ABELHAS EUGLOSSINI (HYMENOPTERA: APIDAE) COMO INDICADORES ECOLÓGICOS DE ÁREAS EM RESTAURAÇÃO NA MATA ATLÂNTICA

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UNIVERSIDADE ESTADUAL DO NORTE FLUMINENSE – UENF

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Tese apresentada ao Centro de Biociências e Biotecnologia da Universidade Estadual do Norte Fluminense Darcy Ribeiro, como parte das exigências para obtenção do título de Doutor em Ecologia e Recursos Naturais.

Orientadora: Profa. Dra. Maria Cristina Gaglianone
Coorientador: Prof. Dr. Milton Cezar Ribeiro (UNESP)

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Orientadora

“Não voltariam nunca mais, resistiriam à saudade que ataca os sertanejos na mata. Então eles eram bois para morrer tristes por falta de espinhos? Fixarse-iam muito longe, adotariam costumes diferentes.”

Vidas Secas, Graciliano Ramos

Dedico este trabalho a todos que mantém o desejo vivo de sonhar. Aos que, através de janelas, enxergam o brilho de um mundo inteiro de possibilidades. Aos que não temem quebrar ciclos através dos sonhos. Aos meus, que vieram e virão para criar espaços em posições historicamente negadas e que me possibilitaram escrever esta dedicatória.

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RESUMO

As mudanças na estrutura da paisagem, dirigidas pela fragmentação dos habitats, têm afetado as respostas ecológicas da biodiversidade e o funcionamento dos ecossistemas. Além da conservação dos remanescentes de habitat em paisagens modificadas, estratégias como a restauração florestal são fundamentais para mitigar os efeitos das alterações na paisagem, assim como para o reestabelecimento das espécies e suas funções ecológicas. Nesse sentido, uma importante estratégia para avaliar o sucesso de projetos de restauração é a utilização de indicadores ecológicos, como as abelhas, insetos essenciais para a manutenção dos ecossistemas através da polinização. Entre esses organismos, as abelhas Euglossini representam importantes modelos de estudo, uma vez que são polinizadores de uma alta diversidade de plantas, apresentam dependência florestal e são sensíveis às perturbações ambientais. Contudo, apesar de muitos estudos verificarem os efeitos negativos das mudanças na paisagem sobre comunidades de Euglossini, poucos avaliaram o reestabelecimento dessas abelhas em habitats restaurados, e determinaram os fatores que influenciam nesse processo. Este estudo avaliou a recuperação de comunidades de abelhas (Hymenoptera: Apoidea) na escala da paisagem em diferentes ecossistemas globalmente (Capítulo I), a influência de fatores locais (*sd*NDVI) e da paisagem (cobertura (%) de floresta e heterogeneidade composicional) sobre a alfa diversidade de comunidades de euglossine em habitats restaurados ativamente, passivamente (regeneração natural), e floresta conservada (Capítulo II), e o efeito de variações na composição da paisagem sobre a composição de espécies de euglossine entre pares de habitats na Mata Atlântica (Capítulo III). Machos de Euglossini foram amostrados em 12 paisagens, com três pontos de amostragens em cada (floresta, restauração ativa e regeneração natural), totalizando 36 pontos de amostragem. Foram amostrados 8,818 machos de euglossine, de quatro gêneros e 21 espécies. Os resultados indicaram que a recuperação de comunidades de abelhas é influenciada por fatores locais e da paisagem (Capítulo I), por variações na vegetação dos habitats restaurados (Capítulo II), e por mudanças na composição da paisagem (Capítulo III). As comunidades de euglossine não diferiram entre habitats restaurados e conservados, indicando o sucesso de estratégias de

restauração ativa e regeneração natural para recuperar esses polinizadores (Capítulo II, Capítulo III). Uma maior variação de NDVI em habitats restaurados afetou negativamente a alfa diversidade de euglossine (Capítulo II), enquanto perturbações na paisagem afetaram negativamente a beta diversidade dessas abelhas (Capítulo III). Este estudo indica a importância da restauração, independente da estratégia, para recuperar a alfa e beta diversidade de comunidades de euglossine na Mata Atlântica. A manutenção e conservação da cobertura de habitat na paisagem é essencial para as dinâmicas ecológicas entre habitats conservados e restaurados.

Palavras-chave: Ecologia da Restauração, Ecologia de Paisagens, Abelhas Euglossini, Mata Atlântica, Indicadores ecológicos

ABSTRACT

Landscape changes, driven by habitat fragmentation, have negatively affected biodiversity and ecosystem functioning. Besides habitat conservation in modified landscapes, forest restoration is essential to mitigate the effects of landscape disturbances and recovery of species and their ecological functions. Restoration outcomes should be evaluated with ecological indicators such as bees, considering their essential role in ecosystem functioning because of pollination. Euglossini bees are important ecological models, since they pollinate a high plant diversity, show forest dependence, and are sensitive to environmental disturbances. Although many studies have evaluated the effects of landscape changes on Euglossini communities, few have assessed the reestablishment of these bees in restored habitats and the factors driving this process. This study evaluated the recovery of bee communities (Hymenoptera: Apoidea) at the landscape scale in different ecosystems globally (Chapter I), the influence of local (sdNDVI) and landscape (forest cover (%) and compositional heterogeneity) attributes on the alpha diversity of euglossine communities in actively restored, passively restored (natural regeneration), and conserved forest habitats (Chapter II), and the effect of variations in landscape composition on euglossine species composition among habitats pairwise in the Atlantic Forest (Chapter III). Euglossine males were sampled in 12 landscapes, with three sampling points in each (forest, active restoration, and natural regeneration), totaling 36 sampling points. We sampled 8,818 euglossine males, from four genera and 21 species. The recovery of bee communities is influenced by local and landscape attributes (Chapter I), vegetation variations of restored habitats (Chapter II), and landscape changes (Chapter III). Euglossine communities did not differ among restored and conserved habitats, indicating the success of active restoration and natural regeneration strategies in recovering these pollinators in the Atlantic Forest (Chapter II, Chapter III). A higher NDVI variation in restored habitats negatively affected euglossine alpha diversity (Chapter II), while landscape changes negatively affected the euglossine beta diversity (Chapter III). This study highlights the role of forest restoration, regardless of the strategy, in recovering the alpha and beta diversity of euglossine communities. The conservation of

forest cover in the landscape is essential for maintaining ecological dynamics between conserved and restored habitats.

Keywords: Restoration Ecology, Landscape Ecology, Euglossini bees, Atlantic Forest, Ecological indicators

APRESENTAÇÃO DA TESE

A restauração em larga escala de ecossistemas perturbados e destruídos é essencial para mitigar os efeitos negativos da emergência climática e a extinção de espécies. Além disso, restaurar a biodiversidade é crucial para manutenção de serviços ecossistêmicos necessário para populações humanas, como a polinização. Avaliar o sucesso de diferentes estratégias de restauração em recuperar a biodiversidade é uma etapa necessária para projetos e iniciativas de restauração, e deve envolver o uso de indicadores ecológicos que influenciam no funcionamento dos ecossistemas, como as abelhas. Neste estudo, avaliou-se o contexto da restauração de comunidades de abelhas na escala da paisagem em um contexto global através de uma revisão sistemática (Capítulo I). Além disso, comunidades de abelhas da tribo Euglossini foram utilizadas como indicadores ecológicos do sucesso de estratégias de restauração ativa e regeneração natural na Mata Atlântica (Capítulo II e III). Os dados apresentados nessa Tese são uma importante contribuição para a Agenda 2030 da Organização das Nações Unidas, especialmente considerando a Década da Restauração Ecológica. Os resultados encontrados podem embasar o manejo de habitats restaurados focados na recuperação de comunidades de abelhas, e consequentemente, do serviço de polinização.

Esta Tese está organizada com a seguinte estrutura:

- **Introdução Geral:** Teoria sobre Ecologia de Paisagens e Ecologia da Restauração, restauração de comunidade de abelhas na escala da paisagem, e efeitos de mudanças no uso do solo sobre as abelhas Euglossini, grupo foco deste estudo;
- **Capítulo I:** Revisão sistemática sobre a restauração de comunidades de abelhas na escala da paisagem em um contexto global;
- **Capítulo II:** Análise do efeito da composição da paisagem e *sd*NDVI sobre a alfa diversidade de comunidades de abelhas Euglossini em habitats restaurados ativamente, regenerados naturalmente, e floresta conservada;

- **Capítulo III:** Análise do efeito da composição da paisagem e do tipo de estratégia de restauração sobre a beta diversidade de comunidades de abelhas Euglossini;
- **Discussão Geral:** Síntese dos resultados obtidos e recomendações sobre a restauração de comunidades de abelhas na escala da paisagem.

O Capítulo I está no formato de artigo publicado no jornal *Apidologie*, com coautoria do coorientador e orientadora desta Tese.

O Capítulo II está no formato de artigo, sob revisão no jornal *Perspective in Ecology and Conservation*, com coautoria do Dr. Taylor Ricketts (análises estatísticas, supervisão, revisão do texto), Dra. Juliana S. S. Santos (análises de NDVI, revisão do texto), Dr. Wilson Frantine-Silva (amostragem, análises estatísticas, revisão do texto), além do coorientador e orientadora desta Tese.

O Capítulo III está em formato de artigo, em preparação para submissão na revista *Biological Conservation*.

Cada capítulo está formatado conforme as normas específicas de cada revista.

1. INTRODUÇÃO GERAL

1.2 Estrutura da paisagem e fragmentação dos habitats

Com o surgimento da Ecologia de Paisagens, disciplina caracteristicamente multidisciplinar proposta pelo biogeógrafo alemão Carl Troll em 1939, ecólogos têm buscado quantificar os atributos espaciais distribuídos no espaço-tempo, e a influência destes fatores sobre as respostas ecológicas da biodiversidade (Turner, 1989; Turner & Gardner, 2015). Uma paisagem pode ser definida como uma área heterogênea para ao menos um fator de interesse (Turner, 2005). Essa heterogeneidade, entendida como os diferentes tipos de componentes distribuídos em diferentes escalas espaço-temporais (Li & Hu, 2005; Turner & Gardner, 2015), pode ser avaliada através de dois elementos que caracterizam a estrutura de uma paisagem: composição e configuração. Enquanto o primeiro refere-se principalmente aos diferentes tipos de manchas que compõe uma paisagem, o segundo reflete o padrão de arranjo desses componentes no contexto espacial (McGarigal & Marks, 1995; Fahrig et al. 2011; Turner & Gardner, 2015).

Atividades antrópicas têm afetado a composição e a configuração da paisagem. Essas alterações são dirigidas principalmente pela fragmentação dos habitats (Fischer & Lindenmayer, 2007; Haddad et al. 2015). Esse processo transforma a estrutura da paisagem ao criar ou extinguir manchas, altera parâmetros como forma, perímetro, tamanho e isolamento das manchas, que por conseguinte, resulta em mudanças em parâmetros microclimáticos associados às novas configurações dos remanescentes e efeito de borda (Fahrig, 2003; Neel et al. 2004; Haddad et al. 2015). Com isso, a fragmentação é uma das principais causas da perda e degradação dos habitats (Fahrig, 2003; Fischer & Lindenmayer, 2007).

Distinguir a fragmentação *per se* da perda de habitat é um desafio para ecólogos, que constantemente confundem esses dois processos (Fahrig, 2003; 2017; Riva et al. 2024). Enquanto a perda de habitat ocorre através da degradação de uma mancha, sem subdivisão da mesma, a fragmentação causa a ruptura do habitat e introduz um novo contexto espacial através da criação de matrizes ao redor dos remanescentes (Fischer & Lindenmayer, 2007; Mortelli et al. 2010; Fahrig, 2017). A perda de habitat interfere principalmente na composição da paisagem, ao alterar a quantidade de habitat, já a fragmentação *per se* influencia a configuração da paisagem ao determinar o arranjo espacial dos elementos no espaço (Hadley & Betts, 2011; Fahrig, 2017). Por isso, estudos que avaliam a influência de atributos das manchas de habitat sobre parâmetros da

biodiversidade, tais como tamanho e isolamento, são referências para o processo da perda de habitat, mas não podem ser indicativos para os efeitos da fragmentação *per se* (Fahrig, 2013; Riva et al. 2024). Isso porque há uma maior quantidade de habitat em manchas maiores que em manchas pequenas, enquanto o maior isolamento dessas manchas de habitat é decorrente da menor quantidade de habitat na paisagem (Fahrig, 2013; 2017). Por isso, é esperado que parâmetros biológicos, como a riqueza de espécies, sejam positivamente influenciados por paisagens com alta quantidade de habitat (ou seja, que possuem manchas grandes e menos isoladas) (Fahrig, 2013; Watling et al. 2020; Rios et al. 2021; Fahrig, 2021).

As diferenças dos efeitos da fragmentação *per se* e da perda de habitat sobre a biodiversidade resultaram em importantes publicações sobre estes assuntos, especialmente na última década (Fahrig, 2003; Haddad et al. 2015; Fahrig, 2017; Pfeifer et al. 2017; Püttker et al. 2021; Riva et al. 2024). Tais discussões foram impulsionadas após publicações de Fahrig (2003; 2017), que mostraram que os efeitos da fragmentação *per se* sobre a biodiversidade e diferentes respostas ecológicas são fracos, e em alguns cenários, positivos. Posteriormente, Fletcher Jr. et al. (2018) trouxeram evidências que questionam os resultados obtidos por Fahrig (2017), baseados principalmente em estudos anteriores que mostraram efeitos negativos da fragmentação sobre a biodiversidade (por exemplo, Haddad et al. 2015; Pfeifer et al. 2017). Essa discussão se mantém como um dos focos atuais na Ecologia de Paisagens (Fahrig et al. 2019; Saura, 2020; Fahrig, 2021; Riva et al. 2024; Galán-Acedo et al. 2024), e é essencial para definir se as estratégias de manejo da paisagem, fundamentais para a conservação da biodiversidade, devem focar nas áreas de habitats ou na configuração desses elementos no contexto espacial.

A fragmentação dos habitats é a principal causa da crise da biodiversidade (Krauss et al. 2010; Haddad et al. 2015; Caro et al. 2022; Zhang et al. 2024). Por exemplo, a redução na qualidade do habitat e na heterogeneidade composicional pode afetar espécies especialistas e raras, que dependem de diferentes requerimentos ecológicos para manutenção das populações na paisagem (Gámez-Virués et al. 2015; Martello et al. 2018; Carneiro et al. 2021). Parâmetros relacionados à alfa diversidade, como a riqueza e abundância de espécies, são negativamente afetados pela redução na quantidade de habitat e heterogeneidade da paisagem (Fahrig, 2003; Olden & Rooney, 2006; Carneiro et al. 2022). Por outro lado, tais perturbações no contexto espacial resultam em uma homogeneização na composição das comunidades, reduzindo a diversidade regional (ou

seja, beta diversidade) na escala da paisagem (Püttker et al. 2014; Morante-Filho et al. 2015; Muzenza et al. 2024).

Além disso, com o isolamento de populações de plantas e animais, pode ocorrer redução no fluxo gênico e interrupção de dinâmicas de metapopulações (Freiria et al. 2012; Storck- Tonon & Peres, 2017), o que resulta em um aumento nos riscos de extinção local de espécies (Crooks et al. 2017; Aguilar et al. 2019). Consequentemente, perturbações na paisagem dirigem mudanças em interações ecológicas, como planta-polinizador e predação (Liu et al. 2018; Wang et al. 2020; Gabara et al. 2021). Serviços ecológicos e ecossistêmicos, como a polinização, qualidade da água, controle de pragas e doenças, também são afetados por mudanças na estrutura da paisagem (Garibaldi et al. 2011; Haddad et al. 2015; Duarte et al. 2018). Com isso, ações para evitar a homogeneização biológica em paisagens modificadas são cruciais para conservação da biodiversidade (Olden & Rooney, 2006), assim como para a manutenção de serviços ecossistêmicos, essenciais para as populações humanas.

1.3 Restauração ecológica e recuperação de comunidades de abelhas

Mitigar os efeitos da fragmentação dos habitats é fundamental para o funcionamento dos ecossistemas. Nesse sentido, além da conservação dos remanescentes de habitats na paisagem, a restauração ecológica é uma importante ferramenta para a recuperação de ecossistemas degradados. A restauração ecológica é definida pela Sociedade de Restauração Ecológica- SER como o processo de auxiliar na recuperação de ecossistemas danificados, degradados ou destruídos (SER, 2024). A Ecologia da Restauração, disciplina que engloba os conceitos teóricos e métodos da restauração ecológica, teve origem na década de 1980 (Jordan et al. 1987; Young et al. 2005). Desde então, essa área do conhecimento tornou-se o centro de discussões sobre políticas ambientais globais. Países membros das Nações Unidas, por exemplo, comprometeram- se em restaurar 350 milhões de hectares de ecossistemas degradados e destruídos, para mitigar a perda da biodiversidade. Diante disso, as Nações Unidas declarou o período 2021-2030 como a “Década da Restauração”, tempo limite para atingir estes importantes objetivos de restauração e reduzir os efeitos das alterações do clima (ONU, 2019; Fischer et al. 2021).

A restauração ecológica objetiva estabelecer sistemas autossustentáveis e resilientes através da recuperação da composição de comunidades de plantas e animais, além do retorno da funcionalidade das espécies nos ecossistemas e o aumento da

conectividade na escala da paisagem (Rodrigues et al. 2009; Suding et al. 2015; Rother et al. 2019). Através dessa prática, espera-se que sistemas degradados ou destruídos retornem às condições ambientais semelhantes ao período anterior à perturbação no sistema (Rodrigues et al. 2009; Suding, 2011). Com isso, a restauração ecológica é importante para a integridade dos ecossistemas, e pode beneficiar as populações humanas que dependem diretamente de serviços ecossistêmicos (Hagger et al. 2017; Zanini et al. 2021; Bergamo et al. 2021).

Locais susceptíveis as práticas de restauração são manejados através da remoção de atividades antrópicas e de espécies exóticas, e criação de um habitat favorável à colonização de diferentes grupos taxonômicos (Rodrigues et al. 2009; Suding, 2011). Essas estratégias são direcionadas por meio de duas técnicas principais de restauração ecológica. Na restauração passiva, há um isolamento da área para reduzir ou debelar os impactos das atividades antrópicas, e o processo de restauração nessa técnica ocorre pela regeneração natural do ambiente (Rodrigues et al. 2009; Suding, 2011; Meli et al. 2017). Em alguns cenários, intervenções são necessárias durante o processo de restauração passiva, como a introdução de algumas espécies específicas (Holl & Aide, 2011). Na restauração ativa, há um manejo direto do homem nas diversas fases da restauração (Suding, 2011; Holl & Aide, 2011). Na primeira fase, é feito o plantio de espécies de plantas primárias com rápido crescimento, que fornecem uma cobertura no solo e condições ambientais para a recuperação posterior de espécies vegetais secundárias, secundárias tardias e de clímax (Rodrigues et al. 2009).

Diferentes fatores podem influenciar a escolha da melhor estratégia para projetos de restauração (Holl & Aide, 2011; Atkinson & Bonser, 2020). Áreas que possuem solos com maior fertilidade e condições microclimáticas adequadas, tais como clima e temperatura, apresentam maior resiliência local e podem ser mais susceptíveis à regeneração natural (Rodrigues et al. 2009; Meli et al. 2017; Zanini et al. 2021). Por outro lado, áreas degradadas (solo infértil e lixiviado, altas temperaturas), com baixa capacidade de resiliência, dependem de diversas intervenções humanas para o processo de restauração (Meli et al. 2017; Atkinson & Bonser, 2021). Além disso, um fator essencial para a direcionar a melhor estratégia de restauração é a estrutura da paisagem (Holl & Aide, 2011; San-José et al. 2022). Áreas degradadas situadas em paisagens com alta cobertura de vegetação nativa podem apresentar uma maior resiliência ecológica devido à maior proximidade dos remanescentes naturais, que servem como manchas-fontes de propágulos e colonizadores, facilitando uma rápida recuperação dos ecossistemas

(Pardini et al. 2010; Cariveau et al. 2020; Carneiro et al. 2024). Da mesma forma, locais degradados inseridos em paisagens altamente modificadas, com baixa cobertura de vegetação nativa e alto isolamento espacial entre os remanescentes de habitat podem apresentar baixa resiliência ecológica devido à maior dificuldade de dispersão das espécies e colonização por migrantes, o que dificulta o sucesso da restauração (Pardini et al. 2010; Aavik & Helm, 2017; Griffin et al. 2021). Por isso, considerar esses atributos espaciais é essencial para tomadas de decisões de quais locais na paisagem a restauração ecológica pode ser mais efetiva, maximizando o tempo de manejo.

Os programas de restauração ecológica geralmente apresentam tempo de execução e recursos financeiros limitados. Por essas características, tais projetos têm concentrado na restauração através de determinados grupos taxonômicos, especialmente plantas (Young, 2000; Williams, 2011). Este grupo de organismos tem sido o foco central da restauração ecológica, baseado principalmente na hipótese dos "Campos dos Sonhos", que prediz que reestabelecer a estrutura do habitat através da vegetação é o primeiro passo para a recolonização de populações de animas e suas funções ecológicas (Palmer et al. 1997). Por isso, a literatura sobre a restauração ecológica tem se concentrado principalmente nos diferentes aspectos das comunidades vegetais (Young, 2000; Gornish et al. 2017; Aavik & Helm, 2017; Durbecq et al. 2020). Contudo, avaliar as comunidades de animais é fundamental para verificar o sucesso de projetos de restauração e direcionar, quando necessário, ações de manejo que resultem em uma recuperação efetiva de ambientes degradados e de relações ecológicas essenciais para manutenção e funcionamento dos ecossistemas, como planta-polinizador.

As abelhas são um grupo chave para avaliar o sucesso de projetos de restauração, uma vez que a recuperação das comunidades desses insetos em habitats restaurados pode indicar o reestabelecimento da relação planta-polinizador nesses sistemas (Dixon, 2009; Exeler et al. 2009; Carneiro et al. 2024). Trabalhos anteriores indicaram que diferentes fatores influenciam o estabelecimento de comunidades de abelhas em habitats restaurados. A composição das comunidades desses polinizadores pode ser afetada pela escolha de quais espécies de plantas são utilizadas para restauração (Lane et al. 2020; Sousa Miranda et al. 2021; Ribeiro et al. 2024), ao mesmo tempo que plantas pioneiras espontâneas e espécies generalistas são essenciais para restauração de polinizadores, pois fornecem recursos florais para uma alta diversidade de insetos (Campbell et al. 2019; Deprá et al. 2021). Além disso, a riqueza e abundância de abelhas são positivamente

relacionadas ao aumento da idade da restauração (Griffin et al. 2017; Gruchowski-Woitowicz et al. 2022). Esse efeito positivo ocorre porque à medida que o tempo passa, há um aumento na complexidade da estrutura da vegetação, o que contribui para uma maior diversidade de recursos florais e de locais de nidificação para diferentes espécies de abelhas (Araújo et al. 2018; Montoya-Pfeiffer et al. 2020). Geralmente, as comunidades de abelhas estabelecem-se em habitats restaurados e atingem uma composição similar aos pontos de referência (ou seja, habitat similar conservado) após os primeiros anos do início da restauração (Exeler et al. 2009; Griffin et al. 2017).

Fatores locais, como a disponibilidade de recursos florais, tornam-se menos relevantes para o estabelecimento de abelhas em habitats restaurados quando estes locais estão inseridos em paisagens com maior cobertura de floresta e próximos aos remanescentes de habitat, que atuam como áreas fontes para os requerimentos ecológicos desses insetos (Griffin et al. 2021). A estrutura da paisagem tem influência direta sobre a colonização de espécies de abelhas habitats restaurados. É importante considerar que estes ambientes podem ser cercados tanto por manchas de habitats, quanto por matrizes com diferentes tipos de usos e manejo, influenciando na dispersão das abelhas na escala da paisagem (Dixon, 2009; Gobatto et al. 2022). Por isso, habitats restaurados localizados em paisagens com uma alta cobertura de habitat podem apresentar uma maior abundância, riqueza, e beta diversidade de abelhas (Cariveau et al. 2020; Griffin et al. 2021; Carneiro et al. 2024). Além do mais, a dispersão desses polinizadores pode ser facilitada por *stepping stones*, e por uma maior conectividade estrutural na paisagem (Dixon, 2009; Griffin et al. 2017; Griffin et al. 2021). Portanto, a restauração na escala da paisagem é essencial para o reestabelecimento das comunidades de abelhas (Dixon, 2009), assim como de suas funcionalidades nos ecossistemas.

1.4 Abelhas Euglossini, mudanças na paisagem e restauração ecológica

As abelhas da tribo Euglossini (Hymenoptera: Apidae) desempenham importantes funções ecológicas nas florestas tropicais úmidas. Os machos dessas abelhas são polinizadores exclusivos de centenas de espécies de Orchidaceae (Cameron, 2004; Roubik & Hanson, 2004), que fornecem perfumes florais utilizados em comportamentos de coorte (Dressler, 1982; Eltz, 2005; Roubik & Hanson, 2004; Henske et al. 2023). Por esse motivo, as abelhas Euglossini são também conhecidas como “abelhas de orquídeas”. Esses insetos também são polinizadores chave para espécies incluídas em

mais de 40 famílias botânicas (Ramírez et al. 2002; Roubik & Hanson, 2004), que são fontes de diferentes recursos florais, tais como néctar, pólen, perfumes e resina (Rocha-Filho et al. 2012; Ospina- Torres et al. 2015). Além disso, uma vez que as abelhas Euglossini apresentam alta capacidade de voo e podem dispersar em amplas áreas contínuas de floresta (Janzen, 1971; Wikelski et al. 2010), esses insetos são importantes vetores de pólen de plantas com distribuição esparsa na paisagem.

A tribo Euglossini é um grupo monofilético, com distribuição geográfica restrita ao Novo Mundo, do sul dos Estados Unidos até o norte da Argentina (Nemésio, 2009; Moure & Melo, 2023). Essas abelhas compreendem mais de 240 espécies em 5 gêneros, *Euglossa* Latreille, *Eulaema* Lepeletier, *Eufriesea* Cockerell, *Exaerete* Hoffmansegg e *Aglae* Lepeletier & Serville (Moure & Melo, 2023; Engel & Rasmussen, 2020). *Euglossa* é o gênero com maior riqueza, com mais de 139 espécies conhecidas, seguido por *Eufriesea*, com 66 espécies, *Eulaema* (33 espécies), Exaerete (8 espécies) e *Aglae* (gênero monoespecífico) (Moure & Melo, 2023). Essas abelhas têm comportamento tipicamente solitário (Michener, 2007), mas muitas espécies, principalmente dos gêneros *Euglossa* e *Eulaema*, podem apresentar comportamentos primitivamente sociais (Zucchi et al. 1969; Garófalo, 1985; Roubik & Hanson, 2004; Andrade-Silva et al. 2016). As espécies de *Exaerete* são cleptoparasitas de ninhos de *Eufriesea* e *Eulaema*, enquanto *Aglae* de ninhos de *Eulaema* (Roubik & Hanson, 2004; Michener, 2007). As espécies de Euglossini são abelhas de médio e grande porte, apresentam brilho metálico em diferentes cores, tais como azul, violeta, dourado, verde e amarelo, e são caracterizadas por uma glossa longa, que em algumas espécies pode ultrapassar o comprimento do corpo (Cameron, 2004; Nemésio, 2009; Engel & Rasmussen, 2020).

A maior diversidade das abelhas Euglossini está concentrada nas regiões quentes e úmidas próximas à linha do Equador, onde os índices pluviométricos excedem os 2000 mm anuais (Dressler, 1982; Cameron, 2004; Roubik & Hanson, 2004). Por isso, a maior riqueza de espécies dessas abelhas é relatada para a Floresta Amazônica, onde também é observado um elevado número de espécies endêmicas (Storck-Tonon et al. 2009; Cândido et al. 2018; Brito et al. 2019; Brown et al. 2024). Nessas florestas tropicais úmidas, as abelhas Euglossini representam cerca de 25% da diversidade de abelhas observada (Roubik & Hanson, 2004). Para o Brasil, a Mata Atlântica é o segundo bioma com maior riqueza de espécies e endemismos, principalmente nas regiões de baixas latitudes, associadas às fitofisionomias que recebem maiores quantidades de chuva anualmente, tais como as florestas ombrófilas densas do Corredor Central e da Serra do

Mar da Mata Atlântica (Nemésio et al. 2009; Ramalho et al. 2009; Aguiar et al. 2014; Garraffoni et al. 2017; Miranda et al. 2019). Por outro lado, observa-se uma redução na riqueza de Euglossini com o aumento da latitude em direção à porção sul da Mata Atlântica (Sofia & Suzuki, 2004; Giangarelli et al. 2015). Além disso, há uma diminuição acentuada na riqueza dessas abelhas para as regiões centrais do Brasil, principalmente na Diagonal Seca, onde insere-se o Cerrado e a Caatinga. O Cerrado detém uma maior riqueza de espécies em relação à Caatinga, o que está associado a maior pluviometria e ocorrência de ecossistemas de florestas úmidas deste bioma, tais como as matas de galeria (Silveira et al. 2015; Martins et al. 2018; Leão-Gomes & Vasconcelos, 2023). Para a Caatinga, a maior riqueza de Euglossini concentra- se em regiões de caatinga arbórea, de maiores altitudes, ou em ecossistemas de encrave com maior umidade (Moura & Schlindwein, 2009; Andrade-Silva et al. 2012; Carneiro et al. 2018; Mariano et al. 2024), enquanto áreas de caatinga arbustiva parecem sustentar poucas espécies, com maior tolerância a estes ambientes (Carneiro et al. 2018).

O conhecimento sobre a biologia e ecologia de Euglossini cresceu amplamente após década de 1970, com a descoberta que machos dessas abelhas são atraídos por compostos aromáticos que poderiam ser sintetizados em laboratório (Dodson et al. 1969). Ainda assim, aspectos relacionados a biologia de nidificação e taxonomia de fêmeas da maioria das espécies de Euglossini ainda são desconhecidos, devido à dificuldade em encontrar ninhos desses insetos e em amostrar fêmeas (Nemésio, 2009). Por isso, a maior parte da literatura de Euglossini é focada nos machos dessas abelhas, que são atraídos por essências aromáticas em coletas ativas (i.e. com rede entomológica) e passivas (i.e. com armadilhas feitas com garrafas PET).

A facilidade para amostragem dos machos de Euglossini torna este grupo de organismos um importante modelo de estudo para responder diferentes perguntas ecológicas (Gonçalves & Faria, 2021; Hipólito et al. 2023). Por exemplo, vários estudos verificaram que a composição das comunidades de Euglossini é influenciada por diferentes variáveis bióticas e abióticas (Aguiar & Gaglianone, 2012; Aguiar et al. 2014; Sobreiro et al. 2019). A riqueza e abundância dessas abelhas é correlacionada à umidade e temperatura (Aguiar & Gaglianone, 2012; Ferronato et al. 2017). Uma menor riqueza dessas abelhas é observada em fitofisionomias de florestas estacionais semideciduais em comparação às formações de florestas ombrófilas (Aguiar et al. 2014; Giangarelli et al. 2015), enquanto uma baixa abundância de Euglossini é encontrada em regiões frias de alta altitude (Pinto et al. 2019; Carneiro et al. 2021). Além disso, a riqueza, abundância

e diversidade de espécies dessas abelhas são positivamente influenciadas por habitats com maior complexidade na estrutura da vegetação (Silveira, 2014; Moreira et al. 2017; Viana et al. 2021; Brown et al. 2024).

