UNIVERSIDADE ESTADUAL DE SANTA CRUZ – UESC
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E CONSERVAÇÃO DA BIODIVERSIDADE – PPGECB

KETLEN BONA BEZERRA DA COSTA

ANT-DIASPORE INTERACTIONS: ANTHROPOGENIC DISTURBANCE INFLUENCES, TRENDS, AND GAPS IN A BRAZILIAN BIODIVERSITY HOTSPOT

ILHÉUS - BAHIA
2023

KETLEN BONA BEZERRA DA COSTA

ANT-DIASPORE INTERACTIONS: ANTHROPOGENIC DISTURBANCE INFLUENCES, TRENDS, AND GAPS IN A BRAZILIAN BIODIVERSITY HOTSPOT

Tese apresentada à Universidade Estadual de Santa Cruz, como parte das exigências para obtenção do título de Doutora em Ecologia e Conservação da Biodiversidade.
Área de concentração: Ecologia e Conservação da Biodiversidade
Discente: Ketlen Bona Bezerra da Costa
Orientadora: Dra. Eliana Cazetta
Co-orientador: Dr. Jacques H.C. Delabie

ILHÉUS – BAHIA
2023

C837 Costa, Ketlen Bona Bezerra da.
Ant-diaspore interactions: anthropogenic disturbance influences, trends, and gaps in a brazilian biodiversity hotspot / Ketlen Bona Bezerra da Costa. – / Ketlen Bona Bezerra da Costa. – Ilhéus, BA: UESC, 2023.
111 f. : il.

Orientadora: Eliana Cazetta.
Tese (Doutorado) - Universidade Estadual de Santa Cruz. Programa de Pós-graduação em Ecologia e Conservação da Biodiversidade.
Inclui referências.

1. Biodiversidade – Conservação. 2. Formigas. 3. Semente – Dispersão. 4. Relação inseto-planta. I. Título.

CDD 333.95

Aos meus pais Francisco & Lúcia e à Luane Karoline Fontenele,
meus exemplos de força, simplicidade e amor puro.

Free as a bird
Like the next best thing to be

John Lennon, Paul McCartney, George Harrison & Ringo Star

AGRADECIMENTOS

Por muitas e muitas vezes, durante árduos quatro anos de uma busca constante para me encaixar na trilha das formigas, pensei que nunca deveria ter tentado segui-la. No entanto, graças às pessoas que aqui agradecerei, esses pensamentos se tornaram a força que me fez chegar aqui e cumprir o que me propus no início desse caminho: fazer ciência com amor, de forma honesta e responsável.

Primeiramente, agradeço o apoio da Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Código de Financiamento 001 e ao PPG em Ecologia e Conservação da Biodiversidade da UESC, em especial à Iky Anne e à Amábille Kruschewsky, obrigada por toda a assistência e ajuda nos momentos de dúvida.

Agradeço à minha orientadora Eliana Cazetta pelos ensinamentos sobre dispersão de sementes e sua contribuição na minha trajetória acadêmica. Obrigada pelo tempo que se dedicou pensando sobre essa tese e pela compreensão nos momentos mais difíceis. Agradeço também ao meu coorientador Jacques Delabie pelos ensinamentos e conselhos, e pelos elogios sobre a escrita e desenvolvimento do trabalho que sem saber chegavam nos momentos de maior desânimo. Vocês são grandes pesquisadores e professores, tenho muita admiração.

Agradeço imensamente aos meus queridos amigos Ana Carla Rodrigues (Cacá) e Hugo C. M. Costa, vocês sempre estarão no meu conjunto de boas lembranças da vida, seja pelo acolhimento na primeira vez que sai do Acre ou pela primeira vez que conheci o mar ou pela primeira vez que tomei cerveja antes das 10 da manhã! Obrigada pelas boas risadas, vocês sempre serão especiais para mim! Agradeço ao meu querido Fernando César Bonfim pela ajuda e disponibilidade de sempre. Sem a sua ajuda certamente eu não conseguiria avançar. Muito obrigada!

Agradeço ao Laboratório de Ecologia de Formigas da UFLA pelo acolhimento no meu penúltimo ano de doutorado. Obrigada Ícaro Wilker, Guilherme Alves, Dara Veiga, Letícia Gomes, Camila Braga, Marília Costa, Chaim Lasmar e Antônio Queiroz pelas boas risadas, pelo café compartilhado e pelas cervejadas que às vezes beiravam à perda de controle total! Adoro vocês!

Agradeço ao Cássio Nunes (parceiro Dudu) e à Natália Carvalho pela parceria, pelas alegrias [e agonias!] compartilhadas. Obrigada pela comemoração inesquecível ao parar o carro no meio de uma ladeira naquela noite de 30 de outubro de 2022 para soltar um grito que estava preso há quatro anos. Vocês são malucos! Obrigada Cássio, por ter sido meu parceiro musical, sua amizade foi um presente enorme e sei que em algum dia desses voltaremos a nos reunir para compartilhar boas histórias e tocar as perfeitas músicas da maior banda do planeta (eles mesmo, The Beatles)!

Agradeço ao meu amigo querido professor Dr. Henrique Mews, que me ensinou tudo o que sei sobre ciência e pesquisa. Mesmo com a participação de outros professores, é sempre em você que penso quando estou aperreada: “calma, como o Henrique escreveria/faria/leria/falaria isso aqui?”. E então faço. Obrigada por tudo!

Agradeço imensamente ao professor Dr. Edson Guilherme pela oportunidade de concluir essa etapa da minha vida acadêmica fazendo parte do Laboratório de Ornitologia da UFAC. Obrigada pela confiança e por abrir as portas para a minha vontade de crescer como cientista. Certamente, farei jus e abraçarei todas as oportunidades nesse novo caminho.

Agradeço às minhas amadas amigas Thábata Richely, Thaynara Rocha, Nayanny Fontenele e Luane Fontenele pela companhia, pelas risadas, pelas conversas muitas vezes sem sentido que, no fim, são sempre as mais sábias. Sempre bom falar coisas nada com nada que,

na realidade, são tudo com tudo. O melhor, saber que a gente se entende com uma falando mais alto que a outra. E, claro, agradeço à Fridinha que finge ser uma cadela perto das pessoas e que sempre está no meio das atribulações (fazendo a atribulação). Amo vocês!

Agradeço à dona Graça Viana Fontenele por sempre ter me tratado como uma filha. A senhora é um dos meus portos mais seguros. Obrigada pelo amor, pelo carinho, pelas comidinhas e abrigo desde a minha graduação! Agradeço também ao Pedro Henrique, pelos sorrisos e olhares genuínos, pelos tons de ameaça "É, Ketinha...". É bom ver você crescendo e ficando maior do que eu. Eu amo vocês de todo meu coração!

