coffee productivity. The presence of birds and bats increased *fruit set* (positive effect; orange areas in Figure 4a) in landscapes with higher *densities of forest-cover edges*, and where there were more than three *different land uses in contact with coffee patches* (Figure 4b).

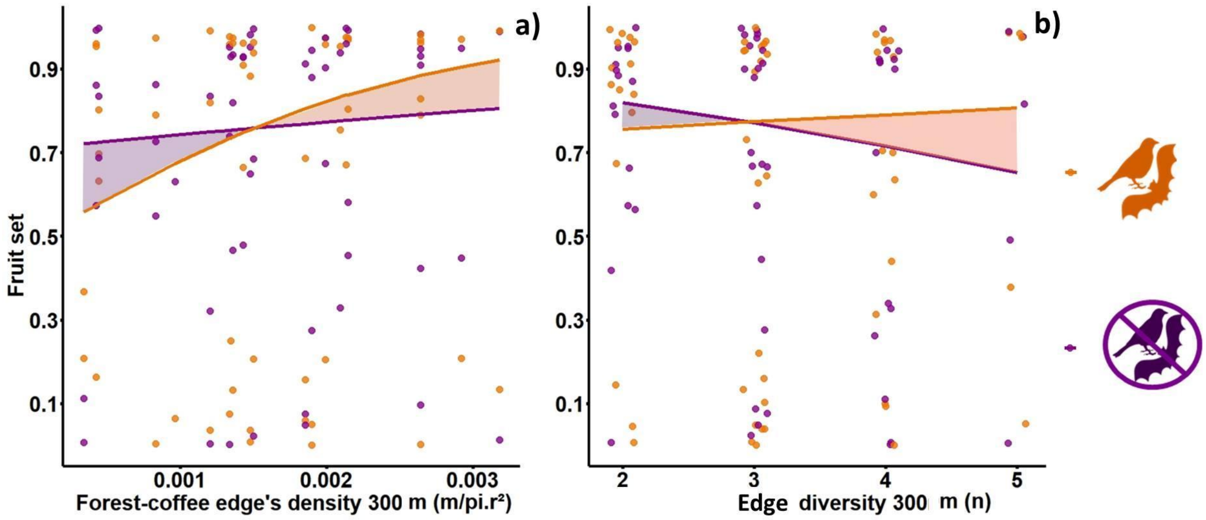


Figure 4. Partial effects of the relationships between the proportion of *fruit set* with (orange lines and dots) and without (purple lines and dots) birds and bats' contribution to CLM pest control and (a) *forest-coffee edge density* (m/pi.r²) and (b) *edge diversity* (n). Shaded areas between curves show the interaction between exclusion experiments (birds and bats presence/absence) and the intensity of provision (width of the shaded area along the gradient of the predictor variable). Shaded areas in orange and purple indicate where birds and bats had positive (i.e., service) and negative effects (i.e., disservice), respectively.

The provision of *Leaf loss control by birds and bats* varied with *forest* and *coffee cover* (within 100 and 500-m, respectively), *forest-coffee edge density* (1-km), and *distance to forest edge* (see models in Table S2). Similar to the patterns observed for *Fruit set*, birds and bats' contribution to *Leaf loss* switched direction with the ranges of predictor variables, thus again representing both service (i.e., a positive effect of the presence of birds and bats) and disservice (i.e., a negative effect of the presence of birds and bats) (Figure 5). The presence of birds and bats was associated with lower proportion of leaf loss (positive effect; orange areas in Figure 5) in landscapes with higher *forest cover* and *forest-coffee edge densities*, and with lower *coffee cover* (Figure 5). Positive effects of the presence of birds and bats on leaf loss were also seen *far (~ >100 m) from forest edges* (Figure 5).

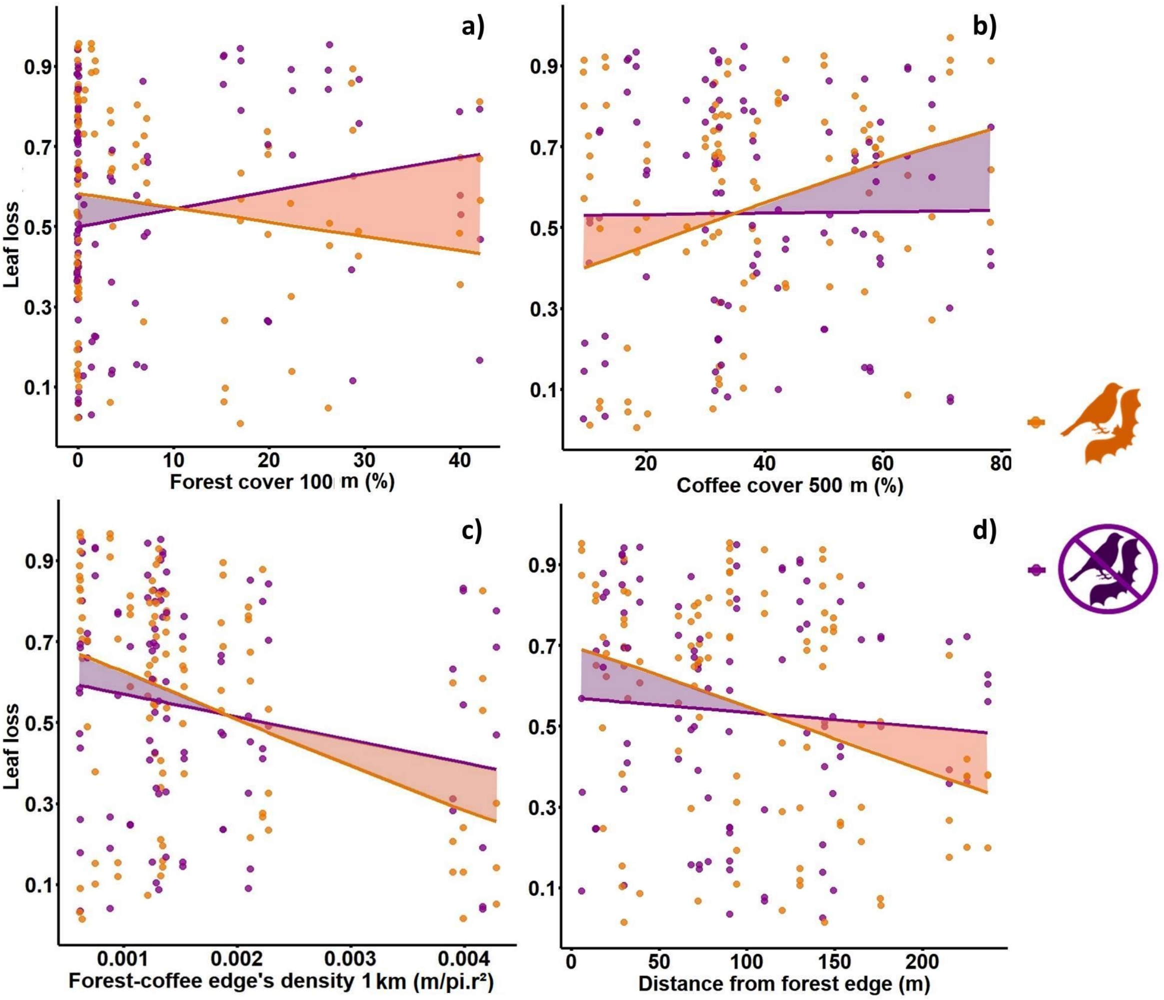


Figure 5. Partial effects of the relationships between the proportion of *leaf loss* with (orange lines and dots) and without (purple lines and dots) birds and bats' contribution to CLM pest control with (a) *forest cover* (%), (b) *coffee cover* (%), (c) *forest-coffee edge density* (m/m²) and (d) *distance to forest edge* (m). Shaded areas between curves show the interaction between exclusion experiments (birds and bats presence/absence) and the intensity of provision (width of the shaded area along the gradient of the predictor variable). Shaded areas in orange and purple represent where birds and bats had positive effects (i.e., service) and negative effects (i.e., disservice), respectively.

Coffee berry borer (CBB) control

For CBB regulation by ants, the final model for *CBB presence* included the additive effects of the interactions between ants exclusion and *1-km-level coffee cover*, and ants exclusion and *200-m-level edge diversity* (Table S2). The contribution of ants to reduce the probability of *CBB presence* (positive effects; orange areas in Figure 6) reduced as *coffee cover* increased (Figure 6a), and increased as *edge diversity* increased (Figure 6b). Therefore, the contribution of ants in the reduction of *CBB presence wa*s highest in landscapes with low *coffee cover* and in *coffee patches surrounded by multiple land uses*.