Devido à alta dependência de ambientes florestais, as abelhas Euglossini são consideradas indicadores ecológicos essenciais para entender os efeitos das perturbações nos habitats e mudanças na paisagem sobre comunidades de abelhas (Brosi, 2009; Storck- Tonon & Peres, 2017; Allen et al. 2019). De fato, muitos estudos têm observado a influência de variáveis dos habitats, assim como da estrutura da paisagem, sobre diferentes atributos das comunidades de Euglossini (Brosi, 2009; Aguiar et al. 2015; Cândido et al. 2018; Carneiro et al. 2021; Côrrea-Neto et al. 2024). A variação na composição da comunidade dessas abelhas foi explicada pelo isolamento entre as manchas florestais e mudanças no tipo de habitat na Floresta Amazônica (Storck-Tonon & Peres, 2017; Côrrea-Neto et al. 2024). Outros estudos neste bioma indicam que o aumento no isolamento entre remanescentes florestais resultou em um declínio da riqueza de espécies de Euglossini (Powell & Powell, 1987; Cândido et al. 2018), enquanto remanescentes com maior conectividade apresentaram uma maior riqueza dessas abelhas (Storck-Tonon et al. 2013). Uma maior riqueza e diversidade de espécies também foi observada em remanescentes de Floresta Amazônica com menor área de borda (Storck-Tonon et al. 2013), dados similares observados na Mata Atlântica, onde a riqueza e abundância de Euglossini foram associadas ao tamanho das áreas centrais dos fragmentos (Nemésio & Silveira, 2010), assim como ao tamanho dos remanescentes florestais (Ramalho et al. 2009; Aguiar & Gaglianone, 2012). Por outro lado, observações nas florestas úmidas da América Central mostraram efeitos positivos da quantidade de borda de fragmentos florestais sobre a abundância e riqueza de Euglossini, ao mesmo tempo que uma maior abundância de espécies foi observada em fragmentos florestais maiores (Brosi, 2009). Além do mais, paisagens na Mata Atlântica e Floresta Amazônica com menor porcentagem de ambientes antrópicos ao redor dos remanescentes florestais influenciaram positivamente a abundância e riqueza de Euglossini (Silveira, 2014; Cândido et al. 2018). Efeitos positivos da heterogeneidade composicional, que representa a diversidade de manchas no contexto espacial, foram observados sobre a riqueza e abundância de espécies raras de Euglossini na Mata Atlântica (Opedal et al. 2020; Carneiro et al. 2021; Carneiro et al. 2022). Com isso, verifica-se que mudanças no habitat e na estrutura da paisagem geralmente resultam em efeitos negativos sobre as comunidades de Euglossini, o que mostra o potencial dessas abelhas como indicadores

ecológicos. Novos estudos considerando outros contextos espaciais são essenciais para corroborar esses padrões, e fornecer evidências que contribuam para estratégias de manejo e conservação desses importantes polinizadores em paisagens modificadas.

Os estudos que avaliaram os efeitos das mudanças nos habitats e na paisagem sobre as comunidades de Euglossini têm usado principalmente parâmetros da alfa diversidade, tais como riqueza e abundância de espécies (Brosi, 2009; Silveira, 2014; Allen et al. 2019; Carneiro et al. 2022). Essas variáveis, especialmente a abundância de espécies, são facilmente obtidas, não requerem análises complexas, e podem apresentar respostas robustas às perturbações na paisagem (Cândido et al. 2018; Allen et al. 2019; Carneiro et al. 2022). Por outro lado, poucos estudos têm avaliado aspectos associados a beta diversidade de comunidades de Euglossini (Nemésio & Vasconcelos, 2013; Costa & Francoy, 2017; Machado et al. 2018; Brown et al. 2024), e o conhecimento sobre como essa beta diversidade responde as mudanças na paisagem é ainda incipiente (Botsch et al. 2017; Brown et al. 2024). Áreas florestais com menor complexidade estrutural têm diferenças na composição de espécies de Euglossini em comparação a habitats com maior complexidade (Allen et al. 2019; Brown et al. 2024). Uma tendência de uma maior substituição na composição de espécies (ou seja, *turnover*) foi observado entre comunidades de floresta contínua com de pequenos fragmentos florestais (Botsch et al. 2017). Além do turnover, o aninhamento (*nestedness*) é outro componente da beta diversidade, e é utilizado para avaliar processos não-aleatórios de perda de espécies entre comunidades (Baselga, 2010). Com isso, é importante considerar a influência do contexto espacial sobre componentes da beta diversidade de Euglossini, para compreender como atributos espaciais dirigem mudanças na composição das comunidades dessas abelhas.

Apesar do potencial das abelhas Euglossini como indicadores ecológicos de diferentes parâmetros ambientais e alterações na paisagem, o uso desses insetos para analisar o sucesso de projetos de restauração é negligenciado. Os poucos dados relacionados as abelhas Euglossini em habitats restaurados na Mata Atlântica indicam que espécies dessas abelhas podem utilizar esses ambientes para nidificação (Gobatto et al. 2021), e que a composição da comunidade dessas abelhas não apresenta diferenças entre habitats restaurados e conservados (Ferronato et al. 2017), apesar das espécies de Euglossini serem mais predominantes em fragmentos conservados (Montoya-Pfeiffer et al. 2020). Isso é um indicativo que as abelhas Euglossini podem rapidamente colonizar essas áreas (Ferronato et al. 2017), contribuindo para o sucesso

da restauração, uma vez que essas abelhas polinizam uma alta diversidade de espécies de plantas. Contudo, são necessários novos trabalhos para analisar os diferentes fatores que influenciam as comunidades de Euglossini em habitats restaurados, especialmente em escalas espaciais mais amplas.

Além do mais, não há dados relacionados as comunidades de abelhas Euglossini como indicadores do sucesso de estratégias de restauração ativa e passiva (ou seja, regeneração natural) na Mata Atlântica. Estudos realizados com comunidades de vespas e abelhas que nidificam em cavidades preexistentes na Floresta Amazônica indicaram que a estratégia de restauração influencia a diversidade funcional e composição de espécies desses insetos, com comunidades de habitats regenerados naturalmente apresentando maior similaridade com de habitats florestais conservados (Araújo et al. 2020; Araújo et al. 2021). Para a Mata Atlântica, a estratégia de restauração não afetou as interações planta-polinizador, e isso pode estar relacionado a uma maior influência do contexto da paisagem sobre essas dinâmicas ecológicas (Souza et al. 2022). Com isso, estudos que analisem o efeito da estratégia de restauração e da estrutura da paisagem são essenciais para entender a interação entre esses fatores sobre a recuperação de comunidades de abelhas.

O objetivo geral deste estudo foi avaliar as respostas das comunidades de abelhas Euglossini aos atributos locais e da paisagem de habitats restaurados e conservados de floresta ombrófila na Mata Atlântica do Sudeste do Brasil. Os dados obtidos fornecem evidências para direcionar estratégias de restauração e manejo dessas áreas, contribuindo para a recuperação das comunidades de abelhas e no sucesso dos projetos de restauração.

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CAPÍTULO I

RESTORATION OF BEE COMMUNITIES (HYMENOPTERA: APOIDEA: ANTHOPHILA) IN LANDSCAPE SCALE: A REVIEW[1]

Abstract: Anthropogenic disturbances have changed the landscape structure and functioning in many ecosystems worldwide. Ecological restoration at the landscape level is important to recover degraded and destroyed ecosystems, as well as increase the habitat amount and spatial connectivity, thus reestablishing biodiversity and essential ecological processes. Different local and landscape factors affect the recovery of animal communities in general, particularly the bees. These insects are essential for restoration success through pollination. Considering the importance of ecological restoration at the landscape level to pollinator conservation, we systematically reviewed the influence of landscape structure on the restoration of bee communities. Our review encompassed the analysis of 18 articles based on specific criteria including the number of bee sampling units within restoration areas and landscape analyses. These studies showed that habitat amount and proximity influence in different ways the bee richness, abundance, diversity, and species composition in the restored environments. We also observed that restoration attributes linked to habitat complexity such as the availability of floral and nesting resources drive the bee species' colonization and persistence. Our findings emphasize the necessity of designing restoration strategies that consider the spatial and temporal distribution of bee species requirements on a landscape scale.

Keywords: bees, pollinators, landscape structure, restoration ecology, restoration success

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1. INTRODUCTION

Anthropic disturbances, accompanied by habitat loss and fragmentation, have substantially altered the compositional and configurational landscape heterogeneity in several ecosystems. In human-modified landscapes, the combination of a low habitat amount and disruptions in the structural connectivity between habitat patches impacts the ability of landscapes to facilitate the flow of individuals (i.e., functional connectivity) (Fahrig 2017; Tonetti et al. 2023). These spatial attributes play an important role in ecological dynamics such as species dispersal, immigration, and colonization influencing landscape resilience and ecosystem restoration (Pardini et al. 2010; Gawecka and Bascompte 2021).

Restoration ecology has been the focus of environmental discussions in the Anthropocene era. Global initiatives such as the "Decade on Ecosystem Restoration" have guided the recovery of millions ha of degraded ecosystems worldwide (UN 2019). Ecological restoration comprises a range of techniques and methods to assist in the recovery of damaged, degraded, or destroyed ecosystems (SER 2004). The restoration is based on the ecological succession to recover species and their functionality, contributing to biodiversity conservation and ecosystem integrity (Rodrigues et al. 2009; Suding et al. 2015). At the same time, large-scale restoration is essential for mitigating the adverse impacts of the ongoing climate crisis and the high rate of species extinctions (Strassburg et al. 2020; Tonetti et al. 2022).

Before implementing restoration strategies, it is imperative to consider various local and landscape attributes. It is crucial to understand the local potential resilience, which depends on environmental factors such as soil quality, disturbance history, type of land use, as well as climatic conditions such as temperature and precipitation (Suding 2011; Cariveau et al. 2020; Zanini et al. 2021). Equally important is the assessment of surrounding landscape resilience (i.e. the capacity of the landscape to provide source areas and facilitate gene flow) (Pardini et al. 2010; Cariveau et al. 2020). A higher species colonization and ecosystem recovery is expected in landscapes with a high and intermediate habitat amount and low spatial isolation because these spatial filters do not impose restrictions on species dispersal (Tscharntke et al. 2005; Pardini et al. 2010). On the other hand, landscapes with a low habitat amount and high isolation can narrow the propagule dispersal and species colonization (Pardini et al. 2010; Williams 2011). Thus, focusing on landscape-scale restoration can boost habitat availability and enhance

structural and functional spatial connectivity contributing to the restoration success (Crouzeilles et al. 2015; Jakovak et al. 2021; González-Chaves et al. 2023).

Evaluating the success of restoration efforts relies on monitoring the recovery of both plant and animal communities. For this, a reference area (i.e. conserved habitat or ecosystem) is recommended considering it as the target scenario for restoration outcome (Rodrigues et al. 2009; Prach et al. 2019). Restoring plant communities has been the main restoration objective because establishing a habitat structure is the first step towards the colonization by animal groups (aka the “Fields of Dreams” hypothesis, Palmer et al. 1997). Assessing the effectiveness of restoration efforts in recovering biodiversity should also encompass non-target organisms, such as bees, as they are essential to restoration success due to their critical role in pollination service.

Bees (Hymenoptera: Apoidea: Anthophila) are the main pollinators in terrestrial ecosystems. The nearly 20,000 bee species known are widely distributed and present diverse life histories (Michener 2007; Orr et al. 2021). While most bee species exhibit solitary behavior, some are social, with caste division or kleptoparasites of solitary and social bee nests (Michener 2007; Danforth et al. 2019). Bee nests vary in location, with some occupying pre-existing cavities above or below ground, while others construct their own nesting cavities (Danforth 2007). These insects feed mainly on pollen and nectar in the larval and adult stages, respectively (Michener 2007). Considering that bee species require different foraging and nesting habitats throughout their life cycles, these insects face threats associated with habitat loss in the landscape. At the same time, the recovery of bee communities may be a proxy for reestablishing plant-pollinator interactions within restored areas contributing to plant reproduction in these environments.

Floral and nesting resources are the principal local drivers acting on the recovery of bee communities in restored areas (Winfree 2010; Onuferko et al. 2018; Gruchowski-Woitowicz et al. 2022). Habitat generalists and below-ground nesting bees are favored in early restoration because of the higher availability of bare soil (Hopwood 2008). This nesting requirement decreases with the ecological succession of plant communities, affecting the species richness, abundance, and composition of below-ground nesting bees (Williams 2011; Onuferko et al. 2018). In contrast, pre-existing cavity nesting bees only colonize restored areas after increasing habitat complexity because these species require nesting resources such as tree cavities (Taki et al. 2013; Gutiérrez-Chacón et al. 2020). Moreover, the plant species used in active restoration plantations influence the bee dispersal to these new habitats (Dixon 2009; Deprá et al. 2021). Early-stage restoration

often features herbaceous and pioneer plant species that support a rich diversity of pollinating insects due to their dense floral resources (Deprá et al. 2021). These plant species may also maintain network interactions over time softening potential fluctuations in floral resources during different seasons (Carvalho et al. 2022).

Many studies have evaluated how habitat enhancement through restoration can benefit bee species, especially in agricultural landscapes (Hopwood 2008; Morandin and Kremem 2013; Kremen and M'Gonigle 2015; Sardiñas et al. 2016). In this practice, plant species, mainly herbaceous, are established in strips or hedgerows in crops to attract bee populations and supply the pollination service (M'Gonigle et al. 2015). There is an increase in bee abundance, richness, and diversity in hedgerows with a high abundance of floral and nesting resources compared to areas lacking habitat improvements (Morandin and Kremen 2013). These resources found only in restored areas shape the bee species composition through the turnover of rare, less mobile, and specialized bee species (Hopwood 2008; Kremen and M'Gonigle 2015). This change in the species composition tends to be less pronounced when environmental factors influencing bee colonization exhibit minimal variation between managed and unmanaged hedgerows (Sardiñas et al. 2016).

The positive effect of different restoration strategies on bees is related to the interplay between local- and landscape-level attributes. When restored areas can not keep the ecological requirements of the different bee species, the habitat remnants in the surrounding landscape act as source areas influencing the ecological dynamics of species colonization and persistence (Kremen et al. 2018; Ponisio et al. 2019). Restored sites are scattered in a spatial context that encompasses both habitat remnants and anthropogenic matrices with varying land uses. Within these mosaics, certain landscape elements can serve as complementary habitats for bee species. High proximity of natural remnants facilitates access to resources still unavailable in restored areas favoring bee species dispersal and colonization from habitat areas (Dixon 2009, Cariveau et al. 2020; Araújo et al. 2021).

Recognizing the essential role of landscape structure in large-scale biodiversity restoration efforts (Crouzeilles et al. 2015), we conducted a systematic review to assess the impact of the landscape attributes on the recovery of both α and β-diversity of bee communities inhabiting ecosystems undergoing restoration. While α-diversity indicates local recovery of parameters such as species richness, abundance, and diversity, the β-diversity could be an important proxy for the maintenance of ecological processes in larger

spatio-temporal scales, such as species turnover and nestedness shedding light on the dynamics of bee communities in the context of landscape restoration.

2. REVIEW METHOD

We did a bibliographic search in the databases *Web of Science* and *Scopus*. For this, the keywords "*bee community*" AND *restoration* AND *landscape* were used. It resulted in 156 and 1351 articles in the *Web of Science* and *Scopus*, respectively. First, we read the *Abstract* of each of these articles. At this step, we selected studies published until 2022 related to bee communities in restored areas with any management strategy, resulting in 34 articles from the *Web of Science* and 54 from *Scopus*. Afterward, we crossed these studies of both databases and eliminated duplicates totaling 70 articles likely to be reviewed. The final step of article selection was based on the following criteria: (1) the study evaluated parameters of α and/or β-diversity of bee communities in several restored areas (replicates), (2) it quantified landscape metrics of composition and/or configuration at the level of patch, class or landscape, and (3) it used uni or multivariate statistical analysis to evaluate the effect of landscape structure on bee communities in the restoration areas. At the end, we selected 18 articles for review (Table S1). We obtained the following information from these studies: (1) the ecosystem where it was carried out (based on the spatial information provided), (2) the number of bee sampling units and if it was considered reference sites (i.e. conserved habitat remnants), (3) buffer size for landscape analyses, (4) landscape explanatory metrics (configuration and/or composition) and level (patch, class, or landscape), (5) evaluating local explanatory variables, and (6) response variables used for the statistical analyses (Table S1).

3. RESULTS AND DISCUSSION

3.1 Overview

We observed that most of the studies were carried out in prairie and grassland ecosystems (n= 14), mainly in the United States (n= 10) and Sweden (n= 4) (Fig 1A-1B, Table S1). Three studies were in the tropical rainforest ecosystems of the Atlantic Forest in Brazil. All articles were published in the last eight years. Tonietto and Larkin (2018) also reported a high study concentration in northern regions in their metanalysis related to restoration management's effect on recovering bee communities. Prairies are widely distributed temperate ecosystems that support high bee richness and have been restored by different initiatives in many countries (Winsa et al. 2017; Denning and Foster 2018; Lane et al. 2021). These studies have contributed to understanding the factors driving the

restoration of rich bee communities at the landscape level. It is interesting to note few studies are being made in tropical forest ecosystems. Restoration in these areas is essential for recovering bee communities and plant-pollinator interaction, especially considering tropical ecosystems maintain several specialized ecological interactions (Dixon 2009).

Bee communities were evaluated in a minimum of four restored areas (Ferronato et al. 2017) and a maximum of 20 (Purvis et al. 2019) (mean = 11.9 sampling points, σ= 5.3) (Fig 1C). To provide a comprehensive perspective, ten studies also conducted bee sampling in reference habitats. While it is not anticipated that bee communities in restored areas perfectly mirror those in habitat remnants, surveying bees in preserved environments can offer valuable insights about potential bee colonization from the available species pool in the landscape (Williams 2011). Among the chosen methods, half of the articles (n= 9) employed entomological nets as the primary bee sampling technique (Fig 1D). Additionally, colored pan traps or bowl traps emerged as other commonly used methods. One study sampled pre-existing cavity nesting bees with trap nests (Gobatto et al. 2022), while another focused on assessing Euglossini bee communities using bait traps (Ferronato et al. 2017) (Fig 1D). This diversity in bee sampling methods has enriched our understanding of various bee groups inhabiting restored areas, contributing significantly to the knowledge about bee restoration. However, different sampling methods affect which bee species are sampled, influencing our understanding of species diversity in restored ecosystems.

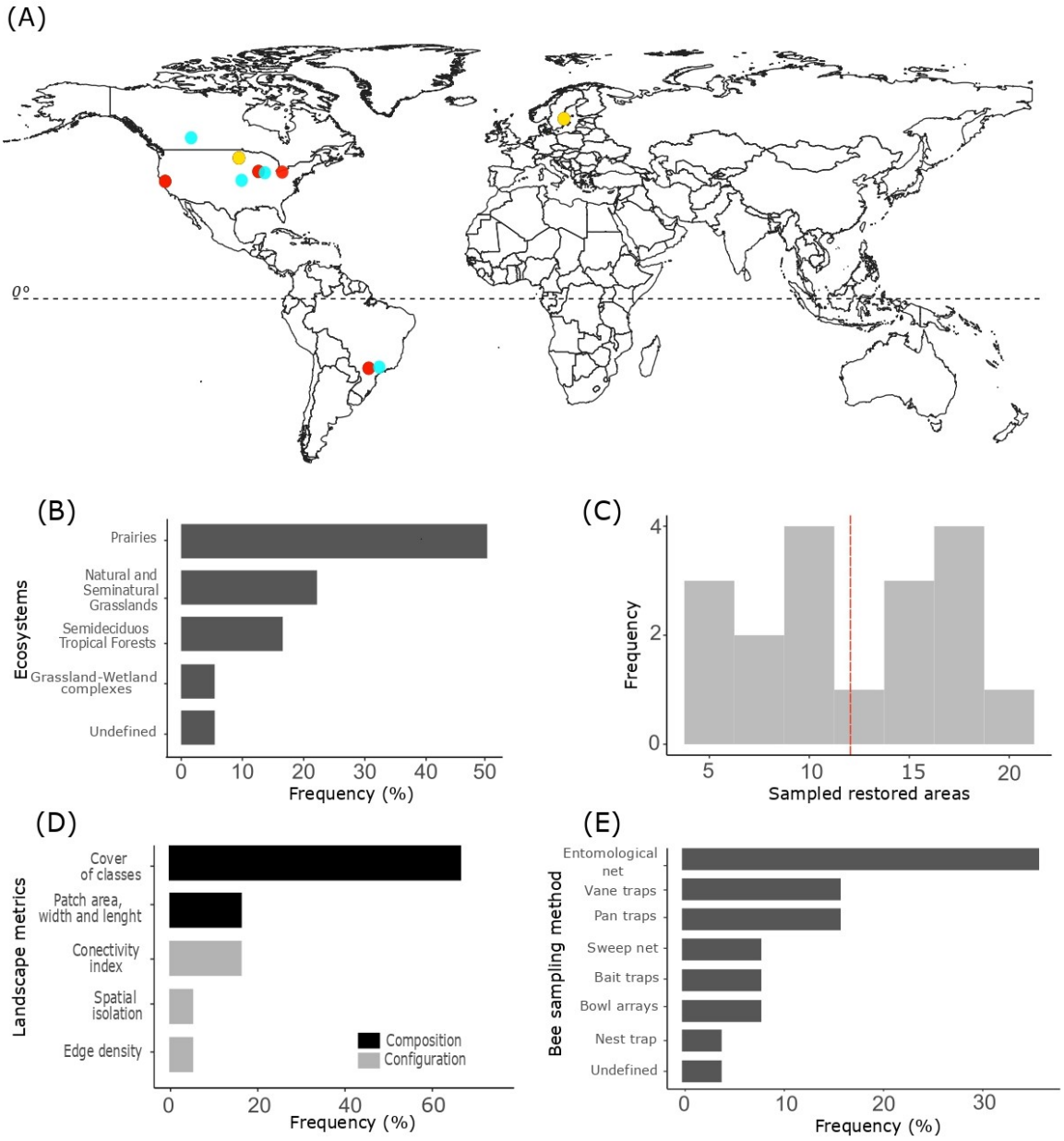

Figure 1. Geographic location of the studies analyzed **(A)**. The map was plotted with 17 studies, in one study it was impossible to locate spatial information of the study area (see Table S1). Blue circles represent one study, and red and yellow circles represent two and three studies carried out in the same region, respectively. **(B)** Frequency (%) of 18 studies by ecosystem related to the effects of landscape on the recovery of bee communities. **(C)** Frequency of the bee sampling points in restored areas. The red dotted line is the mean of sampling points. **(D)** Frequency (%) of methods used to sample bee communities in restored areas. The frequency is not absolute as some articles used multiple sampling methods. (**E)** Frequency (%) of landscape composition and configuration metrics used in the 18 analyzed studies. The frequency is not absolute in relation to 18 analyzed articles because some studies evaluated both landscape metrics (configuration and composition).

The "cover of classes" metric refers to different landscape composition metrics related to the percentage (%) and proportion of classes in the landscape.

Most of the articles (n= 15) used landscape composition metrics, mainly the percentage (%) of classes (Fig 1E). Two studies quantified landscape configuration attributes with connectivity index (Rotchés-Ribalta et al. 2018; Öckinger et al. 2018), while two studies analyzed both configuration and composition metrics (Denning and Foster 2018; Gobatto et al. 2022). Two studies used patch metrics (Ferronato et al. 2017; Montoya-Pfeiffer et al. 2021), while the other articles quantified class and landscape metrics in different buffer sizes. The smaller landscape size was 250 m (Denning and Foster 2018), while three studies quantified the landscape in 5 km buffers considering as the center of the bee sampling points in the restored areas (Winsa et al. 2017; Rotchés-Ribalta et al. 2018; Öckinger et al. 2018). Four studies quantified the landscape attributes with a multiscale approach (Denning and Foster 2018; Ponisio et al. 2019; Novotny and Goodell, 2020; Purvis et al. 2020). The landscape size is usually defined by the species' biological features, such as dispersal potential (Jackson and Fahrig 2012). Bee communities have species with different flight capacities and ecological requirements in space and time (Michener 2007). Assessing the spatial scales at which landscape attributes have a greater influence on the recovery of bee communities through a multiscale landscape analysis is essential for restoration outcomes. It helps to identify the spatial scale at which restoration management can be effective for bee species ("scale of effect", Jackson and Fahrig 2012).

In addition to the landscape predictors, most studies (n= 16) also evaluated the influence of local attributes on bee communities. These parameters predominantly were restoration age, with examples including studies by Griffin et al. (2017), Novotny and Goodell (2020), and Griffin et al. (2021). Furthermore, researchers explored factors related to habitat structure and complexity, such as vegetation height and bare soil cover, as exemplified in Tonietto et al. (2017) and Purvis et al. (2020). Additionally, floral resources, including the richness, abundance, and diversity of flowering plants, were considered important elements influencing bee communities in investigations like Denning and Foster (2018), Tonietto et al. (2017), and Novotny and Goodell (2020). Given the significance of these local restoration attributes in shaping bee communities, we also highlight the importance of these factors within the bee restoration context.

Most of the articles (n=17) evaluated α-diversity indexes of bee communities (e.g., bee richness, abundance, and diversity), and ten articles also analyzed β-diversity (e.g.,

community dissimilarity and species turnover). One of the articles evaluated metacommunity networks (Ponisio et al. 2019). These different parameters of bee communities are essential to understanding how restoration at the landscape scale drives local and regional ecological dynamics related to the reestablishment of bee species.

3.1 Restoring bee communities: influence of local and landscape attributes

The restoration age affected the α and β-diversity of bee communities, but this influence was not uniform across ecosystems. In prairies, there was a positive correlation between restoration age and bee richness, abundance, and diversity (Griffin et al. 2017; Purvis et al. 2020). A few years after the beginning of the restoration, these alpha diversity parameters began to mirror levels observed in conserved prairie remnants (e.g. 2-3 years in Griffin et al. 2017: 1-4 years in Purvis et al. 2020). This underscores restoration age as a proxy for evolving habitat complexity over time (see Fig. 2A). The positive effect of restoration age on bees may be linked to the temporal availability of floral and nesting resources over time. On the other hand, some studies reported no substantial effects of restoration age on bee richness and abundance (Öckinger et al. 2018; Novotny and Goodell 2020; Lane et al. 2021). However, the species composition in restored areas differed from prairie remnants, especially in younger restored areas (< 20 years, Tonietto et al. 2017). At this stage, the colonizing bee species were typically generalists and represented a subset of the species present in the region (Tonietto et al. 2017; Novotony and Goodell 2020). In younger restorations, the higher availability of bare soil and the limited floral resources facilitated colonization by below-ground nesting bees and floral generalist species (Tonietto et al. 2017). Therefore, the time expected to restore species abundance should be smaller as it represents mainly the individuals coming from source areas and birth rates (see Fig. 2A). The diversification of floral resources over time linked to the succession of plant communities and the establishment of nesting cavities contributes to the colonization by above-ground nesting bees and specialists' species (Lane et al. 2021; Griffin et al. 2021). This facilitates the recovery of species richness while there is a species turnover during the restoration trajectory (Tonietto et al. 2017). Finally, the time to restore the species composition would be longer because depends on the reestablishment of conditions and resources required for the entire bee community (> 20 years, Tonietto et al. 2017). Because of these reasons, we hypothesized that the expected time to restore the α-diversity of bee communities (e.g., richness, abundance) seems to be lesser than β-diversity (Fig. 2A). Therefore, the bee species composition emerges as a particularly informative indicator for evaluating the recovery of bee

communities, especially as it underscores the bee species' ecological roles within the communities, as supported by Lane et al. (2021).

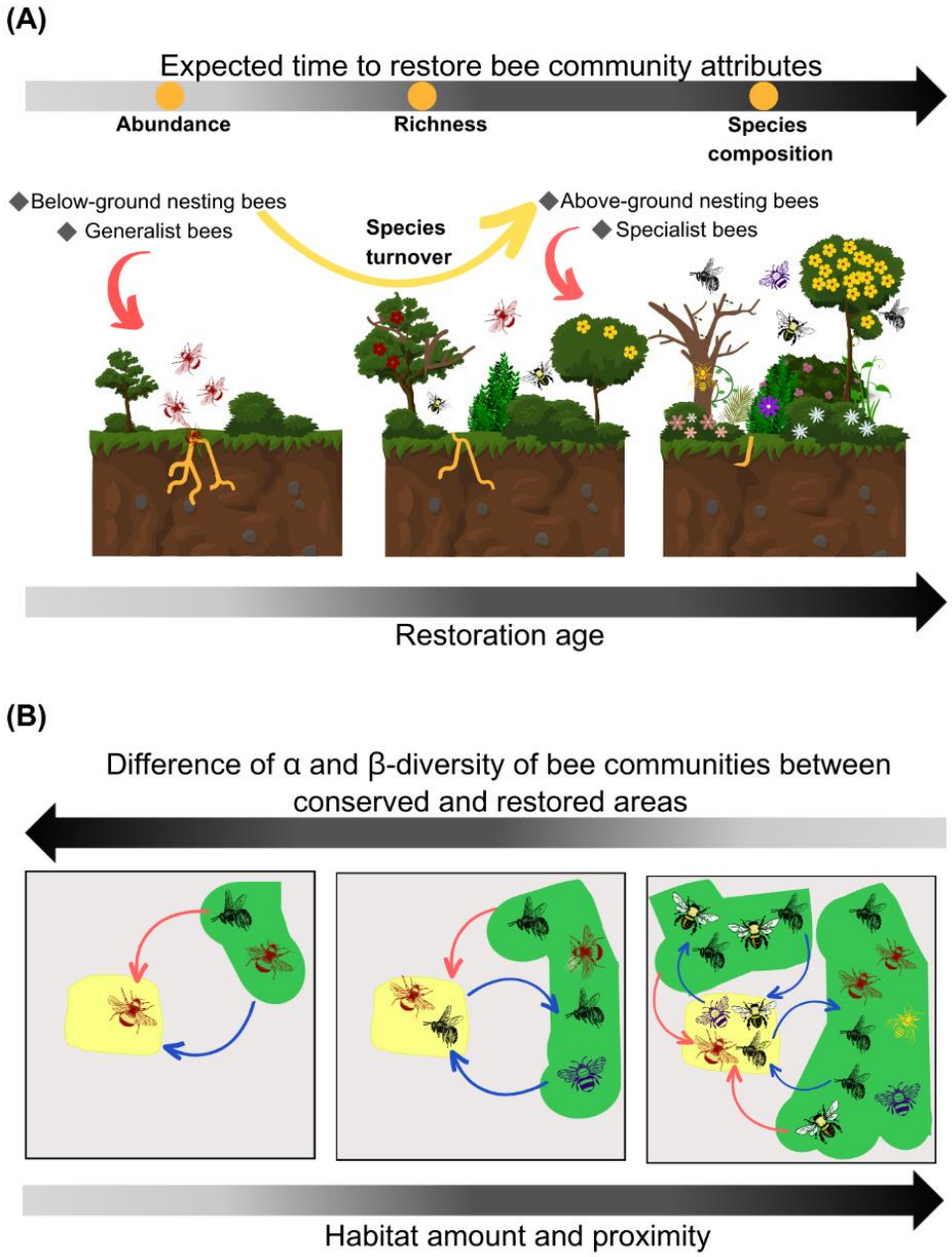

Figure 2. Influence of local **(A)** and landscape attributes **(B)** on restoring bee communities. In **(2B)**, each frame is a hypothetical landscape disregarding the effect of landscape matrices. Red arrows denote species colonization, and blue arrows dispersal processes. Green patches represent habitat areas, and yellow restored.