Agradeço imensamente à minha família pela força, incentivo e, principalmente, pelo gás que me deram nesse finalzinho, quando pensei que não conseguiria tocar em frente. É sempre bom voltar para casa, sentir que a minha presença importa, sentir que sou aguardada com o carinho e o amor mais sincero sempre e, principalmente, saber que tenho, sim, um lugar. Agradeço ao meu pai Francisco e à minha mãe Lúcia, pelo amor incondicional e pelo exemplo que vocês sempre foram para mim. Vocês são o que tenho de mais importante na vida. Agradeço à minha irmã Kérollen, porque é o meu bem mais precioso, a minha única irmã, mesmo com o nosso jeito torto de se amar, obrigada por sentir orgulho de mim e cuidar. Agradeço ao Adryan, meu lindo sobrinho, por sempre me esperar ansioso e muitas vezes tentar me ajudar com as figuras e mapas, mas também por muitas vezes agoniar meu juízo até me fazer desistir de trabalhar para ir jogar vídeo game, futebol ou apenas ouvir você falar por tempo indeterminado. E agora agradeço ao meu mais novo sobrinho Nícollas que tem alegrado a titia desde o dia 01/09/2023, você é o meu mais novo amor! Me perdoem por tantos momentos de ausência e por todas as vezes em que meu orgulho não me deixou pedir ajuda em momentos de dificuldade, sei que gostariam de ter participado de tudo, inclusive dos momentos ruins dessa trajetória. No entanto, o simples fato de sentir que eu tinha para onde correr quando tudo desandasse completamente, era [e sempre será] a maior ajuda que vocês poderiam me dar.

Enfim, agradeço à Luane Karoline Fontenele por ser o meu cais, por ser o meu melhor horário do dia, por ser a minha inspiração. Te agradeço por todas as vezes em que você me levantou, por todas as vezes que acreditou em mim, por todo o incentivo, por cada olhar de amor e de orgulho. Obrigada por sempre estar ao meu lado. Obrigada pela sua calma e pelo seu companheirismo. Obrigada por enxergar em mim um potencial que muitas vezes eu não acredito que exista. Tem sorte aquele que te encontra pelo caminho em algum momento da vida. Você é um ser humano incrível, uma cientista admirável. Você é a minha sorte! Eu amo muito você, Karoline!

Na trilha das formigas, sinto que cumpri o meu dever, entreguei todo o meu amor e sinto que, da parte delas, [experimentando o que disseram os Beatles em "The End"] no fim todo o amor que recebi foi igual ao amor que dei. Esse é um ciclo que se encerra aqui. E, hoje, sempre que penso que ele nunca deveria ter sido iniciado, sinto que foi um aprendizado necessário. Apesar de tudo, é um alívio sentir orgulho de ter feito parte desse pequeno, mas gigantesco, universo das formigas!

SUMÁRIO

RESUMO GERAL

As modificações no uso da terra representam uma crescente ameaça à biodiversidade global. Além da diversidade de espécies, interações essenciais para o desempenho de importantes funções ecossistêmicas, como a dispersão de sementes, estão sendo perdidas. Diante do cenário da grande perda de vertebrados dispersores devido a mudanças no uso da terra e a consequente defaunação, as formigas representam um componente importante para auxiliar a manutenção da estabilidade desses ecossistemas. Esta tese busca compreender os efeitos das perturbações antrópicas sobre as interações entre formigas e diásporos e direcionar pesquisas futuras em um dos *hotspots* mais ameaçados do mundo, a Mata Atlântica brasileira. Para isso, delineamos essa tese em dois capítulos. Primeiramente, realizamos uma meta-análise global com o objetivo de verificar o impacto das perturbações antrópicas sobre a remoção de diásporos por formigas. Revelamos uma redução de 26% na remoção de diásporos por formigas em ambientes perturbados, com reduções consideráveis em áreas de mineração (83%) e fragmentação de habitats (24%). Surpreendentemente, não observamos efeitos significativos em áreas agrícolas (decréscimo de 0,09%). Nossos achados destacam a vulnerabilidade da dispersão de sementes por formigas às atividades humanas, o que ressalta a urgência da conservação de áreas naturais para a manutenção dos ecossistemas. No segundo capítulo, compilamos 26 anos de pesquisa sobre interações formiga-diásporo na Mata Atlântica brasileira e apontamos lacunas de conhecimentos sobre aspectos qualitativos da dispersão de sementes por formigas. Verificamos a escassez de estudos que avaliam os efeitos de distúrbios antrópicos sobre interações formiga-diásporo na Mata Atlântica. Fornecemos uma lista de espécies-chave de formigas que removem e limpam diásporos e revelamos que as espécies *Pachycondyla striata* e *Odontomachus chelifer* são fundamentais para a dispersão de sementes na Mata Atlântica. Além disso, demonstramos que diásporos menores e ricos em lipídios são mais suscetíveis à remoção e limpeza por formigas. Finalmente, apontamos locais prioritários para futuras amostragens com base em características ambientais, incluindo as ecorregiões da Mata Atlântica brasileira. Todas essas informações enfatizam a necessidade da conservação das formigas, uma vez que podem contribuir para a manutenção de processos ecológicos cruciais.

Palavras-chave: Interações formiga-diásporo; Dispersão de sementes; Formicidae; Mutualismo.

GENERAL ABSTRACT

Changes in land use represent a growing threat to global biodiversity. In addition to species diversity, interactions essential for the performance of important ecosystem functions, such as seed dispersal, are being lost. Given the scenario of great loss of dispersing agents due to defaunation and deforestation of natural areas, ants represent an important component to help maintain the stability of these ecosystems. This thesis seeks to understand the effects of anthropogenic disturbances on interactions between ants and diaspores and direct future research in one of the most threatened hotspots in the world, the Brazilian Atlantic Forest. To this end, we outline this thesis in two chapters. First, we carried out a global meta-analysis with the aim of verifying the impact of anthropogenic disturbances on the removal of diaspores by ants. We revealed a 26% reduction in diaspore removal by ants in disturbed environments, with considerable reductions in mining areas (83%) and habitat fragmentation (24%). Surprisingly, we did not observe significant effects in agricultural areas (0.09% decrease). Our findings highlight the vulnerability of seed dispersal by ants to human activities, which highlights the urgency of conserving natural areas to maintain ecosystems. In the second chapter, we compile 26 years of research on ant-diaspore interactions in the Brazilian Atlantic Forest and point out gaps in knowledge about qualitative aspects of seed dispersal by ants. We verified the scarcity of studies that evaluate the effects of anthropogenic disturbances on ant-diaspore interactions in the Atlantic Forest. We provide a list of key ant species that remove and clean diaspores and reveal that the species *Pachycondyla striata* and *Odontomachus chelifer* are fundamental for seed dispersal in the Atlantic Forest. Furthermore, we demonstrate that smaller, lipid-rich diaspores are more susceptible to removal and scavenging by ants. Finally, we point out priority sites for future sampling based on environmental characteristics, including the ecoregions of the Brazilian Atlantic Forest. All this information emphasizes the need for ant conservation, as they can contribute to the maintenance of crucial ecological processes.