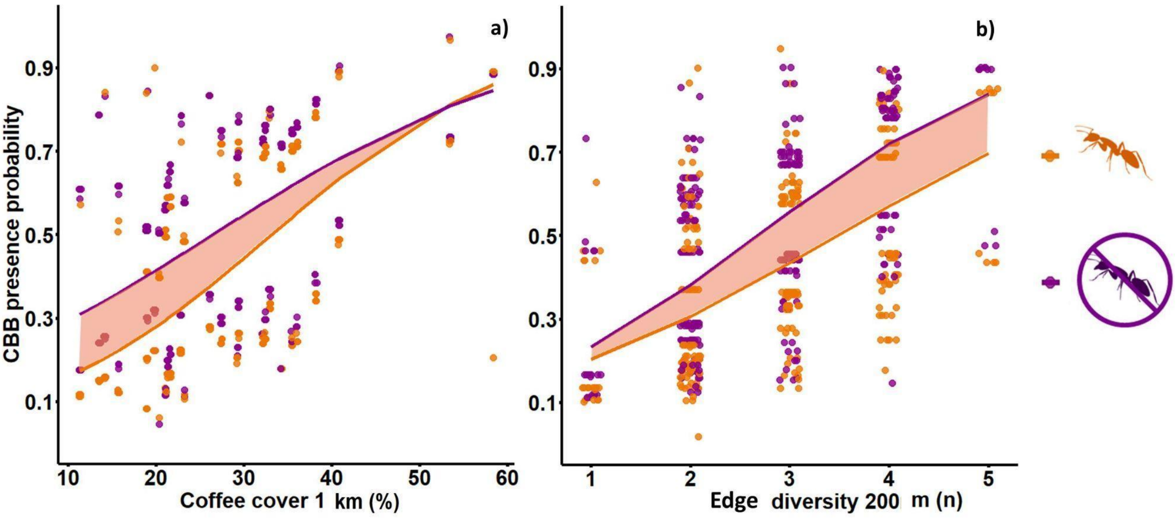


Figure 6. Partial effects of the relationships between the probability of *CBB presence* with (orange lines and dots) and without (purple lines and dots) ants' contribution to CBB pest control with *coffee cover* (%) and *edge diversity* (n). Shaded areas between curves show the interaction between exclusion experiments (ants presence/absence) and the intensity of provision (width of the shaded area along the gradient of the predictor variable). Shaded areas in orange represent where ants had positive effects (i.e., service) and in purple, negative effects (i.e., disservice).

For *CBB infestation*, the final model included the interactions between ants exclusion and *1-km-level amount of forest-coffee edge density*, and ants exclusion and *30-m-level coffee-edge diversity* (Table S2). Similar to the complex relationships for CLM control by birds and bats, ants' contribution to *CBB infestation* also switched direction with the ranges of predictor variables, thus resulting in both service (i.e., a positive effect of the presence of ants) and disservice (i.e., a negative effect of the presence of ants). However, compared to the effects of CLM control by birds and bats on *Fruit set*, the relationships between *CBB infestation* and *forest-coffee edge density* and *edge diversity* had the opposite effect (orange and purple areas in Figure 7). Specifically, ants' contribution to the reduction of *CBB infestation* (positive effect; orange areas in Figure 7) was higher in landscapes with lower *forest-coffee edge density* and *edge diversity* (Figure 7a and b, respectively). At higher *densities of forest-coffee edges* and high *diversity of edges*, *CBB infestation* was higher when ants were present (negative effect; purple areas in Figure 7).

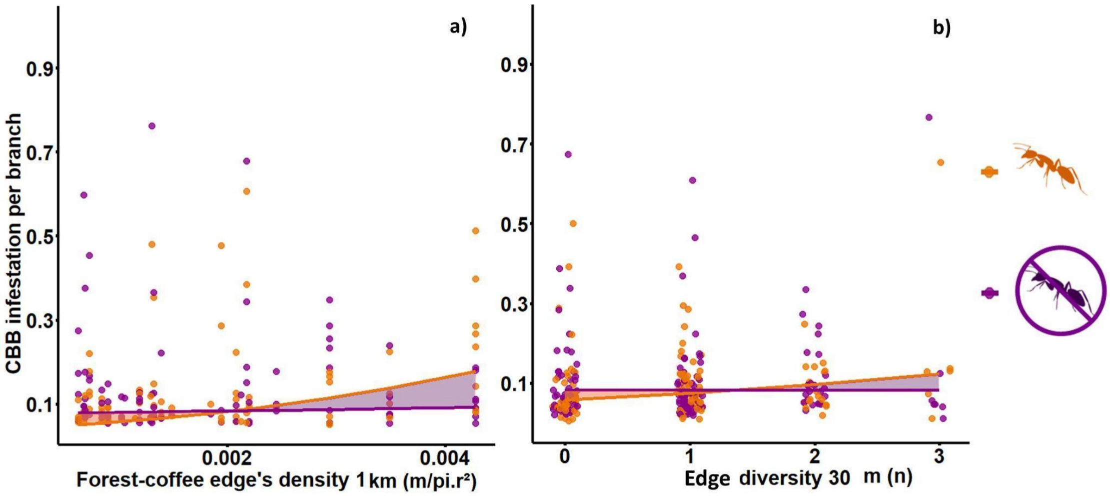


Figure 7. Partial effects of the relationships between the proportion of *CBB infestation* with (orange lines and dots) and without (purple lines and dots) ants' contribution to CBB pest control with *forest-coffee edge density* (m/pi.r²) and *edge diversity* (n). Shaded areas between curves show the interaction between exclusion experiments (ants presence/absence) and the intensity of provision (width of the shaded area along the gradient of the predictor variable). Shaded areas in orange and purple represent where ants had positive effects (i.e., service) and negative effects (i.e., disservices), respectively.

Once CBB was present, the final model for *CBB damage* on coffee beans included the interaction between ants exclusion and *2-km-level forest cover* (Table S2). Similar to other results for pest control, ants' contribution to *CBB damage* shifted as *forest cover* increased. As *forest cover increases*, the provision of *damage control* reduces. Despite this reduction in the provision, up to approximately 40% of *forest cover*, the presence of ants effectively reduces *CBB damage* (positive effect; orange areas in Figure 8). After this point, the provision of this service ceases and the presence of ants is detrimental to the amount of *CBB damage* (negative effect; purple areas in Figure 8).

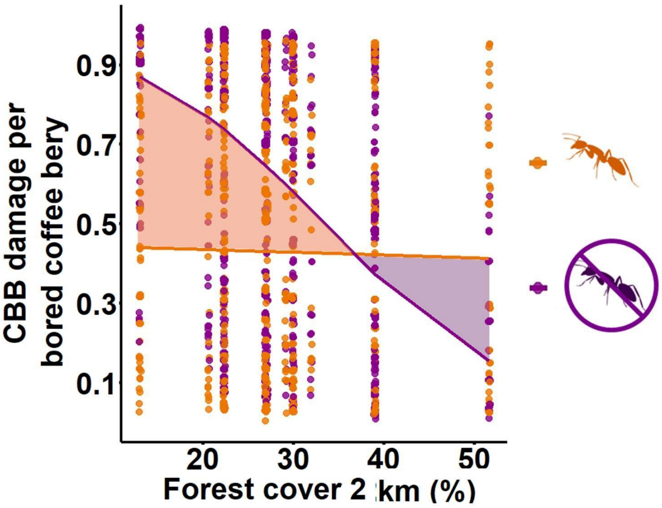
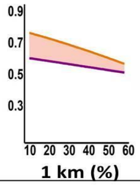
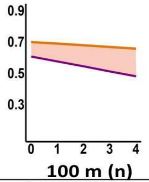
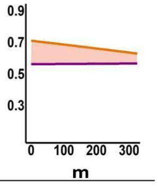
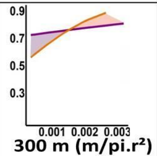
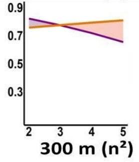
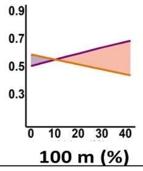
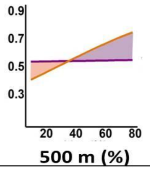
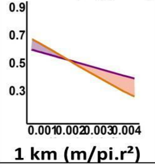
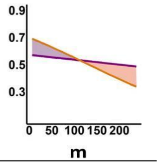
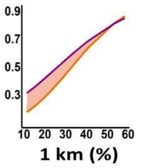
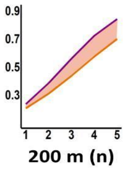
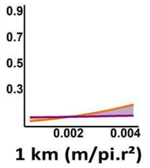
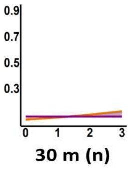
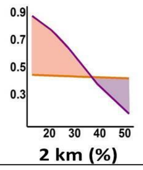


Figure 8. Partial effects of the relationship between the proportion of *CBB damage* with (orange lines and dots) and without (purple lines and dots) ants' contribution to CBB pest control with *forest cover* (%). Shaded areas between curves show the interaction between exclusion experiments (ants presence/absence) and the intensity of provision (width of the shaded area along the gradient of the predictor variable). Shaded areas in orange and purple represent where ants had positive effects (i.e., service) and negative effects (i.e., disservice), respectively.