The way that restored sites attracted and maintained bee species was related to different local characteristics, particularly those of plant communities. In this sense, the studies found different correlations between attributes of bee and plant communities. There was a higher bee diversity and richness in restored areas with higher flowering plants'

richness, abundance, and diversity (Scheper et al. 2015; Kremen et al. 2018; Denning and Foster 2018; Lane et al. 2020; Novotny and Goodell 2020). Bee communities were also influenced by the functional traits of plant communities with colonizing bee species displaying functional traits aligned with the morphological attributes of the available flowers (Winsa et al. 2017; Rotchés-Ribalta et al. 2018). For instance, higher polylectic bee abundance was observed in restored sites characterized by elevated generalist plant diversity (Lane et al. 2021). Meanwhile, functional bee traits such as body size and seasonal flight activity were associated with floral abundance (Tonietto et al. 2017; Winsa et al. 2017; Rotchés-Ribalta et al. 2018). The availability of nesting sites also influenced the recovery of the bee communities. Higher availability of bare soil positively affected the richness and abundance of below-ground nesting bees (Tonietto et al. 2017; Denning and Foster 2018; Purvis et al. 2020). Then, these local attributes (floral and nesting resources availability) are the main filters to restore bee communities at the local scale (Fig. 2A).

The influence of the local restoration characteristics on bee communities depends on the landscape context (Scheper et al. 2015; Ponisio et al. 2019). In restored sites spatially isolated from habitat remnants, the landscape context played a more important role than local attributes on bee α-diversity, as noted by Griffin et al. (2017) and Denning and Foster (2018). The bee richness, diversity, and abundance were positively related to a higher cover of natural and conserved habitats (Denning and Foster 2018; Kremen et al. 2018; Griffin et al. 2017; Griffin et al. 2021). The spatial isolation and connectivity also influenced the bee species diversity, abundance, and occurrence in the restored environments (Öckinger et al. 2018; Montoya-Pfeiffer et al. 2020; Gobatto et al. 2022). While higher isolation of source habitats negatively affected the colonization and persistence of bee species in restored sites (Gobatto et al. 2022; Öckinger et al. 2018; Ponisio et al. 2019), some studies observed a lack of correlation between bee communities and landscape variables (e.g. Ferronato et al. 2017; Lane et al. 2020; Lane et al. 2021)

Landscape metrics are essential to understanding how landscape structure influences the recovery of bee species. Landscapes with low connectivity can spatially limit organism dispersal between patches (Griffin et al. 2021; Gobatto et al. 2022), especially for small bees exhibiting a low dispersal potential. On the other hand, landscapes with high and intermediate habitat amounts can facilitate higher bee colonization and dispersal from habitat to restored areas due to the low spatial isolation from source areas, as observed by Griffin et al. (2021) in prairies. Consequently, the high habitat cover at the landscape level can facilitate bee dispersion between habitat and restored patches in both ways

(Tscharntke et al. 2005; Pardini et al. 2010, see Fig. 2B). Furthermore, modified landscapes with poor resources may restrict colonization by specialist large-bodied bees, even for species showing a high dispersal potential, as noted by Ponisio et al. (2019). This leads to notable differences in bee community composition between restored and remnant areas in which bee species within restored sites often exhibit remarkable environmental plasticity (Tonietto et al. 2017; Öckinger et al. 2018).

In more complex landscapes with high compositional heterogeneity, bee communities quickly recovered, as shown in Griffin et al. (2017). This spatial and environmental heterogeneity allows a habitat complementation for bee species. Even when floral and nesting resources remain scarce in restored sites, bee species can access these resources in other patches scattered across the landscape (Denning and Foster 2018; Novotny and Goodell 2020; Griffin et al. 2021). Functional bee traits, including sociality and nest location, demonstrated correlations with habitat cover, with solitary bee species benefiting from habitat enhancement through restoration (Kremen et al. 2018). In addition, easy access to floral and nesting resources in habitat patches in the surrounding landscapes can increase bee persistence in restored areas (Kremen et al. 2018). A high habitat amount at the landscape level resulted in a low variation in the β-diversity of bee communities between restored and habitat patches because they facilitate many ecological processes affecting the bee communities (e.g. dispersal, migration, colonization), as highlighted by Lane et al. (2020) (see Fig. 2B).

Diverse restoration strategies demonstrated distinct impacts on bee communities. In ecosystems with a historical legacy of human management, such as seminatural grasslands, the land use (e.g., abandoned, actively restored, intact grasslands) did not influence the composition of functional traits of bee communities (Winsa et al. 2017). For example, the abundance of short and long-tongued bees was positively associated with the floral resource abundance independently of the strategy used on grassland restoration (Rotchés-Ribalta et al. 2018). In prairie restoration, habitat management using bison grazing negatively affected bee abundance (Griffin et al. 2021). These large mammals can diminish the availability of floral resources and alter soil conditions affecting below-ground nesting bee species (Griffin et al. 2021). This management strategy and prescribed fire in prairie ecosystems would be better designed in a rotation system to minimize negative effects on some bee groups such as above-ground bees (Tonietto et al. 2017; Griffin et al. 2021).

The land use also in the landscape influenced the bee community's attributes. There was a lower bee diversity in disturbed environments before restoration, a trend that reversed after restoration (Kremen et al. 2018; Purvis et al. 2020). A higher bee abundance was also observed within conserved and restored tropical forest areas compared to other land uses such as crops (Montoya-Pfeiffer et al. 2020). Changes in the land use in these tropical ecosystems negatively affected several functional bee traits. This effect was lower for small and medium-sized ground-nesting bee species and polylectic diet than for medium and large above-ground nesting bee species with social or parasitic behavior, which were more prevalent in conserved and restored areas (Montoya-Pfeiffer et al. 2020). Consequently, there is a species turnover in conserved and restored forests about other human land uses (Montoya-Pfeiffer et al. 2020). Thus, ecological restoration initiatives for increasing habitat amount at the landscape level are essential for promoting the recovery of bee communities.

4. FINAL REMARKS

Bees, as primary pollinators of flowering plants, play a crucial role in ecosystem functioning. Therefore, the recovery of these hymenopteran communities is essential to the restoration outcomes. Many restoration initiatives towards creating bee-friendly habitats have been implemented in agricultural landscapes, thus favoring bee colonization and crop pollination (Winfree 2010; Kremen et al. 2018). Our study underscores that restoration initiatives focusing on wild bee communities should be based on the ecological requirements of bee species found in the nearest remaining habitat patches. Additionally, we emphasized the importance of landscape variables such as habitat cover and spatial isolation on bee recovery.

Few studies concerning the effects of landscape structure on the recovery of bee communities highlight the importance of new studies evaluating how the landscape context influences different ecological processes in restored areas. It caught our attention that most of the studies were carried out in temperate ecosystems. However, studies must be considered in other ecosystems (e.g., tropical forests) to expand our understanding of how local and landscape attributes influence biodiversity recovery.

The recovery of bee communities is a process influenced by a complex interplay of local and landscape factors. While the bee abundance and richness seem to be easily recoverable after restoration, the species composition experiences a time lag and is shaped by various factors including plant community characteristics, landscape

composition, and configuration. Based on this systematic literature review, we indicate some remarks related to the restoration of bee communities:

(1) ***Resource availability matters***: The availability of floral and nesting resources emerges as the primary local filters influencing bee species colonization. Implementing management strategies like establishing patches with plant species blooming in different seasons, along with providing nesting resources such as wood or other structures with cavities, can significantly enhance bee colonization in restored areas, particularly for species that nest in pre-existing cavities;

(2) ***Landscape habitat amount is crucial***: Landscapes with a higher habitat amount often exhibit a faster recovery in bee communities in restored sites. This scenario is friendly to species dispersal from source areas, involving diverse bee groups. Consequently, management strategies should be focused on increasing habitat amount and connectivity;

(3) ***Mindful management in ecosystems***: In ecosystems characterized by natural disturbance dynamics, such as prairies and temperate forests, caution should be exercised when implementing management strategies like fire and canopy opening during restoration. These actions, even benefiting some bee groups, can also diminish essential bee nesting resources, such as dry wood and wood cavities.

It's paramount to underscore that each ecosystem harbors its distinct biodiversity linked to its specific environmental characteristics. Strategies that prove effective in restoring bee communities within one region may yield different results elsewhere. Therefore, each restoration plan must be designed and based on the requirements of wild bee species and local and landscape attributes. This approach not only enhances the bee community recovery but also the re-establishment of crucial plant-pollinator ecological interaction, culminating in overall restoration success.

5. SUPPLEMENTARY INFORMATION

The online version contains supplementary material available at https:// doi. org/ 10. 1007/ s13592- 024- 01095-3.

6. AUTHORS' CONTRIBUTIONS

LSC, MCR, and MCG designed the systematic review. LSC wrote the manuscript draft. MCG and MCR edited and reviewed the manuscript.

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8. AVAILABILITY OF DATA AND MATERIAL

Additional data is available in the Supplementary Material.

9. CODE AVAILABILITY

Not applicable.

10. DECLARATIONS

10.1 Ethics approval

Not applicable.

10.2 Consent to participate

Not applicable.

10.3 Consent for publication

Not applicable.

10.4 Conflict of interest

The authors declare no conflict of interest.

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Supplementary Appendix A. Articles used to evaluate the effects of landscape structure on the recovery of bee communities.

Reference	Year	Title	Journal	Study area	Ecosystem	Reference habitat	Number of bee sampling points	Bee sampling method	Buffer size
Denning and Foster	2018	Taxon-specific associations of tallgrass prairie flower visitors with site-scale forb communities and landscape composition and configuration	Biological Conservation	Kansas, United States	Prairie	Yes	10 (5 habitat remnants and 5 restorations)	Entomological net	250 m, 1 km
Ferronato et al	2017	Orchid Bee (Apidae: Euglossini) Communities in Atlantic Forest Remnants and Restored Areas in Paraná State, Brazil	Neotropical Entomology	Paraná, Brazil	Semideciduous tropical forest	Yes	8 (4 habitat remnants and 4 restorations)	Bait traps	-
Gobatto et al	2022	Agricultural landscape infuences on the solitary bees and wasps that nest in ecological restoration sites	Biodiversity and Conservation	Paraná, Brazil	Semideciduous tropical forest	No	9 (all restorations)	Nest traps	2 km
Griffin et al	2017	Wild bee community change over a 26-year chronosequence of restored tallgrass prairie	Restoration Ecology	Illinois, United States	Prairie	Yes	18 (3 cornfields, 12 restorations and 3 habitat remnants)	Pan traps and vane traps	500 m
Griffin et al	2021	Bee communities in restored prairies are structured by landscape and management, not local floral resources	Basic and Applied Ecology	Illinois, United States	Prairie	No	14 (all restorations)	Bowl arrays and blue vane traps	500 m
Lane et al	2020	Floral resource diversity drives bee community diversity in prairie restorations	Journal of Applied Ecology	Minnesota, United States	Prairie	No	16 (all restorations)	Entomological net	1.5 km

		along an agricultural landscape gradient							
Lane et al	2022	Differences in bee community composition between restored and remnant prairies are more strongly linked to forb community differences than landscape differences	Journal of Applied Ecology	Minnesota, United States	Prairie	Yes	20 (10 habitat remnants, and 10 restorations)	Entomological net, bee bowl arrays and blue vane trap	1.5 km
Montoya-Pfeiffer et al	2020	Bee pollinator functional responses and functional effects in restored tropical forests	Ecological Applications	São Paulo, Brazil	Semideciduous tropical forest	Yes	52 (4 conserved fragments, 5 disturbed fragments, 15 restoration plantings, 12 anthropogenic wetlands, and 16 sugarcane fields	Pant traps and bait traps	1 km
Novotny and Goodell	2020	Rapid recovery of plant-pollinator interactions on a chronosequence of grassland-reclaimed mines	Journal of Insect Conservation	Ohio, United States	Grasslands	No	10 (all restorations)	Entomological net	1,5 km (scale defined from a previous multiscale analysis)
Öckinger et al	2018	Mobility and resource use influence the occurrence of pollinating insects in restored seminatural grassland fragments	Restoration Ecology	Central region of Sweden	Seminatural grasslands	Yes	18 (14 habitat remnants, 18 restorations)	Entomological net	5 km
Purvis et al	2020	Wild bee community recovery in restored grassland-wetland complexes of prairie North America	Biological Conservation	Alberta, Canada	Grassland-wetland complexes	Yes	25 (20 restorations, 3 prairie-wetland remnants, and 2 unrestored wetlands)	Blue vane trap, pan traps	500 m, 2 km

Ritchie et al	2020	Pollination of a bee-dependent forb in restored prairie: No evidence of pollen limitation in landscapes dominated by row crop agriculture	Restoration Ecology	Minnesota, United States	Prairie	No	7 (although the study considered 8 restorations, bees were sampled in only 7)	Entomological net	1.5 km
Rotchés-Ribalta et al	2018	Associations between plant and pollinator communities under grassland restoration respond mainly to landscape connectivity	Journal of Applied Ecology	South central region of Sweden	Seminatural grasslands	Yes	38 (10 abandoned grasslands, 18 restored grasslands, and 10 intact grasslands with grazing)	Sweep net	5 km
Tonietto et al	2017	Bee communities along a prairie restoration chronosequence: Similar abundance and diversity, distinct composition	Ecological Applications	Illinois, United States	Prairie	Yes	18 (4 abandoned agricultural fields, 4 habitat remnants, and 10 restorations)	Entomological net and pan traps	1 km
Winsa et al	2017	Sustained functional composition of pollinators in restored pastures despite slow functional restoration of plants	Ecology and Evolution	Central region of Sweden	Seminatural grasslands	Yes	38 (10 abandoned grasslands, 18 restored grasslands, and 10 grasslands with grazing)	Sweep net	5 km
Kremen et al	2018	Pollinator community assembly tracks changes in floral resources as restored hedgerows mature in agricultural landscape	Frontiers in Ecology and Evolution	California, United States	Prairie	No	15 (5 restored edges and 10 non-restored control edges)	Entomological net	1 km

Scheper et al	2015	Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries	Journal of Applied Ecology	Germany, Sweden, the Netherlands and the United Kingdom	Undefined (the study did not bring any reference to location or coordinates)	No	64 (16 by country- 8 restored wildflower strips and 8 field unrestored boundaries)	Unable to set	1 km
Ponisio et al	2019	Proximity of restored hedgerows interacts with local floral diversity and species' traits to shape long-term pollinator metacommunity dynamics	Ecology Letters	California, United States	Prairie	No	39 (18 restored hedgerows, 21 unrestored field margins)	Entomological net	50 m on a log scale (1 km, 7 km)

Reference	Year	Landscape metric level (patch, class or landscape)	Explanatory landscape metrics (Composition and/or Configuration)	Local explanatory variables	Response variables of bee communities
Denning and Foster	2018	Class, Landscape	Composition and Configuration (proportion of warm-season grasslands, proportion of natural/semi-natural (NSN) lands, and edge density)	Yes (forb abundance, richness and species composition)	Species richness, abundance, diversity and composition, interaction network
Ferronato et al	2017	Patch	Composition (patch size, width and length)	Yes (mean local temperature, relative humidity)	Species abundance and composition
Gobatto et al	2022	Class	Composition (reforestation area (ha), forest fragment area, and soybean/corn monoculture area (ha), distances (m) between the restorations and the nearest forest patch)	No	Species richness, abundance, diversity and composition
Griffin et al	2017	Class	Composition (percentage wooded land, and percentage agricultural land)	Yes (restoration size and age)	Richness rarefied, abundance, species compostion, beta diversity components (species replacement and richness effects)
Griffin et al	2021	Class	Composition (percentage of prairie and percentage of forest)	Yes (restoration age, management restoration variables- presence of bison and burning regime)	Bee richness and abundance

Lane et al	2020	Class	Composition (percentage of agriculture)	Yes (floral resource richness, restoration size and age)	Effective number of species, beta diversity- Bray–Curtis dissimilarity
Lane et al	2022	Class	Composition (amount of agricultural land use)	Yes (forb community dissimilarity, restoration age)	Effective number of species, species composition and dissimilarity, bee functional traits (bee tongue length and lecticity)
Montoya-Pfeiffer et al	2020	Patch	Compostion (Fragment cover area)	Yes (habitat type- conserved fragments, disturbed fragments, restoration plantings, anthropogenic wetlands, and sugarcane fields, and plant communities)	Overall bee abundance and plant frequency, functional richness, diversity, dissimilarity of bees and plants, interaction network indices, bee abundance/plant frequency, functional richness and diversity, functional dissimilarity)
Novotny and Goodell	2020	Class	Composition (proportion of forest, herbaceous and pasture, crop, and developed land)	Yes(site age, flower richness, flower abundance, flower diversity, flowering plant community composition)	Bee richness and abundance, bee community composition, plant–bee networks
Öckinger et al	2018	Landscape	Configuration (connectivity index described by Hanski et al. (2000))	Yes (time since restoration and area of the restored pasture)	Occurrence of solitary bee and bumblebees species in restored and intact pastures, species traits (intertegular distance, diet breadth- oligolectic or polylectic, nest site preferences- parasitic, renters, carders, ground excavators) and number of indicator species
Purvis et al	2020	Class	Composition (proportion of non-cropped land cover)	Yes (time since restoration, site type, floral diversity and abundance, percent bare ground, soil compaction)	Bee abundance and diversity (bumble bees excluded and bumble bees alone), species composition
Ritchie et al	2020	Class	Composition (proportion of surrounding agriculture)	No	Bee abundance
Rotchés-Ribalta et al	2018	Landscape	Configuration (connectivity index described by Hanski et al. (2000))	Yes (grassland type- abandoned, restored or intact,flowering plant abundance, species richness, species evenness, functional richness and functional composition)	Bee abundance, richness, evenness, functional richness and functional evenness, abundance of feeding guilds- oligolectic and polylectic bees, species traits (body size, sociality, lecticity, tongue length, nesting type and the start date and length of the flight period)
Tonietto et al	2017	Class	Composition (proportion of natural area)	Yes (blooming plant abundance and diversity, mean bare ground,restoration age, site type)	Bee abundance and diversity, species composition, community-weighted mean

					trait values, beta diversity (taxonomic and functional differentiation)
Winsa et al	2017	Class, Landscape	Composition and Configuration (proportion of tree and shrub cover, connectivity index described by Hanski et al. (2000))	Yes (time since restoration, abandonment time, pasture area, mean vegetation height, mean flower abundance, grassland type- abandoned, restored or intact)	Species composition and community trait composition (intertegular distance, sociality, lecty, tongue length, nesting trait, flight start, flight period)
Kremen et al	2018	Class	Composition (area of surrounding natural habitat)	Yes (floral diversity, nesting resources- percentages of bare ground and dead wood)	Abundance, Richness, Evenness and diversity of bees; functional traits (sociality, nesting location, nesting habit and lecty, the species pollinate crops, mean body size and floral resource specialization)
Scheper et al	2015	Class	Composition (cover of the land-use types, proportion of semi-natural habitat suitable as foraging and nesting sites for bees)	Yes (land-use intensity- N input; floral resource availability- flower cover and richness)	Bee abundance and richness (bumblebees and solitary bees), abundance and species richness of Red List species
Ponisio et al	2019	Class	Composition (amount of remnant habitat)	Yes (floral diversity)	Metacommunity network, colonization and persistence

CAPÍTULO II

NDVI PREDICTS THE OUTCOMES OF NATURAL REGENERATION AND ACTIVE RESTORATION ON BEE COMMUNITIES WITHIN THE ATLANTIC FOREST, BRAZIL[2]

Abstract: Biodiversity monitoring is essential for assessing restoration outcomes, and this relies on ecological indicators sensitive to environmental changes. Remotely sensed metrics are efficient and increasingly available, but their ability to predict plant and animal diversity still requires careful evaluation. Here, we assessed the power of spectral diversity and landscape composition metrics to predict the alpha diversity of Euglossini bee communities in the Atlantic Forest of Brazil. Within 12 landscapes, we recorded euglossine males in three habitat types: conserved forests, habitats undergoing natural regeneration, and habitats under active restoration. We used Generalized Linear Mixed Models to assess the influence of spectral and landscape structure on bee diversity. Euglossine abundance and richness did not differ statistically among habitat types. Standard deviation of NDVI was a better predictor of euglossine richness, abundance, and diversity than landscape composition variables (forest cover (%) and landscape heterogeneity). The effect of spectral diversity was positive on bee abundance and richness in the forest but negative on euglossine communities in restored habitats. Our study shows that spectral diversity can predict bee diversity and assess restoration outcomes. It highlights the importance of forest restoration regardless of management practices for biodiversity recovery in fragmented landscapes.

Keywords: Orchid bees, restoration strategies, NDVI, spectral diversity, landscape composition, biodiversity monitoring

[2] Manuscrito em revisão no periódico *Perspectives in Ecology and Conservation*: Carneiro, L.S., Ribeiro, M.C., Ricketts, T., Santos, J.S.S., Frantine-Silva, W., Gaglianone. NDVI predicts the outcomes of natural regeneration and active restoration on bee communities within the Atlantic Forest, Brazil.

1. INTRODUCTION

Biodiversity loss due to unsustainable land use intensification and climate change has affected ecosystems worldwide. These threats are particularly concerning because of the important role played by biodiversity in providing ecosystem services, such as crop pollination, water supply, pest and natural enemies responses, and disease control (Zhang et al. 2007; Duarte et al. 2018).

The increasing demand for ecosystem services driven by human population growth underscores the urgency of restoring degraded ecosystems, thereby contributing to biodiversity conservation. As a consequence, the "Decade of Ecological Restoration" established by the United Nations - UN recognizes the essential role of ecological restoration in the recovery of ecosystems (UN, 2019). Initiatives such as the Bonn Challenge aim to recover 350 million hectares of forest ecosystems worldwide to mitigate the effects of the climate crisis and the anticipated species extinctions in the coming decades (Strassburg et al. 2020).

Ecological restoration encompasses diverse methods for recovering degraded and destroyed ecosystems and enhancing their resilience (SER, 2004). Two primary strategies adapted to the specificities of ecosystems have guided restoration practices worldwide: passive and active restoration. In passive restoration (hereafter natural regeneration), the environments regenerate naturally with reduced human participation (Rodrigues et al. 2009; Suding, 2011; Meli et al. 2017). In certain instances, the success of this strategy depends on ecosystem resilience, which is gathered by interventions such as introducing species with low colonization potential (Holl and Aide, 2011). On the other hand, active restoration is driven by human management and spans from improving local conditions (e.g., increasing soil fertility) to selecting and planting target species for restoration (Suding, 2011; Holl and Aide, 2011).

The assessment of restoration outcomes is commonly performed via indicators measured in the field such as species taxonomic and functional diversity, community composition, and vegetation structural characteristics (Taddeo and Dronova, 2020; Oliveira et al. 2021). However, survey of biological data demands high sampling effort and financial resources, which is challenging over wide spatial areas and over time (Palmer, 1995; Magurran, 2013). As a result, remote sensing data such as satellite images have been used to predict plant taxonomic and functional diversity (Perrone et al. 2023) and assess

the restoration outcomes (Taddeo and Dronova, 2018; Taddeo and Dronova, 2020; McKenna et al. 2022). These data can offer accessible information and provide crucial insights into large-scale biodiversity dynamics (Pettorelli et al. 2005; Pettorelli et al. 2014), including information on restoration success (McKenna et al. 2022).

In particular, spectral indexes derived from satellite images such as NDVI (Normalized Difference Vegetation Index, Rouse et al. 1973) have been used to predict species diversity in different ecosystems (Wu et al. 2021; Benedetti et al. 2023). Spectral indexes combine the spectral reflectance from two or more wavelengths to synthesize information about land surface features such as vegetation. Spectral indexes have been long employed to map vegetation dynamics and to test the Spectral Variability Hypothesis (Palmer et al. 2000; Palmer et al. 2002), which argues that the variability in spectral signals is linked to variation in plant community parameters, indicating spatial heterogeneity within habitats (Palmer et al. 2002; Wang and Gamon, 2019; Fassnacht et al. 2022). Spectral heterogeneity is expected to positively correlate with species richness in situ since heterogeneous habitats support higher niche availability and consequently, a higher number of species (Palmer et al. 2002; Perrone et al. 2023). Mature forest habitats exhibit greater complexity in the vegetation strata and lower spectral variability compared to young restored areas, which experience rapid vegetation changes due to ecological succession dynamics (Valtonen et al. 2021). In conserved vegetation areas, disturbances can increase spectral variability, positively affecting species diversity (Palmer et al. 2002; Stein et al. 2014; Fassnacht et al. 2022). However, in restored and open habitats with low vegetation complexity, this relationship may be negative (Gillespie, 2005; Oindo and Skidmore, 2002). Thus, remote sensing metrics show promise but must be carefully evaluated against a range of taxa, especially in biodiversity hotspots where ecosystem restoration is a global priority (Perrone et al. 2023).

Despite being primarily employed for monitoring plant community dynamics, spectral index variability is valuable for understanding ecological responses at higher trophic levels, such as animal communities (Pettorelli et al. 2005; Camarreta et al. 2020). Spectral variability linked to vegetation variations and land use changes has explained animal abundance and richness in natural and modified ecosystems (Levanoni et al. 2012; Leong and Roderick, 2015; Wu et al. 2021; Benedetti et al. 2023). Consequently, spectral indexes can be useful for understanding the influence of vegetation variations and habitat diversity on the recovery of animal communities in natural ecosystems.

Importantly, animal community recovery within a site is influenced by attributes of

the surrounding landscape such as habitat amount and isolation, because they affect ecological dynamics such as species dispersal and migration in restored habitats (Fahrig, 2003; Pardini et al. 2010). Positive effects of the habitat amount and land use diversity (i.e. landscape compositional heterogeneity) on biodiversity recovery have been observed in different animal groups, such as mammals (Mérő et al. 2015), birds (San-José et al. 2022) and bees (Kremen et al. 2018; Gobatto et al. 2022).

Bees are key organisms for restoration outcomes. Considering the mutualistic interaction between plants and bees, the restoration of both communities is self-reinforcing, driven by positive feedback. The restoration of plant communities depends on bees because of their essential role as primary pollinators of flowering plants, especially in tropical habitats (Dixon, 2009, Deprá et al. 2022). On the other hand, the reestablishment of bee communities in restored habitats depends on the availability of nesting sites and floral resources, factors influenced by vegetation structural complexity, and species composition (Dixon, 2009; Cariveau et al. 2020). Besides these local factors, landscape variables such as habitat amount, spatial isolation, and land use diversity surrounding restored areas influence bee colonization and persistence in these new habitats (Dixon, 2009; Kremen et al. 2018; Cariveau et al. 2020).

One of the main bee groups in the forest habitats in the Neotropical region, Euglossini bees, or orchid bees, are crucial pollinators for over 40 botanical families (Roubik and Hanson, 2004). These bees could be important proxies to evaluate restoration effectiveness, especially considering the easy sampling of euglossine males (Roubik and Hanson, 2004; Hipólito et al. 2023). Moreover, most 250 euglossine species have biological requirements typically found in conserved forests. Euglossine males rely on fragrant resources primarily sourced from orchid flowers, while females depend on forest-provided nesting sites (Roubik and Hanson, 2004). These bees also respond to local habitat variations (Sobreiro et al. 2019; Hipólito et al. 2023), as well as landscape composition and configuration (Carneiro et al. 2021; Sousa et al. 2022). Euglossine communities can therefore be important ecological indicators for assessing the recovery of bee communities in restored forest habitats with different management strategies.

Given the importance of biodiversity monitoring in restored areas, here we address the effects of spectral diversity (standard deviation of NDVI – *sd*NDVI, Rouse et al. 1973) and landscape composition variables (forest cover (%) and landscape compositional heterogeneity) on euglossine alpha diversity (abundance, richness, Shannon and inverse Simpson diversities) within different forest habitats in the Atlantic Forest in Brazil. We

recorded bee data in conserved forest sites (hereafter forest) and habitats undergoing natural regeneration and active restoration. We hypothesized a higher explanatory power of forest cover (%) on the euglossine alpha diversity since euglossine species show a high dependence on forest cover in the landscape (Carneiro et al. 2022; Corrêa-Neto et al. 2024) (Fig. 1A). Also, we expected a greater explanatory power of *sd*NDVI than landscape compositional heterogeneity, considering that euglossine species are sensitive to environmental heterogeneity within habitats (Houbik and Hanson, 2004; Brito et al. 2017; Sobreiro et al. 2019) (Fig. 1A). In forest habitats, we expected a positive effect of forest cover (%), *sd*NDVI, and landscape compositional heterogeneity on euglossine communities (Carneiro et al. 2022; Corrêa-Neto et al. 2024) (Fig. 1B-1D). Considering the positive effect of habitat amount in the landscape on biodiversity recovery and euglossine bees (Pardini et al. 2010; Carneiro et al. 2022), we expected positive effects of forest cover (%) on euglossine communities in restored habitats (Fig. 1B). Finally, we expected negative effects of *sd*NDVI and landscape compositional heterogeneity on euglossine communities in restored habitats because of the lower habitat heterogeneity and forest cover (%) in the landscape (Brito et al. 2017; Corrêa-Neto et al. 2024) (Fig. 1C-1D).

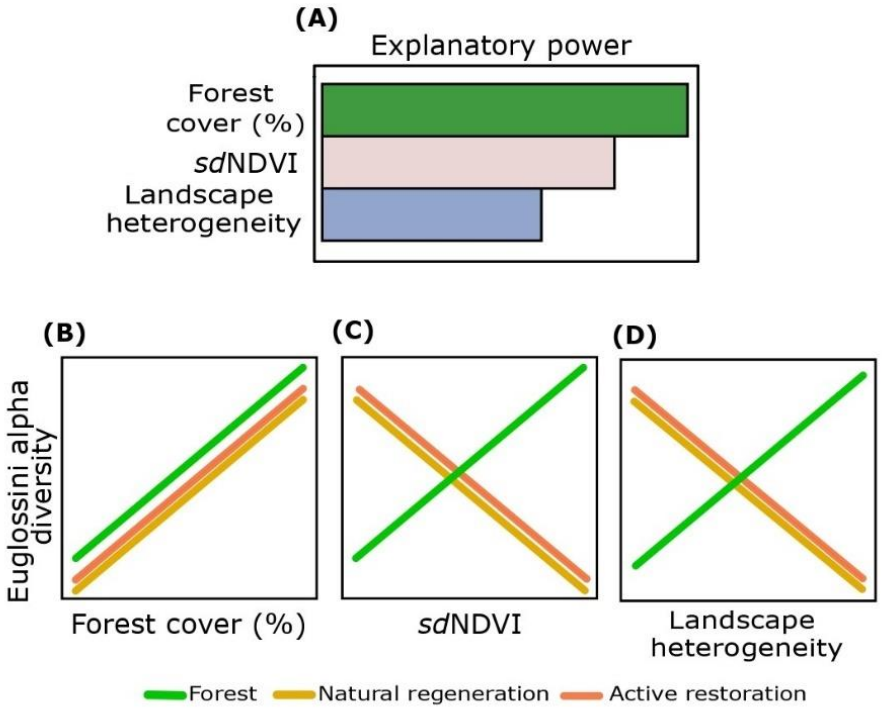

Figure 1. Expected explanatory power **(A)** and expected patterns **(B-D)** about the influence of forest cover (%), landscape heterogeneity, and *sd*NDVI on the alpha diversity of

euglossine bees in natural habitats with different management in the Atlantic Forest (forest, natural regeneration, and active restoration).