Keywords: Ant-diaspore interactions; Seed dispersal; Formicidae; Mutualism.

INTRODUÇÃO GERAL

As mudanças no uso da terra têm impulsionado a perda de biodiversidade nos ecossistemas terrestres de todo o mundo (DECAËNS et al., 2018; HADDAD et al., 2015; RODRÍGUEZ-ECHEVERRY et al., 2018). Evidências empíricas apontam que a perda de habitat reduz a complexidade de habitats remanescentes, induzindo a diminuição local de atributos estruturais fundamentais para as espécies (e.g., diversidade de plantas, disponibilidade de recursos, variabilidade de nicho) (ECHEVERRÍA et al., 2007; ROCHA-SANTOS et al., 2016). Além disso, as perturbações no solo e simplificação da estrutura da vegetação causada pela conversão de áreas naturais em pastagens, mineração e áreas urbanas também reduzem drasticamente a diversidade de espécies (ALROY, 2017; BARLOW et al., 2016; CASTRO PENA et al., 2017). Tudo isso compromete a estabilidade dos ecossistemas, uma vez que a perda de espécies reflete na perda de interações essenciais para sua manutenção e funcionamento (NAEEM et al., 2009; SYMSTAD et al., 2006).

As interações ecológicas desempenham um papel fundamental na manutenção da biodiversidade (BASCOMPTE; JORDANO, 2007). Relações como a predação, competição e mutualismo contribuem para a estabilidade dos ecossistemas, uma vez que possibilitam a coexistência das espécies (BASCOMPTE; JORDANO, 2007). As interações entre formigas e plantas, por exemplo, abrangem desde relações obrigatórias, como a simbiose em que formigas protegem plantas (COLEY; BARONE, 1996; LONGINO, 1991), até relações facultativas, como plantas que fornecem recursos alimentares às formigas, mas não dependem delas (BEATTIE, 1985; GORB; GORB, 2003). É possível observar um sistema de serviços fornecidos por formigas em troca de recompensas fornecidas por plantas, no qual a qualidade do recurso pode influenciar o desempenho do serviço (BEATTIE, 1985). Os diversos mutualismos provenientes dessas interações formigas-plantas resultam em funções ecológicas essenciais para os ecossistemas terrestres, como a polinização e a dispersão de sementes (BEATTIE, 1985). A compreensão e a conservação dessas interações são fundamentais para a manutenção dos ecossistemas e da biodiversidade global.

A dispersão de sementes por formigas (i.e., mirmecocoria) apresenta um papel significativo na estrutura das comunidades de plantas de regiões temperadas e tropicais (BEATTIE, 1985). Nessas interações, as sementes são levadas para longe da planta-mãe, o que reduz a predação denso-dependente e a competição de plântulas parentais (GORB; GORB, 2003). Além disso, as formigas depositam as sementes em locais ideais para germinação (i.e., ninhos de formigas) e podem reduzir a infestação por fungos ao remover a polpa ou arilo dos frutos (BEATTIE, 1985; GORB; GORB, 2003; LEAL; LEAL; ANDERSEN, 2015). Ecossistemas temperados apresentam uma diversidade expressiva de plantas mirmecocóricas, nos quais a mirmecocoria particularmente e outras interações animal-planta provavelmente moldaram comunidades de plantas temperadas (JIA et al., 2018; LENGYEL et al., 2009). As plantas mirmecocóricas são plantas que produzem sementes com um apêndice rico em lipídios e carboidratos chamado elaiossomo, o qual atrai especificamente formigas (VAN DER PIJL, 1982). Algumas plantas chegam a sincronizar sua frutificação com a melhor época de forrageio de formigas (YOUNGSTEADT et al., 2009), o que demonstra a forte relação entre formigas em plantas de regiões temperadas. Nas regiões tropicais, especificamente em florestas úmidas, essas interações formiga-diásporo são facultativas, a maioria ocorrendo entre diásporos não-mirmecocóricos e formigas sem especialidade de alimentação (FERNÁNDEZ et al., 2003). A dispersão de sementes não-mirmecocóricas por formigas em regiões tropicais é crucial, uma vez que atua de forma complementar a dispersão primária realizada por vertebrados (CAMARGO et al., 2016; CHRISTIANINI; MAYHÉ-NUNES; OLIVEIRA, 2007; CHRISTIANINI; OLIVEIRA, 2009).

Dentre a gama de interações existentes nos ecossistemas, vários estudos concentram-se em mutualismos uniformemente difusos, no qual múltiplos parceiros atuam com a mesma importância em termos de frequência e consequências de suas interações (e.g., dispersores de sementes) (GOVE; MAJER; DUNN, 2007). Nesses mutualismos, a perda de espécies parceiras não altera o resultado do mutualismo (e.g., dispersão de sementes), uma vez que há redundância funcional. Nos mutualismos desigualmente difusos uma espécie desempenha um papel chave, sendo fundamental para o resultado do mutualismo (GOVE; MAJER; DUNN, 2007). Nesse tipo de mutualismo, reduções na diversidade das espécies parceiras acarretam consequências para o resultado do mutualismo dependendo de qual espécie é perdida. A dispersão de diásporos por formigas parece corresponder a um mutualismo desigualmente difuso, uma vez que alguns estudos verificaram a presença de espécies-chave nessas interações (FONTENELE; SCHMIDT, 2021; GOVE; MAJER; DUNN, 2007; HEITHAUS; HEITHAUS; LIU, 2005; NESS, 2004). Essas evidências são muito relevantes, uma vez que a dispersão de sementes é mais eficaz onde uma ou duas espécies de formigas dispersoras eficazes dominam (GORB; GORB, 2003). Nesse sentido, verificar a existência de espécies-chave de formigas para a dispersão de sementes é crucial, principalmente diante da grande perda de biodiversidade em regiões tropicais e temperadas.

As formigas estão presentes numerosamente em quase todo o globo terrestre (SCHULTHEISS et al., 2022) e a maior diversidade de espécies pode ser encontrada do Brasil (FEITOSA et al., 2022). Diferentes habitats com características particulares de flora e fauna, os quais formam uma alta diversidade de ecorregiões, contribuem para que o Brasil apresente esta maior biodiversidade do mundo (LEWINSOHN; PRADO, 2005). No entanto, o aumento de explorações e conversões de habitats naturais em diferentes usos do solo no Brasil têm ameaçado diversos ecossistemas, o qual apresenta dois *hotspots* mundiais de biodiversidade. Os *hotspots* de biodiversidade são pontos críticos para conservação, uma vez que apresentam alta diversidade de espécies, alto grau de endemismo e estão sob alto risco de extinção (MYERS et al., 2000). A Mata Atlântica brasileira está entre os *hotspots* mais criticamente ameaçados do mundo (MYERS et al., 2000), o que se deve à exploração antrópica desde 1500 com o descobrimento do Brasil (REZENDE et al., 2018; SÁ, 1996). A perda de espécies devido às modificações antrópicas na Mata Atlântica é altamente preocupante, uma vez que as interações entre as espécies também são perdidas. Por exemplo, evidências empíricas apontam que a fragmentação de habitats e as modificações no uso do solo reduz a diversidade de formigas e de grupos funcionais de formigas na Mata Atlântica (LEAL et al., 2012; RABELLO et al., 2018), o que acarreta efeitos negativos em funções que as formigas executam, como a dispersão de sementes (QUEIROZ et al., 2021).