4. Discussion

Our results provide evidence that the provision of pollination, pest control by ants and pest control by birds and bats in coffee plantations are modulated by landscape attributes associated with the supply, demand and flow of these services (Table 1). Specifically, the number of land uses in contact with coffee (*edge diversity*) was the main common driver of both pollination and pest control services. This suggests that land uses surrounding coffee areas may enhance service provision by supplying a diverse set of pollinators and pest controllers. Additionally, the 'scale of effect' of *edge diversity* effects was consistently small for both services (up to 300-m), suggesting that local flow of species (e.g., species spillover) are key to the provision of pollination and pest control in coffee plantations. The presence of pollinators and pest controllers increased coffee productivity through influences on fruit set, leaf loss and pest infestation. However, while the presence of pollinators consistently resulted in service provision (i.e., the presence of pollinators resulting in higher yield), pest control was both positively (i.e., service provision) and negatively (i.e., disservice provision) influenced by ants, and by birds and bats. Finally, besides *edge diversity,* pollination, pest control by ants and pest control by birds and bats were also affected by other components of landscape structure (*forest cover, coffee cover and forest-coffee edge density*) (see Table 1). However, the scale of these effects varied greatly between services. These differences in the 'scale of effect' along with the provision of pest control service and disservice highlight the complexity behind planning multiple service provision. Our results then emphasise that landscape management focused on increasing pollination and pest control needs to consider multiscalar approaches that account for disservice, as well for service provisions.

Table 1: Summary of the relationships between configuration and compositional aspects of the landscape linked to the supply (*Forest cover* and *Edge diversity*), demand (*Coffee cover*) and flow (*Forest-coffee edge density*, *Edge diversity* and *Distance to forest edge*), and the provision of pollination (*Fruit set*), CLM control by birds and bats (*Fruit set* and *Leaf loss*), and CBB control by ants (*CBB presence*, *CBB infestation* and *CBB damage*). Shaded areas between curves show the interaction between exclusion experiments (pollinators or pest controllers *presence*: orange lines; *absence*: purple lines) and the intensity of provision (width of the shaded area along the gradient of the predictor variable). Shaded areas in orange represent where service providers (pollinators, birds and bats, or ants) had *positive effects* on provision (i.e., *service)* and in purple *negative effects (*i.e., *disservice)*.

Ecosystem service (ES)		**Forest cover (%)**	**Coffee cover (%)**	**Forest-coffee edge density (m)**	**Edge diversity (n)**	**Distance to forest edge (m)**
Pollination	**Fruit Set**					
Coffee leaf miner (CLM) control by birds and bats	**Fruit Set**					
	Leaf loss					
Coffee berry borer (CBB) control by ants	**CBB presence**					
	CBB infestation					
	CBB damage					

Landscape structure effects on the supply, demand and flows of pollination and pest control

Our work shows that pollination and pest control provision rely on landscape attributes associated with the supply (*Forest cover* and *Edge diversity*), demand (*Coffee cover*) and flows (*Forest-coffee edge density*, *Edge diversity* and *Distance to forest edge*). Regarding the supply of these services, the amount of native forest was particularly important to the provision of pest control. At local scales, higher forest cover resulted in reduction of *leaf loss mediated by birds and bats*, suggesting that forest patches may indeed be acting as supply areas of pest controllers. Higher local forest cover may favour connectivity between patches and thus foster species movement across the landscape (Martensen et al., 2012; Brudivig et al., 2009). In contrast, low forest cover may drastically reduce the number of edges between native habitat and matrix and increase patch isolation (Villard & Metzger, 2014), which could then reduce the probability of species spilling over from habitat patches. At larger landscape scales, however, increases in forest cover reduced the provision of *CBB damage* control by ants. In landscapes with higher forest cover (~>40%), as the diversity of birds increases, ants' contribution to the service may be hindered due to higher predation pressure upon ants by birds (Librán-Embid et al., 2017). This intraguild predation by birds can then limit ants’ ability to control CBB damage, resulting in a disservice via the release of predation pressure on CBB. However, for landscapes with up to 40% of forest cover, the presence of ants was particularly important to reduce *CBB damage* (Figure 8). In these landscapes (~<40%), as the community of birds becomes less diverse (Boesing et al 2018a), intraguild predation pressure on ants is expected to be relaxed, thus increasing ants' relevance as natural controllers of CBB.

Regardless of the scale, higher demand (i.e., *coffee cover*) reduces the provision of both pollination and pest control. Increases in coffee cover may reduce service provision due to dilution effects, meaning that there is more demand for pollinators and pest controllers than they can actually meet (Vanbergen 2013). Additionally, increasing coffee cover can also reduce the diversity of pest controllers and pollinators due to the negative effects of landscape simplification and homogenization (Gámez-Virués et al., 2015; Aguilera et al 2020; Gonzalez-Chaves et al., 2020), while facilitating pest movement and spread (Avelino et al., 2012; Medeiros et al 2019; Beasley et al. 2020 Preprint). Finally, the negative effects of large amounts of coffee cover on pollination and pest control are in accordance with the positive effects of higher edge diversity on the provision of these services, reinforcing the relevance of higher matrix heterogeneity to pollination and pest control provision (Turner et al., 2013; Baillod et al., 2017; Aguilera et al 2020).

Besides the effects of the amount of supply (i.e., native forest areas) and demand (i.e., coffee areas), our results show that pollination and biological pest control provision is also shaped by flow-related landscape attributes. This applies to the service of *CLM control by birds and bats*, for which higher contact between supply and demand resulted in higher provision. These positive effects may be a result of higher flow of species from the supply to demand. Indeed, higher edge densities in the region have been reported to have positive effects on the spillover of birds probably due to the higher chance of edge encounters by habitat species (Boesing et al 2018b). Furthermore, our results also suggest that the flow of species and, therefore, service provision are not only shaped by *the amount of contact between supply and demand*, but also by the *distance to supply*. As the distance to forest edge increased, pollination provision decreased, suggesting that although the contact between supply and demand patches is important, the benefit derived from this connection is stronger near habitat-matrix edges. This can be due to the movement resistance that anthropogenic matrices impose on the species, thus altering the service they provide (Boesing et al 2018b; Hohlenwerger et al 2022). As foraging outside the habitat boundaries may inflict a higher predation risk (Brown, 1999; Hernández and Laundré, 2005). Longer incursions into the matrix may be thus avoided by the species, resulting in lower service provision far from the forest edge. Indeed, the diversity of species of bees tends to decrease as distance to forest increases (Gonzalez-Chaves et al 2020).

It is important, however, to point out that not all services may be similarly affected by *higher forest-coffee edge densities* and *distance to forest*. This was the case for the *regulation of CBB infestation by ants* and *leaf loss by birds and bats*. For these services, the provision of pest control happened in landscapes with lower forest-coffee edge density and far from the forest, respectively. Higher contribution of non-forested species or intraguild predation are two of the main processes which could be underlying these results. An increase in forest-coffee edge densities and proximity to forest could result in higher competition for resources with forest species and lower abundance of generalists species, especially near habitat-matrix edges

(Lacasella et al., 2015; Boesing et al., 2018b). Similarly to patterns found for forest cover effects on CBB damage control, it is possible that the mechanisms underlying the higher contribution of birds and bats to CLM control in landscapes with high forest-coffee edges, may also be resulting in higher predation pressure on ants by birds (Martin et al., 2013). This intraguild predation may thus result in a reduced contribution of ants to the control of CBB infestation at higher forest-coffee edge densities. Likewise, it is possible that near forest edges, birds and bats exert predation pressure on other invertebrates besides crop pests, including predatory arthropods such as ants and wasps (Karp and Daily, 2014), thus diluting their contribution to pest control and reducing the ability of other pest controllers to provide the service themselves (Martin et al., 2013).

Landscape diversity as a common driver of pollination and pest control

Edge diversity was the main common driver for both ecosystem services, suggesting heterogeneous landscapes may favour multiple service provisions. The positive effects of the diversity of land uses and land covers surrounding coffee plots suggests that these areas may be acting as supply of multiple service-providing species or facilitating the flow of those species, contributing thus to higher service provision. Heterogeneous landscapes may increase service provision by i) offering a greater diversity of pollinators and natural pest controllers (Aguilera et al. 2020); ii) providing complementary or supplementary resources to forest-dependent pollinators and natural pest controllers (e.g., nesting areas and secondary food resources) (Alignier et al., 2019; Aguilera et al. 2020); and by iii) increasing landscape connectivity (Martensen et al., 2012; Ries et al., 2014), which may also result in a higher diversity and spillover of pollinators and natural pest controllers in coffee plantations. Finally, higher landscape heterogeneity may hinder pest movement and thus reduce pests abundance (Bosem-Baillod et al., 2017). However, contrary to the positive effects found for the control of *CBB presence* and for *fruit set from pollination and CLM control*, higher edge diversity resulted in a disservice to *CBB infestation*, although this effect is weak. As ant species involved in controlling CBB colonisation may not be the same as the ones regulating CBB infestation levels (Moris and Perfecto, 2016; Prata-Gonçalves, 2016; Aristizábal and Metzger, 2019), it is, therefore, possible that the positive effects of edge diversity on the control of CBB presence via higher species richness may not reflect in higher regulation of CBB infestation. Finally, as the efficiency in removing pests varies among ant species (Way and Khoo, 1992), an increase in edge diversity may indirectly be altering the diversity species that are more efficient pest controllers once CBB is present.