2. MATERIAL AND METHODS

2.1 Study area

Our study area comprises the Mosaic of Conservation Reserves of the Golden Lion Tamarin (*Leonthopithecus rosalia rosalia* L., ICMBio, 2023) within the Atlantic Forest ecoregion in the north-central Rio de Janeiro state, Southeast Brazil (Fig. 2A, Supplementary Material Appendix A). The region includes 21 protected areas under different levels of public and private protection (ICMBio, 2023). The Atlantic Forest is one of the world's most endangered biodiversity hotspots (Mittermeier et al. 2011), and this region keeps a high species diversity, with several endemic and threatened species (ICMBio, 2023).

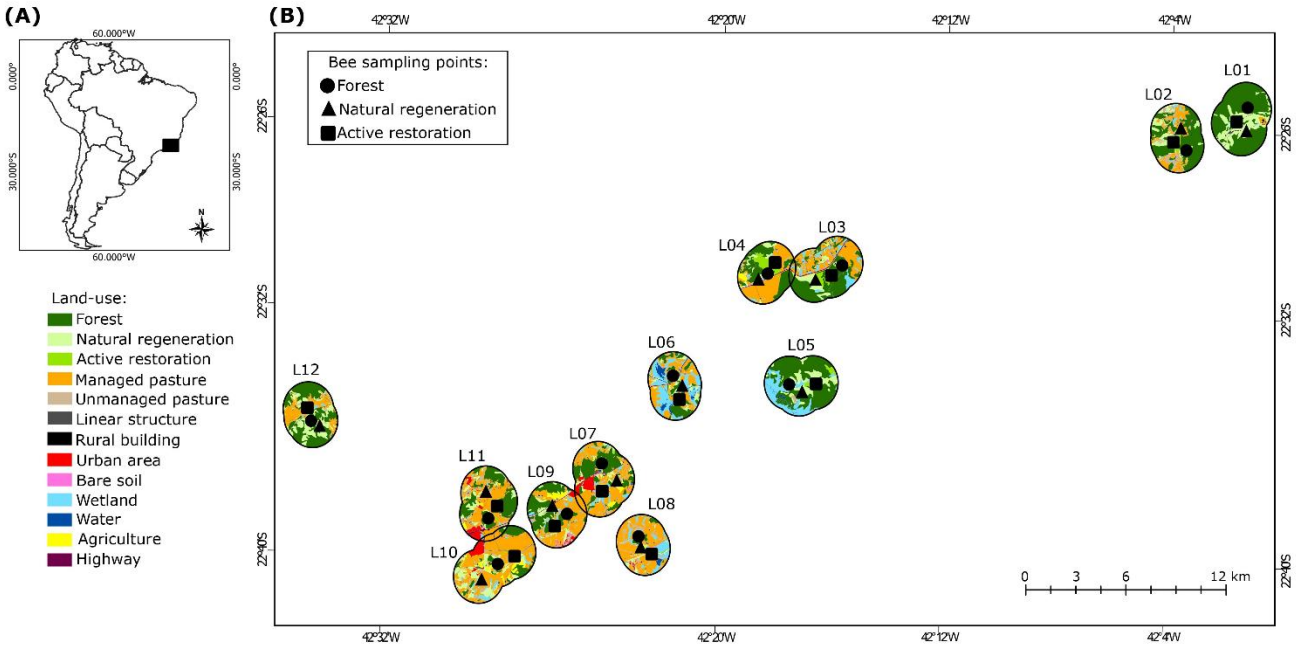

Figure 2. **(A)** Location of the study area, within the Atlantic Forest ecoregion, Rio de Janeiro state, Southeast Brazil; **(B)** Land cover composition of the studied landscapes (L1-L12) and the location of 36 sampling sites of euglossine bees in three habitat types (forest- circles, naturally regenerated- triangles, and actively restored- squares) in each landscape. Each landscape represents three 1,500-m dissolved buffers, using bee sampling points in the forest, natural regeneration, and active restoration sites as the center.

The forest loss in our study area resulted from various anthropic pressures over centuries, from agricultural activities in the 19th to current urban expansion (Lima et al. 2006; ICMBio, 2023). In this sense, habitat restoration in the Atlantic Forest is a global priority (Strassburg et al. 2020). Due to different public and private incentives, several regions of the Atlantic Forest present a mosaic of areas undergoing natural regeneration and active restoration, including our study area (Fig. 2B, Supplementary Material Appendix A). The areas of natural regeneration in this region have replaced degraded lands previously covered by pasture or agriculture (Tonetti et al. 2023).

The natural vegetation types within the study area correspond to lowland and submontane-dense ombrophilous forests (Carvalho et al. 2008; ICMBio, 2023). Besides conserved and restored forests, the study area presents other land covers such as pasture, agriculture, building areas, and wetlands (Fig. 2B). The region has a humid tropical climate of *Aw* type according to the Köppen classification, with a hot, rainy summer and a short dry winter. The average temperature ranges between 18°C and 24°C, and the average rainfall between 1100 mm and 2400 mm (ICMBio, 2023).

2.2 Sampling design

We sampled bees in 12 landscapes in different habitat types (forest, natural regeneration, and active restoration), being three habitats per landscape and 36 sampling sites in total (three sampling points * 12 landscapes) (see Fig. 2B, Supplementary Material Appendix A). Thus, each landscape (L01 to L12) was three dissolved nested landscapes, each corresponding to one habitat type. The selection criteria for the 12 landscapes were based on the presence of regenerated and actively restored areas surrounding conserved forest patches. The minimum distance between the bee sampling points within each nested landscape was 300 m (mean= 787.6 ± 438.6 m). We delimited each landscape by performing a join of concentric circles (buffers) of 1,500 m-radius size (706.9 ha) around each sampling site (Fig. 2B). This buffer size has been used to evaluate the influence of landscape composition on euglossine bees (Carneiro et al. 2021; Côrrea-Neto et al. 2023).

2.3 Conserved forests, active restoration program, and natural regeneration areas

We chose conserved forest patches of different sizes (minimum= 17.6 ha, maximum= 494.0 ha, mean= 167.4 ± 165.5 ha) with low or none anthropogenic pressure in the last 30 years to represent our reference site in each landscape. Forest patches in the Atlantic Forest aged beyond four decades can be classified as old forests, considering their vegetation structure and composition (Toledo et al. 2020). We used the time series of

Google Earth images to ensure that the forest patches were not young regenerated forests (Landsat TM images: 1985 to 2008, high-resolution images: from 2008). In addition, most of the forest patches chosen are located in nature reserves within the Mosaic of Conservation Reserves of the Golden Lion Tamarin.

The actively restored habitats are initiatives undertaken by the Golden Lion Tamarin Association (AMLD; *Associação Mico-Leão-Dourado*) to protect golden lion tamarin populations, a primate species at extinction risk (AMLD, 2022). To achieve this goal, the AMLD has planted 816,000 seedlings across 440 hectares in partnership with decision-makers and local communities (AMLD, 2022). In general, these areas are managed by the removal of human-induced activities, enhancement of local conditions, and plantation of native tree species of the Atlantic Forest. The seedlings encompass successional stages ranging from pioneer to late-secondary of botanical families characterized by high species richness and abundance in the biome (e.g., Fabaceae, Rubiaceae, Verbenaceae, Malvaceae, Urticaceae) (Silva et al. 2023). Seedlings are planted in parallel rows with a minimum distance of two meters between them, following the management guidelines of the Atlantic Forest Restoration Pact (https://www.pactomataatlantica.org.br). Initial restoration management spans the first two years and includes the removal of exotic species and replanting of seedlings. Plantings established in degraded areas such as pastures show vegetation with no canopy structure during the first years of restoration, with many open areas and a poor understory (Silva et al. 2023). Old restored areas usually had closed canopies because of the successful growth of planted tree species, although certain areas may still lack a developed understory. The selected AMLD restoration projects were implemented between 2002 and 2018, varying in size from 0.6 to 56.0 ha (mean= 10.2 ± 15.2 ha).

We chose naturally regenerated habitats based on a gradient of vegetation recovery. In general, these environments had no animal grazing. Young regenerated areas in this region exhibit a scattered distribution of trees and an open canopy, with a high plant species abundance from early successional stages of the Atlantic Forest (e.g., *Miconia* spp, *Attalea* spp) and a dense understory predominantly composed of pioneer plant species (Lima et al. 2006). In contrast, old regenerated areas show dense canopies featuring tree species from secondary to late successional stages (e.g., *Tibouchina* spp, *Nectandra* spp) (Lima et al. 2006). Anthropogenic disturbances in these sites include logging, and in some areas, we visually observed some exotic plant species (e.g.,

Artocarpus heterophyllus). The size of these sites ranged from 1.7 to 91.2 ha (mean= 33.5 ± 49.5 ha).

The age of active restoration sites ranges from 5 to 21 years, with a closed canopy visually observed from 7 to 10 years of growing. The naturally regenerated sites aged from 10 to 24 years. Details about the relationship between restoration age and euglossine communities can be found in Supplementary Material B.

2.4 Euglossini bee sampling

We sampled euglossine males with five bait traps (eucalyptol, eugenol, methyl cinnamate, methyl salicylate, and vanillin). These traps were built with polyethylene terephthalate (PET) bottles. In each one, three lateral bottle cones allowed bees access to a cotton ball soaked with bait inside the trap (Aguiar and Gaglianone, 2008). This passive sampling method is essential for large-scale ecological studies, facilitating standardized sampling across multiple areas (Carneiro et al. 2021; Hipólito et al. 2023).

Field expeditions occurred during the rainy season in November 2021, December 2022, and March 2023, coinciding with the peak activity period of euglossine bees, particularly when seasonal species emerge (Roubik and Hanson, 2004). Bee sampling occurred in the 36 sites during two field expeditions, each lasting three days, totaling six sampling days. The sampling was simultaneous in the three habitat types within each landscape (i.e. forest, active restoration, and natural regeneration). The five bait traps within each sampling site were placed in the vegetation at a height of 1.5 m and a minimum distance of 2.0 m between each (Aguiar and Gaglianone, 2008; Carneiro et al. 2021).

The traps were set up early in the morning of the first sampling day (06:00 am to 08:00 am) and remained until the afternoon of the third sampling day (3:00 pm to 5:00 pm) when the bees were collected. Bait traps keep their attractiveness to euglossine males for several days even without bait replenishment (Coswosk et al. 2019). However, considering the rapid evaporation of eucalyptol and its high attractiveness for euglossine males (Aguiar and Gaglianone, 2008; Ramalho et al. 2009), we left a 5 ml eppendorf filled with eucalyptol into the trap connected to the cotton by a nylon string allowing bait auto-recharge by capillarity (Sobreiro et al. 2019).

The sampled bees were pinned, tagged, and deposited in the Bee Collection of the Experimental Ecology Sector of the Laboratório de Ciências Ambientais (LCA), Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF). The bees were identified using taxonomic keys (Rebêlo and Moure, 1995; Nemésio, 2009), comparison to

reference specimens sampled in the study area (Ramalho et al. 2009), and validated by a taxonomist specialist.

2.5 Response variables

We calculated four response variables of the alpha diversity of euglossine communities: bee abundance, and Hill numbers in q= 0 (species richness), q= 1 (Shannon entropy, hereafter Shannon diversity), and q= 2 (inverse Simpson diversity) (Supplementary Material Appendix C). Hill numbers incorporate the exponent q to express the effective number of species, increasing sensitivity to species dominance as q rises (Hill, 1973; Chao et al. 2014). We used the *hillR* function from the hill R package to obtain the Hill numbers (Li, 2018). Bee abundance accounted for species abundance excluding the highly dominant species *Euglossa cordata* (Linnaeus). This orchid bee species exhibits remarkable environmental plasticity with high dominance across different ecosystems in the Atlantic Forest ecoregion (Aguiar and Gaglianone, 2008; Ramalho et al. 2009), resulting in underestimation of the effect of predictor variables on rare species abundance (Carneiro et al. 2021). Indeed, the null model best explained total abundance (see Supplementary Material Appendix C). Then, all results correlating spectral and landscape variables with bee abundance excluded the *E. cordata* abundance.

2.6 Land cover mapping

We mapped the land cover within each landscape by performing a visual interpretation in high-resolution satellite images available in the basemap of ArcGIS Pro software version 3.1.0 (CommunityArcGIS Pro 3.1.0, 2023). We performed a manual classification, using vectorial tools available in ArcGIS in a scale of 1:2,500. We identified the land cover classes based on our knowledge of the study area and fieldwork experience. In total, we mapped 13 land cover classes: forest, active restoration, natural regeneration, managed pasture, unmanaged pasture, linear structure, rural building, urban area, bare soil, wetland, water, agriculture, and highway (Fig. 2B). Most of these classes have been used to predict euglossine communities in fragmented landscapes (Carneiro et al. 2021; Carneiro et al. 2022). We identified the areas of active restoration using the spatial data (shapefiles) from the AMLD restoration project described before (2.3 item). To identify the areas of natural regeneration, we used the map of secondary vegetation freely available in the MapBiomas database (Collection 8: 2022, Souza et al. 2020), and multitemporal high-resolution images from Google Earth. The landscape classification was validated during the field expeditions.

2.7 Landscape composition metrics and spectral index at multi-scales

We rasterized the previously described land cover map (5-m resolution) to quantify forest cover (%) (Percentage of Classes- PLAND metric), and landscape compositional heterogeneity using the Shannon Diversity Index (SHDI metric) (McGarigal, 2015). To assess the scale of effect, which represents the spatial extent to which variable responses are best predicted by landscape variables (Jackson and Fahrig, 2012), we estimated each landscape metric (forest cover (%) and SHDI) in concentric buffers of different radius sizes ranging from 250 to 1500 m, with 250 m of interval (Supplementary Material Appendix C). To calculate the landscape metrics, we used the *lsm* function available in the landscapemetrics package (Hesselbarth et al. 2019).

To assess the spectral diversity of different types of forest habitats by remote sensing data, we calculated the standard deviation (*sd*) of the Normalized Difference Vegetation Index (NDVI; Rouse et al. 1973) from Sentinel 2A and B satellite images with 10 m of spatial resolution available in the Google Earth Engine platform - product COPERNICUS/S2_SR_HARMONIZED, using the cloud mask calculated from QA60 band. We chose the NDVI because this index has been widely used to describe vegetation conditions, and spectral diversity indexes derived from NDVI images have demonstrated high power to predict plant taxonomic and functional diversity (Bailey et al. 2004; Valtonen et al. 2021; Perrone et al. 2023). The NDVI corresponds to the normalized difference between the reflectance in the electromagnetic spectrum's near-infrared (NIR) and red (Red) wavelengths. We downloaded a total of 596 images from January/2021 to March/2023, corresponding to the scenes 23KQR, 23KQQ, 23KRR, and 24KTA. The total of images acquired for 2021, 2022, and 2023 were 267, 256, and 73, respectively. We defined this period of image searching based on the duration of bee sampling.

Firstly, we calculated the NDVI for all images using the formula NDVI = (NIR – Red) / (NIR + Red). Second, we quantified the *sd*NDVI pixel-to-pixel for the set of NDVI images. Lastly, we calculated the average of *sd*NDVI for all polygons of natural vegetation corresponding to each habitat type (forest, natural regeneration, and active restoration). The average of *sd*NDVI was obtained in concentric buffers ranging from 250 to 1500 m, as described previously (Supplementary Material Appendix C). The natural vegetation polygons were obtained from our land cover map.

2.8 Statistical analyses

We used a one-way ANOVA with a 95% significance level to assess variations in species richness and abundance among the three habitat types (i.e., forest, active restoration, and natural regeneration). Afterward, we used the *multifit* R function (Huais, 2018) to identify the scale of effect of each predictor variable (*sd*NDVI, forest cover (%), and SHDI) on euglossine communities. Linear Models (LMs) were fitted using the predictor variables quantified previously in multi-scale (250 to 1500 m) and habitat type as a covariate. The scale with the highest value of R^2 was selected for the subsequent analyses (Supplementary Material Appendix D Fig. A-D).

To assess the influence of predictor variables on response variables (bee abundance, species richness, Shannon and inverse Simpson diversities), we modeled the data using Generalized Linear Mixed Models (GLMMs). Fixed effects included *sd*NDVI, forest cover (%), and landscape heterogeneity (SHDI). Also, we considered the habitat type (forest, natural regeneration, and active restoration) as a fixed effect because our objective was to evaluate the variation in the euglossine communities associated with habitat management. We considered the landscape code (L01 to L12) the random effect because the landscapes are spatially nested (i.e., each of the 12 landscapes represents three nested landscapes).

The bee abundance showed overdispersion and was modeled with negative binomial error distribution, while Hill numbers (species richness, Shannon, and inverse Simpson diversities) were analyzed with normal error distribution. Initially, we tested the best structure of the fixed effect habitat type through two alternatives: (a) y~ forest cover + landscape heterogeneity * habitat type + (1|landscape), and (b) y~ forest cover + landscape heterogeneity + habitat type + (1|landscape). We used the Maximum Likelihood method (ML) with the ANOVA test to determine the best model structure (Zuur et al. 2009). Both structures were feasible for all response variables following the ML results (*Chisq p* > 0.05). Then, we built univariate GLMMs considering habitat type in additive and interaction structures (Supplementary Material Appendix E). A null model was used to test the hypothesis of no statistical relationship between response and explanatory variables. We used the *lmer* and *glmer.nb* functions from the lme4 R package for GLMM analyses (Bates et al. 2015). The models were plotted through the *lmerPredictionPlot* function from the r4eco package (http://github.com/wilsonfrantine/R4eco).

To identify which predictor variable had the greatest predictive power on euglossine alpha diversity, we ranked the models using the Akaike Information Selection Criterion

corrected for small samples (AICc) (Burnham and Anderson, 2002). The model with the lowest ΔAICc was considered the most parsimonious (Burnham and Anderson, 2002) (Supplementary Material Appendix E). Models with ΔAICc < 2.0 and model weight (*wi*) > 0.1 were also considered plausible to explain the patterns (Burnham and Anderson, 2002). We used the *ICtab* function from the bbmle package for model selection (Ben Bolker and R Development Core Team, 2020). The model assumptions were verified with Q-Q plots. Finally, we analyzed the proportion of variance in the models explained solely by fixed effects and by both fixed and random effects using marginal-R^2 and conditional-R^2, respectively (Nakagawa and Schielzeth, 2013). The *r.squareglmm* function from the MuMIn package was used to quantify marginal and conditional R^2 (Barton, 2023)

We performed all analyses using the R software 4.3.2 (R Core Team, 2021).

3. RESULTS

We sampled 8,818 euglossine males from four genera and 21 species (Supplementary Material Appendix F). Forest sites showed high euglossine total abundance and richness (*N*= 3,146, mean= 262.2 ± 82.9; *S*= 19, mean= 10.7 ± 2.2), followed by natural regeneration (*N*= 3,001, mean= 250.1 ± 78.8; *S*= 18, mean= 9.1 ± 2.2) and active restoration (*N*= 2,671, mean= 222.5 ± 72.7; *S*= 17, mean= 9.3 ± 2.2). We did not find statistical differences among habitat types for bee abundance (one-way ANOVA: F= 2.8, *p*= 0.06, df= 2; Fig. 3A) and richness (one-way ANOVA: F= 2.23, *p*= 0.12, df= 2, Fig. 3B).

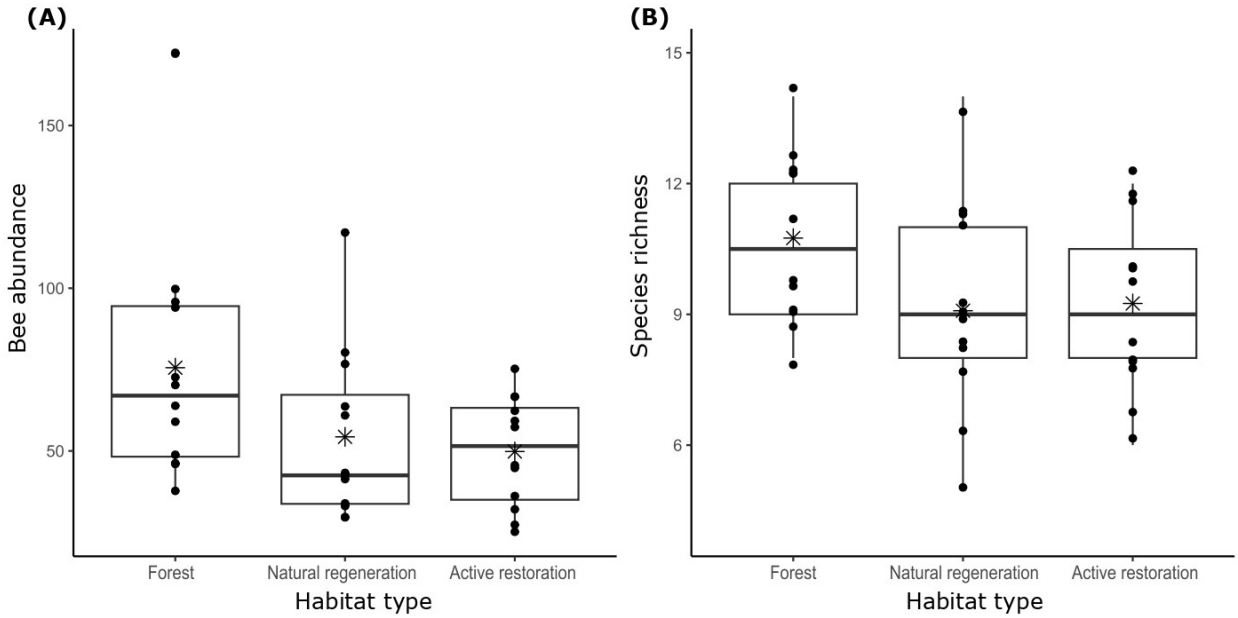

Figure 3. Variation in euglossine bee abundance **(A)** and species richness **(B)** among forest, natural regeneration, and active restoration sites in the Atlantic Forest. Bee

abundance excluded the dominant species *Euglossa cordata*. Each point is a Euglossini bee sampling site (12 by habitat type). The asterisk represents the mean.

Euglossa cordata was the most abundant species, representing 75.5% of the total sampled bees. The forest sites featured three singletons (*Euglossa townsendi* Cokerell, *Euglossa viridis* (Perty), and *Eufriesea violacea* (Blanchard)), while one singleton was recorded in natural regeneration (*Eulaema bombiformis* (Packard)) (Supplementary Material Appendix F).

We found no influence of landscape composition on euglossine communities. A consistent and strong effect of *sd*NDVI was found on orchid bee communities at fine spatial scales (i.e., 250 and 500 m) for species richness, Shannon diversity, and inverse Simpson diversity, and at larger scales (1250 m; Table 1) for bee abundance. The only plausible models for all response variables included *sd*NDVI interacting with habitat type as fixed effects. Models in Table 1 show high fit probabilities according to the model weights (> 80%).

Table 1. Best Generalized Linear Mixed Models - GLMMs ranked by the Akaike Information Selection Criterion corrected for small samples (AICc) to explain the alpha diversity of euglossine bees (i.e. ΔAICc= 0.0 and model weight (*wi*) > 0.1). Fixed effects included *sd*NDVI and habitat type (i.e., forest, natural regeneration, active restoration). Landscape code (L01 to L12) was a random effect in all models. *wi* vary between 0 and 1. The numbers in parentheses following *sd*NDVI are the scale of effect of this variable on the response variables. The asterisk is the interaction term between fixed effects. Marginal-R^2 represents the proportion of model variance explained only by fixed effects, while conditional-R^2 considers both fixed and random effects.

Variable Response	Best model	*wi*	Marginal R^2	Conditional R^2
Bee abundance	*sd*NDVI (1250 m) * Habitat type	0.83	0.41	0.59
Specie richness (Hill *q*0)	*sd*NDVI (500 m) * Habitat type	0.99	0.32	0.49
Shannon diversity (Hill *q*1)	*sd*NDVI (250 m) * Habitat type	0.99	0.29	0.33

Inverse Simpson diversity (Hill *q2*)	*sd*NDVI (250 m) * Habitat type	0.93	0.21	0.27

However, the effect of *sd*NDVI on response variables differed among habitat types. In forest areas, *sd*NDVI positively affected euglossine abundance and richness but had no discernible effect on Shannon or Simpson diversities (Table 2, Fig. 4A-B). On the other hand, in sites of natural regeneration and active restoration, *sd*NDVI negatively affected all four measures of bee communities (Fig. 4A-D). The model estimated coefficients indicated a stronger negative effect of *sd*NDVI on bee diversity mainly in natural regeneration sites ($p < 0.01$, Table 2).

Table 2. Parameters of the best Generalized Linear Mixed Models - GLMMs to explain the alpha diversity of euglossine bees. *sd*NDVI and habitat type were the fixed effects. The interaction between the fixed effects is indicated by the asterisk (*). The *p*-values of the model parameters were obtained from the *Z*-statistic to bee abundance and the *t*-statistic to species richness, Shannon diversity, and inverse Simpson diversity. *p*-values in italics are statistically significant ($p < 0.05$). SE: Standard Error.

Response variable	**Model parameters**	**Estimate**	**SE**	***p*-value**
Bee abundance	Intercept	2.976	0.986	*0.002*
	*sd*NDVI (1250 m)	6.843	5.129	0.182
	Habitat type (Natural regeneration)	3.804	1.097	*0.000*
	Habitat type (Active restoration)	2.229	1.167	0.056
	*sd*NDVI (1250 m) * Habitat type (Natural regeneration)	-21.845	5.738	*0.000*
	*sd*NDVI (1250 m) * Habitat type (Active restoration)	-13.858	6.124	*0.023*
Specie richness (Hill *q*0)	Intercept	5.194	5.130	0.319
	*sd*NDVI (500 m)	29.117	26.732	0.285
	Habitat type (Natural regeneration)	18.797	6.163	*0.006*
	Habitat type (Active restoration)	6.845	6.232	0.284

	*sd*NDVI (500 m) * Habitat type (Natural regeneration)	-105.427	31.772	*0.003*
	*sd*NDVI (500 m) * Habitat type (Active restoration)	-43.610	32.338	0.192
Shannon diversity (Hill *q*1)	Intercept	3.206	1.625	0.057
	*sd*NDVI (250m)	0.039	8.465	0.996
	Habitat type (Natural regeneration)	3.312	2.379	0.176
	Habitat type (Active restoration)	1.741	2.496	0.492
	*sd*NDVI (250 m) * Habitat type (Natural regeneration)	-20.009	12.044	0.109
	*sd*NDVI (250 m) * Habitat type (Active restoration)	-13.261	13.036	0.319
Inverse Simpson diversity (Hill *q2*)	Intercept	2.165	0.957	*0.031*
	*sd*NDVI (250m)	-0.845	4.982	0.866
	Habitat type (Natural regeneration)	1.619	1.394	0.257
	Habitat type (Active restoration)	0.814	1.463	0.583
	*sd*NDVI (250 m) * Habitat type (Natural regeneration)	-9.313	7.058	0.199
	*sd*NDVI (250 m) * Habitat type (Active restoration)	-6.258	7.639	0.420

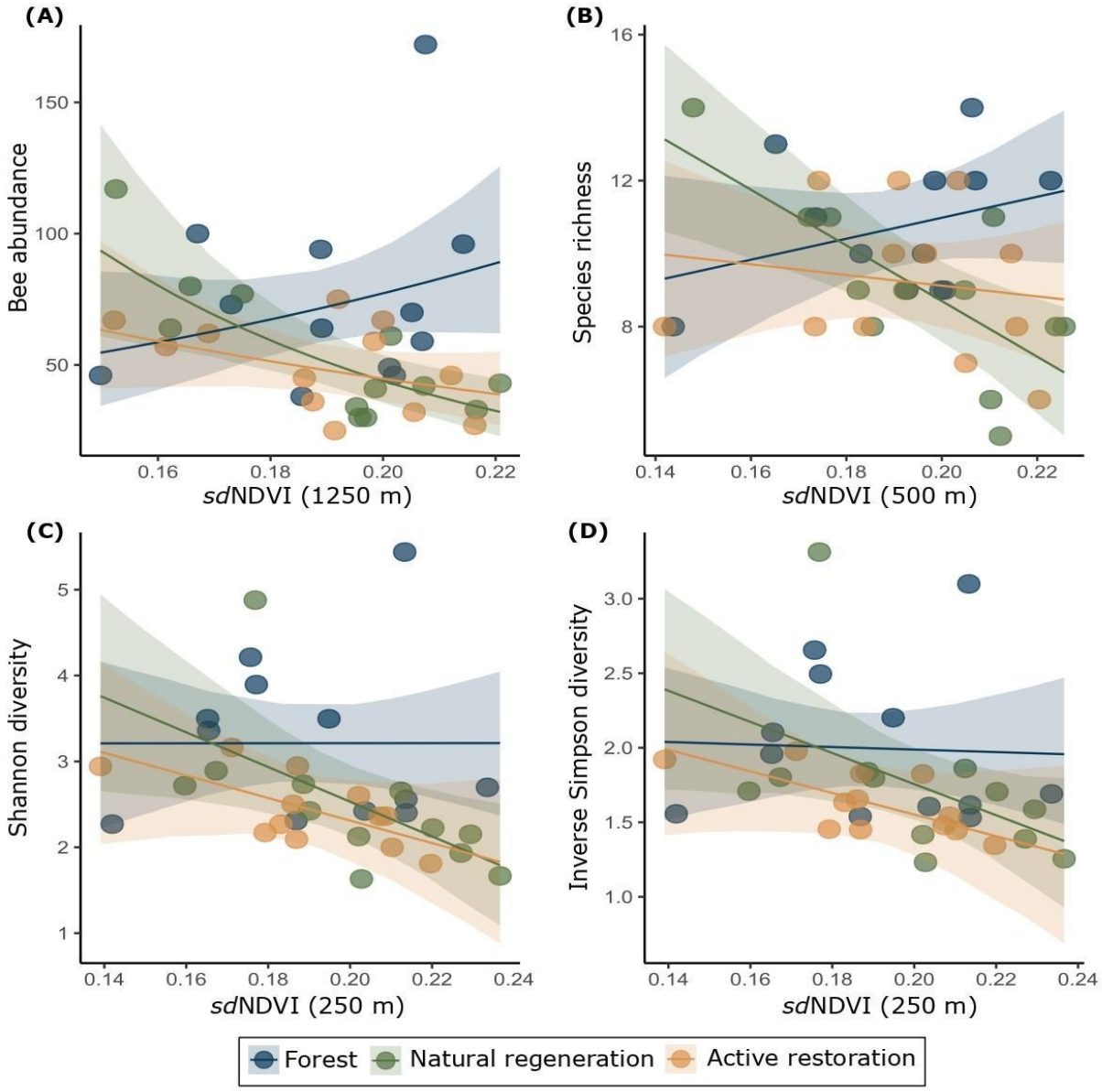

Figure 4. Influence of *sd*NDVI on bee abundance **(A),** species richness **(B),** Shannon diversity **(C),** and inverse Simpson diversity **(D)** of euglossine communities in forest, natural regeneration, and active restoration sites in the Atlantic Forest. Bee abundance represents the species abundance excluding the dominant species *Euglossa cordata*. Species richness, Shannon diversity, and inverse Simpson diversity were quantified by Hill numbers at q= 0, q=1, and q= 2, respectively. Each circle is an euglossine bee sampling point. The line represents the model fit, while shaded areas are the 95% confidence interval.

4. DISCUSSION

Our findings suggest that euglossine bee communities are strongly related to the spectral diversity of different habitat types in the Atlantic Forest. Conversely, we found no effect of landscape metrics on euglossine communities. Our results did not support the

hypothesized explanatory power of forest cover (%) on euglossine communities. Interestingly, *sd*NDVI was the only explanatory variable explaining euglossine communities. These results highlight the potential role of spectral indexes in accessing bees' diversity in restored ecosystems. We did not find a significant difference in euglossine richness and abundance among habitat types, and this result is similar to those observed in other studies (Rasmussen, 2009; Allen et al. 2019). This indicates the remarkable capacity of orchid bee species to colonize new forest habitats independently of the restoration strategy adopted, supporting the importance of forest restoration in recovering biodiversity.