Devido à ampla distribuição geográfica das formigas, facilidade de coleta e respostas rápidas a alterações no habitat, as formigas são muito utilizadas em estudos ecológicos (RIBAS et al., 2012; SCHMIDT; RIBAS; SCHOEREDER, 2013). Além disso, as formigas são consideradas um táxon modelo que pode refletir os padrões de outros grupos biológicos (PAKNIA; PFEIFFER, 2011). A importância desses organismos vai além da alta representatividade em termos de biomassa (SCHULTHEISS et al., 2022), as formigas desempenham funções ecossistêmicas essenciais para a manutenção de ecossistemas temperados e tropicais (e.g., ciclagem de nutrientes, dispersão de sementes, polinização, predação) (DEL TORO; RIBBONS; PELINI, 2012). Assim, as formigas são utilizadas como modelo biológico para o monitoramento não apenas de diversidade taxonômica, mas também de funções ecossistêmicas. Diante de vários anos de esforços voltados para aumentar a compreensão sobre as formigas e suas interações com diásporos, compilar essas informações e crucial, uma vez que essas interações podem influenciar a dinâmica dos ecossistemas. A partir disso, é possível avaliar fatores que influenciam a dispersão de sementes por formigas em diferentes escalas e apontar lacunas de conhecimento para direcionar estratégias de conservação em locais ameaçados.

Nesse contexto, para aumentar a compreensão sobre as interações entre formigas e diásporos e sobre fatores que influenciam essas interações, realizamos uma meta-análise em escala global (**capítulo 1**) de estudos que compararam a remoção de diásporos por formigas em áreas conservadas e perturbadas. Além da quantificação do efeito geral de perturbações sobre a remoção de diásporos por formigas, verificamos características específicas de cada estudo, como região (i.e., temperada e tropical) e tipo de perturbação (e.g., agricultura, fragmentação, incêndio, mineração etc.). Além disso, realizamos um levantamento de estudos (**capítulo 2**) que avaliaram interações entre formigas e diásporos e construímos um banco de dados para a Mata Atlântica brasileira. Além da revisão da literatura sobre o tema, construímos um panorama qualitativo geral sobre os objetivos centrais dos estudos e espécies que participam dessas interações. Além disso, avaliamos os principais tipos de interação (limpeza/remoção) frequentemente observados ou estudados, verificamos a existência de espécies-chaves de formigas e relacionamos o comportamento das mesmas com características dos diásporos para verificar se a morfologia e a qualidade nutricional dos diásporos determinam o tipo da interação. Por fim, procuramos por lacunas de estudos ao longo da Mata Atlântica para definir locais prioritários para futuras amostragens de interações formigas-diásporos.

REFERÊNCIAS

ALROY, J. Effects of habitat disturbance on tropical forest biodiversity. **Proceedings of the National Academy of Sciences of the United States of America**, v. 114, n. 23, p. 6056–6061, 2017.

BARLOW, J. et al. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. **Nature**, v. 535, n. 7610, p. 144–147, 2016.

BASCOMPTE, J.; JORDANO, P. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. **Annual Review of Ecology, Evolution, and Systematics**, v. 38, n. 1, p. 567–593, 2007.

BEATTIE, A. J. **The evolutionary ecology of ant–plant mutualisms**. New York: Cambridge University Press, 1985.

CAMARGO, P. H. S. A. et al. Bird and ant synergy increases the seed dispersal effectiveness of an ornithochoric shrub. **Oecologia**, v. 181, n. 2, p. 507–518, 2016.

CASTRO PENA, J. C. et al. Impacts of mining activities on the potential geographic distribution of eastern Brazil mountaintop endemic species. **Perspectives in Ecology and Conservation**, v. 15, n. 3, p. 172–178, 2017.

CHRISTIANINI, A. V.; MAYHÉ-NUNES, A. J.; OLIVEIRA, P. S. The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a neotropical savanna. **Journal of Tropical Ecology**, v. 23, n. 3, p. 343–351, 2007.

CHRISTIANINI, A. V.; OLIVEIRA, P. S. The relevance of ants as seed rescuers of a primarily bird-dispersed tree in the Neotropical cerrado savanna. **Oecologia**, v. 160, n. 4, p. 735–745, 2009.

COLEY, P. D.; BARONE, J. A. Herbivory and plant defenses in tropical forests. **Annual Review of Ecology and Systematics**, v. 27, n. 1, p. 305–335, nov. 1996.

DECAËNS, T. et al. Biodiversity loss along a gradient of deforestation in Amazonian agricultural landscapes. **Conservation Biology**, v. 32, n. 6, p. 1380–1391, 2018.

DEL TORO, I.; RIBBONS, R. R.; PELINI, S. L. The little things that run the world revisited: A review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). **Myrmecological News**, v. 17, n. August, p. 133–146, 2012.

ECHEVERRÍA, C. et al. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. **Global Ecology and Biogeography**, v. 16, n. 4, p. 426–439, 2007.

FEITOSA, R. M. et al. Ants of Brazil: an overview based on 50 years of diversity studies. **Systematics and Biodiversity**, v. 20, n. 1, 2022.

FERNÁNDEZ, F. et al. **Introducción a las hormigas de la región Neotropical**. Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, 2003.

FONTENELE, L. K.; SCHMIDT, F. A. Forest-pasture shifting alters the assemblages of seed-removing ants in southwestern Brazilian Amazon. **Journal of Insect Conservation**, v. 25, n. 2, p. 213–220, 9 fev. 2021.

GORB, E.; GORB, S. **Seed dispersal by ants in a Deciduous Forest Ecosystem**. Dordrecht: Springer Netherlands, 2003.

GOVE, A. D.; MAJER, J. D.; DUNN, R. R. A keystone ant species promotes seed dispersal in a “diffuse” mutualism. **Oecologia**, v. 153, n. 3, p. 687–697, 8 ago. 2007.

HADDAD, N. M. et al. Habitat fragmentation and its lasting impact on Earth’s ecosystems. **Science Advances**, v. 1, n. 2, p. e1500052, mar. 2015.

HEITHAUS, E. R.; HEITHAUS, P. A.; LIU, S. Y. Satiation in collection of myrmecochorous diaspores by colonies of Aphaenogaster rudis (Formicidae: Myrmicinae) in Central Ohio, USA. **Journal of Insect Behavior**, v. 18, n. 6, p. 827–846, 2005.