The effect of edge diversity on service provision was consistently local, despite the direction of the effect. This small ‘scale of effect’ suggests that processes associated with the local flow of species, such as species spillover at the edges of the coffee fields, are key to the provision of both services. Our results add to previous findings which highlighted the importance of species spillover to pollination and pest control provision (Boesing et al. 2018b; Aristizábal and Metzger, 2019; Gonzalez-Chaves et al., 2020), by showing that other types of land use besides forest patches can also shape service provision by determining access to supply areas through local species flow. Our study brings new evidence on the importance of considering different land uses when assessing the local flows of pollination and pest control. Furthermore, as different land uses have different degrees of usability to the species due to their structural characteristics and resource availability (Hohlenwerger et al., 2022; Travassos-Britto et al. 2022), we suggest incorporating the effect of the degree of matrix usability on service-providers species and on service provision itself in future studies.

Challenges and implications for landscape management

One of the main challenges when planning multiple service provisions is avoiding disservices and taking advantage of the potential synergies among services (Martin et al., 2013; Garibaldi et al., 2018; Martínez-Salinas et al., 2022). This is particularly important when considering the provision of natural pest control, for which we had both services and disservices. Deservices seem to be all linked to antagonist interactions between different pest controllers (e.g., birds and ants). As the community of species in the landscape shifts, so do species interactions (Moreira et al., 2015; Librán-Embid et al., 2021). Landscape structure effects on the diversity of species that contribute to pest control, such as higher abundance and richness of birds in highly forested landscapes (Boesing et al 2018a), could also be shaping intraguild predation, and ultimately altering predatory pressures on pests. Indeed, changes in birds and bats' abundance have been reported to have an effect on the abundance of predatory arthropods including ants (Karp and Daily, 2014; Mass et al 2013), as well as intraguild predation having a negative effect on pest control (Martin et al 2013). Therefore, we suggest that these distinct contributions of birds, bats and ants to the provision of pest control can be a product of the complex trophic interactions between pest controllers and their common prey, and thus must be incorporated in landscape management practices that focus on enhancing biological pest control.

Our results also present evidence that supports the pressing need to integrate multiple scales when assessing several ecosystem services provision in working landscapes (Spake et al., 2019; Metzger et al., 2021). Apart from *edge diversity*, the ‘scale of effects’ of all other scale-dependent variables (*forest cover, coffee cover and forest-coffee edge density*) varied across services (Table 1). Specifically, from the management perspective, these results present opportunities to combine within-farm and landscape-level management actions (Tscharntke et al., 2005; Garibaldi et al 2018). At smaller scales, farmers may manage the areas around the cultivation plots seeking to increase the proximity to forest edge, forest-coffee edge density and edge diversity. However, at broader-scales, landscape management actions should focus on reaching the amount of coverage needed to avoid disservices and stimulate service provision (González-Chaves et al 2022). Such management actions may benefit from legislation and incentive programs on native forest restoration that combine both local and regional targets. Those benefits may be obtained through environmental schemes such as federal legislations like the Brazilian environmental legislation which obliges landowners to maintain a determined amount of native vegetation within their properties (Metzger et al. 2019). Similarly, those benefits may also be obtained through economic incentives like payment for ecosystem services that focus on promoting or ensuring long-term service provision through native vegetation protection or regeneration (Ruggiero et al., 2019). Such management schemes may thus ensure service provision by promoting native vegetation conservation while still allowing landowners to better manage the arrangement of native vegetation patches and crop plantations to optimize flow-related landscape attributes.

5. Conclusion:

We present novel evidence on how landscape structural attributes linked to the supply, demand and flow of ecosystem services shape the provision of pollination and pest control in coffee plantations. Our work adds to the current literature on the interacting effects of services provision by showing that landscape structure plays an essential role in promoting multiple service provision, and thus should be considered in ecosystem service assessments focused on enhancing synergies and avoiding trade-offs. Furthermore, our results highlight the importance of local edge diversity as the main common driver of pollination and pest control provision, reinforcing the relevance of local flow and landscape heterogeneity to ensure service provision. Finally, we show that management challenges such as the complex relationships for pest control service and disservice provision, as well as the wide range of ‘scale of effects’ of the relationships between landscape structure and pollination and pest control should be taken into account when planning multiple service provision. Our results suggest maintaining intermediate levels of landscape forest cover (~40%) while controlling for local forest cover (up to 20%), as well as maintaining less than 40% of local coffee cover to ensure that demand does not surpass supply. Moreover coffee fields and other anthropogenic matrices (e.g., pastures and eucalyptus) should be arranged in a way to increase forest-coffee edge density and the diversity of land uses in the surrounding coffee fields. We then suggest that combining local and landscape management strategies to protect and restore native vegetation at multiple scales whilst allowing for different crop and forest configurations could benefit multiple service provision while avoiding disservices.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References:

Aguilera, G., Roslin, T., Miller, K., Tamburini, G., Birkhofer, K., Caballero-Lopez, B., ... & Bommarco, R. (2020). Crop diversity benefits carabid and pollinator communities in landscapes with semi-natural habitats. *Journal of Applied Ecology*, *57*(11), 2170-2179. https://doi.org/10.1111/1365-2664.13712

Alignier, A., Solé-Senan, X. O., Robleño, I., Baraibar, B., Fahrig, L., Giralt, D., ... & Batáry, P. (2020). Configurational crop heterogeneity increases within-field plant diversity. *Journal of Applied Ecology*, *57*(4), 654-663. https://doi.org/10.1111/1365-2664.13585

Aristizabal, N., & Metzger, J. P. (2019). Landscape structure regulates pest control provided by ants in sun coffee farms. *Journal of Applied Ecology*, *56*(1), 21-30. https://doi.org/10.1111/1365-2664.13283

Avelino, J., Romero-Gurdi´an, A., Cruz-Cuellar, H.F., Declerck, F.A. (2012). Landscape context and scale differentially impact coffee leaf rust, coffee berry borer, and coffee root-knot nematodes. Ecological applications 22 (2), 584–596. https://doi.org/10.1890/11-0869.1

Barton, K., & Barton, M. K. (2015). Package 'mumin'. Version, 1(18), 439.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Grothendieck, G., Eigen, C., Rcpp, L. (2015). Package 'lme4'. Convergence 12.

Beasley, E. M., Aristizábal, N., Bueno, E., & White, E. R. (2020). The spore of the beans: Spatially explicit models predict coffee rust spread in fragmented landscapes. *bioRxiv*. https://doi.org/10.1101/2020.10.16.343194

Boesing, A. L., Nichols, E., & Metzger, J. P. (2018a). Biodiversity extinction thresholds are modulated by matrix type. *Ecography*, *41*(9), 1520-1533.

Boesing, A.L., Nichols, E., Metzger, J.P. (2018b). Land use type, forest cover and forest edges modulate avian cross-habitat spillover. *Journal of Applied Ecology* 55, 1252–1264. https://doi.org/10.1111/1365-2664.13032.

Bolker, B. M., Gardner, B., Maunder, M., Berg, C. W., Brooks, M., Comita, L. et al (2013). Strategies for fitting nonlinear ecological models in R, AD M odel B uilder, and BUGS. *Methods in Ecology and Evolution*, 4(6), 501-512. https://doi.org/10.1111/2041-210X.12044

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, 28(4), 230–238. https://doi.org/10.1016/j.tree.2012.10.012

Bosem-Baillod, A., Tscharntke, T., Clough, Y., & Batáry, P. (2017). Landscape-scale interactions of spatial and temporal cropland heterogeneity drive biological control of cereal aphids. *Journal of Applied Ecology*, *54*(6), 1804-1813. https://doi.org/10.1111/1365-2664.12910

Brown, J. S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary ecology research*, *1*(1), 49-71.