4.1 *sd*NDVI explaining euglossine bee communities

Many studies have detected an association between euglossine alpha diversity and landscape structure. For example, a higher euglossine richness and abundance have been observed in landscapes with high forest cover (%) and compositional heterogeneity (Cândido et al. 2018; Carneiro et al. 2022; Corrêa-Neto et al. 2024). In addition, fragmentation per se negatively affected euglossine richness (Sousa et al. 2022). Nevertheless, our result underscores the additional importance of spectral metrics to predict habitat (Wang and Gamon, 2019) and bee diversity. Response variables such as euglossine richness and abundance respond to environmental heterogeneity within habitats (Ambruster, 1983; Brito et al. 2017), which is lost in categorical land cover maps (Gould, 2000; Galbraith et al. 2015). Therefore, spectral metrics sensitive to local habitat variations such as the *sd*NDVI are essential to evaluate the effect of spatial attributes on biodiversity (Levanoni et al. 2011; Benedetti et al. 2023).

The *sd*NDVI positively explained bees' abundance and richness in conserved forests, indicating that the higher *sd*NDVI results in higher bees' diversity, corroborating with the Spectral Variability Hypothesis. Previous studies have already reported the *sd*NDVI as a good predictor of biodiversity, including birds' taxonomic, functional, and phylogenetic diversity (Nieto et al. 2015; Benedetti et al. 2023), mammal diversity (Oindo, 2002) and plant taxonomic (Taddeo et al. 2019) and functional diversity (Perrone et al. 2023). Thus, as well as biodiversity measures obtained in the field (Tian et al. 2023), our findings demonstrated that a spectral diversity metric could also provide information on bees' diversity in conserved and restored habitats.

Conversely, *sd*NDVI negatively explained bee diversity in natural regeneration and active restoration habitats, indicating that the higher *sd*NDVI lowers bee diversity. The power of spectral data to predict habitat diversity is associated with vegetation types

(Perrone et al. 2023), as well as with confounding factors such as the presence of bare soil, litter, gaps, shade, understory, and rocks (Taddeo et al. 2019; Perrone et al. 2023). These factors affect the pixel reflectance, which should be referent only from vegetated areas (Taddeo et al. 2019; Wang et al. 2022; Perrone et al. 2023). For example, in areas of homogeneous vegetation, spectral data tends to provide better predictions than in areas of less vegetation density or open canopy due to a smaller number of mixed pixels (Wang et al. 2022). The higher spectral heterogeneity in restored areas, leading to lower bee diversity, can be related to the confounding factors described above which can increase mixed pixels and spectral diversity (Torresani et al. 2024). In this way, obtaining data in situ from conserved areas is essential to validate and understand the conditions of restored habitats by spectral index.

The negative effect of *sd*NDVI on bee communities highlights the need to understand better the relationship between spectral data and species diversity in restored habitats. Studies have shown that spectral heterogeneity can influence animal diversity in conserved and restored habitats both positively (Oindo and Skidmore, 2002; Bailey et al. 2004) and negatively (Bailey et al. 2004; Benedetti et al. 2023). This variety of results indicates a need for further research to clarify these patterns. We propose some hypotheses that may explain the negative effect of *sd*NDVI on bee communities in restored habitats.

First, spectral heterogeneity within actively restored sites may be related to the death of some planted species that can increase vegetation gaps, decrease vegetation density, and compose more open canopies. Also, the restored areas have different ages. Areas of young restoration tend to have a higher variation in plant physiological traits (Silva et al. 2023), and they tend to be colonized by a few bee species (Cariveaeu et al. 2020), which can decrease bee diversity.

Second, spectral heterogeneity in naturally regenerated sites may be linked to the plant species colonizing these habitats. In the Atlantic Forest, natural regeneration areas tend to be colonized by a few generalist plant species (Pessoa et al. 2012), with long-established sites displaying a closed canopy structure. At the same time, these regenerated habitats present higher understory biomass (Cardoso et al. 2022). Euglossine communities in the regenerated sites may be negatively associated with ecological succession in the understory, large open areas, and temporal delay for tree reestablishment and canopy structure (Ferronato et al. 2017).

Also, it is interesting to note that the negative relationship between *sd*NDVI and bee diversity was significantly stronger in naturally regenerated than in actively restored habitats. Actively restored habitats may show higher predictability in restoration outcomes due to human management. In contrast, the lower predictability in the successional trajectories of naturally regenerated habitats may lead to delayed biodiversity recovery (Arroyo-Rodriguez et al. 2023). Considering the influence of spatial isolation of source areas on natural regeneration success, it is reasonable to infer that the negative relationship of *sd*NDVI with bees' diversity in naturally regenerated sites can reflect the ecological challenges of colonization by plant species, as well as deteriorated local conditions only allowing colonization by generalist plant species with high environmental plasticity. Different forest restoration strategies (e.g., passive, assisted) have been recognized to influence the reestablishment of bee communities in tropical forests (Araújo et al. 2020).

Less complex habitats can negatively affect bee communities. For example, a lower canopy complexity and epiphyte diversity negatively affect the euglossine communities (Allen et al. 2019). Many euglossine species depend on conserved forest habitats for nesting and feeding (Roubik and Hanson, 2004), while collecting perfumes mainly in orchid flowers is essential for the reproductive success of euglossine males (Henske et al. 2023). The absence of these requirements in the restored sites can explain why some species were exclusive in the forest habitats. Species like *Eufriesea violacea* have declined in abundance in small and degraded forest patches (Giangarelli et al. 2009). A recent initiative executed in some actively restored habitats involved habitat enrichment by epiphytes such as orchid species (AMLD, 2024). This restoration strategy may enhance the restoration of orchid bee communities in the region, as most euglossine males depend on this forest compartment in tropical ecosystems (Roubik and Hanson, 2004).

5. CONCLUSION

Our results showed the power of spectral diversity to predict bee diversity in response to habitat local management. These variables should be considered not only in vegetation monitoring but also to understand how the spectral diversity can predict the recovery of animal communities. Given the advancements in remote sensing technology, ecological restoration studies can benefit through the temporal and spatial data monitoring of the different restoration phases. Our results demonstrated the power of this spectral data to predict an ecological indicator with a high sensitivity to habitat and landscape changes,

such as euglossine bees. Despite the great field effort in collecting biological data, this provides an overview of biodiversity recovery in restored ecosystems, thereby contributing valuable insights to support ecological restoration and conservation strategies.

Here, we indicated that remote sensing data can assess differences in bee diversity between conserved and restored forests. However, as in the field, measuring different restoration strategies outcomes by remote sensing needs to be better comprehended. Further studies need to be performed to confirm the patterns found here, including other taxa and ecosystems under restoration. Obtaining field data to validate the relationship between biological and spectral diversity is essential since it can improve our understanding of the relationship between these variables, mainly in areas with high habitat heterogeneity. Finally, our findings highlight that restored Atlantic Forest habitats, regardless of the management strategy used, support euglossine bee communities at levels comparable to those in conserved forests.

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7. DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

The authors have declared no use of AI related technologies.

8. DECLARATION OF COMPETING INTEREST

The authors have declared no competing interests.

9. DATA AVAILABILITY

Additional data is available in the supplementary material.

10. CREDIT AUTHORSHIP CONTRIBUTION STATEMENT

Lázaro S. Carneiro: Conceptualization, Data Curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing - Original Draft, Writing - Review & Editing. **Milton Cezar Ribeiro:** Conceptualization, Formal analysis, Methodology, Supervision, Writing - Review & Editing. **Taylor Ricketts**: Software, Supervision, Writing - Review & Editing. **Juliana Silveira S.S. Santos:** Formal analysis, Software, Writing - Review & Editing. **Wilson Frantine-Silva**: Investigation, Methodology, Software, Formal analysis, Writing - Review & Editing. **Maria Cristina Gaglianone:** Conceptualization, Data Curation, Funding acquisition, Methodology, Project administration, Resources, Visualization, Supervision, Writing - Review & Editing.

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Supplementary Material Appendix A. Geographic coordinates of the 12 landscapes (L01-L12) with three bee sampling points (FOR: Forest, NRG: Natural regeneration, ATR: Active restoration) in the Rio de Janeiro state, Southeast Brazil.

Landscape	Coordinates	Municipality
L01	FOR (22°25'15.8"S 42°01'57.2"W)	Rio das Ostras
	NRG (22°25'51.2"S 42°02'06.2"W)	
	ATR (22°25'41.5"S 42°02'16.5"W)	
L02	FOR (22°26'24.3"S 42°04'16.0"W)	Casimiro de Abreu
	NRG (22°25'56.6"S 42°04'22.2"W)	
	ATR (22°26'14.5"S 42°04'22.1"W)	
L03	FOR (22°30'08.7"S 42°16'00.5"W)	Silva Jardim
	NRG (22°30'31.3"S 42°16'49.0"W)	
	ATR (22°30'22.9"S 42°16'17.2"W)	
L04	FOR (22°30'26.25"S 42°18'28.1"W)	Silva Jardim
	NRG (22°30'36.2"S 42°18'35.6"W)	
	ATR (22°30'20.43"S 42°18'20"W)	
L05	FOR (22°33'46.9"S 42°17'36.2"W)	Silva Jardim
	NRG (22°33'57.3"S 42°17'16.1"W)	
	ATR (22°33'45.3"S 42°16'47.6"W)	
L06	FOR (22°33'42.9"S 42°21'38.4"W)	Silva Jardim
	NRG (22°33'54.3"S 42°21'31.9"W)	
	ATR (22°34'09.1"S 42°21'33.2"W)	
L07	FOR (22°36'26.4"S 42°24'10.6"W)	Silva Jardim
	NRG (22°36'46.7"S 42°23'48.0"W)	
	ATR (22°37'06.4"S 42°24'07.4"W)	
L08	FOR (22°38'37.9"S 42°22'38.8"W)	Silva Jardim
	NRG (22°38'43.3"S 42°22'36.6"W)	
	ATR (22°38'50.5"S 42°22'31.2"W)	
L09	FOR (22°37'52.0"S 42°25'25.8"W)	Silva Jardim
	NRG (22°37'41.8"S 42°25'45.2"W)	
	ATR (22°38'03.8"S 42°25'36.2"W)	
L10	FOR (22°39'16.5"S 42°27'39.4"W)	Silva Jardim
	NRG (22°39'46.4"S 42°28'16.4"W)	
	ATR (22°39'02.4"S 42°27'10.7"W)	
L11	FOR (22°37'54.0"S 42°28'05.5"W)	Silva Jardim
	NRG (22°37'15.5"S 42°28'03.8"W)	
	ATR (22°37'29.9"S 42°27'50.8"W)	
L12	FOR (22°35'10.5"S 42°34'07.1"W)	Silva Jardim
	NRG (22°35'03.3"S 42°34'14.3"W)	
	ATR (22°34'49.2"S 42°34'16.3"W)	

Supplementary Material Appendix B. Effect of restoration age on euglossine bees.

The manuscript section "**2.3 Conserved forests, active restoration program and natural regeneration areas**" highlights the age variation in actively restored and naturally regenerated habitats. Restoration age has been shown to positively influence bee community recovery in several ecosystems worldwide. Restoration age is a proxy of the habitat complexity over time, since increasing restoration age the habitat becomes more complex and similar to conserved (i.e. reference) habitats. A discussion of the effect of restoration age on the recovery of bee communities can be found in Carneiro et al. (2024).

Given the different ages of restored habitats where euglossine bees were sampled, it is reasonable to expect that this factor might influence euglossine alpha diversity and should be included in the models. We tested models incorporating restoration age and compared them with the best-fitting models presented in the "Results" section. However, the models including “Age” as a fixed effect did not fit, as demonstrated in the following table:

Table A. Model comparison including the fixed effect “Age”. Bee abundance excludes the dominant species *Euglossa cordata*. Species richness, Shannon diversity, and inverse Simpson diversity were quantified using Hill numbers at q= 0, q= 1, and q= 2, respectively.

Response variable	Model structure	ΔAICc	weight
Bee abundance	**Mean_NDVI_SD_1250*Habitat_type+(1|Landscape)**	**0.0**	**0.79**
	Mean_NDVI_SD_1250+Age*Habitat_type+(1|Landscape)	2.66	0.20
Species richness	**Mean_NDVI_500*Habitat_type +(1|Landscape)**	**0.0**	**1**
	Mean_NDVI_SD_500+Age*Habitat_type+(1|Landscape)	16.58	0
Shannon diversity	**Mean_NDVI_SD_250*Habitat_type+(1|Landscape)**	**0.0**	**1**
	Mean_NDVI_SD_250+Age*Habitat_type +(1|Landscape)	17.38	0
Inverse Simpson diversity	**Mean_NDVI_SD_250*Habitat_type +(1|Landscape)**	**0.0**	**1**
	Mean_NDVI_SD_250+Age*Habitat_type +(1|Landscape)	17.63	0

When analyzing a linear model- LM correlating Age and *sd*NDVI in the spatial scales of Table A (250 m, 500 m, and 1250 m), we found no statistically significant results ($p > 0.05$), and low coefficients of determination ($R^2 < 0.1$). Therefore, the “Age” was excluded from our analysis.

Several factors may explain these findings. In active restored areas, the outcomes may be influenced by specific restoration management practices. In natural regeneration areas, the unpredictability of succession trajectories may play a role, as natural regeneration depends on factors such as land-use legacy and the availability of surrounding habitats. Further details are provided in the "Discussion" section.

Cited reference:

Carneiro, LS, Ribeiro MC, Gaglianone, MC (2024) Restoration of bee communities (Hymenoptera: Apoidea: Anthophila) in landscape scale: a review. Apidologie, 55(4), 1-13.

Supplementary Material Appendix C. Multiscale variables used to assess the scale of effect of spatial attributes on euglossine communities sampled in forest, natural regeneration, and active restoration sites. The predictor variables landscape heterogeneity (shdi), *sd*NDVI, and forest cover (%) (pct10) were quantified in multi-buffers between 250-1500 m, interspersed by 250 m. The bee abundance variable excluded the abundance of the dominant species *Euglossa cordata*. Hill numbers *q*=0: species richness, *q*= 1: Shannon diversity, *q*=2: inverse Simpson diversity.

Landscape	Habitat type	Total abundance	Bee abundance	Hill q0	Hill q1	Hill q2	Shdi 250	Shdi 500	Shdi 750	Shdi 1000	Shdi 1250	Shdi 1500
L01	Forest	376	172	14	5.439	3.100	0.653	0.705	0.760	0.875	0.944	0.910
L02	Forest	300	59	12	2.402	1.532	0.767	1.148	1.404	1.438	1.377	1.336
L03	Forest	223	46	8	2.270	1.557	0.635	1.083	1.438	1.451	1.561	1.568
L04	Forest	341	100	13	3.498	1.957	1.187	1.615	1.592	1.586	1.564	1.556
L05	Forest	293	64	9	2.559	1.616	0.918	1.066	1.082	1.174	1.184	1.177
L06	Forest	175	73	11	4.214	2.655	1.084	1.507	1.768	1.774	1.699	1.645
L07	Forest	210	70	12	3.360	2.103	1.335	1.215	1.243	1.453	1.599	1.673
L08	Forest	274	94	9	3.497	2.202	1.028	1.628	1.577	1.479	1.367	1.382
L09	Forest	403	96	12	2.698	1.691	1.114	1.465	1.360	1.491	1.591	1.615
L10	Forest	224	49	10	2.423	1.606	1.432	1.622	1.553	1.438	1.443	1.513
L11	Forest	231	46	9	2.310	1.539	1.048	1.214	1.429	1.590	1.629	1.696
L12	Forest	96	38	10	3.894	2.495	0.750	1.132	1.346	1.380	1.386	1.347
L01	Natural_regeneration	252	41	9	2.125	1.417	0.590	1.192	1.240	1.103	1.025	0.980
L02	Natural_regeneration	267	42	11	1.933	1.388	1.584	1.687	1.651	1.542	1.486	1.457

L03	Natural_regeneration	479	117	14	2.718	1.709	1.336	1.673	1.736	1.758	1.687	1.601
L04	Natural_regeneration	241	64	11	2.891	1.803	1.605	1.677	1.643	1.601	1.606	1.594
L05	Natural_regeneration	274	77	9	2.425	1.797	1.052	1.155	1.281	1.226	1.208	1.194
L06	Natural_regeneration	284	80	11	2.735	1.840	1.200	1.746	1.747	1.685	1.669	1.661
L07	Natural_regeneration	194	43	8	2.152	1.587	1.581	1.819	1.770	1.825	1.796	1.779
L08	Natural_regeneration	215	61	6	2.653	1.862	1.808	1.770	1.611	1.511	1.418	1.398
L09	Natural_regeneration	302	33	8	1.667	1.255	1.402	1.503	1.681	1.654	1.568	1.567
L10	Natural_regeneration	133	34	5	2.224	1.706	1.199	1.453	1.505	1.548	1.547	1.594
L11	Natural_regeneration	299	30	9	1.632	1.232	1.584	1.437	1.426	1.547	1.543	1.498
L12	Natural_regeneration	61	30	8	4.878	3.313	1.257	1.473	1.457	1.454	1.415	1.355
L01	Active_restoration	327	59	12	2.360	1.479	1.640	1.461	1.236	1.088	0.983	0.919
L02	Active_restoration	230	46	10	2.364	1.541	1.023	1.435	1.465	1.460	1.427	1.410
L03	Active_restoration	229	67	8	2.942	1.921	1.200	1.308	1.486	1.508	1.625	1.657
L04	Active_restoration	187	57	12	3.162	1.977	0.821	1.065	1.546	1.567	1.528	1.503
L05	Active_restoration	193	45	10	2.501	1.656	1.059	1.112	1.059	0.983	0.937	1.001
L06	Active_restoration	264	62	8	2.269	1.634	1.632	1.648	1.666	1.633	1.634	1.652
L07	Active_restoration	183	32	8	1.999	1.444	1.024	1.797	1.809	1.817	1.844	1.782
L08	Active_restoration	271	75	7	2.601	1.825	1.875	1.844	1.638	1.536	1.516	1.456
L09	Active_restoration	190	27	6	1.811	1.346	1.458	1.255	1.437	1.462	1.530	1.659
L10	Active_restoration	206	36	10	2.171	1.454	1.063	0.903	0.970	1.173	1.299	1.334
L11	Active_restoration	248	67	12	2.946	1.826	0.597	1.052	1.363	1.453	1.412	1.432
L12	Active_restoration	143	25	8	2.093	1.450	0.638	1.551	1.515	1.453	1.416	1.370

Landscape	Habitat type	MeanNDVI_SD_250	Mean_NDVI_SD_500	Mean_NDVI_SD_750	Mean_NDVI_SD_1000	Mean_NDVI_SD_1250	Mean_NDVI_SD_1500	pct10_250	pct10_500	pct10_750	pct10_1000	pct10_1250	pct10_1500
L01	Forest	0.213	0.206	0.202	0.205	0.208	0.204	64.106	68.032	68.145	65.781	65.730	66.951
L02	Forest	0.214	0.207	0.211	0.208	0.207	0.210	47.268	55.454	53.606	53.132	55.661	57.557
L03	Forest	0.142	0.144	0.147	0.147	0.150	0.152	77.824	69.035	48.202	43.444	37.519	37.115
L04	Forest	0.165	0.165	0.166	0.167	0.167	0.168	59.100	32.778	26.681	27.070	32.872	36.490
L05	Forest	0.214	0.201	0.195	0.190	0.189	0.183	30.552	43.735	45.883	51.803	54.552	52.895
L06	Forest	0.176	0.174	0.175	0.173	0.173	0.175	70.321	51.926	32.653	20.568	17.748	18.124
L07	Forest	0.165	0.199	0.197	0.206	0.205	0.205	53.209	68.496	66.358	57.864	46.824	39.949
L08	Forest	0.195	0.200	0.199	0.195	0.189	0.192	62.530	35.601	16.322	9.181	6.087	5.647
L09	Forest	0.234	0.223	0.218	0.216	0.214	0.214	53.586	34.404	31.968	27.982	25.006	25.820
L10	Forest	0.204	0.196	0.198	0.203	0.201	0.204	41.126	22.640	13.704	8.845	7.148	7.181
L11	Forest	0.187	0.193	0.196	0.200	0.202	0.201	63.534	38.580	26.903	24.377	27.299	27.666
L12	Forest	0.177	0.183	0.184	0.182	0.186	0.188	57.582	41.855	36.583	35.687	37.729	41.252
L01	Natural_regeneration	0.202	0.205	0.200	0.200	0.199	0.197	9.197	23.671	41.242	44.648	53.234	60.296
L02	Natural_regeneration	0.227	0.211	0.212	0.211	0.207	0.210	34.344	30.774	37.462	45.269	49.362	50.697
L03	Natural_regeneration	0.160	0.148	0.148	0.149	0.153	0.155	3.528	7.164	18.438	26.890	36.916	44.291
L04	Natural_regeneration	0.167	0.172	0.167	0.165	0.162	0.164	20.716	39.613	34.380	26.483	25.818	31.151
L05	Natural_regeneration	0.190	0.182	0.179	0.175	0.175	0.170	30.875	41.381	37.898	47.550	53.097	52.719
L06	Natural_regeneration	0.189	0.177	0.175	0.168	0.166	0.165	48.833	33.681	29.143	24.456	19.722	17.390

L07	Natural_regeneration	0.229	0.224	0.218	0.216	0.221	0.214	11.802	20.784	23.618	28.416	32.033	34.491
L08	Natural_regeneration	0.212	0.210	0.210	0.207	0.201	0.199	21.656	28.200	16.324	9.181	5.876	4.939
L09	Natural_regeneration	0.237	0.226	0.221	0.214	0.217	0.218	16.312	38.932	34.615	37.951	43.182	42.740
L10	Natural_regeneration	0.220	0.212	0.201	0.197	0.195	0.194	0.000	3.839	5.236	5.300	6.100	7.497
L11	Natural_regeneration	0.203	0.192	0.199	0.201	0.196	0.195	17.096	9.738	11.107	19.725	28.409	34.505
L12	Natural_regeneration	0.177	0.185	0.187	0.191	0.197	0.203	30.713	31.691	31.198	31.024	34.222	38.499
L01	Active_restoration	0.207	0.203	0.204	0.201	0.198	0.200	35.325	27.846	31.086	42.789	54.043	62.273
L02	Active_restoration	0.209	0.215	0.214	0.213	0.212	0.213	20.079	37.885	47.363	50.606	54.036	53.960
L03	Active_restoration	0.139	0.142	0.148	0.149	0.152	0.155	56.258	61.204	52.975	52.810	45.170	41.359
L04	Active_restoration	0.171	0.174	0.166	0.161	0.161	0.161	33.112	18.777	15.698	27.587	35.372	37.934
L05	Active_restoration	0.186	0.190	0.188	0.188	0.186	0.182	18.464	27.876	39.174	54.332	62.075	63.169
L06	Active_restoration	0.183	0.173	0.172	0.168	0.169	0.169	21.788	29.663	24.477	24.362	23.723	22.007
L07	Active_restoration	0.210	0.216	0.206	0.204	0.206	0.205	0.000	2.835	10.517	10.652	17.791	23.064
L08	Active_restoration	0.202	0.205	0.206	0.201	0.192	0.195	0.115	6.772	13.248	9.181	5.876	4.329
L09	Active_restoration	0.220	0.220	0.215	0.215	0.216	0.215	45.212	56.075	44.365	34.441	30.982	26.467

L10	Active_restoration	0.179	0.197	0.183	0.189	0.188	0.192	0.000	0.000	0.000	4.417	12.454	18.945
L11	Active_restoration	0.187	0.191	0.199	0.200	0.200	0.201	0.000	13.252	19.430	27.910	36.200	39.498
L12	Active_restoration	0.187	0.184	0.186	0.189	0.191	0.196	0.000	18.270	28.256	33.430	36.605	42.183

Supplementary Material Appendix D. Scale of effect of the landscape attributes (forest cover (%), landscape heterogeneity) and *sd*NDVI on euglossine communities in restored and forest habitats in the Atlantic Forest, Brazil.

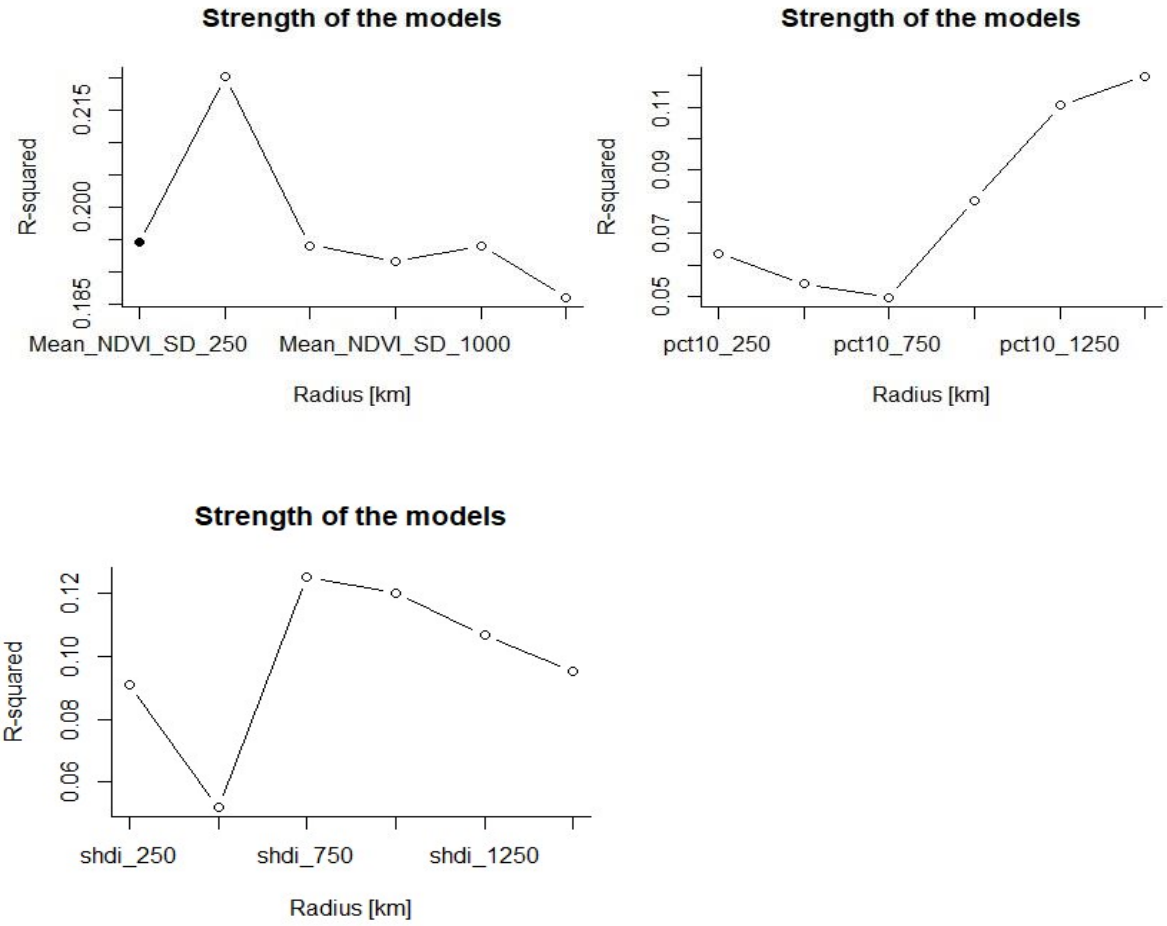

Fig. A. Scale of effect of *sd*NDVI (top left), forest cover (%) (pct10- top right), and landscape heterogeneity (shdi- bottom) on total abundance. The scale of effect was the one that presented the highest R^2 (y-axis). On the x-axis, each mark represents a spatial scale, from 250 to 1,500 m, with 250 m intervals.

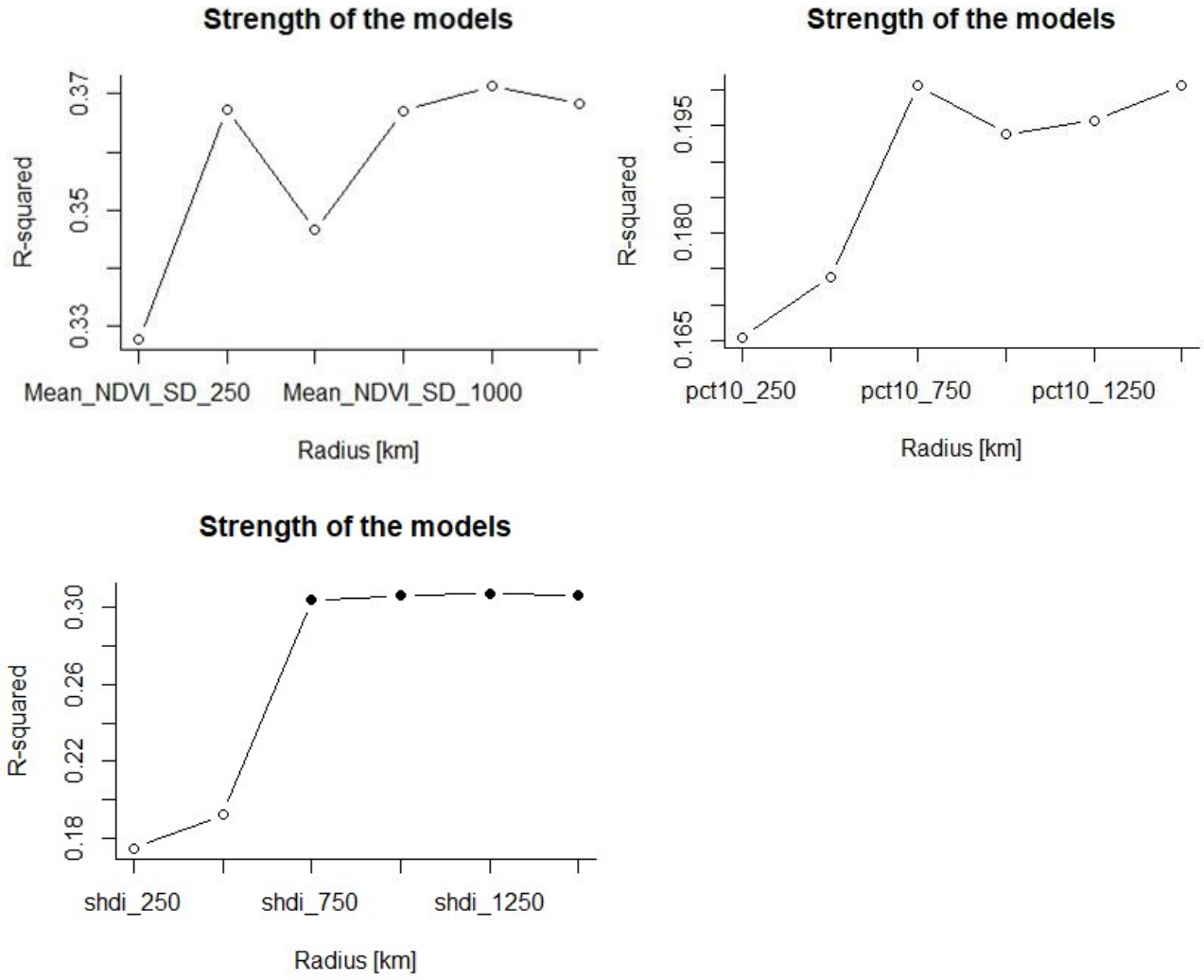

Fig. B. Scale of effect of *sd*NDVI (top left), forest cover (%) (pct10- top right), and landscape heterogeneity (shdi- bottom) on bee abundance. This abundance variable excluded the abundance of *Euglossa cordata*. The scale of effect was the one that presented the highest R^2 (y-axis). On the x-axis, each mark represents a spatial scale, from 250 to 1,500 m, with 250 m intervals.