JIA, S. et al. Global signal of top-down control of terrestrial plant communities by herbivores. **Proceedings of the National Academy of Sciences of the United States of America**, v. 115, n. 24, p. 6237–6242, 2018.

LEAL, I. R. et al. Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. **Biodiversity and Conservation**, v. 21, n. 7, p. 1687–1701, 2012.

LEAL, I. R.; LEAL, L. C.; ANDERSEN, A. N. The benefits of myrmecochory: A matter of stature. **Biotropica**, v. 47, n. 3, p. 281–285, 2015.

LENGYEL, S. et al. Ants sow the seeds of global diversification in flowering plants. **PLoS ONE**, v. 4, n. 5, p. 1–6, 2009.

LEWINSOHN, T. M.; PRADO, P. I. Biodiversidade brasileira: Síntese do estado atual do conhecimento. In: **Síntese do conhecimento atual da biodiversidade brasileira**. [s.l: s.n.]. p. 21–112.

LONGINO, J. T. Taxonomy of the cecropia-inhabiting azteca ants. **Journal of Natural History**, v. 25, n. 6, p. 1571–1602, 1991.

MYERS, N. et al. Biodiversity hotspots for conservation priorities. **Nature**, v. 403, n. 7326, p. 853–858, 2000.

NAEEM, S. et al. **Biodiversity, Ecosystem Functioning, and Human Wellbeing**. New York: Oxford University Press Inc., 2009.

NESS, J. H. Forest edges and fire ants alter the seed shadow of an ant-dispersed plant. **Oecologia**, v. 138, n. 3, p. 448–454, 2004.

PAKNIA, O.; PFEIFFER, M. Hierarchical partitioning of ant diversity: Implications for conservation of biogeographical diversity in arid and semi-arid areas. **Diversity and Distributions**, v. 17, n. 1, p. 122–131, 2011.

QUEIROZ, A. C. M. et al. Diaspore Removal by Ants Does Not Reflect the Same Patterns of Ant Assemblages in Mining and Rehabilitation Areas. **Neotropical Entomology**, v. 50, n. 3, p. 335–348, 2021.

RABELLO, A. M. et al. Habitat attribute similarities reduce impacts of land-use conversion on seed removal. **Biotropica**, v. 50, n. 1, p. 39–49, 2018.

REZENDE, C. L. et al. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. **Perspectives in Ecology and Conservation**, v. 16, n. 4, p. 208–214, 2018.

RIBAS, C. R. et al. Ants as indicators in Brazil: A review with suggestions to improve the use of ants in environmental monitoring programs. **Psyche**, v. 2012, 2012.

ROCHA-SANTOS, L. et al. The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. **Biological Conservation**, v. 196, p. 1–9, 2016.

RODRÍGUEZ-ECHEVERRY, J. et al. Impact of land-use change on biodiversity and ecosystem services in the Chilean temperate forests. **Landscape Ecology**, v. 33, n. 3, p. 439–453, 2018.

SÁ, M. R. A ferro e fogo: a história e a devastação da Mata Atlântica Brasileira. **História, Ciências, Saúde-Manguinhos**, v. 3, n. 3, p. 558–559, 1996.

SCHMIDT, F. A.; RIBAS, C. R.; SCHOEREDER, J. H. How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators. **Ecological Indicators**, v. 24, p. 158–166, 2013.

SCHULTHEISS, P. et al. The abundance, biomass, and distribution of ants on Earth. **Proceedings of the National Academy of Sciences of the United States of America**, v. 119, n. 40, p. 1–9, 2022.

SYMSTAD, A. J. et al. Species loss and ecosystem functioning: Effects of species identity and community composition. **Oikos**, v. 81, n. 2, p. 389, 2006.

VAN DER PIJL, L. **Principles of dispersal in higher plants**. Berlin, Heidelberg: Springer Berlin Heidelberg, 1982.

YOUNGSTEADT, E. et al. Species-Specific Seed Dispersal in an Obligate Ant-Plant Mutualism. **PLoS ONE**, v. 4, n. 2, p. e4335, 2009.

CAPÍTULO I

EFFECTS OF ANTHROPOGENIC DISTURBANCES ON DIASPORE REMOVAL BY ANTS: A META-ANALYSIS

(https://doi.org/10.1016/j.actao.2023.103893)
Artigo publicado na revista *Acta Oecologica*.

Effects of anthropogenic disturbances on diaspore removal by ants: a meta-analysis

Bona, Ketlen[1,2]*, Delabie, Jacques H.C.[2,3] and Cazetta, Eliana[1,4]

[1]Applied Ecology and Conservation Lab, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Ilhéus, BA, Brazil.

[2]Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, CEPLAC, Ilhéus, BA, Brazil.

[3]Universidade Estadual de Santa Cruz, Departamento de Ciências Agrárias e Ambientais, Ilhéus, BA, Brazil.

[4]Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, BA, Brazil.

*Corresponding author. E-mail address: bonaketlen@gmail.com

ORCID ID

Ketlen Bona (0000-0002-8874-2919)

Jacques H.C. Delabie (0000-0002-2695-1061)

Eliana Cazetta (0000-0002-2209-2554)

Abstract

Anthropogenic changes in natural landscapes are identified as a major driver of biodiversity loss worldwide. Consequently, important ecosystem functions, such as seed dispersal by animals, can be lost, which threaten the stability of essential ecological processes. Given the current scenario of large seed disperser's loss, secondary dispersal by ants has been identified as an important alternative to mitigate the impacts caused by human changes. However, empirical evidence shows contradictory effects of anthropogenic disturbances on diaspore removal by ants. Here, we conducted a global meta-analysis from 22 studies (65 comparisons) comparing diaspore removal by ants in disturbed versus preserved areas to investigate general trends to different anthropogenic disturbances. Specifically, we evaluate: (i) the effects of anthropogenic disturbances on diaspore removal by ants comparing temperate and tropical regions, and (ii) comparing different disturbance types (agriculture related disturbances, fragmentation, mining, fire, etc.) on diaspore removal by ants. We found an overall negative effect of anthropogenic disturbances on diaspore removal by ants (26% decrease), both in temperate and tropical regions (38% and 19% decrease, respectively). In addition, diaspore removal by ants responded negatively to disturbances related to fragmentation (24% decrease) and mining (83% decrease). However, we found no evidence of effects in areas subjected to agricultural processes (0.9% decrease). Our findings suggest that human disturbances might compromise crucial early stages to the natural regeneration in ecosystems such the seed dispersal.

Keywords

Ecosystem functions; Fragmentation; Mining; Seed dispersal; Seed removing ants; Secondary dispersal.