Brudvig, L.A., Damschen, E.I., Tewksbury, J.J., Haddad, N.M., Levey, D.J., (2009). Landscape connectivity promotes plant biodiversity spillover into non-target habitats. PNAS 106, 9328–9332. https://doi.org/10.1073/pnas.0809658106

Carlucci, M. B., Marcilio-Silva, V., Torezan, J. M. (2021). The southern Atlantic Forest: use, degradation, and perspectives for conservation. In The Atlantic Forest (pp. 91-111). Springer, Cham. DOI: 10.1007/978-3-030-55322-7_56

Chain-Guadarrama, A., Martínez-Salinas, A., Aristizábal, N., & Ricketts, T. H. (2019). Ecosystem services by birds and bees to coffee in a changing climate: A review of coffee berry borer control and pollination. *Agriculture, Ecosystems & Environment*, 280, 53-67. https://doi.org/10.1016/j.agee.2019.04.011

Conab (2018). Levantamento da companhia nacional de abastecimento de café. http://www.conab.gov.br/OlalaCMS/uploads/arquivos

Dainese, M., Martin, E. A., Aizen, M. A., Albrecht, M., Bartomeus, I., Bommarco, R.et al (2019). A global synthesis reveals biodiversity-mediated benefits for crop production. *Science advances*, *5*(10), eaax0121. DOI: 10.1126/sciadv.aax0121

Dias FP, Souza CAS (2015) Caracterização de progênies do cafeeiro (Coffea arabica L.) selecionadas em Minas Gerais: II-caracteres relacionados à produção. Ceres 52(299).

FAO. (2019). Top 20 Commodities, Export Value by country. http://www.fao.org/faostat/en/#rankings/major_commodities_exports.

Fox, J., Friendly, G. G., Graves, S., Heiberger, R., Monette, G., Nilsson, H. et al (2007). The car package. R Foundation for Statistical Computing, 1109.

Gagic, V., Marcora, A., & Howie, L. (2019). Additive and interactive effects of pollination and biological pest control on crop yield. *Journal of Applied Ecology*, 56(11), 2528-2535. https://doi.org/10.1111/1365-2664.13482

Gámez-Virués, S., Perović, D. J., Gossner, M. M., Börschig, C., Blüthgen, N., De Jong, H., ... & Westphal, C. (2015). Landscape simplification filters species traits and drives biotic homogenization. *Nature communications*, *6*(1), 1-8. DOI: 10.1038/ncomms9568

Garibaldi, L. A., Andersson, G. K., Requier, F., Fijen, T. P., Hipólito, J., Kleijn, D. et al (2018). Complementarity and synergisms among ecosystem services supporting crop yield. *Global food security*, *17*, 38-47. https://doi.org/10.1016/j.gfs.2018.03.006

González-Chaves, A., Jaffé, R., Metzger, J. P., & de MP Kleinert, A. (2020). Forest proximity rather than local forest cover affects bee diversity and coffee pollination services. *Landscape Ecology*, 35(8), 1841-1855. https://doi.org/10.1007/s10980-020-01061-1

Harrison, X.A., (2015). A comparison of observation-level randomeffect and beta-binomial models for modelling overdispersion in binomial data in ecology & evolution. *PeerJ* 3, e1114. https://doi.org/10.7717/peerj.1114.

Hartig, F. (2020). DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.3, 3.

Hernández, L., & Laundré, J. W. (2005). Foraging in the 'landscape of fear'and its implications for habitat use and diet quality of elk Cervus elaphus and bison Bison bison. *Wildlife Biology*, *11*(3), 215-220. https://doi.org/10.2981/0909-6396(2005)11[215:FITLOF]2.0.CO;2

Hohlenwerger, C., Tambosi, L. R., & Metzger, J. P. (2022). Forest cover and proximity to forest affect predation by natural enemies in pasture and coffee plantations differently. Agriculture, Ecosystems & Environment, 333, 107958. https://doi.org/10.1016/j.agee.2022.107958

Huais, P. Y. (2018). multifit: an R function for multi-scale analysis in landscape ecology. *Landscape Ecology*, 33(7), 1023-1028.

Jackson, H. B., & Fahrig, L. (2015). Are ecologists conducting research at the optimal scale?. *Global Ecology and Biogeography*, *24*(1), 52-63. https://doi.org/10.1111/geb.12233

Joly, C.A., Metzger, J.P., Tabarelli, M. (2014). Experiences from the brazilian atlantic forest: ecological findings and conservation initiatives. *New Phytologist*. 204, 459–473. https://doi.org/10.1111/nph.12989

Karp DS and Daily GC (2014) Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95(4):1065–1074. https://doi.org/10.1890/13-1012.1

Karp, D.S., Chaplin-Kramer, R., Meehan, T.D., Martin, E.A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A.E., Martínez-Salinas, A., et al., (2018) Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences*, 201800042. https://doi.org/10.1073/pnas.1800042115.

Lacasella, F., Gratton, C., De Felici, S., Isaia, M., Zapparoli, M., Marta, S., & Sbordoni, V. (2015). Asymmetrical responses of forest and “beyond edge” arthropod communities across a forest–grassland ecotone. Biodiversity and Conservation, 24(3), 447-465. https://doi.org/10.1007/s10531-014-0825-0

Librán-Embid, F., De Coster, G., & Metzger, J. P. (2017). Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. *Landscape Ecology*, *32*(9), 1907-1920. https://doi.org/10.1007/s10980-017-0555-2

Librán‐Embid, F., Grass, I., Emer, C., Ganuza, C., & Tscharntke, T. (2021). A plant–pollinator metanetwork along a habitat fragmentation gradient. Ecology Letters, 24(12), 2700-2712. https://doi.org/10.1111/ele.13892

Maas B, Clough Y, Tscharntke T (2013) Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters* 16(12):1480–1487. https://doi.org/10.1111/ele.12194

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M. et al (2017). Package ‘glmmTMB’. R Package Version 0.2. 0.

Martensen, A.C., Ribeiro, M.C., Banks-leite, C., Prado, P.I., Metzger, J.P. (2012). Associations of forest cover, fragment area, and connectivity with neotropical understory bird species richness and abundance. Conserv. Biol. 26, 1100–1111. https://doi.org/10.1111/j.1523-1739.2012.01940.x

Martin, E. A., Reineking, B., Seo, B., & Steffan-Dewenter, I. (2013). Natural enemy interactions constrain pest control in complex agricultural landscapes. *Proceedings of the National Academy of Sciences*, 110, 5534–5539. https://doi.org/10.1073/pnas.1215725110

Martin, A. E. (2018). The spatial scale of a species’ response to the landscape context depends on which biological response you measure. *Current Landscape Ecology Reports*, *3*(1), 23-33. https://doi.org/10.1007/s40823-018-0030-z

Martínez-Salinas, A., Chain-Guadarrama, A., Aristizábal, N., Vilchez-Mendoza, S., Cerda, R., & Ricketts, T. H. (2022). Interacting pest control and pollination services in coffee systems. *Proceedings of the National Academy of Sciences*, *119*(15), e2119959119. https://doi.org/10.1073/pnas.2119959119

Medeiros, H.R., Martello, F., Almeida, E.A., Mengual, X., Harper, K.A., Grandinete, Y.C., Metzger, J.P., Righi, C.A., Ribeiro, M.C. (2019). Landscape structure shapes the diversity of beneficial insects in coffee producing landscapes. Biol. Cons. 238, 10819. https://doi.org/10.1016/j.biocon.2019.07.038

Meyer, S. T., Koch, C., & Weisser, W. W., 2015. Towards a standardized rapid ecosystem function assessment (REFA). Trends Ecol Evolut, 30(7), 390-397. https://doi.org/10.1016/j.tree.2015.04.006

Metzger, J. P., Bustamante, M. M., Ferreira, J., Fernandes, G. W., Librán-Embid, F., Pillar, V. D., ... & Overbeck, G. E. (2019). Why Brazil needs its legal reserves. *Perspectives in Ecology and Conservation*, *17*(3), 91-103. https://doi.org/10.1016/j.pecon.2019.07.002

Metzger, J. P., Villarreal-Rosas, J., Suárez-Castro, A. F., López-Cubillos, S., González-Chaves, A., Runting, R. K., ... & Rhodes, J. R. (2021). Considering landscape-level processes in ecosystem service assessments. *Science of The Total Environment*, *796*, 149028. https://doi.org/10.1016/j.scitotenv.2021.149028

Moreaux, C., Meireles, D. A., Sonne, J., Badano, E. I., Classen, A., González-Chaves, A. et al (2022). The value of biotic pollination and dense forest for fruit set of Arabica coffee: A global assessment. *Agriculture, Ecosystems & Environment*, *323*, 107680. https://doi.org/10.1016/j.agee.2021.107680

Moreira, E. F., Boscolo, D., & Viana, B. F. (2015). Spatial heterogeneity regulates plant-pollinator networks across multiple landscape scales. PloS one, 10(4), e0123628. https://doi.org/10.1371/journal.pone.0123628

Morris, J. R., & Perfecto, I. (2016). Testing the potential for ant predation of immature coffee berry borer (Hypothenemus hampei) life stages. Agriculture, Ecosystems & Environment, 233, 224-228.https://doi.org/10.1016/j.agee.2016.09.018

Muschler, R. (1997). Shade or sun for ecologically sustainable coffee production: a summary of environmental key factors.