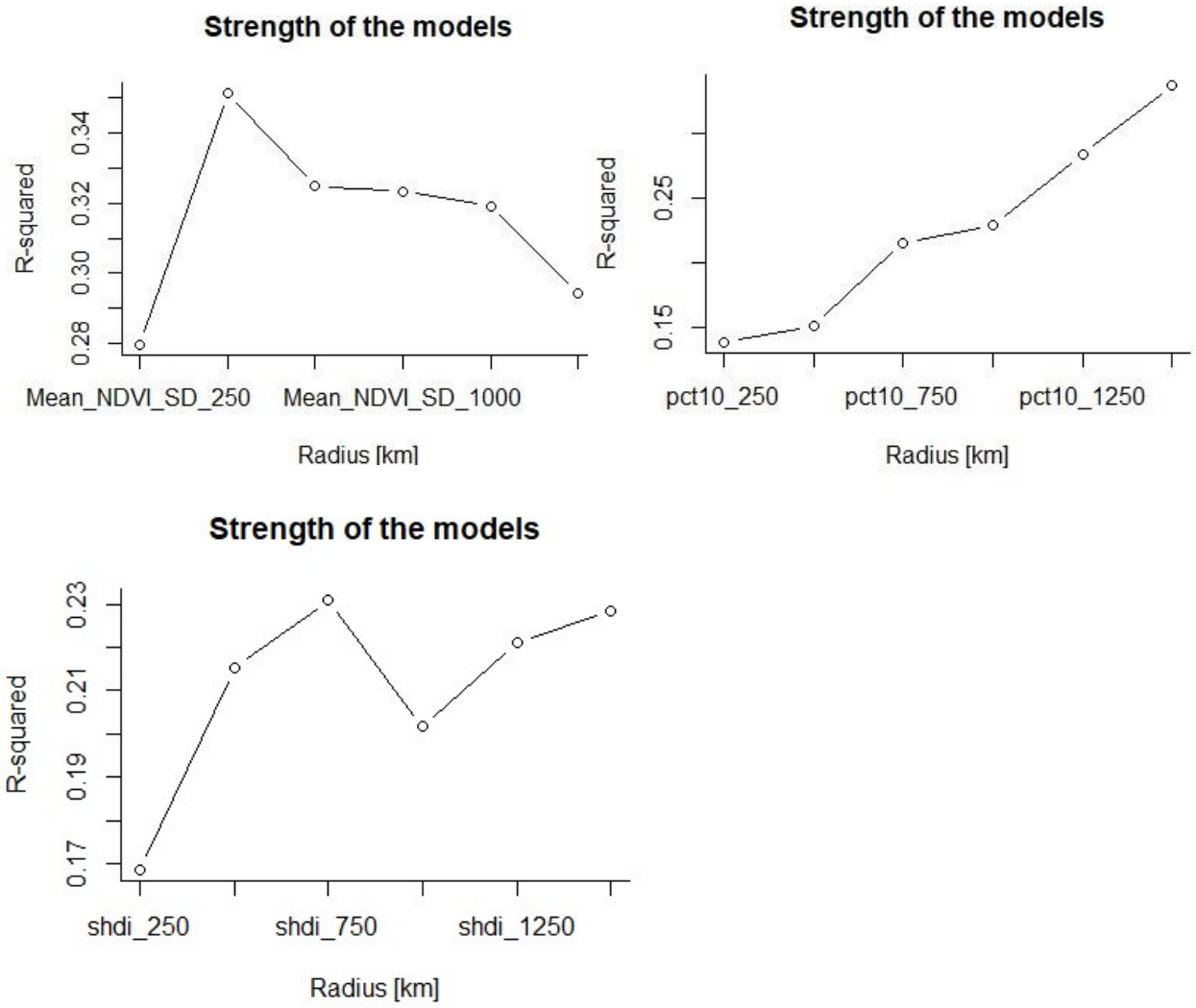

Fig. C. Scale of effect of *sd*NDVI (top left), forest cover (%) (pct10- top right), and landscape heterogeneity (shdi- bottom) on Hill numbers q= 0 (species richness). The scale of effect was the one that presented the highest R^2 (y-axis). On the x-axis, each mark represents a spatial scale, from 250 to 1,500 m, with 250 m intervals.

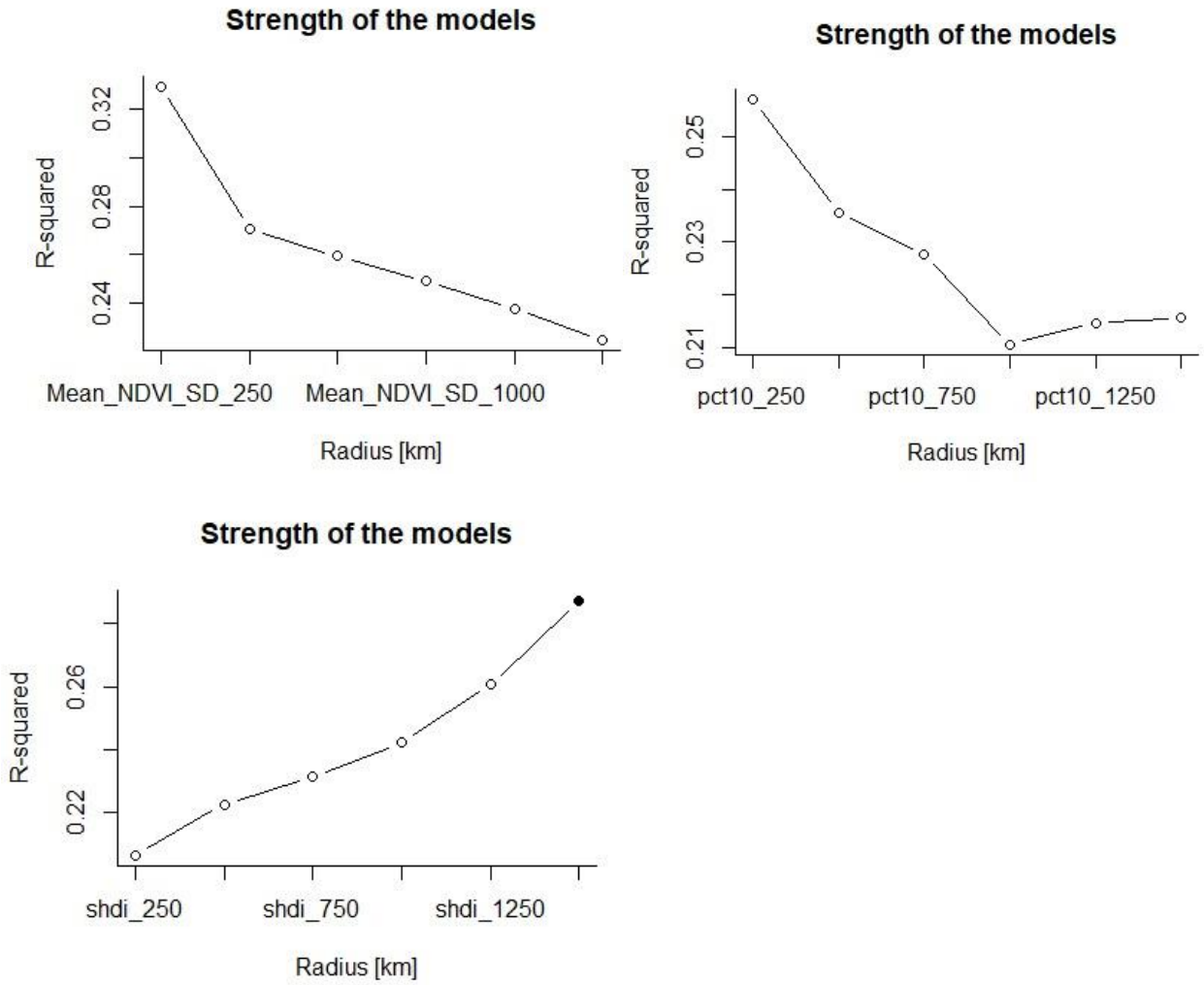

Fig. D. Scale of effect of *sd*NDVI (top left), forest cover (%) (pct10- top right), and landscape heterogeneity (shdi- bottom) on Hills number *q*= 1 (Shannon diversity). The scale of effect was the one that presented the highest R^2 (y-axis). On the x-axis, each mark represents a spatial scale, from 250 to 1,500 m, with 250 m intervals.

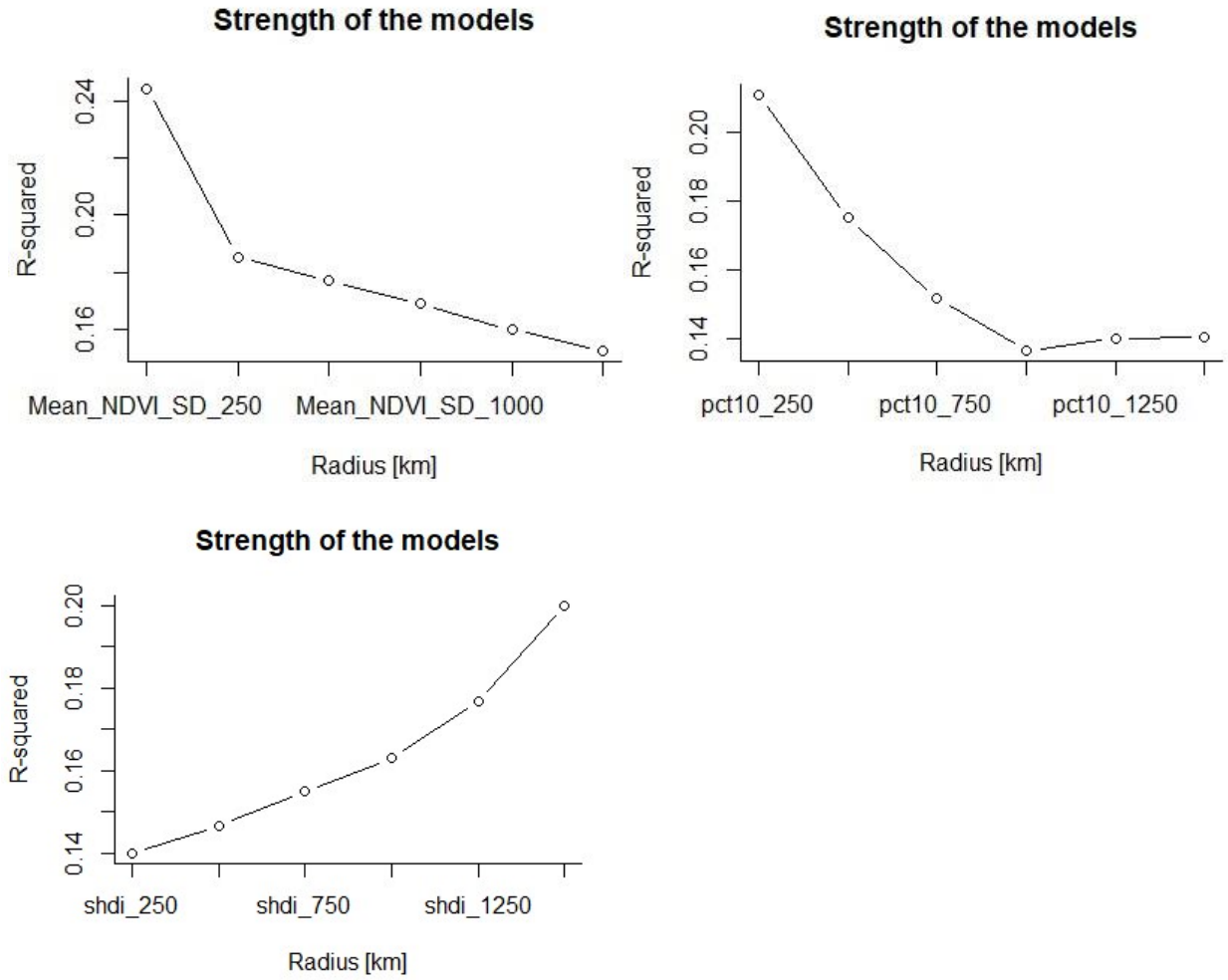

Fig. E. Scale of effect of *sd*NDVI (top left), forest cover (%) (pct10- top right), and landscape heterogeneity (shdi- bottom) on Hills number *q*= 2 (inverse Simpson diversity). The scale of effect was the one that presented the highest R^2 (y-axis). On the x-axis, each mark represents a spatial scale, from 250 to 1,500 m, with 250 m intervals.

Supplementary Material Appendix E. Generalized Linear Mixed Models- GLMMs used to access the effects of sdNDVI, forest cover (%), and landscape heterogeneity on the total abundance, bee abundance (excluded *Euglossa cordata*), and Hill numbers *q*= 0 (species richness), *q*=1 (Shannon diversity), *q*= 2 (inverse Simpson diversity). *sd*NDVI, forest cover (%), landscape heterogeneity, and habitat type (i.e. forest, natural regeneration, active restoration) were fixed effects. Landscape code was the random effect. The GLMMs were ranked using the Akaike Information Selection Criterion corrected for small samples (AICc). The best models (i.e. ΔAICc < 2.0 and model weight (wi) > 0.1) are in bold. df= degrees of freedom.

Response variables	Models	dLogLik	ΔAICc	df	model weight (wi)
Total abundance	**Total abundance ~ 1 + (1|Landscape)**	**0.0000**	**0.0000**	**3**	**0.8312**
	Total abundance ~ Forest cover (1500 m) + Habitat type + (1|Landscape)	1.4388	5.2690	6	0.0596
	Total abundance ~ Mean sdNDVI (500 m) + Habitat type + (1|Landscape)	0.8595	6.4275	6	0.0334
	Total abundance ~ Mean sdNDVI (500 m) * Habitat type + (1|Landscape)	0.8595	6.4275	6	0.0334
	Total abundance ~ Landscape heterogeneity (750 m) + Habitat type + (1|Landscape)	0.8227	6.5011	6	0.0322
	Total abundance ~ Landscape heterogeneity (750 m) * Habitat type + (1|Landscape)	2.3497	9.8838	8	0.0059
	Total abundance ~ Forest cover (1500 m) * Habitat type + (1|Landscape)	1.9837	10.6160	8	0.0041
Bee abundance (excluded *Euglossa cordata*)	**Bee abundance ~ Mean sdNDVI (1250 m) * Habitat type + (1|Landscape)**	**7.2915**	**0.0000**	**8**	**0.8310**
	Bee abundance ~ Mean sdNDVI (1250 m) + Habitat type + (1|Landscape)	1.5601	5.0261	6	0.0673
	Bee abundance ~ 1 + (1|Landscape)	0.0000	5.2497	5	0.0602
	Bee abundance ~ Forest cover (750 m) + Habitat type + (1|Landscape)	0.2282	7.6899	6	0.0178
	Bee abundance ~ Landscape heterogeneity (1250 m) + Habitat type + (1|Landscape)	0.2142	7.7178	6	0.0175
	Bee abundance ~ Landscape heterogeneity (1250 m) * Habitat type + (1|Landscape)	2.1649	10.2533	8	0.0049
	Bee abundance ~ Forest cover (750 m) * Habitat type + (1|Landscape)	0.7985	12.9860	8	0.0013
Species richness (Hill *q*= 0)	**hill_q0 ~ Mean sdNDVI (500 m) * Habitat type + (1|Landscape)**	**21.8957**	**0.0000**	**8**	0.9999

Shannon diversity (Hill *q*= 1)	hill_q0 ~ Landscape heterogeneity (750 m) * Habitat type + (1|Landscape)	12.1406	19.5102	8	0.0001
	hill_q0 ~ Landscape heterogeneity (750 m) + Habitat type + (1|Landscape)	5.7064	25.9417	6	0.0000
	hill_q0 ~ Forest cover (1500 m) + Habitat type + (1|Landscape)	4.8814	27.5918	6	0.0000
	hill_q0 ~ 1 + (1|Landscape)	0.0000	29.2080	3	0.0000
	hill_q0 ~ Mean sdNDVI (500 m) + Habitat type + (1|Landscape)	3.4232	30.5081	6	0.0000
	hill_q0 ~ Forest cover (1500 m) * Habitat type + (1|Landscape)	0.5471	42.6970	8	0.0000
	hill_q1 ~ Mean sdNDVI (250 m) * Habitat type + (1|Landscape)	**20.8767**	**0.0000**	**8**	**0.9922**
	hill_q1 ~ Mean sdNDVI (250 m) + Habitat type + (1|Landscape)	12.6682	9.9803	6	0.0068
	hill_q1 ~ Landscape heterogeneity (1500 m) * Habitat type + (1|Landscape)	13.2189	15.3158	8	0.0005
	hill_q1 ~ Landscape heterogeneity (1500 m) + Habitat type + (1|Landscape)	9.7448	15.8270	6	0.0004
	hill_q1 ~ 1 + (1|Landscape)	5.3265	16.5172	3	0.0003
	hill_q1 ~ Forest cover (250 m) + Habitat type + (1|Landscape)	5.4936	24.3295	6	0.0000
	hill_q1 ~ Forest cover (250 m) * Habitat type + (1|Landscape)	0.0000	41.7535	8	0.0000
Inverse Simpson diversity (Hill *q*= 2)	**hill_q2 ~ Mean sdNDVI250 * Habitat type + (1|Landscape)**	**19.9920**	**0.0000**	**8**	**0.9382**
	hill_q2 ~ Mean_sdNDVI (250 m) + Habitat type + (1|Landscape)	13.3722	6.8028	6	0.0313
	hill_q2 ~ 1 + (1|Landscape)	9.2139	6.9728	3	0.0287
	hill_q2~ Landscape heterogeneity (1500 m) + Habitat type + (1|Landscape)	10.1941	13.1589	6	0.0013
	hill_q2 ~ Landscape heterogeneity (1500 m) * Habitat type + (1|Landscape)	12.3921	15.1997	8	0.0005
	hill_q2 ~ Forest cover (250 m) + Habitat type + (1|Landscape)	6.5428	20.4615	6	0.0000
	hill_q2 ~ Forest cover (250 m) * Habitat type +(1|Landscape)	0.0000	39.9839	8	0.0000

Supplementary Material Appendix F. Composition of Euglossini bee communities sampled in 12 landscapes in the Rio de Janeiro state, Southeast Brazil. Each landscape (L01-L12) has three bee sampling points in different habitat types: Forest (FOR), Natural regeneration (NRG), and Active restoration (ATR). *Ef: Eufriesea, Eg: Euglossa, El: Eulaema, Ex: Exaerete.*

	L01			**L02**			**L03**			**L04**			**L05**			**L06**		
	L01 ATR	**L01 NRG**	**L01 FOR**	**L02 ATR**	**L02 NRG**	**L02 FOR**	**L03 ATR**	**L03 NRG**	**L03 FOR**	**L04 ATR**	**L04 NRG**	**L04 FOR**	**L05 ATR**	**L05 NRG**	**L05 FOR**	**L06 ATR**	**L06 NRG**	**L06 FOR**
Ef surinamensis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Ef violacea	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Eg bembei	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0
Eg cordata	268	211	204	184	225	241	162	362	177	130	177	241	148	197	229	202	204	102
Eg clausi	2	3	13	4	4	4	2	6	3	2	5	19	1	0	2	3	10	15
Eg despecta	0	3	2	0	2	0	0	2	0	1	0	3	1	1	0	0	0	3
Eg fimbriata	1	0	2	1	1	0	0	0	0	2	1	1	0	1	0	0	1	0
Eg gaianii	5	1	15	1	0	1	0	3	0	1	11	4	0	0	0	1	1	12
Eg ignita	5	10	17	3	1	1	18	36	13	3	3	18	3	0	8	0	0	1
Eg iopoecila	7	0	23	5	1	7	2	2	3	0	0	9	2	1	10	2	1	0
Eg marianae	13	8	39	7	1	8	0	0	0	0	0	0	0	1	0	0	0	0
Eg milenae	1	0	0	0	1	0	0	0	0	0	0	6	0	0	0	0	0	2
Eg pleosticta	2	3	8	1	0	2	3	2	1	6	2	6	2	3	5	4	9	2
Eg securigera	9	8	11	6	1	9	10	9	4	20	11	6	2	16	6	42	44	26
Eg townsendi	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eg truncata	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0

Eg viridis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
El bombiformis	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
El cingulata	4	0	6	0	0	4	0	4	0	2	5	4	2	2	3	4	2	1
El nigrita	10	5	32	18	26	21	23	41	20	18	24	20	21	52	13	6	10	7
Ex smaragdina	0	0	1	0	4	1	9	9	2	1	1	4	11	0	17	0	1	4

	L07			**L08**			**L09**			**L10**			**L11**			**L12**		
	L07 ATR	**L07 NRG**	**L07 FOR**	**L08 ATR**	**L08 NRG**	**L08 FOR**	**L09 ATR**	**L09 NRG**	**L09 FOR**	**L10 ATR**	**L10 NRG**	**L10 FOR**	**L11 ATR**	**L11 NRG**	**L11 FOR**	**L12 ATR**	**L12 NRG**	**L12 FOR**
Ef surinamensis	1	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Eg bembei	0	1	1	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0
Eg cordata	151	151	140	196	154	180	163	269	307	170	99	175	181	269	185	118	31	58
Eg clausi	0	0	34	3	4	16	3	3	21	2	0	5	5	11	8	3	5	6
Eg despecta	0	1	0	0	0	0	0	0	2	1	0	1	1	0	1	1	2	1
Eg fimbriata	3	0	1	0	0	0	0	1	1	2	0	0	1	1	0	0	2	0
Eg gaianii	1	1	10	18	12	13	14	10	26	3	1	4	19	0	14	2	0	2
Eg ignita	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1
Eg iopoecila	0	0	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Eg marianae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Eg milenae	0	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	2	0
Eg pleosticta	0	2	4	1	2	4	0	0	6	9	2	3	6	2	2	3	6	3
Eg securigera	18	8	6	14	18	23	5	4	24	13	22	13	11	4	8	3	8	14
Eg townsendi	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0

Eg viridis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
El bombiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
El cingulata	1	0	1	3	0	1	0	0	3	1	0	1	1	1	1	1	0	1
El nigrita	7	29	3	36	25	25	4	13	7	4	9	20	19	9	11	12	5	9
Ex smaragdina	1	1	6	0	0	10	1	1	4	0	0	1	0	1	0	0	0	1

CAPÍTULO III

FOREST COVER OUTWEIGHS RESTORATION STRATEGY IN EXPLAINING BEE BETA DIVERSITY IN THE ATLANTIC FOREST, BRAZIL[3]

Abstract: Ecosystem restoration is essential to recover biodiversity and ecosystem services. The results of active and passive restoration strategies should be evaluated through ecological indicators, such as bees. Euglossini bees are essential pollinators in neotropical ecosystems and respond negatively to landscape disturbances. Understanding how forest cover (%) and landscape heterogeneity influence their communities is essential for guiding restoration and conservation efforts. We analyzed the effects of habitat type (forest, active restoration, and natural regeneration), forest cover (%), and landscape compositional heterogeneity on species composition and beta diversity components of euglossine communities in the Atlantic Forest. We found that forest cover (%) significantly influences species composition, beta diversity, and turnover, while habitat type did not affect bee communities. Both active and natural restoration strategies effectively recovered euglossine communities. Landscapes with a higher forest cover (%) supported forest-dependent species, while a low forest cover (%) favored species with higher environmental plasticity, increasing turnover. We found that landscape changes negatively affected bee communities by increasing community similarity among habitat types. These results emphasize the importance of forest conservation and restoration for maintaining pollinator diversity and re-establishing ecosystem services. Our findings provide important insights for landscape restoration and biodiversity conservation in fragmented tropical landscapes.

Keywords: Orchid bees, active restoration, natural regeneration, landscape composition, community composition.

[3] Manuscrito em preparação para submissão no periódico *Biological Conservation.*

1. INTRODUCTION

Ecosystem restoration at the landscape scale is a global challenge of the 2030 Agenda, essential for addressing biodiversity loss and mitigating the climate crisis. Ecological restoration comprises different approaches to recover and enhance the resilience of degraded and destroyed ecosystems (SER, 2004). By supporting biodiversity, restoration plays an important role in sustaining ecosystem services essential to human well-being.

Evaluating restoration outcomes in recovering biodiversity is crucial to ensure effective restoration management (Holl and Aide, 2011). Restoration outcomes are typically assessed with diversity indicators of plant and animal communities (Rodrigues et al. 2009). Metrics such as species richness and abundance are often used as proxies for local biodiversity recovery in restored habitats (Crouzeilles et al. 2016; Carneiro et al. 2024). However, high taxonomic diversity and singletons can mask species identity and broader ecological processes at the landscape scale, affecting our understanding of ecological dynamics between restored and conserved habitats (Jost 2010). Then, assessing variations in regional species diversity (i.e. beta diversity) can provide a better evaluation of restoration outcomes (Lane et al. 2021; Carneiro et al. 2024).

Beta diversity is essential for evaluating restoration effectiveness, as it reflects variations in species composition between restored and reference (conserved) habitats (Whittaker, 1960). These variations result from different filters operating synergistically across spatial and temporal scales. Large-scale filters, such as climatic and historical factors shape community patterns, while local filters, including resource availability and ecological interactions, influence community composition in small scales (Legendre et al. 2005; Barton et al. 2013).

Differences in species composition arise from replacement (i.e. turnover) and species loss (i.e. nestedness) among local communities (Baselga, 2010). Among several factors, turnover highlights the role of environmental gradients in community structure, and nestedness reflects the influence of niche availability and barriers on species dispersal and colonization (Legendre, 2014). Considering that recovering community composition is a primary goal of ecological restoration (Rodrigues et al. 2009; Crouzeilles et al. 2016), understanding how environmental variations drive species replacement and loss is important for conserving the ecological processes that underpin community arrangement (Barton et al. 2013; Legendre, 2014).

Landscape structure also affects beta diversity patterns due to the influence of habitat amount and configuration on ecological dynamics (Pardini et al. 2010). Habitat loss and fragmentation driven by anthropogenic disturbances act as strong ecological filters, intensifying processes such as species extinction within communities (Püttker et al. 2014). These disturbances lead to biotic homogenization, decreasing differences in species composition between local communities (Olden and Rooney, 2006; Püttker et al. 2014). Therefore, forest restoration is essential for re-establishing and maintaining ecological processes that affect species composition at the landscape scale.

Many studies have evaluated the effect of landscape context on animal beta diversity in different ecosystems (Morante et al. 2015; Medeiros et al. 2019; Regolin et al. 2020; Lane et al. 2021). Overall, these studies suggest that landscapes with lower habitat amount and compositional heterogeneity support subsets of species from landscapes with higher habitat availability and heterogeneity. Consequently, a higher habitat amount is expected to enhance the recovery of species composition at the landscape scale (Pardini et al. 2010; Carneiro et al. 2024). Understanding how landscape structure influences beta diversity in restored ecosystems can provide information for designing management strategies focused on recovering and maintaining regional species diversity.

This study investigated how variations in landscape composition influence orchid bee community composition between restored and conserved habitats in the Atlantic Forest. Euglossine bees, distributed from the southern United States to northern Argentina, are key pollinators in the Neotropical rainforests (Roubik and Hanson, 2004). They are highly forest-dependent and important ecological indicators of habitat quality (Allen et al. 2019; Brown et al. 2024) and landscape disturbances (Carneiro et al. 2022). Changes in landscape structure negatively affect the alpha diversity of euglossine communities (Allen et al. 2019; Côrrea-Neto et al. 2024), as well as species composition (Cândido et al. 2018). Nonetheless, these bees respond positively to habitat restoration, with species abundance, richness, and composition showing no significant differences between conserved and restored habitats (Ferronato et al. 2017; Capítulo II).

Here, we analyzed variations in the composition of euglossine bee communities in response to landscape changes in actively restored, passively restored (natural regeneration hereafter), and conserved forest habitats. Specifically, we addressed the following questions: (1) Do variations in forest cover (%) and compositional heterogeneity within landscapes influence total beta diversity and its components (turnover and nestedness)? (2) Do euglossine species exhibit specificity to habitat type (active

restoration, natural regeneration, and conserved forest) and forest cover (%) level in the landscape? (3) Does forest cover (%) affect the probability of occurrence of the indicator species? We hypothesized that changes in forest cover (%) and compositional heterogeneity drive variations in bee species composition (Cândido et al. 2018), whereas habitat type has no significant effect (Ferronato et al. 2017). Additionally, we hypothesized that total beta diversity, turnover, and nestedness increase with higher differences in landscape composition (Regolin et al. 2020). We expected that low forest cover (%) and compositional heterogeneity would lead to the homogenization of euglossine communities among habitats pairwise, given the negative effect of habitat loss and the positive influence of compositional heterogeneity on these bees (Cândido et al. 2018; Carneiro et al. 2022). This study highlights the influence of landscape composition on the beta diversity of euglossine communities among restored and conserved habitats, emphasizing the essential role of landscape structure in shaping ecological dynamics in restored ecosystems.

2. MATERIAL AND METHODS

2.1 Study area

This study was carried out in 12 landscapes within the Mosaic of Conservation Reserves of the Golden Lion Tamarin in the Rio de Janeiro state, Southeast Brazil (Figure 1). Originally covered by the Atlantic Forest, this region currently consists of a mosaic of protected and restored forest patches scattered by anthropic matrices, including pastures, urban areas, and linear structures (Figure 1). The predominant vegetation comprises dense submontane and lowland forests, characteristic of a humid tropical climate with rainy summers and short, dry winters (ICMBio, 2023).

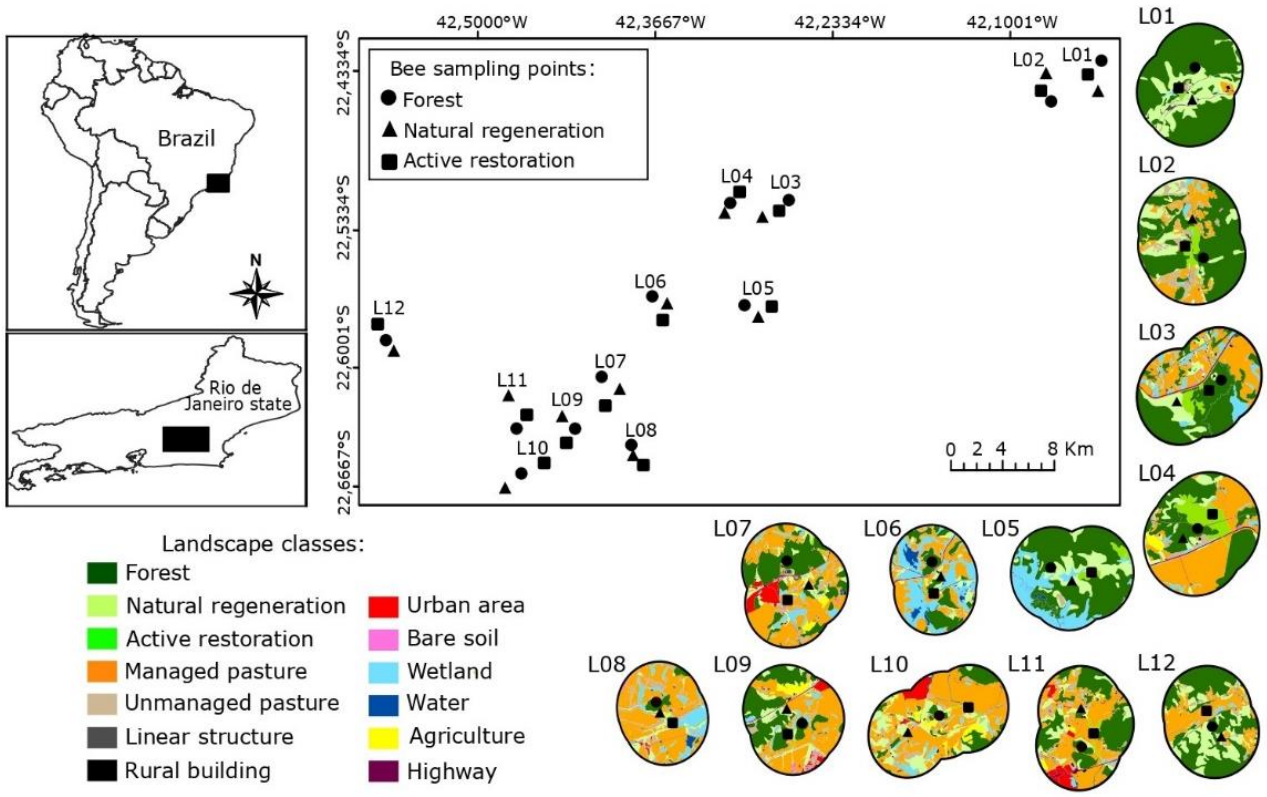

Figure 1. Study area showing sampling sites of Euglossini bees in forest (*N*= 12, circles), natural regenerated (*N*= 12, triangles), and active restored (*N*=12, squares) habitats within 12 landscapes in the Rio de Janeiro state, Southeast Brazil. Each landscape represents three 1,500 m dissolved buffers. The landscapes were mapped using a thematic resolution of 13 classes.