1. Introduction

The constant exploitation of natural resources by human population has driven unprecedented changes in landscapes around the world (Steffen et al., 2011). As consequence, native environments were frequently subjected to a range of impacts (*e.g.*, logging, agriculture, mining, urbanization), which makes human activities one of the main drivers of the considerable loss of biodiversity at a global scale (Castro Pena et al., 2017; McKinney, 2008; McLaughlin and Mineau, 1995; Steffen et al., 2011; Thorn et al., 2018). This is mainly due to the loss of habitat and the consequently decrease in the available resources and changes in the essential conditions that allow the persistence of species in the remaining habitats (Echeverría et al., 2007; Rocha-Santos et al., 2016). In addition, disturbances in the soil and simplification of vegetation structure caused by abrupt transformation of forests or other vegetation types into pastures, mining, and expansion of urban areas also drastically reduce species diversity (Alroy, 2017; Barlow et al., 2016; Castro Pena et al., 2017). Consequently, it might occur a disruption in plant-animal interactions fundamental for the provision of ecological services (Bascompte and Jordano, 2007; Naeem et al., 2009; Symstad et al., 2006; Tylianakis et al., 2008).

Seed dispersal is an essential ecological process of paramount importance in anthropogenic landscapes, due to its key role to the stability of plant community or the recovery of degraded areas (Howe and Miriti, 2004; McConkey et al., 2012). In both tropical and temperate regions, the occurrence of seed dispersal agents is especially important and can considerably increase the chances of reproductive success of many plant species that produce fleshy fruits (McConkey et al., 2012; Van der Pijl, 1982). However, the loss of important seed dispersers (*e.g.*, medium and large sized vertebrates) due to defaunation of anthropogenic landscapes has threatened the maintenance of the seed dispersal process, with detrimental consequences for forest regeneration in the long term (Gardner et al., 2019; Haddad et al., 2015; Traveset et al., 2012; Vellend et al., 2006). On the other hand, the consequences of anthropogenic disturbance on other groups of seed dispersers, such as ants are still poorly understood. Ants can act as primary dispersers of fallen diaspores (*i.e.*, units dispersal; Van der Pijl, 1982) under parent plants, even of plants not specialized on ant dispersal (*i.e.*, those bearing an elaiosome) (Munguía-Rosas et al., 2009; Passos and Oliveira, 2002). Yet ants can also act as secondary seed dispersers removing seeds previously dispersed (Christianini and Oliveira, 2009, 2010).

Ants are social insects that actively participate in many ecosystem functions (Lach et al., 2010a) and are identified as the main animal group that redistributes resources in tropical forests floor (Griffiths et al., 2018). Among these resources are myrmecochorous diaspores (*i.e.*, diaspores with an elaiosome, a specialized comestible appendage dedicated to ant attraction; Beattie 1985) and non-myrmecochorous diaspores (*i.e.*, plants that are primarily dispersed by vertebrates, wind or authocoric species) (Anjos et al., 2020; Santana et al., 2013; Vander Wall and Longland, 2004). Diaspore removal by ants is a crucial stage in the dispersal process, whenever diaspores escape from high competition close to parent plants and increases the possibility of colonization of new habitats (Howe and Smallwood, 1982; Lengyel et al., 2009; Van der Pijl, 1982). In addition, diaspores can be carried by ants to higher quality microhabitats (*e.g.*, nest compartments), which have microclimate properties and soil nutrients suitable for germination and early growth of the seedling and are safe for recruitment (Christianini et al., 2007; Farji-Brener and Werenkraut, 2017). The diaspore cleaning by ants may also prevent infestation by fungi, and increases seed germination success (Guimarães and Cogni, 2002; Passos and Oliveira, 2002). Taking together, this highlights the fundamental role of ants in seed dispersal of myrmecochorous (Leal et al., 2015) and non-myrmecochorous (Christianini et al., 2007) diaspores in terrestrial ecosystems (Rico-Gray and Oliveira, 2007).

Although several studies have found negative impacts of anthropogenic disturbances on ant biodiversity (Lach et al., 2010b; Queiroz et al., 2017; Solar et al., 2016), the understanding of these impacts on ecosystem functions performed by ants is still limited. In addition, published studies evaluating the impacts of anthropogenic disturbances on diaspore removal by ants have pointed out to contradictory results. Some studies have shown that anthropogenic disturbances negatively affect diaspore transport by ants by reducing removal events (Almeida et al., 2013; Dominguez-Haydar and Armbrecht, 2011). Also, human impacts may reduce the occurrence of high-quality ants for diaspore removal (*i.e.*, larger ants, with solitary foraging and ability to remove over long distances), which may decrease seed dispersal quality (Leal et al., 2014a, 2014b). In contrast, other studies have pointed out to a lack of effects (Ness, 2004) or to an increase in diaspore removal by ants, suggesting positive anthropogenic impacts on removal rates (Fontenele and Schmidt, 2021). However, this increase in removal is mainly attributed to low-quality ants for diaspore removal (*i.e.*, smaller ants, with mass recruitment and removal over short distances; see Leal et al., 2014a, 2014b) (Fontenele and Schmidt, 2021). Thus, the overall effects of anthropogenic disturbances on diaspore removal by ants are still unclear. Unraveling these effects can provide theoretical support to increase our understanding on how anthropogenic disturbances affect animal-plant interactions and might trigger cascading effects on natural regeneration of ecosystems.

Here, we performed a meta-analytical approach to investigate at a global scale the occurrence of a consistent effect of anthropogenic disturbances on diaspore removal by ants. We tested the hypothesis that anthropogenic disturbances negatively affect diaspore removal by ants. This expectation is supported by the fact that environmental changes negatively influence the diversity and activity pattern of ants (Crist, 2009). In addition, we verified specific characteristics of each study, such as region (*i.e.*, temperate, and tropical) and type of disturbance (*i.e.*, agriculture, fragmentation, fire, mining, etc.). Specifically, we expected: (i) overall negative effects of anthropogenic disturbances on diaspore removal by ants in both temperate and tropical regions, and (ii) overall negative effects of anthropogenic disturbances on diaspore removal by ants. Our expectations are supported by the fact that anthropogenic disturbances are related to reducing habitat complexity, landscape structure and soil (Barlow et al., 2016; Decaëns et al., 2018; Holec and Frouz, 2005; Leal et al., 2012; Leal et al., 2014a; Solar et al., 2016). These effects are responsible to strongly contribute to the decline of species and, consequently, of essential functions in ecosystems, such as the secondary seed dispersal by ants.

2. Methods

2.1. Dataset

We performed a systematic review of the literature at a global scale focusing on studies that investigated the relationship between any type of anthropogenic disturbance and diaspore removal by ants from 1980 up to August 5th, 2020. Our searches were carried out in SCOPUS databases (http://www.scopus.com), ISI Web of Knowledge (http://www.webofknowledge.com) and Google Scholar (https://scholar.google.com.br) search engines. We used the following search terms: “ant diaspore” OR “ant fruit interaction” OR “ant removal” OR “myrmecochory” OR “myrmecochorous seeds” OR “non-myrmecochorous seeds” OR “harvester ants” AND “fragment*” OR “patch size” OR “habitat loss” OR “land-use change” OR “degradation” OR “alteration” OR “disturbance” OR “perturbation” OR “forest loss” OR “deforestation” OR “edge effects” OR “edge influence” OR “urban” OR “agriculture” OR “mining” OR “dam” OR “fire disturbance”. These keywords were searched in the title, abstract and keywords of the references.