Pierre LSR (2011) Níveis populacionais de Leucoptera coffeella (Lepidoptera: Lyonetiidae) e Hypothenemus hampei (Coleoptera: Scolytidae) e a ocorrência de seus parasitoides em sistemas de produção de café orgânico e convencional. PhD, Universidade de São Paulo. http://www.sbicafe.ufv.br:80/handle/123456789/9037

Pompeu, P., Costa, M., Fontes, M., Carvalho, L., Pereira, J., Pellicciottii, A.,Gomes, D., Cipriani, H., Martins, M. (2009). Classificação e apresentação dos parâmetros climáticos de poços de caldas-mg, in: III Congresso Latino Americano de Ecologia, São Lourenço-MG.

Power, A. G. (2010). Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical transactions of the royal society B: biological sciences*, *365*(1554), 2959-2971. https://doi.org/10.1098/rstb.2010.0143

Prata-Gonçalves, G., 2016, Influência da cobertura florestal sobre a composiç ão de espécies de formigas em agroecossistemas de café. Trabalho de Conclus ão de Curso (Graduação em Ciências Biológicas) – Universidade Federal de São Paulo – Campus Diadema.

Qiu, J., Queiroz, C., Bennett, E. M., Cord, A. F., Crouzat, E., Lavorel, S. et al (2021). Land-use intensity mediates ecosystem service tradeoffs across regional social-ecological systems. *Ecosystems and People*, *17*(1), 264-278.https://doi.org/10.1080/26395916.2021.1925743

R Development Core Team (2014). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. ISBN 3-900051-07-0.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M. (2009). The brazilian atlantic forest: How much is left, and how is the remaining forest distributed? implications for conservation. Biol Cons 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021.

Rosa, M. R., Brancalion, P. H., Crouzeilles, R., Tambosi, L. R., Piffer, P. R., Lenti, F. E., Hirota, M., Santiami, E., Metzger, J. P., 2021. Hidden destruction of older forests threatens Brazil's Atlantic Forest and challenges restoration programs. *Scientific Advancements*, 7(4), eabc4547.https://doi.org/10.1126/sciadv.abc4547

Ruggiero, P. G., Metzger, J. P., Tambosi, L. R., & Nichols, E. (2019). Payment for ecosystem services programs in the Brazilian Atlantic Forest: Effective but not enough. *Land use policy*, *82*, 283-291. https://doi.org/10.1016/j.landusepol.2018.11.054

Saturni, F. T., Jaffe, R., & Metzger, J. P. (2016). Landscape structure influences bee community and coffee pollination at different spatial scales. *Agriculture, Ecosystems & Environment*, *235*, 1-12. https://doi.org/10.1016/j.agee.2016.10.008

Spake, R., Bellamy, C., Graham, L. J., Watts, K., Wilson, T., Norton, L. R., ... & Eigenbrod, F. (2019). An analytical framework for spatially targeted management of natural capital. *Nature Sustainability*, *2*(2), 90-97. https://doi.org/10.1038/s41893-019-0223-4

Travassos-Britto, B., Hohlenwerger, C., Miranda, J., da Rocha, P.L.B. (2022). Quantity and quality of suitable matrices matter in reducing the negative effect of fragmentation on populations extinction risk. https://doi.org/10.1101/2020.08.10.244178

Tscharntke, T., Klein, A. M., Kruess, A., Steffan‐Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology letters*, *8*(8), 857-874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Turner, M. G., Donato, D. C., & Romme, W. H. (2013). Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. *Landscape ecology*, *28*(6), 1081-1097. https://doi.org/10.1007/s10980-012-9741-4

Vanbergen AJ (2013) Threats to an ecosystem service: pressures on pollinators. Front Ecol Environ 11:251–259. https://doi.org/10.1890/120126

Villard, M. A., & Metzger, J. P. (2014). Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, *51*(2), 309-318. https://doi.org/10.1111/1365-2664.12190

Way, M. J., & Khoo, K. C. (1992). Role of ants in pest management. *Annual review of Entomology*, *37*(1), 479-503.

Winqvist, C., Ahnström, J., & Bengtsson, J. (2012). Effects of organic farming on biodiversity and ecosystem services: taking landscape complexity into account. Annals of the New York Academy of Sciences, 1249(1), 191-203.

Zuur, A., Ieno, E., Walker, N., Saveliev, A., Smith, G. (2009). Mixed-effects models and extensions in ecology with R. Springer Science & Business Media.

Appendix: Supplementary Material

S1- Landscape metrics and Data analysis:

Table S1: Selection of the "scale of effect" of each landscape metric based on the Akaike Information Criterion corrected for small sample sizes (AICc). Showing the selected most significant scales (lowest AICc) for the effects of forest cover (FC), coffee cover (CC), edge diversity (ED) and forest-coffee edge density (FCED) considering several scales (30, 50, 100 up to 500 with 100 m intervals, 1000, 2000 and 3000 m).

Ecosystem Service	Landscape attributes	AICc	delta	weight
Pollination	FC_200 m	12010.1	0.00	0.82
	CC_1 km	12003.6	0.00	0.966
	ED_100 m	11996.5	0.00	0.914
	FCED_30 m	12010.5	0.00	0.785
Pest control by ants - Infestation	FC_50 m	1316.3	0.00	0.990
	CC_1 km	1315.8	0.00	0.606
	ED_30 m	1326.9	0.00	0.537
	FCED_1 km	1309.3	0.00	0.873
Pest control by ants - Presence	FC_30 m	649.3	0.00	0.240
	CC_1 km	648.5	0.00	0.249
	ED_200 m	648.7	0.00	0.258
	FCED_500 m	649.3	0.00	0.184
Pest control by ants - Damage	FC_2 km	13343.5	0.00	0.902
	CC_3 km	13351.2	0.00	0.991
	ED_200 m	13360.9	0.00	0.331
	FCED_300 m	13358.3	0.00	0.705
Pest control by birds and bats - Fruit set	FC_300 m	774.8	0.00	0.365
	CC_200 m	776.0	0.00	0.140
	ED_300 m	774.6	0.00	0.251

	FCED_300 m	769.2	0.00	0.729
Pest control by birds and bats - Leaf Loss	FC_100 m	1740.2	0.00	0.556
	CC_500 m	1742.8	0.00	0.255
	ED_1 km	1735.3	0.00	0.458
	FCED_1 km	1743.1	0.00	0.463

Table S2: Model average output showing the significant relationships between landscape attributes (forest cover (FC), coffee cover (CC), edge diversity (ED) and forest-coffee edge density (FCED) and pollination and pest control provision that form the final model for each service.

Ecosystem Service	Landscape attribute	Estimate	Std.Error	z value	P value
Pollination	CC_1 km	-0.106176	0.022108	3.798	1.6e-06
	ED_100 m	0.071022	0.022227	3.192	0.00141
	Dist	-0.076845	0.026099	2.942	0.00326
Pest control by ants - Infestation	ED_30 m	-0.23531	0.08511	2.754	0.00589
	FCED_1 km	-0.34190	0.07768	3.383	1.17e-05
Pest control by ants - Presence	CC_1 km	0.76623	0.29548	2.587	0.00967
	ED_200 m	0.63660	0.27981	2.270	0.02320
Pest control by ants - Damage	FC_2 km	-0.76141	0.17136	3.441	9.0e-06
Pest control by birds and bats - Fruit set	ED_300 m	-0.22441	0.10393	2.135	0.03278
	FCED_300 m	0.57065	0.20827	2.713	0.00666
Pest control by birds and bats - Leaf Loss	FC_100 m	-0.433534	0.087599	3.918	9.00e-07
	CC_500 m	0.443223	0.115784	3.806	0.000141
	FCED_1 km	-0.297711	0.102719	2.880	0.003973
	Dist	-0.322368	0.080823	3.962	7.45e-05

S2- Exclusion experiments:

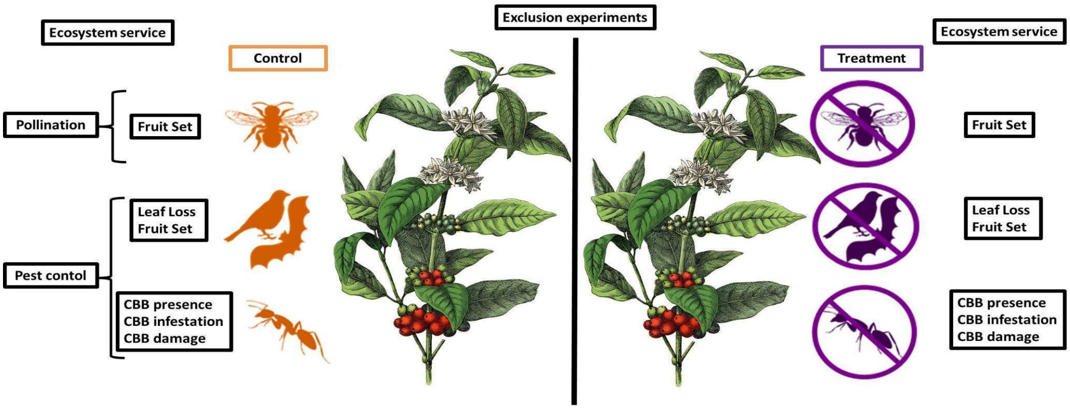

Figure S1: Simplified schematic representation of exclusion experiments for pollination and pest control and their respective indicators.