In each landscape, we selected three habitat types for bee sampling: conserved forest, natural regeneration, and active restoration, resulting in 36 sampling points (three points * 12 landscapes) (Capítulo II). Conserved forest patches (i.e. reference habitat) represent areas with minimal or no anthropogenic disturbance in the last 30 years. Actively restored areas are part of projects implemented by the *Associação Mico Leão Dourado* (AMLD) to enhance habitat connectivity on the landscape scale. Restoration management includes planting native tree species in parallel rows at least two meters apart. Natural regenerated habitats are characterized by spontaneous vegetation recovery without human management. The two restored habitat types were selected along a gradient of forest recovery and age, ranging from sparsely vegetated young restorations to older patches with well-developed vegetation. The age of active restoration sites ranges from 5 to 21 years, while naturally regenerated sites aged from 10 to 24 years.

Detailed descriptions of each habitat type (conserved forest, active restoration, and natural regeneration) are provided in Capítulo II.

2.2 Bee sampling

We sampled euglossine males during the rainy season in November 2021, December 2022, and March 2023, coinciding with their peak activity period, including seasonal species (Roubik and Hanson, 2004). In each habitat type, euglossine bees were sampled using five aromatic traps made from PET bottles (eucalyptol, eugenol, methyl cinnamate, methyl salicylate, and vanillin) (Aguiar and Gaglianone, 2008; Capítulo II). Sampling was conducted in two field expeditions, each lasting three consecutive days, totaling six sampling days per habitat type. Traps were set up in the early morning of the first day and collected in the afternoon of the third day. Details of bee sampling are available in Capítulo II.

Bees were identified using taxonomic keys and confirmed by a taxonomist. Dry specimens are deposited in the Bee Collection of the Experimental Ecology Sector at Universidade Estadual do Norte Fluminense Darcy Ribeiro (UENF).

2.3 Landscape composition analysis

We created 1,500-meter concentric buffers around each sampling point in the three habitat types (forest, active restoration, and natural regeneration). Thus, each of the 12 landscapes represents three nested dissolved buffers (Capítulo II; Figure 1). Land use within these landscapes was mapped in a 1:2,500 scale using high-resolution satellite images in the ArcGIS Pro software version 3.1.0 (Community ArcGIS Pro 3.1.0, 2023). The landscapes were classified into 13 classes: forest, active restoration, natural regeneration, managed pasture, unmanaged pasture, linear structure, rural building, urban area, bare soil, wetland, water, agriculture, and highway (Figure 1; Capítulo II). These categories were chosen based on the ecological requirements of euglossine bees and previous studies (Carneiro et al. 2021; Carneiro et al. 2022).

Afterward, we rasterized the landscape vector map (5-meter resolution) to quantify the forest cover (%) and compositional landscape heterogeneity, using the PLAND and SHDI metrics, respectively (McGarigal, 2015). These metrics were calculated in multi-buffers around each habitat type, from 250 to 1,500 meters, in 250-meter intervals (Capítulo II; Supplementary Material Appendix A). Multiscale approaches are essential to detect the scale of effect, which represents the spatial scale at which landscape attributes most strongly influence ecological variables (Jackson and Fahrig, 2012).

To evaluate how variations within landscapes influence total beta diversity and its components, we calculated differences in forest cover (%) and landscape heterogeneity among landscapes pairwise for each spatial scale (Medeiros et al. 2022). Specifically, we subtracted the metric values of one nested landscape from another for each pair: forest vs. active restoration, forest vs. natural regeneration, and natural regeneration vs. active restoration (Figure 1; Supplementary Material Appendix B).

Landscape metrics were calculated using the *lsm* function from the R package landscapemetrics (Hesselbarth et al. 2019).

2.4 Beta diversity

We used a presence-absence matrix (Supplementary Material Appendix C) to quantify total beta diversity and its turnover and nestedness components among habitats pairwise within each nested landscape (forest vs. active restoration; forest vs. natural regeneration; and natural regeneration vs. active restoration; Supplementary Material Appendix B). Total beta diversity was assessed using Sorensen's dissimilarity (βsor), turnover using Simpson's dissimilarity (βsim), and nestedness as the difference between Sorensen's and Simpson's dissimilarities (βsor - βsim) (Baselga, 2010). All analyses were conducted with the *beta.pair* function from the R package betapart (Baselga et al. 2023).

2.5 Data analysis

We analyzed the influence of habitat type (forest, active restoration, and natural regeneration), forest cover (%), and landscape heterogeneity on species composition using Jaccard dissimilarity matrices. To evaluate variations in species composition among habitat types, we used a Multivariate Analysis of Permutational Variance (PERMANOVA). To assess the effects of landscape composition, we built multiple PERMANOVA models using the landscape metrics as explanatory variables in multi-scale (250 – 1,500 m; Supplementary Material Appendix A). The optimal PERMANOVA model was selected based on the landscape metric with the highest statistical explanatory power on species composition ($p < 0.05$, $R^2 > 0.1$; Supplementary Material Appendix D). This approach was used to detect the scale of the effect of landscape structure on the euglossine composition. We found that forest cover (%) at 1,000 m had the highest explanatory power on species composition (Supplementary Material Appendix D). Then, we classified landscapes into three forest cover levels at 1,000 m: low (0 – 25%), medium (25 – 50%), and high cover (> 50%) (Supplementary Material Appendix A). We used these levels due to the low forest cover in the study area, where few landscapes were more than 50% covered. A new PERMANOVA was performed using these forest cover (%) levels as

explanatory variables. Statistical significance was based on 999 permutations. Additionally, we performed a Permutational Multivariate Dispersion Analysis (PERMDISP) to verify heterogeneity within groups (i.e. habitat type and forest cover (%) levels) (Anderson et al. 2006). For significant PERMANOVA results ($p < 0.05$), a Pairwise PERMANOVA test was used to identify differences in community composition among groups. PERMANOVA results were graphically visualized using a Non-Metric Multidimensional Scaling analysis (NMDS). Jaccard dissimilarity, PERMANOVA, and PERMDISP analyses were performed using the *vegdist*, *adonis2*, and *betadisper* functions of the R package vegan (Oksanen et al. 2022).

We evaluated the relationship between euglossine species occurrence and habitat type (forest, natural regeneration, and active restoration), and forest cover (%) levels (1,000 m) using the Individual Indicator Value Method (IndVal), with 999 permutations. This method identifies species specificity and fidelity to particular habitat groups (Dufrene and Legendre, 1997). This analysis was conducted with the *multipatt* function from the R package indicspecies (Cáceres and Legendre, 2009).

To determine whether the probability of occurrence of the indicator species (IndVal: $p < 0.05$) is influenced by forest cover (%), we built Generalized Linear Models (GLMs) using presence-absence data for each indicator species as the response variable. The predictor variable was forest cover (%) at 1,000 m. This scale was chosen due to its higher influence on species composition, as previously indicated by PERMANOVA. These logistic models were built with a binomial distribution and a "logit" link. We ranked each GLM against null models using the Akaike Information Selection Criterion Corrected for small samples (AICc). The model with the best fit was the one with the lowest ΔAICc value (Burnham and Aderson, 2002). Model assumptions were accessed with Q-Q plots. Model selection was performed using the model.sel function in the R MuMIn package (Barton, 2023).

Finally, we assessed the correlation between beta total diversity, turnover, and nestedness with differences in forest cover (%) and compositional heterogeneity for each habitat pairwise (i.e. forest vs. active restoration, forest vs. natural regeneration, and natural regeneration vs. active restoration). We scaled the values derived from the differences in landscape metrics pairwise (section 2.3) to account for the high variation in both positive and negative axes. To evaluate the effects of variations in landscape composition in different scales on total beta diversity and its components, we used a Multiple Regression Distance analysis - MRM with 999 permutations (Linchstein, 2007).

We presented results only for the models with the highest R^2 and lowest *p*-value for each response variable, representing the scale of the effect of landscape composition on total beta diversity and its components (Supplementary Material Appendix F). These analyses were carried out using the *MRM* function of the R package ecodist (Goslee & Urban, 2007).

All analyses were performed in the R 4.3.2 software (R Core Team, 2021).

3. RESULTS

We found that habitat type does not significantly influence euglossine species composition (PERMANOVA: R^2= 0.05, *pseudo*-F= 1.04, *p*= 0.40; Figure 2A). However, the variability in species composition differed within habitat types (PERMDISP: *F*= 5.44, *p*= 0.01). In contrast, changes in forest cover (%) at 1,000 m led to variations in community composition, and this pattern was not significantly influenced by variability in the forest cover levels (PERMANOVA: R^2= 0.16, *pseudo*-F= 3.33, *p*= 0.001; PERMDISP: *F*= 1.68, *p*= 0.21; Figure 2B). The first two NMDS axes showed that landscapes with high and medium forest cover have different species compositions compared to landscapes with low forest cover (PERMANOVA Pairwise: High x Medium: *p*= 0.054; High x Low: *p*= 0.006, Medium x Low: *p*= 0.014; Figure 2B).

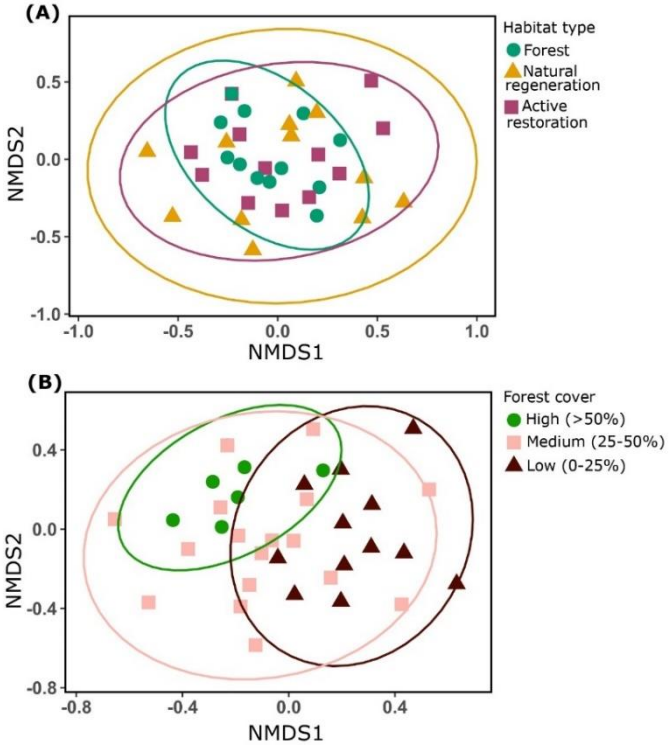

Figure 2. Non-metric Multidimensional Scaling (NMDS) of euglossine bee communities among habitat types (forest, active restoration, natural regeneration) (**A**) and forest cover

levels (%) at 1,000 m (high: > 50%, medium: 25-50%, and low: 0-25%) (**B**). Each point represents a bee sampling site, and ellipses 95% confidence intervals.

We found no bee indicator species for habitat type (IndVal: p > 0.05; (Supplementary Material Appendix E). However, two euglossine species were indicators of the forest cover level (%). *Euglossa iopoecila* Dressler (IndVal= 0.81, p= 0.001) and *Euglossa ignita* Smith (IndVal= 0.79, p= 0.001) are indicators of landscapes with high (> 50%), and high and medium forest cover (25 - 50%), respectively (Supplementary Material Appendix E). Logistic models for both species fitted better than the null model (*E. iopoecila:* ΔAICc= 0.0, *wi*= 1.0; *E. ignita:* ΔAICc= 0.0, *wi*= 0.98). Logistic regression curves showed that *E. iopoecila* was more likely to occur in landscapes with higher forest cover (Figure 3A), whereas this pattern was not evident for *E. ignita* (Figure 3B).

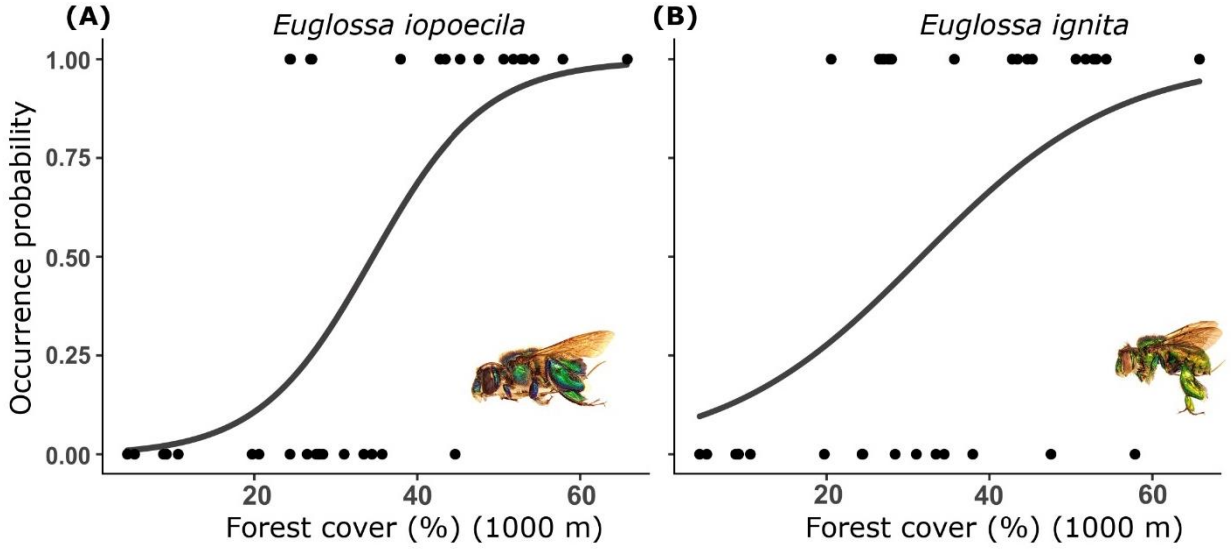

Figure 3. Logistic regression curves indicating the occurrence probability of *Euglossa iopoecila* Dressler (**A**) and *Euglossa ignita* Smith (**B**) with forest cover (%) at 1,000 m.

Total beta diversity and turnover showed different responses to variations in landscape composition (Supplementary Material Appendix F). Increased variation in forest cover (%) positively influenced total beta diversity pairwise, particularly between forest and active restoration, and natural regeneration and active restoration (R^2= 0.24, p= 0.002; Figure 4A). A higher variation in compositional heterogeneity negatively affected total beta diversity pairwise between forest and active restoration (R^2= 0.13, p= 0.03; Figure 4B). Additionally, a higher variation in forest cover (%) was associated with increased species turnover, mainly between forest and active restoration (R^2= 0.11, p=

0.02; Figure 4C). The nestedness component was unaffected by any landscape variable (Supplementary Material Appendix F).

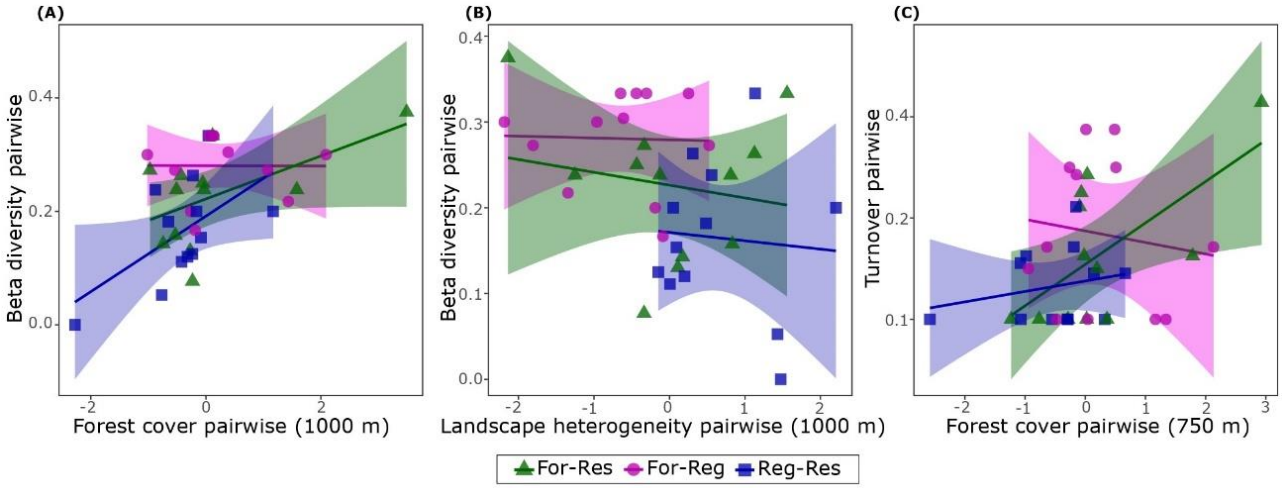

Figure 4. Relation of the total beta diversity (**A, B**) and turnover (**C**) of euglossine communities among habitat pairwise (Green: forest x active restoration; Pink: forest x natural regeneration; Blue: natural regeneration x active restoration) with variations in forest cover (%) (**A**, **C**) and landscape heterogeneity (**B**) among landscapes pairwise. The *x*-axis is scaled. The 95% confidence interval is represented by the shaded area.

4. DISCUSSION

Our findings support the hypothesis that euglossine species composition is influenced by landscape composition but is unaffected by habitat type. The results suggest that actively and naturally restored habitats support species compositions similar to those of conserved forest areas. Euglossine bees exhibit a high flight capacity, facilitating bee dispersal and colonization to restored habitats. These findings align with previous studies that reported no significant differences in euglossine communities between restored and conserved habitats (Ferronato et al. 2017; Capítulo II). However, we observed that forest cover (%) drives changes in species composition, total beta diversity, and turnover among habitats pairwise. These results underscore the essential role of forest cover (%) in shaping ecological dynamics and regional species diversity (Püttker et al. 2014; Maurenza et al. 2024).

4.1 Landscape composition affects euglossine communities

The influence of forest cover (%) and landscape heterogeneity on beta diversity has been indicated for different animal groups, such as birds (Morante et al. 2015), mammals (Regolin et al. 2020), and insects (Medeiros et al. 2019; Medeiros et al. 2022). These

landscape attributes are crucial for the recovery of species composition in restored habitats. The habitat amount is particularly important for restoration outcomes, as it reflects the available species pools and facilitates colonization and migration dynamics at the landscape scale (Pardini et al. 2010). Compositional heterogeneity, which represents land-use diversity, can enhance animal community recovery by providing landscape complementation and supplementation for species with different ecological requirements (Fahrig et al. 2011; Regolin et al. 2020; Carneiro et al. 2024).

Landscapes with a low forest cover (%) presented different composition of euglossine communities in relation to landscapes with a high forest cover (%). Forest loss acts as an important ecological filter, increasing the role of deterministic processes in shaping community composition (Morante et al. 2015; Maurenza et al. 2024). Habitat loss favors species with higher plasticity to environmental disturbances in the landscape (Püttker et al. 2014; Morante et al. 2015). For instance, euglossine species such as *Euglossa cordata* (Linnaeus) and *Eulaema nigrita* Lepeletier were recorded in all habitat types across landscapes, showing their high plasticity to landscape changes (Aguiar and Gaglianone, 2008; Carneiro et al. 2022). On the other hand, species like *Euglossa marianae* Nemésio and *Eufriesea violacea* Blanchard were only found in landscapes with a high forest cover (%), indicating their sensitivity to landscape disturbances (Ramalho et al. 2009; Giangarelli et al. 2009). These findings highlight the importance of habitat amount in maintaining euglossine species composition at the landscape scale.

We found that two euglossine species were associated with landscapes with a higher forest cover (%). *E. opecila* and *E. ignita* have been commonly recorded in conserved forest areas (Ramalho et al. 2009; Rosa et al. 2015). Many euglossine species are dependent on forests for floral and nesting resources (Roubik and Hanson, 2004). Forest loss negatively impacts euglossine bees by reducing the spatial availability of these critical ecological resources (Cândido et al. 2018; Carneiro et al. 2022). Our results reinforce that euglossine species can be good indicators of environmental and landscape changes (Brown et al. 2024).

A higher variation in forest cover (%) led to increased dissimilarity and species replacement among habitats pairwise, particularly between forest and active restored, and natural regenerated and active restored habitats. This suggests that species found in landscapes with high forest cover are replaced by other species in landscapes with low forest cover. Forest cover (%) is essential in maintaining a high beta diversity of euglossine communities, promoting species turnover between restored and conserved habitat

patches. Species turnover is a proxy of species' ecological tolerance and occurs when species exhibit a high habitat specificity (Barton et al. 2013; Legendre, 2014). Consequently, changes in landscape composition can increase euglossine community dissimilarity across habitats (Cândido et al. 2018; Allen et al. 2019).

The high turnover of euglossine species between conserved and actively restored habitats may contribute to the success of this restoration strategy. While species replacement may be linked to the fact that many euglossine species are habitat specialists, this bee group tends to exhibit a generalist behavior in collecting floral resources (Roubik and Hanson, 2004). As a result, pollination services provided by species in conserved habitats may be maintained by other species in restored areas, supporting the recovery of pollination services in restored habitats (Winfree et al. 2018).

We found that a higher landscape heterogeneity reduced species dissimilarity between forest and actively restored habitats. Some studies have shown positive effects of variations in compositional landscape heterogeneity on total beta diversity and its components (Medeiros et al. 2019; Regolin et al. 2020). However, it is important to note that these studies were conducted in agricultural landscapes, where increased heterogeneity benefits biodiversity (Fahrig et al. 2011). In our study area, the increase in compositional heterogeneity reflects habitat loss, since the most predominant matrix is pasture. In this context, increased heterogeneity negatively impacted euglossine diversity (Corrêa-Neto et al. 2024). Anthropogenic disturbances, such as habitat loss, are major drivers of biotic homogenization, leading to increased community similarity on large scales (Püttker et al. 2014; Maurenza et al. 2024).

5. FINAL REMARKS

Our study highlights the essential role of forest cover (%) in shaping beta diversity and turnover of euglossine communities in conserved and restored forest habitats in the Atlantic Forest. The findings indicate that forest loss negatively affects bee communities by changing species composition. Variations in euglossine communities between forested and deforested landscapes indicate that landscape structure is an important filter for bee occurrence. Species with higher environmental plasticity are favored in landscapes with low forest cover, while species sensitive to environmental disturbances are more common in landscapes with higher habitat availability.

Furthermore, forest cover is essential for the recovery of euglossine communities in restored habitats. Our study demonstrates that increased habitat availability enhances

species dispersal and colonization, thereby promoting the recovery of different dimensions of animal community diversity. These findings suggest that both restored and conserved forest patches hold a similar conservation value, as they contribute to maintaining a high regional species diversity.

Finally, it is important to emphasize that active and natural regeneration restoration strategies are equally effective in restoring the composition of euglossine communities in the Atlantic Forest. This supports that "restore it, and they will come" is a valid assumption for restoration projects aimed at biodiversity conservation, particularly for bees. Although bees are not a target group for restoration initiatives, the successful recovery of their community composition serves as an indicator of the re-establishment of pollination ecological service in restored habitats.

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Supplementary Material Appendix A. Compositional heterogeneity (shdi) and forest cover (%) (pct10) quantified at multi-scale (250 - 1,500 m) in 12 landscapes (L01 – L12) in Rio de Janeiro state, Southeastern Brazil. Each landscape represents three nested landscapes around the euglossine sampling points: ATR: active restoration, NRG: Natural regeneration, and FOR: Forest. “Level 1000” means the forest cover (%) levels at the 1,000 m scale: High: >50%, Medium: 25 - 50%, Low: 0 – 25%).

Landscape	Habitat type	Shdi 250	Shdi 500	Shdi 750	Shdi 1000	Shdi 1250	Shdi 1500	pct10 250	pct10 750	pct10 1250	pct10 1500	Level 1000
L01	ATR	1.640	1.461	1.236	1.088	0.983	0.919	35.325	31.086	54.043	62.273	Medium
L01	NRG	0.590	1.192	1.240	1.103	1.025	0.980	9.197	41.242	53.234	60.296	Medium
L01	FOR	0.653	0.705	0.760	0.875	0.944	0.910	64.106	68.145	65.730	66.951	High
L02	ATR	1.023	1.435	1.465	1.460	1.427	1.410	20.079	47.363	54.036	53.960	High
L02	NRG	1.584	1.687	1.651	1.542	1.486	1.457	34.344	37.462	49.362	50.697	Medium
L02	FOR	0.767	1.148	1.404	1.438	1.377	1.336	47.268	53.606	55.661	57.557	High
L03	ATR	1.200	1.308	1.486	1.508	1.625	1.657	56.258	52.975	45.170	41.359	High
L03	NRG	1.336	1.673	1.736	1.758	1.687	1.601	3.528	18.438	36.916	44.291	Medium
L03	FOR	0.635	1.083	1.438	1.451	1.561	1.568	77.824	48.202	37.519	37.115	Medium
L04	ATR	0.821	1.065	1.546	1.567	1.528	1.503	33.112	15.698	35.372	37.934	Medium
L04	NRG	1.605	1.677	1.643	1.601	1.606	1.594	20.716	34.380	25.818	31.151	Medium
L04	FOR	1.187	1.615	1.592	1.586	1.564	1.556	59.100	26.681	32.872	36.490	Medium
L05	ATR	1.059	1.112	1.059	0.983	0.937	1.001	18.464	39.174	62.075	63.169	High
L05	NRG	1.052	1.155	1.281	1.226	1.208	1.194	30.875	37.898	53.097	52.719	Medium
L05	FOR	0.918	1.066	1.082	1.174	1.184	1.177	30.552	45.883	54.552	52.895	High
L06	ATR	1.632	1.648	1.666	1.633	1.634	1.652	21.788	24.477	23.723	22.007	Low
L06	NRG	1.200	1.746	1.747	1.685	1.669	1.661	48.833	29.143	19.722	17.390	Low
L06	FOR	1.084	1.507	1.768	1.774	1.699	1.645	70.321	32.653	17.748	18.124	Low
L07	ATR	1.024	1.797	1.809	1.817	1.844	1.782	0.000	10.517	17.791	23.064	Low
L07	NRG	1.581	1.819	1.770	1.825	1.796	1.779	11.802	23.618	32.033	34.491	Medium
L07	FOR	1.335	1.215	1.243	1.453	1.599	1.673	53.209	66.358	46.824	39.949	High
L08	ATR	1.875	1.844	1.638	1.536	1.516	1.456	0.115	13.248	5.876	4.329	Low

L08	NRG	1.808	1.770	1.611	1.511	1.418	1.398	21.656	16.324	5.876	4.939	Low
L08	FOR	1.028	1.628	1.577	1.479	1.367	1.382	62.530	16.322	6.087	5.647	Low
L09	ATR	1.458	1.255	1.437	1.462	1.530	1.659	45.212	44.365	30.982	26.467	Medium
L09	NRG	1.402	1.503	1.681	1.654	1.568	1.567	16.312	34.615	43.182	42.740	Medium
L09	FOR	1.114	1.465	1.360	1.491	1.591	1.615	53.586	31.968	25.006	25.820	Medium
L10	ATR	1.063	0.903	0.970	1.173	1.299	1.334	0.000	0.000	12.454	18.945	Low
L10	NRG	1.199	1.453	1.505	1.548	1.547	1.594	0.000	5.236	6.100	7.497	Low
L10	FOR	1.432	1.622	1.553	1.438	1.443	1.513	41.126	13.704	7.148	7.181	Low
L11	ATR	0.597	1.052	1.363	1.453	1.412	1.432	0.000	19.430	36.200	39.498	Medium
L11	NRG	1.584	1.437	1.426	1.547	1.543	1.498	17.096	11.107	28.409	34.505	Low
L11	FOR	1.048	1.214	1.429	1.590	1.629	1.696	63.534	26.903	27.299	27.666	Low
L12	ATR	0.638	1.551	1.515	1.453	1.416	1.370	0.000	28.256	36.605	42.183	Medium
L12	NRG	1.257	1.473	1.457	1.454	1.415	1.355	30.713	31.198	34.222	38.499	Medium
L12	FOR	0.750	1.132	1.346	1.380	1.386	1.347	57.582	36.583	37.729	41.252	Medium

Supplementary Material Appendix B. Total beta diversity, nestedness and turnover of euglossine communities calculated between pairs of habitats of each landscape (L01-L12): FOR x ATR, FOR x NRG, and NRG x ATR (FOR: Forest, ATR: Active restoration, NRG: Natural Regeneration). The values of the metrics percentage of forest (%) (pct) and landscape heterogeneity (shdi) were calculated through the difference between the value of each pair of landscape (FOR x ATR, FOR x NRG, and NRG x ATR) for each scale (between 250 to 1500 m, see Supplementary Material Appendix A).