We selected studies that met the following inclusion criteria: (i) clear comparison between disturbed and undisturbed environments by assessing ant-diaspore (myrmecochorous and non-myrmecochorous diaspores) removal events; (ii) presentation of average values and sample sizes for both treatments; and (iii) exclusively anthropogenic disturbances. We excluded papers that: (i) evaluated indirect effects of anthropogenic disturbances (*e.g.*, invasive ants); (ii) experimental and natural disturbances (*e.g.*, experimental fire or natural periodic fire). Here, our focus was to reveal how different anthropogenic changes in natural landscapes (*e.g.*, forest loss, fragmentation, agriculture, mining, etc.) interfere in the process of seed dispersal by ants; and (iii) studies with unavailable data (*e.g.*, studies without information of mean and standard deviance). After this screening, we ended up with 22 studies (See Supplementary Material, Fig. S1), encompassing a total of 10 types of anthropogenic disturbances (Fig. 1). The selected studies were published between 1985 and 2020 (Table S1) and were distributed in nine countries (Fig. 1 and Fig. S2).

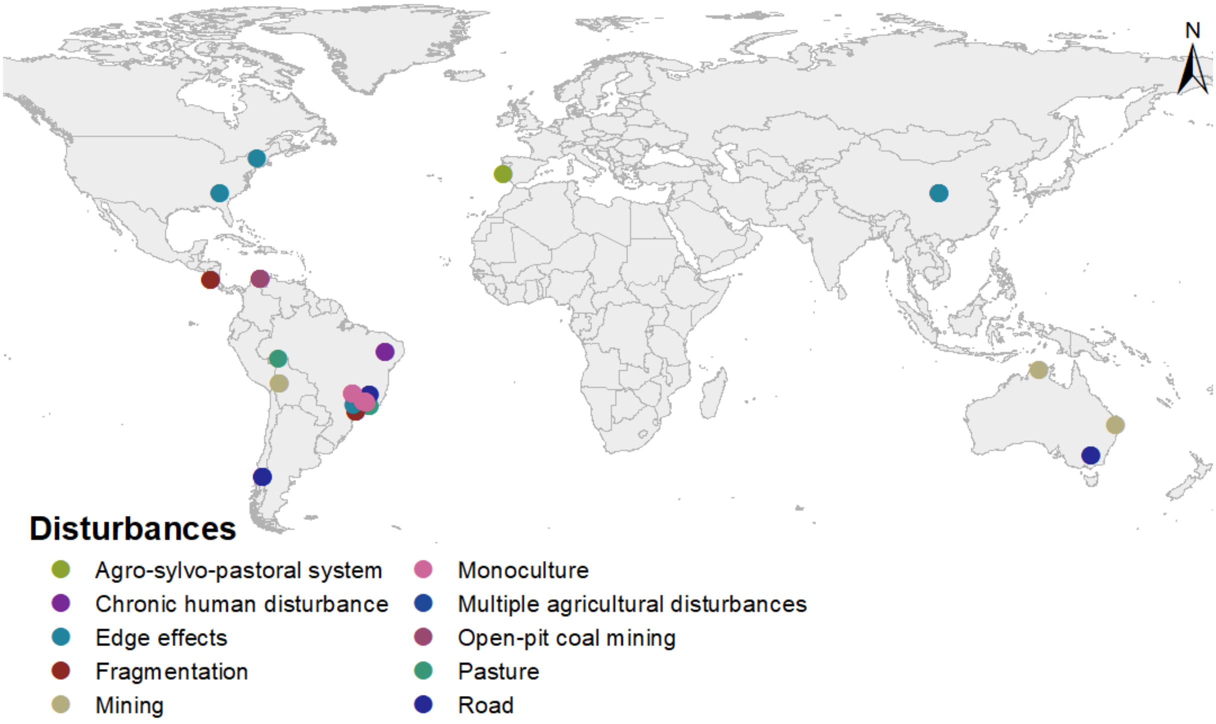


Fig. 1 World distribution of study sites included in the meta-analysis. The different colors indicate the type of disturbance reported in each study.

2.2. Meta-analytical procedure

For each comparison of disturbed *versus* control areas, we extracted the sample size and the mean value of diaspore removal events by ants (number of removed diaspore) with the estimated error (error or standard deviation) for treatment and control. We used the DataThief III software (Tummers, 2006) to extract raw values from figures whenever authors presented the data in graphs (N = 7). However, most of the data (N = 15) were obtained from values given by authors in the studies. We used Hedges' g as the effect size measure in our meta-analysis due to our small sample size (Borenstein et al., 2009). Our database was mainly composed by studies that presented more than one comparison (85.7% total) for multiple species, time periods, response, or predictor values. Thus, we performed a meta-analysis of random effects with 10,000 bootstrap randomizations, drawing a comparison per study to control for possible bias due to lack of independence among effect sizes within studies (Adams et al., 1997; Gibson et al., 2011). Thus, we calculated the mean bootstrapped effect size with 95% confidence intervals, which we considered significant when it did not include zero (Borenstein et al., 2009). We estimated the heterogeneity of the effect size using the I^2 statistic, which describes the proportion of variation between the studies through the heterogeneity of the data (Higgins et al., 2003). In addition, we performed subgroup analysis per geographic region and types of disturbances (See Supplementary Material, Table S1) to verify the heterogeneity of responses. Due to the low number of studies in each of the 10 different disturbance type found (Fig. 1), we combine studies into three major categories (*i.e.*, Agriculture, Fragmentation and Mining) (Table 1).

Table 1 Subgroups and categories used in the meta-analysis. Not all the categories of types of disturbance were included, due to the low number of studies. Therefore, we created subsets with similar disturbance in three categories. Numbers in parentheses are the number of studies/comparisons for each moderator variable.

Subgroup	**Moderator variables**
1. Region	**1.1 Temperate (9/20)** Latitude > 23.5° N/S **1.2 Tropical (13/45)** Latitude < 23.5° N/S
2. Disturbance	**2.1 Agriculture (7/22)** Pasture, monoculture, agro-sylvo-pastoral system, chronic human disturbance, and multiple agricultural disturbances **2.2 Fragmentation (11/26)** Edge effects (edge *vs.* interior comparisons), road, and fragmentation metrics (local and landscape studies, matrix effects) **2.3 Mining (4/17)** Mining and open-pit coal mining

To evaluate the publication bias and verify the robustness of our meta-analysis, we performed the Rosenthal's fail-safe number (FSN) analysis, which calculates the number of studies with no effects necessary to change the overall effect size ($FSN \geq 5*N + 10$, where N is the number of used studies) (Rosenthal, 1991). Then, the Egger's test was applied, which performs a linear regression of the effect sizes standardized in their precision to verify asymmetry in the funnel graph, where $p > 0.05$ indicates a symmetric funnel graph (Egger et al., 1997). All analyzes were performed with R software (R Core Team, 2020) using the Metafor package (Viechtbauer, 2010).