Pollination:

For the first data on pollination, 15 experimental sites each containing a pollination-exclusion experiment were placed in a coffee bush across nine landscapes. At each experiment, three randomly selected branches in which pollinators were excluded, were compared to another three randomly selected branches in which flowers were opened and accessible to pollinators, resulting in a total of 405 branches per treatment. For the second data on pollination, eight experimental sites each containing three coffee bushes with pollination-exclusion experiments were placed across three landscapes. At each experimental site, a total of 15 randomly selected coffee branches (five per coffee bush) in which pollinators were excluded, were compared to another 15 randomly selected coffee branches (five per coffee bush) in which flowers were opened and accessible to pollinators, resulting in 360 branches per treatment.

Coffee leaf miner control:

For CLM control by birds and bats, four experimental sites each containing two units of birds and bats-exclusion experiments were placed across six landscapes. At each unit, four coffee bushes in which birds and bats were excluded, were compared to another four adjacent coffee bushes that were accessible to all potential pest controllers. Each coffee bush had nine randomly marked branches with four marked leaves on each branch, resulting in 864 branches per treatment. For each of the marked branches, the number of remaining leaves in each coffee plant were counted every 30–45 days during the six peak months of CLM infestation (June-November). Also for six of the nine marked branches, the number of young coffee berries (early fruits, 4–6 weeks after main blossom) and ripped berries (harvestable fruits, 6–28 weeks after main blossom) were counted, resulting in 576 branches per treatment. To exclude birds and bats while still allowing arthropods to enter, a nylon monofilament mesh was used to cover each of the four coffee bushes that comprehended one of the two units of pest control-exclusion experiments. Care was taken to assure minimal spatial distance between experimental sites, variation in the surrounding local forest cover, and to control for coffee varieties (see Librán-Embid et al. 2017 for procedure detail).

Coffee berry borer control:

For CBB control by ants, three experimental sites each containing 10 coffee bushes with ant-exclusion experiments were placed across 10 landscapes right before the main flowering to ensure CBB absence (October 2014-June 2015). At each coffee bush, one randomly selected branch in which ants were excluded was compared to another randomly selected neighbouring branch which was accessible to ants, resulting in 300 branches per treatment. To ensure ants exclusion, Tree Tanglefoot Insect Barrier was spread along 10 cm of the branch after the seventh plant node starting from the branch tip, and ant-excluded branches were isolated from other branches that could potentially come into contact. A small dot of Tanglefoot was also placed on control branches to control for any effect of Tanglefoot on CBB. Maintenance of ant-excluded branches was done once a month (see Aristizábal and Metzger, 2019 for procedure details). For each branch, the number of berries produced and berries bored was counted and right before farmers' harvest time, all coffee berries in experimental branches were collected. Care was taken to ensure a similar number of flowers, height, and position to all experimental branches (see Aristizábal and Metzger for procedure details).

Discussão geral

Não há dúvidas que as sociedades dependem da provisão de diversos serviços ecossistêmicos, como os de produção de alimentos, limpeza da água e do ar, e do valor cultural e estético que a natureza tem para o ser humano (Constanza et al. 2014; IPBES 2019). Ainda, é sabido que muitos destes serviços que são fundamentais para o bem-estar humano atualmente se encontram em declínio ou sob pressão de extinção futura em função das alterações ambientais, como as transformações de áreas naturais em áreas agrícolas ou urbanas, das mudanças climáticas e da poluição (Kubiszewski et al. 2020). Dessa forma, para reduzir a degradação ambiental e gerir os recursos de modo a garantir a provisão longa e sustentável de serviços ecossistêmicos, é necessário entender não só como esses serviços ocorrem em paisagens antrópicas, mas também como mudanças nestas paisagens podem dificultar ou aumentar as provisões (Boesing et al. 2020). Dentro desse contexto, *essa tese assumiu como central a importância de se considerar o efeito do espaço nos três componentes da cadeia de provisão* (i.e., *oferta, demanda* e *fluxo*), e buscou avançar no conhecimento de *como atributos da paisagem afetam a provisão de diferentes serviços através de mudanças na quantidade e qualidade da oferta, demanda e do fluxo entre estes componentes*.

No primeiro capítulo da tese, nós mostramos que a contribuição de inimigos naturais para o *controle natural de pragas* depende de como esses organismos respondem aos diferentes tipos de matrizes antrópicas. Nossos resultados mostram que t*axas de predação por artrópodes são consistentemente maiores em matrizes de café, entretanto, a depender da escala espacial, essas taxas podem aumentar ou reduzir com a quantidade de cobertura florestal do entorno*. Em uma escala local, o aumento na cobertura florestal tende a reduzir a taxa de predação por artrópodes, entretanto, esse efeito é invertido em escalas mais amplas, com paisagens com maior cobertura florestal contribuindo para maiores taxas de predação. Já *a taxa de predação por aves é maior próxima à borda de fragmentos florestais e similar às taxas por artrópodes, em matrizes de café*. Por fim, se considerarmos toda a comunidade de inimigos naturais, ou seja, sem separar grupos específicos, as taxas de predação são maiores em matrizes de café próximas à borda dos fragmentos florestais e em paisagens com alta cobertura florestal. Assim, dada à clara importância do tipo da matriz para a provisão potencial do serviço de controle de pragas, nós recomendamos que *o manejo de paisagens foque não apenas em aumentar a quantidade e proximidade das florestas em relação às matrizes na paisagem, mas também reduzir o contraste estrutural entre o habitat nativo e a matriz*. Para isso, nós propomos uma série de ações no nível das fazendas que podem levar a uma maior heterogeneidade e permeabilidade da matriz e, portanto, beneficiar a provisão do serviço ecossistêmico de controle de pragas.

No segundo capítulo, nós desenvolvemos uma abordagem de redes para avaliar como a estrutura da paisagem afeta a provisão do *serviço de polinização de café* através dos seus efeitos no número e quantidade de conexões (i.e., fluxo de polinização) entre áreas de oferta e demanda. Nós mostramos que *ao modelar o serviço de polinização como uma rede espacialmente explícita de interações entre oferta e demanda, é possível identificar como a paisagem afeta a provisão através de efeitos tanto estruturais como funcionais*. Por exemplo, nossos resultados mostram que a produção de café é afetada pela competição entre áreas de demanda por áreas de oferta. Ou seja, *características do arranjo espacial* (e.g., grau de interpolação entre áreas de oferta e demanda) *e da capacidade de ofertar recursos* (e.g., quantidade limite de recurso ofertado por uma mesma área de oferta) *afetam conjuntamente o serviço de polinização*. Diante desses e dos demais resultados deste capítulo, nós discutimos que a abordagem de redes permitiu que nós identificássemos quais características da paisagem são mais relevantes para produção de café, considerando em particular o efeito desses atributos nos fluxos que ligam a oferta à demanda. Nós discutimos a importância de se identificar esses padrões para *melhor desenhar estratégias de manejo que permitam aumentar e intensificar os fluxos de polinização e, portanto, as conexões entre oferta e demanda, aumentando assim a provisão do serviço e a produção do café.*.

No terceiro capítulo, nós buscamos avançar no conhecimento de como atributos da paisagem associados à oferta, demanda e fluxo podem atuar como motores comuns do *serviço de polinização e controle de pragas em cafezais*. Esse estudo surge da necessidade de se criar paisagens multifuncionais que possam atender à alta demanda por produção, reduzindo os níveis de degradação ambiental e, portanto, promover a provisão sinérgica de serviços de forma sustentável ao longo do tempo. Nossos resultados mostram que *os serviços de controle de pragas e de polinização são diferentemente afetados pela estrutura da paisagem, e que esses efeitos se dão em escalas espaciais distintas*. Apesar disso, nossos resultados também mostram que *a diversidade de tipo de matriz ao redor das áreas de café age como um motor comum a ambos os serviços ecossistêmicos*. Ainda, esse efeito ocorre predominantemente em escalas locais (até 300 m da área de cultivo), o que reforça a *importância de processos ecológicos associados ao fluxo local de espécies* para a provisão da polinização e controle de pragas. Por fim, nossos resultados sobre a complexidade da provisão do controle de pragas sugerem que *o desenho de paisagens multifuncionais deve considerar não só a provisão de serviços, como a de desserviços*.