Landscape	Habitat pairwise	betatotal	nestedness	turnover	pct10_250	pct10_500	pct10_750	pct10_1000	pct10_1250	pct10_1500	shdi_250	shdi_500	shdi_750	shdi_1000	shdi_1250	shdi_1500
L01	FOR_ATR	0.238	0.127	0.125	28.782	40.185	37.06	22.992	11.687	4.677	-0.987	-0.756	-0.476	-0.213	-0.039	-0.009
L01	FOR_NRG	0.217	0.217	0	54.909	44.361	26.904	21.133	12.496	6.655	0.062	-0.487	-0.48	-0.229	-0.081	-0.07
L01	NRG_ATR	0.154	0.071	0.091	-26.12	-4.176	10.156	1.859	-0.809	-1.978	-1.05	-0.269	0.004	0.016	0.042	0.061
L02	FOR_ATR	0.238	0.038	0.222	27.189	17.569	6.243	2.526	1.625	3.597	-0.255	-0.288	-0.061	-0.022	-0.05	-0.074
L02	FOR_NRG	0.304	0.032	0.3	12.924	24.68	16.144	7.863	6.299	6.86	-0.817	-0.539	-0.247	-0.104	-0.108	-0.121
L02	NRG_ATR	0.182	0.082	0.111	14.265	-7.111	-9.901	-5.337	-4.674	-3.263	0.561	0.251	0.187	0.082	0.058	0.047
L03	FOR_ATR	0.273	0.273	0	21.567	7.83	-4.774	-9.365	-7.651	-4.244	-0.565	-0.225	-0.048	-0.057	-0.064	-0.089
L03	FOR_NRG	0.273	0.273	0	74.296	61.87	29.764	16.555	0.603	-7.176	-0.701	-0.59	-0.298	-0.307	-0.126	-0.033
L03	NRG_ATR	0	0	0	-52.73	-54.04	-34.53	-25.92	-8.254	2.932	0.136	0.365	0.25	0.25	0.063	-0.056
L04	FOR_ATR	0.13	0.04	0.1	25.988	14.001	10.983	-0.517	-2.5	-1.444	0.366	0.55	0.046	0.019	0.035	0.052
L04	FOR_NRG	0.167	0.076	0.1	38.385	-6.835	-7.699	0.588	7.054	5.339	-0.418	-0.062	-0.051	-0.015	-0.042	-0.039
L04	NRG_ATR	0.12	0.037	0.091	-12.39	20.837	18.682	-1.105	-9.554	-6.783	0.784	0.612	0.097	0.034	0.078	0.091
L05	FOR_ATR	0.263	0.041	0.25	12.087	15.859	6.709	-2.528	-7.523	-10.274	-0.141	-0.045	0.023	0.191	0.248	0.177
L05	FOR_NRG	0.333	0	0.375	-0.323	2.354	7.986	4.253	1.455	0.176	-0.134	-0.089	-0.199	-0.052	-0.024	-0.016
L05	NRG_ATR	0.053	0.053	0	12.411	13.505	-1.277	-6.781	-8.978	-10.45	-0.007	0.043	0.222	0.243	0.272	0.193
L06	FOR_ATR	0.158	0.158	0	48.533	22.263	8.176	-3.794	-5.974	-3.882	-0.548	-0.141	0.102	0.141	0.065	-0.007

L06	FOR_NRG	0.273	0	0.3	21.488	18.245	3.51	-3.888	-1.974	0.734	-0.116	-0.239	0.021	0.089	0.03	-0.016
L06	NRG_ATR	0.263	0.138	0.143	27.046	4.018	4.666	0.094	-4	-4.617	-0.432	0.098	0.081	0.052	0.035	0.009
L07	FOR_ATR	0.375	0	0.429	53.209	65.662	55.841	47.212	29.033	16.886	0.311	-0.581	-0.565	-0.364	-0.245	-0.109
L07	FOR_NRG	0.3	0.175	0.143	41.406	47.713	42.74	29.448	14.791	5.459	-0.246	-0.604	-0.527	-0.372	-0.197	-0.106
L07	NRG_ATR	0.2	0.2	0	11.802	17.949	13.101	17.764	14.242	11.427	0.557	0.023	-0.038	0.008	-0.048	-0.003
L08	FOR_ATR	0.077	0.077	0	62.416	28.829	3.074	-0.001	0.211	1.318	-0.847	-0.216	-0.06	-0.057	-0.149	-0.073
L08	FOR_NRG	0.2	0.2	0	40.874	7.401	-0.002	0	0.211	0.709	-0.78	-0.142	-0.034	-0.032	-0.05	-0.015
L08	NRG_ATR	0.125	0.125	0	21.541	21.428	3.076	0	0	0.61	-0.067	-0.074	-0.026	-0.025	-0.098	-0.058
L09	FOR_ATR	0.143	0.143	0	8.373	-21.67	-12.39	-6.46	-5.977	-0.646	-0.344	0.21	-0.077	0.029	0.061	-0.044
L09	FOR_NRG	0.3	0.175	0.143	37.273	-4.528	-2.646	-9.969	-18.176	-16.92	-0.288	-0.038	-0.321	-0.164	0.023	0.048
L09	NRG_ATR	0.333	0.333	0	-28.9	-17.14	-9.75	3.509	12.199	16.273	-0.056	0.248	0.244	0.193	0.038	-0.092
L10	FOR_ATR	0.333	0.333	0	41.126	22.64	13.704	4.428	-5.306	-11.765	0.368	0.719	0.583	0.265	0.144	0.179
L10	FOR_NRG	0.333	0.333	0	41.126	18.801	8.468	3.545	1.048	-0.316	0.232	0.169	0.048	-0.11	-0.105	-0.081
L10	NRG_ATR	0.2	0	0.222	0	3.839	5.236	0.883	-6.354	-11.449	0.136	0.55	0.535	0.375	0.249	0.26
L11	FOR_ATR	0.238	0.127	0.125	63.534	25.328	7.473	-3.533	-8.901	-11.832	0.452	0.161	0.067	0.138	0.217	0.264
L11	FOR_NRG	0.333	0	0.375	46.438	28.841	15.796	4.652	-1.109	-6.839	-0.536	-0.223	0.003	0.043	0.086	0.198
L11	NRG_ATR	0.238	0.127	0.125	17.096	-3.514	-8.323	-8.185	-7.791	-4.993	0.988	0.385	0.063	0.095	0.131	0.066
L12	FOR_ATR	0.25	0	0.286	57.582	23.585	8.327	2.258	1.124	-0.931	0.112	-0.419	-0.169	-0.074	-0.031	-0.022
L12	FOR_NRG	0.333	0.083	0.286	26.868	10.164	5.385	4.663	3.508	2.752	-0.508	-0.341	-0.111	-0.075	-0.029	-0.007
L12	NRG_ATR	0.111	0.111	0	30.713	13.422	2.942	-2.406	-2.384	-3.684	0.619	-0.078	-0.058	0.001	-0.002	-0.015

Supplementary Material Appendix C. Presence-absence matrix used to quantify Jaccard dissimilarity and beta diversity of euglossine bee communities sampled in 12 landscapes (L01-L12) in the Atlantic Forest. In each landscape, bees were sampled in three habitat types (ATR: Active restoration, NRG: Natural regeneration, and FOR: Forest). The first two letters in the species names (columns) represent the genus of each species: *Eg: Euglossa, El: Eulaema, Ex: Exaerete, Ef: Eufriesea.*

Sites	*Egcordata*	*Elnigrita*	*Elbombiformis*	*Elcingulata*	*Egignita*	*Egiopoecila*	*Egclausi*	*Egdespecta*	*Egmilenae*	*Egmarianae*	*Egtruncata*
L01ATR	1	1	0	1	1	1	1	0	1	1	0
L01NRG	1	1	0	0	1	0	1	1	0	1	0
L01FOR	1	1	0	1	1	1	1	1	0	1	0
L02ATR	1	1	0	0	1	1	1	0	0	1	0
L02NRG	1	1	0	0	1	1	1	1	1	1	0
L02FOR	1	1	0	1	1	1	1	0	0	1	0
L03ATR	1	1	0	0	1	1	1	0	0	0	0
L03NRG	1	1	1	1	1	1	1	1	0	0	1
L03FOR	1	1	0	0	1	1	1	0	0	0	0
L04ATR	1	1	0	1	1	0	1	1	0	0	1
L04NRG	1	1	0	1	1	0	1	0	0	0	0
L04FOR	1	1	0	1	1	1	1	1	1	0	0
L05ATR	1	1	0	1	1	1	1	1	0	0	0
L05NRG	1	1	0	1	0	1	0	1	0	1	0
L05FOR	1	1	0	1	1	1	1	0	0	0	0

L06ATR	1	1	0	1	0	1	1	0	0	0	0
L06NRG	1	1	0	1	0	1	1	0	0	0	0
L06FOR	1	1	0	1	1	0	1	1	1	0	0
L07ATR	1	1	0	1	0	0	0	0	0	0	0
L07NRG	1	1	0	0	0	0	0	1	0	0	0
L07FOR	1	1	0	1	0	1	1	0	0	0	0
L08ATR	1	1	0	1	0	0	1	0	0	0	0
L08NRG	1	1	0	0	0	0	1	0	0	0	0
L08FOR	1	1	0	1	0	0	1	0	0	0	0
L09ATR	1	1	0	0	0	0	1	0	0	0	0
L09NRG	1	1	0	0	0	1	1	0	0	0	0
L09FOR	1	1	0	1	1	0	1	1	1	0	0
L10ATR	1	1	0	1	0	0	1	1	1	0	0
L10NRG	1	1	0	0	0	0	0	0	0	0	0
L10FOR	1	1	0	1	0	0	1	1	0	0	0
L11ATR	1	1	0	1	1	0	1	1	1	0	0
L11NRG	1	1	0	1	0	0	1	0	0	0	0
L11FOR	1	1	0	1	0	0	1	1	0	0	0
L12ATR	1	1	0	1	0	0	1	1	0	0	0

L12NRG	1	1	0	0	0	0	1	1	1	0	0
L12FOR	1	1	0	1	1	0	1	1	0	0	0

Sites	*Egtownsendi*	*Eggaianii*	*Egsecurigera*	*Egfimbriata*	*Egbembei*	*Egpleosticta*	*Egviridis*	*Efviolacea*	*Efsurinamensis*	*Exsmaragdina*
L01ATR	0	1	1	1	0	1	0	0	0	0
L01NRG	0	1	1	0	0	1	0	0	0	0
L01FOR	0	1	1	1	1	1	0	0	0	1
L02ATR	0	1	1	1	0	1	0	0	0	0
L02NRG	0	0	1	1	0	0	0	0	0	1
L02FOR	0	1	1	0	0	1	0	1	0	1
L03ATR	0	0	1	0	0	1	0	0	0	1
L03NRG	0	1	1	0	1	1	0	0	0	1
L03FOR	0	0	1	0	0	1	0	0	0	1
L04ATR	0	1	1	1	0	1	0	0	0	1
L04NRG	0	1	1	1	0	1	0	0	1	1
L04FOR	0	1	1	1	0	1	0	0	0	1
L05ATR	0	0	1	0	0	1	0	0	0	1
L05NRG	0	0	1	1	0	1	0	0	0	0
L05FOR	0	0	1	0	0	1	0	0	0	1
L06ATR	0	1	1	0	0	1	0	0	0	0
L06NRG	0	1	1	1	1	1	0	0	0	1

L06FOR	0	1	1	0	0	1	0	0	0	1
L07ATR	0	1	1	1	0	0	0	0	1	1
L07NRG	0	1	1	0	1	1	0	0	0	1
L07FOR	0	1	1	1	1	1	0	0	1	1
L08ATR	0	1	1	0	0	1	0	0	0	0
L08NRG	0	1	1	0	0	1	0	0	0	0
L08FOR	0	1	1	0	0	1	0	0	1	1
L09ATR	0	1	1	0	0	0	0	0	0	1
L09NRG	0	1	1	1	0	0	0	0	0	1
L09FOR	0	1	1	1	0	1	0	0	0	1
L10ATR	0	1	1	1	0	1	0	0	0	0
L10NRG	0	1	1	0	0	1	0	0	0	0
L10FOR	1	1	1	0	0	1	0	0	0	1
L11ATR	0	1	1	1	1	1	0	0	0	0
L11NRG	0	0	1	1	1	1	0	0	0	1
L11FOR	0	1	1	0	0	1	1	0	0	0
L12ATR	0	1	1	0	0	1	0	0	0	0
L12NRG	0	0	1	1	0	1	0	0	0	0
L12FOR	0	1	1	0	0	1	0	0	0	1

Supplementary Material Appendix D. Permutational Multivariate Analysis of Variance (PERMANOVAs) used to evaluate the effect of landscape heterogeneity (shdi) and forest cover (%) (pct) on the dissimilarity of euglossine communities sampled in the Atlantic Forest. The “shdi” and “pct” metrics were quantified at multi-scale, from 250 to 1500 m, with a 250 m interval. In each modeling round, PERMANOVAs with a p-value < 0.05 (italics) were selected for the subsequent modeling round. The final round included the PERMANOVA in which the landscape metric had the higher explanatory power on community dissimilarity. Df: Degrees of freedom; Sum of Sqs: Sum of Squares.

Modeling round	PERMANOVA models	Df	Sum of Sqs	R^2	F	Pr(>F)
1°	Jaccard_dissim$shdi_250	1	0.116	0.034	1.408	0.22
	Jaccard_dissim$shdi_500	1	0.057	0.017	0.697	0.676
	Jaccard_dissim$shdi_750	1	0.069	0.020	0.842	0.547
	Jaccard_dissim$shdi_1000	*1*	*0.182*	*0.054*	*2.208*	*0.044*
	Jaccard_dissim$shdi_1250	1	0.048	0.014	0.589	0.737
	Jaccard_dissim$shdi_1500	1	0.120	0.035	1.461	0.21
	Jaccard_dissim$pct10_250	1	0.122	0.036	1.477	0.198
	Jaccard_dissim$pct10_500	*1*	*0.201*	*0.059*	*2.439*	*0.017*
	Jaccard_dissim$pct10_750	*1*	*0.217*	*0.064*	*2.639*	*0.012*
	Jaccard_dissim$pct10_1000	*1*	*0.197*	*0.058*	*2.396*	*0.031*
	Jaccard_dissim$pct10_1250	1	0.084	0.025	1.026	0.434
	Jaccard_dissim$pct10_1500	1	0.083	0.024	1.004	0.46
2°	Jaccard_dissim$shdi_1000	1	0.194	0.057	2.394	0.019
	Jaccard_dissim$pct10_500	*1*	*0.257*	*0.076*	*3.177*	*0.005*
	Jaccard_dissim$pct10_750	1	0.176	0.052	2.167	0.041
	Jaccard_dissim$pct10_1000	*1*	*0.250*	*0.074*	*3.090*	*0.006*
3°	*Jaccard_dissim$pct10_500*	*1*	*0.272*	*0.080*	*3.306*	*0.004*
	Jaccard_dissim$pct10_1000	*1*	*0.398*	*0.117*	*4.832*	*0.001*
Final PERMANOVA model	*Jaccard_dissim$pct10_1000*	*1*	*0.531*	*0.157*	*6.318*	*0.001*
	Residual	34	2.858	0.843		
	Total	35	3.389	1.000		

Supplementary Material Appendix E. Individual Indicator Value (IndVal) of euglossine communities sampled in the Atlantic Forest. The IndVal analysis was used to verify if euglossine species occurrence is an indicator of habitat type (FOR: Forest, NRG: Natural regeneration, and ATR: Active restoration), and level of forest cover (%) in the landscape (1,000 m): High cover (> 50%), Medium cover (25-50%) and Low cover (0-25%). Columns "s." with zeroes and ones represent the sites included in the combination of each species. Missing *p*-values (NA) mean that the species occurred in all groups. Significant *p*-values (> 0.05) are indicated in bold.

Species	s.FOR	s.NRG	s.ATR	IndVal (Habitat type)	*p*-value	s.High	s.Medium	s.Low	IndVal (Forest cover (%)	*p*-value
Euglossa_cordata	1	1	1	1	NA	1	1	1	1	NA
Eulaema_nigrita	1	1	1	1	NA	1	1	1	1	NA
Eulaema_bombiformis	0	1	0	0.289	1	0	1	0	0.243	1
Eulaema_cingulata	1	1	1	0.833	NA	1	1	1	0.833	NA
Euglossa_ignita	1	1	1	0.707	NA	1	1	0	**0.819**	**0.001**
Euglossa_iopoecila	1	1	1	0.667	NA	1	0	0	**0.796**	**0.001**
Euglossa_clausi	1	1	1	0.943	NA	1	1	1	0.943	NA
Euglossa_despecta	1	1	1	0.707	NA	1	1	1	0.707	NA
Euglossa_milenae	1	1	1	0.471	NA	0	1	1	0.525	0.214
Euglossa_marianae	1	1	1	0.441	NA	1	1	0	0.540	0.076
Euglossa_truncata	0	1	1	0.289	1	0	1	0	0.343	0.388
Euglossa_townsendi	1	0	0	0.289	1	0	0	1	0.289	0.539
Euglossa_gaianii	1	1	1	0.882	NA	1	1	1	0.882	NA
Euglossa_securigera	1	1	1	1.000	NA	1	1	1	1.000	NA
Euglossa_fimbriata	1	1	1	0.687	NA	1	1	1	0.687	NA
Euglossa_bembei	1	1	0	0.463	0.459	1	1	1	0.441	NA
Euglossa_pleosticta	1	1	1	0.943	NA	1	1	1	0.943	NA
Euglossa_viridis	1	0	0	0.289	1	0	0	1	0.289	0.532
Eufriesea_violacea	1	0	0	0.289	1	1	0	0	0.378	0.177
Eufriesea_surinamensis	1	1	1	0.333	NA	1	0	1	0.364	0.812
Exaerete_smaragdina	1	1	1	0.799	NA	1	1	1	0.799	NA

Supplementary Material Appendix F. Multiple Regression Models (MRM) used to evaluate the scale of effect of forest cover (%) (pct10) and landscape heterogeneity (shdi) on total beta diversity, nestedness, and turnover. Landscape metrics were quantified in multi-buffers, from 250 to 1500 m, with a 250 m interval. Models with p-value < 0.05 are indicated in italics. The scale of effect was the one that presented the highest R^2-value for each response variable.

Response variable	Explanatory variable	R^2	*p*
Total beta diversity	pct10_250	0.09	0.06
	pct10_500	*0.14*	*0.01*
	pct10_750	*0.2*	*0.004*
	pct10_1000	*0.24*	*0.002*
	pct10_1250	*0.12*	*0.03*
	pct10_1500	0.01	0.4
	shdi_250	0	0.62
	shdi_500	0.09	0.09
	shdi_750	0.08	0.1
	shdi_1000	*0.13*	*0.03*
	shdi_1250	0.06	0.14
	shdi_1500	0	0.6
Nestedness	pct10_250	0.04	0.22
	pct10_500	0	0.62
	pct10_750	0	0.89
	pct10_1000	0.01	0.54
	pct10_1250	0	0.72
	pct10_1500	0	0.88
	shdi_250	0	0.89
	shdi_500	0	0.64
	shdi_750	0	0.75
	shdi_1000	0.01	0.44
	shdi_1250	0.03	0.32
	shdi_1500	0.04	0.25
Turnover	pct10_250	0	0.7
	pct10_500	0.05	0.17
	pct10_750	*0.11*	*0.03*
	pct10_1000	0.09	0.06
	pct10_1250	0.05	0.19
	pct10_1500	0	0.6
	shdi_250	0	0.77
	shdi_500	0.09	0.06
	shdi_750	0.07	0.08
	shdi_1000	0.02	0.3
	shdi_1250	0	0.75
	shdi_1500	0.01	0.51

2. DISCUSSÃO GERAL

A restauração dos habitats na escala da paisagem é essencial para atingir as metas da Década da Restauração dos Ecossistemas definida pela Organização das Nações Unidas (ONU). Recuperar ecossistemas e conservar a biodiversidade é um desafio mundial, que têm envolvido diferentes públicos, desde escalas locais até globais. Nesse sentido, estudos ecológicos que avaliam o sucesso de diferentes estratégias de restauração representam importantes contribuições para essa Agenda. Para isso, é necessário o uso de indicadores ecológicos para o monitoramento dos resultados de projetos de restauração, o que pode fornecer evidências para um manejo da restauração beneficiando a biodiversidade. Este trabalho mostra a importância de comunidades de abelhas Euglossini como *proxies* dos resultados da restauração na Mata Atlântica. Esses polinizadores responderam aos atributos locais de habitats restaurados (**Capítulo I, Capítulo II**), assim como o contexto espacial da paisagem (**Capítulo I, Capítulo III**). Diante disso, este estudo indica que: (1) fatores locais como disponibilidade de recursos de nidificação, recursos florais e dinâmicas da vegetação são importantes filtros para a recuperação das comunidades de abelhas, e (2) a composição e configuração da paisagem afetam diretamente as dinâmicas ecológicas de dispersão, colonização e persistência de espécies de abelhas em habitats restaurados.

Variações na disponibilidade de recursos ao longo da trajetória da restauração afetam o reestabelecimento da alfa e beta diversidade de comunidades de abelhas (**Capítulo I**). Enquanto espécies generalistas rapidamente colonizam habitats restaurados, facilitando a recuperação da alfa diversidade, espécies especialistas dependem do reestabelecimento de condições e requerimentos ecológicos para colonização, o que resulta em um atraso na recuperação da composição de espécies (Tonietto et al. 2017; **Capítulo I, Capítulo II**). Apesar desse padrão variar entre diferentes ecossistemas, os resultados observados indicam que estratégias de manejo focadas nos requerimentos de espécies de abelhas podem favorecer a recuperação da alfa e beta diversidade das comunidades desses polinizadores (**Capítulo I, Capítulo II, Capítulo III**).

É esperado que características locais dos habitats, especialmente ligados as comunidades de plantas, desempenhem um papel essencial sobre a recuperação das comunidades de abelhas devido ao mutualismo planta-polinizador (Dixon, 2009; Cariveau et al. 2020). Contudo, é necessário também considerar o contexto da paisagem, porque as espécies de abelhas colonizadoras são provenientes de áreas fontes, que estão

inseridas em um mosaico de manchas, incluindo matrizes de uso antrópico (Cariveau et al. 2020). Os resultados encontrados indicam que características associadas à estrutura e complexidade dos habitats (**Capítulo I, Capítulo II**), assim como da estrutura da paisagem (**Capítulo I, Capítulo III**) interagem sinergicamente no espaço e tempo, afetando a recuperação das comunidades em habitats restaurados.

Este estudo ressalta que variáveis ecológicas como riqueza, abundância, diversidade, e dissimilaridade na composição de espécies de Euglossini em habitats restaurados e conservados podem apresentar diferentes respostas a uma mesma variável preditora relacionada à estrutura dos habitats (**Capítulo II**), e da paisagem (**Capítulo III**). Com isso, para avaliar o sucesso de projetos de restauração, estudos devem considerar diferentes variáveis respostas, e quando possível, em uma perspectiva multi-táxon. Isso pode indicar as diferenças nas dinâmicas ecológicas das comunidades entre habitats restaurados e conservados, e fornecer informações para embasar estratégias de manejo de restauração que maximizem a recuperação da biodiversidade.

É interessante notar que enquanto a alfa diversidade de Euglossini foi fortemente correlacionado ao *sd*NDVI (**Capítulo II**), a composição de espécies respondeu à composição da paisagem (**Capítulo III**). O *sd*NDVI representa variações de *greenness* da vegetação ao longo do tempo, e no caso de habitats restaurados, fatores de confusão como áreas não vegetadas e solo exposto (Perrone et al. 2023). A associação da alfa diversidade de Euglossini com o *sd*NDVI pode refletir o fato que as espécies dessas abelhas respondem às variações locais dos habitats (Roubik & Hanson, 2004; Sobreiro et al. 2017). Por outro lado, é importante observar o papel da cobertura de floresta sobre variações na beta diversidade de Euglossini entre habitats conservados e restaurados. As abelhas Euglossini têm alta dependência de habitats florestais, e variações na quantidade de habitat devem afetar as dinâmicas de dispersão e colonização de espécies entre habitats restaurados e conservados, e consequentemente, a beta diversidade (**Capítulo III**). Este estudo ressalta que entender o sucesso de estratégias de restauração sobre a biodiversidade requer a utilização de atributos que refletem as variações dos habitats, como *sd*NDVI, assim como da estrutura da paisagem. Apesar do papel essencial do contexto da paisagem sobre dinâmicas ecológicas, métricas como a cobertura de floresta não quantificam a heterogeneidade dentro dos habitats, o que pode dificultar nossa compreensão sobre os fatores que influenciam a restauração da biodiversidade (**Capítulo II**).

Além disso, é importante que estudos que avaliam o sucesso da restauração através de indicadores ecológicos utilizem métricas relacionadas às diferentes dimensões da diversidade de comunidades (**Capítulo I, Capítulo II, Capítulo III**). A riqueza e abundância de espécies é essencial para entender o reestabelecimento do número de espécies e quantidade de indivíduos nos habitats restaurados (**Capítulo I, Capítulo II**). Contudo, algumas questões como a ocorrência de *singletons* e variações na identidade de espécies entre áreas são negligenciadas por métricas de alfa diversidade. Nesse sentido, a beta diversidade é crucial para compreender as variações na composição de espécies entre habitats restaurados e conservados (**Capítulo I, Capítulo III)**. Ambas dimensões (alfa e beta diversidade) devem ser utilizadas de forma complementar, para acessar a diversidade local e regional de espécies em paisagens de restauração. Além disso, estudos futuros podem utilizar outras dimensões, tais como diversidade funcional e filogenética.

Este estudo também indica o papel de abelhas Euglossini como indicadores ecológicos do sucesso da restauração (**Capítulo II, Capítulo III**), assim como de mudanças na paisagem (**Capítulo III**). Os resultados reforçam que espécies de Euglossini podem ser importantes indicadores da quantidade de habitat. Apesar de *Euglossa ignita* e *Euglossa iopoecila* apresentarem ampla distribuição em diferentes biomas (Moure & Melo, 2023), ambas espécies são sensíveis a redução da quantidade de habitat na paisagem (**Capítulo III**). Isso mostra que o desflorestamento pode afetar negativamente a manutenção de populações dessas abelhas, e consequentemente, o serviço de polinização. Além disso, *E. ignita* e *E. iopeocila* são as espécies com os maiores comprimentos de língua em relação ao tamanho do corpo registradas na área de estudo. É possível que esse traço pode resultar em maior especificidade na coleta de recursos florais, aumentando a sensibilidade dessas espécies aos distúrbios na paisagem, como observado para outras espécies de abelhas na Mata Atlântica (Montoya-Pfeiffer et al. 2020).

Além do mais, populações de *Euglossa marianae* Nemésio foram restritas às florestas e habitats restaurados dentro de duas reservas biológicas- REBIO (União- L01-L02, e Poço das Antas- L05; **Capítulo II, Capítulo III**). Estas reservas representam os maiores e mais conservados fragmentos de Mata Atlântica na região centro norte do estado do Rio de Janeiro. No entanto, é interessante notar que apenas um indivíduo de *E. marianae* foi amostrado na REBIO Poço das Antas (**Capítulo II)**. Esta espécie de abelha foi indicada como sensível às perturbações ambientais (Nemésio, 2013), e foi

recentemente categorizada como Quase Ameaçada- NT (Portaria ICMBio 1145/2022). Isso ressalta o papel essencial da restauração ecológica para aumentar a quantidade de habitat para as populações de abelhas. Ao mesmo tempo, enfatiza-se a importância de unidades de conservação para a manutenção das populações de *E. marianae,* assim como de estratégias para aumentar as populações dessa abelha na escala da paisagem.

Este trabalho indica que estratégias de restauração ativa e passiva são igualmente eficientes para recuperar a alfa (**Capítulo II**) e beta diversidade (**Capítulo III**) de comunidades de Euglossini na Mata Atlântica. A restauração dessa floresta tropical é essencial para restauração global de ecossistemas, e no Brasil, tem sido guiada desde 2009 pelo Pacto Nacional de Restauração da Mata Atlântica, que objetiva recuperar milhões de hectares de floresta. Os objetivos de restaurar a Mata Atlântica têm sido atingidos primariamente através da regeneração natural (Crouzeilles et al. 2017). Essa estratégia de restauração será essencial para recuperar milhões de hectares de ecossistemas nos próximos anos (Crouzeilles et al. 2020; Vancine et al. 2024), e como indicado pelo nosso trabalho, para recuperar a biodiversidade.

Contudo, muitas áreas na Mata Atlântica apresentam condições locais extremamente deterioradas, associadas a um legado antigo de perturbações antrópicas e uso do solo, com alto isolamento espacial de áreas fontes de propágulo. Isso demanda manejo antrópico através de técnicas de restauração passiva assistida ou ativa para atingir o sucesso da restauração (Jakovak et al. 2021). É importante destacar que a restauração ativa contribui para um rápido estabelecimento da vegetação por meio do plantio de espécies nativas. Tomadores de decisão devem considerar estratégias para aumentar a complexidade de habitats restaurados, pois muitos requerimentos necessários para a recuperação de espécies de animais têm um atraso no tempo (**Capítulo I, Capítulo II**). Por exemplo, estratégias de restauração para criar um sub-bosque podem ser importantes para recuperação da biodiversidade, uma vez que maximiza a disponibilidade de nichos para diferentes espécies. Considerando os requerimentos de polinizadores, o manejo dessas áreas deve incluir o plantio de uma diversidade de espécies nativas que são fontes de pólen e néctar, com florescimento em diferentes períodos do ano, e manutenção de espécies que regeneram naturalmente (Deprá et al. 2021; **Capítulo I**). A introdução de recursos de nidificação também pode maximizar a colonização de espécies de abelhas em habitats restaurados ativamente (Gobatto et al. 2022; **Capítulo I**).

É interessante também ressaltar que dinâmicas que resultam em um aumento na heterogeneidade de habitats florestais conservados podem afetar positivamente a

diversidade de abelhas Euglossini (**Capítulo II**). Essas áreas conservadas são fundamentais porque influenciam na quantidade e isolamento do habitat na escala da paisagem. Além disso, a conservação dessas manchas de floresta garante a manutenção do conjunto de espécies, que podem colonizar os habitats restaurados ativamente e passivamente (**Capítulo III)**.

2.1 Considerações sobre a restauração de polinizadores na Mata Atlântica

Com base nos resultados apresentados nos três capítulos desta Tese, é importante ponderar algumas indicações que podem embasar estratégias de restauração benéficas à recuperação das comunidades de abelhas na Mata Atlântica:

(1) **Restaurar é o que importa**: Independente da estratégia (ativa ou regeneração natural), as comunidades de abelhas são positivamente beneficiadas pela maior disponibilidade de habitat na paisagem. Enquanto restaurar ativamente é necessário para projetos de conservação, como da Associação Mico Leão Dourado, restaurar passivamente reduz o tempo de manejo e custos financeiros. O manejo específico de áreas que regeneram naturalmente é importante para recuperar espécies nativas com baixo potencial de colonização e remoção de espécies exóticas, o que pode maximizar o sucesso dessa estratégia. Contudo, é importante a interação entre governos, organizações e comunidades locais em prol da restauração, uma vez que a maioria das áreas em regeneração está inserida em propriedades particulares;

(2) **O habitat filtra a colonização de espécies**: Atributos relacionados a complexidade de habitas restaurados são um dos principais fatores que afetam as dinâmicas de reestabelecimento de espécies. Enquanto a recuperação da complexidade de habitats restaurados passivamente tem um atraso no tempo, estratégias de manejo em restaurações ativas podem contribuir para um maior sucesso na recuperação dessa complexidade. Isso pode incluir ações de enriquecimento ambiental através da recuperação de compartimentos de habitats florestais, como epífitas, estratégia que tem sido adotada pela Associação Mico-Leão-Dourado. A introdução de cavidades de nidificação para espécies de abelhas em habitats restaurados também deve ser considerada;

(3) **A quantidade habitat na paisagem influencia o sucesso da restauração**: Paisagens com alta quantidade de habitat facilitam a eficácia da restauração, e como consequência, há uma otimização na gestão de recursos financeiros e tempo

de manejo. A restauração em paisagens com baixa cobertura de habitat apresentará maior custo e tempo de manejo, mas é essencial para o aumento da quantidade habitat e conectividade nessas paisagens perturbadas. Dessa forma, tomadores de decisão devem sempre ponderar o contexto da paisagem previamente para maximizar o sucesso da restauração;

(4) **Habitats restaurados têm alto valor para conservação**: Habitats restaurados e conservados sustentam comunidades de abelhas Euglossini similares. Isso indica que ambas áreas possuem um alto valor para conservação, em que os grupos de espécies de abelhas presentes nesses habitats contribuem conjuntamente para uma alta diversidade regional. Dessa forma, áreas restauradas, principalmente através de regeneração natural, têm uma importante contribuição para a manutenção da diversidade de polinizadores, assim como do serviço de polinização em paisagens fragmentadas da Mata Atlântica.

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