No conjunto dos três capítulos, fica claro que é necessário considerar os efeitos da estrutura da paisagem para promover sinergias entre os serviços de polinização e controle de pragas, e que estes estudos requerem análises espaciais em múltiplas escalas. Enquanto o nosso primeiro capítulo destaca a importância do maior grau de permeabilidade da matriz para o serviço de controle de pragas, o segundo capítulo adiciona a necessidade de se considerar como a matriz (neste contexto, a demanda) está distribuída na paisagem em relação aos fragmentos florestais (a oferta). Ainda, este capítulo realça a importância de manter vários e grandes fragmentos florestais próximos às áreas de demanda, para aumentar o fluxo e, portanto, a provisão do serviço de polinização. Estes resultados reforçam a importância de sistemas de manejo que combinem o aumento do contato matriz-floresta e mantenham níveis médios (30-40%) de coberturas florestais na paisagem (González-Chaves et al. 2022) como uma via potencial para reduzir os efeitos negativos de competição pela oferta. Ainda, o nosso terceiro capítulo avança na discussão sobre os efeitos da oferta na provisão de múltiplos serviços ecossistêmicos mostrando que outros tipos de uso da terra também podem atuar como áreas de oferta para uma demanda focal (aqui, as plantações de café), provavelmente devido ao seu potencial em oferecer recursos complementares àqueles presentes em fragmentos florestais (Prevedello and Vieira, 2010; Blitzer et al., 2012). Por fim, nossos trabalhos apontam para a necessidade do manejo em múltiplas escalas como uma via de gerir a paisagem de modo a evitar demandas conflitantes entre os serviços de polinização e controle de pragas. Nós propomos, então, que essas estratégias de manejo ocorram tanto em escalas locais, no nível das fazendas, buscando diversificar a produção e o arranjo espacial das matrizes agrícolas, como em escalas regionais, através de incentivos e regulamentações governamentais para a gestão dos recursos naturais em propriedades privadas (Metzger et al. 2019; González-Chaves et al. 2022).

É importante destacar que o desenvolvimento destes três capítulos muito se beneficiou da produção paralela à tese de três abordagens espaciais de avaliações de serviços ecossistêmicos. O capítulo um permitiu que nós expandíssemos o entendimento de como características da composição das matrizes antrópicas, que até recentemente costumavam ser ignoradas no manejo de paisagens agrícolas, modulam a provisão potencial do serviço de controle de pragas. Esse capítulo dialoga muito proximamente, portanto, com a abordagem desenvolvida em *Metzger et al (2021a)*, a qual ressalta a necessidade de se considerar o efeito de processos no nível da paisagem na provisão de serviços. Esta mesma abordagem foi também fundamental para o desenvolvimento do capítulo dois, visto que ela permitiu com que nós tivéssemos clareza tanto: i) da importância de se considerar os efeitos da estrutura da paisagem; ii) da necessidade de considerar estes efeitos sobre a oferta, demanda e fluxo conjuntamente; quanto iii) do potencial da abordagem de redes socioecológicas para a avaliação espacial da provisão de serviços ecossistêmicos. Esse capítulo também se beneficiou muito da abordagem produzida em *Metzger et al. (2021b)*, visto que ela elucida a importância de se identificar corretamente a oferta, demanda, e fluxo de um serviço para que haja o manejo adequado do mesmo. Ainda, a abordagem proposta em *Metzger et al. (2021b)* permite entender como diferentes estratégias de gestão da oferta e da demanda atuam aumentando ou reduzindo o fluxo que sai e chega até esses componentes. Esse entendimento foi particularmente útil para que nós, frente aos resultados do capítulo dois, pudéssemos propor estratégias de manejo que promovessem a provisão do serviço de polinização em paisagens cafeeiras.

Por fim, o conhecimento produzido em *Boesing et al. (2020)* serviu de base teórica e de motivador para o desenvolvimento do capítulo três. Embora haja evidências na literatura dos efeitos da paisagem sobre a provisão dos serviços de polinização e controle de pragas separadamente (Saturni et al., 2016; Librán-Embid et al., 2017; González-Chaves et al., 2020), é preciso considerar esses serviços conjuntamente para que estratégias de manejo permitam estimular sinergias e evitar demandas conflitantes (Chain-Guadarrama et al. 2022). Ainda, somente ao considerar paisagens multifuncionais, ou seja, paisagens que permitem a provisão de múltiplos serviços, é que podemos corretamente acessar o potencial destas paisagens em ofertar esses serviços no longo prazo. Assim, a abordagem proposta em *Boesing et al. (2020)* elucida as implicações dos nossos resultados frente a necessidade de evitar padrões espaço-temporais de redução ou extinção da provisão de serviços ecossistêmicos.

O conhecimento produzido nesta tese e ao longo desse período permitiram, assim, avançar na compreensão de como o espaço modula as relações entre a oferta, demanda e fluxo de múltiplos serviços ecossistêmicos. Mais especificamente, nossos trabalhos apontam para a necessidade de considerar e caracterizar corretamente esses componentes da cadeia de provisão ao longo do espaço e tempo. Nesse contexto, nós mostramos a importância e potencial da diversidade de tipos de uso da terra para provisão de múltiplos serviços ecossistêmicos ligados à produção de café. Por fim, nós evidenciamos como diferentes estratégias de gestão da demanda e da oferta podem afetar a provisão dos serviços através do efeito da paisagem sobre os fluxos. Nós esperamos que esses trabalhos avancem o conhecimento científico da área, bem como fortaleçam propostas de manejo da paisagem que favoreçam tanto a sociedade como a biodiversidade.

Referências:

Boesing, A. L., Prist, P. R., Barreto, J., Hohlenwerger, C., Maron, M., Rhodes, J. R., ... & Metzger, J. P. (2020). Ecosystem services at risk: integrating spatiotemporal dynamics of supply and demand to promote long-term provision. One Earth, 3(6), 704-713.

Blitzer, E. J., Dormann, C. F., Holzschuh, A., Klein, A. M., Rand, T. A., & Tscharntke, T. (2012). Spillover of functionally important organisms between managed and natural habitats. Agriculture, Ecosystems & Environment, 146(1), 34-43.

Costanza, R., De Groot, R., Sutton, P., Van der Ploeg, S., Anderson, S. J., Kubiszewski, I., ... & Turner, R. K. (2014). Changes in the global value of ecosystem services. Global environmental change, 26, 152-158.

González-Chaves, A., Jaffé, R., Metzger, J. P., & de MP Kleinert, A. (2020). Forest proximity rather than local forest cover affects bee diversity and coffee pollination services. Landscape Ecology, 35(8), 1841-1855.

González-Chaves, A., Carvalheiro, L. G., Garibaldi, L. A., & Metzger, J. P. (2022). Positive forest cover effects on coffee yields are consistent across regions. Journal of Applied Ecology, 59(1), 330-341.

Chain-Guadarrama, A., Martínez-Salinas, A., Aristizábal, N., & Ricketts, T. H. (2019). Ecosystem services by birds and bees to coffee in a changing climate: A review of coffee berry borer control and pollination. Agriculture, Ecosystems & Environment, 280, 53-67.

IPBES. (2019). The global assessment report on summury on policymakers of the IPBES global asessment report on biodiversity and ecosystem services. (and C. N. Z. S. Díaz, J. Settele, E. S. Brondízio E.S., H. T. Ngo, M. Guèze, J. Agard, A. Arneth, P. Balvanera, K. A. Brauman, S. H. M. Butchart, K. M. A. Chan, L. A. Garibaldi, K. Ichii, J. Liu, S. M. Subramanian, G. F. Midgley, P. Miloslavich, Z. Molnár, D. Obura, A, Ed.). Bonn, Germany.

Kubiszewski, I., Costanza, R., Anderson, S., & Sutton, P. (2020). The future value of ecosystem services: Global scenarios and national implications. In Environmental Assessments. Edward Elgar Publishing.

Librán-Embid, F., De Coster, G., & Metzger, J. P. (2017). Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. Landscape Ecology, 32(9), 1907-1920.

Metzger, J. P., Bustamante, M. M., Ferreira, J., Fernandes, G. W., Librán-Embid, F., Pillar, V. D., ... & Overbeck, G. E. (2019). Why Brazil needs its legal reserves. Perspectives in Ecology and Conservation, 17(3), 91-103.

Metzger, J. P., Villarreal-Rosas, J., Suárez-Castro, A. F., López-Cubillos, S., González-Chaves, A., Runting, R. K., ... & Rhodes, J. R. (2021a). Considering landscape-level processes in ecosystem service assessments. Science of The Total Environment, 796, 149028.

Metzger, J. P., Fidelman, P., Sattler, C., Schroter, B., Maron, M., Eigenbrod, F., ... & Rhodes, J. R. (2021b). Connecting governance interventions to ecosystem services provision: A social-ecological network approach. People and Nature.

Prevedello, J. A., & Vieira, M. V. (2010). Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation, 19(5), 1205-1223.

Saturni, F. T., Jaffe, R., & Metzger, J. P. (2016). Landscape structure influences bee community and coffee pollination at different spatial scales. Agriculture, Ecosystems & Environment, 235, 1-12.