3. Results

We found 65 comparisons of anthropogenic disturbances on diaspore removal by ants, in 22 studies (mean ± standard deviation (SD) = 2.95 ± 1.67 comparisons per study). Most studies were conducted in tropical regions (13 studies, 45 comparisons) and nine studies in temperate regions (20 comparisons) (Table 1). Regarding the types of disturbances, most studies evaluated fragmentation effects (11 studies, 26 comparisons), followed by agriculture (7 studies, 22 comparisons) and mining (4 studies, 17 comparisons) (Table 1). Most studies were zoocentric with ant active collection (N = 15) (See the seed-removing ant species list of each study in Table S2) and seven studies were focusing on specific plant species or exclusion experiments (no active collection of ants) (Table S3). Three studies used artificial diaspores (See Table S3).

The mean bootstrapped effect size indicated an overall negative effect of anthropogenic disturbances on diaspore removal by ants (-0.26 [95% CI: -0.48, -0.08]). A moderate heterogeneity among effect sizes (Mean I^2 = 65%; 95% CI: 81%, 29%), was partially explained by different effects of our moderator variables (*i.e.*, Temperate and Tropical regions, Agriculture, Fragmentation and Mining disturbances). Subgroup analyzes revealed that diaspore removal by ants responded negatively to anthropogenic disturbances both in tropical (-0.19 [95% CI: -0.34, -0.07]) and temperate regions (-0.38 [95% CI: -0.86, -0.02]) (Fig. 2). In addition, diaspore removal by ants responded negatively to fragmentation (-0.24 [95% CI: -0.50, -0.005]) and mining (-0.83 [95% CI: -1.52, -0.40]), while there was little evidence of an overall effect of agriculture (-0.09 [95% CI: -0.21, 0.02]) (Fig. 2).

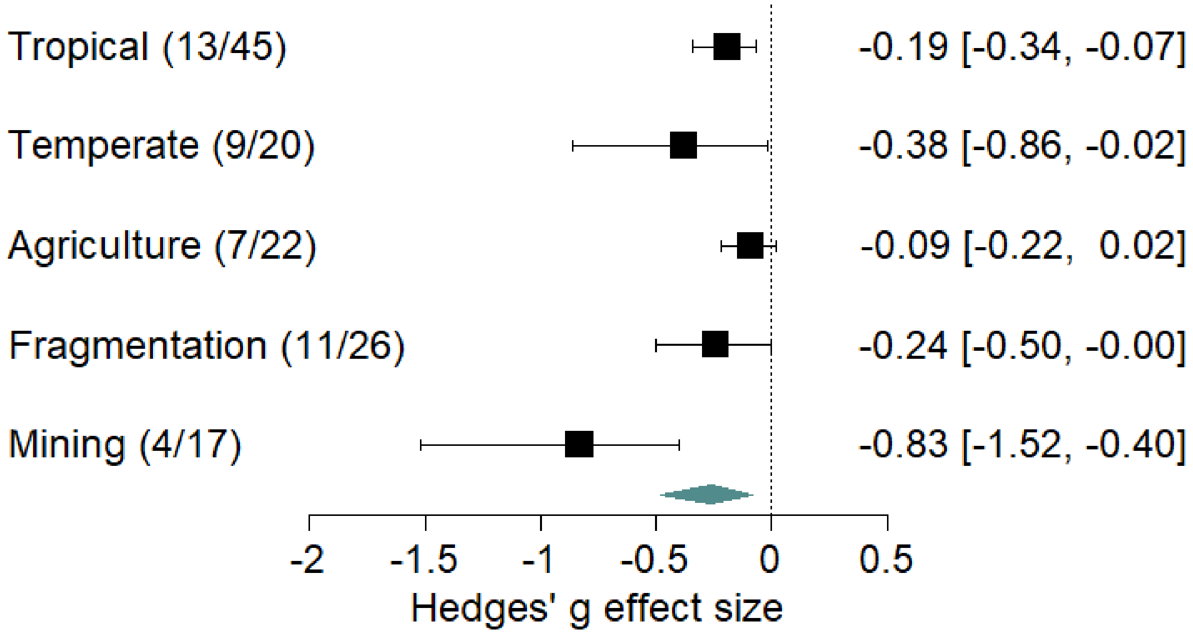


Fig. 2 Mean effect size (Hedges' g (squares)) and the 95% CIs values (horizontal lines) of the effects of anthropogenic disturbances on diaspore removal by ants. The categories of each subgroup are pointed on the left, with the number of studies/comparisons in parentheses. The blue diamond indicates global mean effect size of the meta-analysis.

Regarding publication bias, Rosenthal's fail-safe number (FSN) test showed that 73 studies with no effect would be needed to transform the result of this meta-analysis into a non-significant overall effect size. We found a threshold below to that suggested by Rosenthal (1991) (*i.e.*, 5*22 studies used in meta-analysis + 10 = 120). Moreover, the Egger's test resulted in a mean z-value of -0.55 (95% CI: -1.95; 1.06) and a mean p-value of 0.44 (95% CI: 0.05; 0.95), indicating a symmetric funnel plot. Thus, our results are unaffected by publication bias.

4. Discussion

Our study provides unprecedented information on the interference of anthropogenic disturbances on diaspore removal by ants at a global scale. It reveals that the negative effects of different anthropogenic disturbances occurs both in temperate and tropical regions. In addition, we found a general negative effect of disturbances related to fragmentation and mining on diaspore removal by ants, but none on disturbances arising from agriculture. Our findings may suggest that anthropogenic disturbances reduce the quantitative contribution of ants to seed removal with possible consequences to a key process for plant reproductive success (Leal et al., 2015; Passos and Oliveira, 2002). Although our study has possible limitations due to the relatively low number of studies and knowledge gaps in some continents of the world that have not yet investigated the effects of anthropogenic disturbances on diaspore removal by ants, we discuss below possible explanations and interpretations of our results.

We found an overall negative effect of anthropogenic disturbances on diaspore removal by ants (26% decrease). In general, disturbance can lead to the increase of specialized ants in open and arid environments, or behaviorally dominant ant species (Kuate et al., 2015; Parr and Gibb, 2009). Consequently, there is an increase in competitive exclusion of more specialized species belonging to functional groups important to perform functions such as seed dispersal (Hoffmann and Andersen, 2003; Parr and Gibb, 2009; Philpott et al., 2009). This may explain our findings, which demonstrate that overall anthropogenic disturbance can negatively impact ecosystem functions. Furthermore, it is known that the same disturbance can have different effects on ant species at the community level (Andersen, 2018). This is because characteristics such as the natural openness of the habitat can interfere with the resilience and adaptations of species (Andersen, 2018; Arnan et al., 2006). For instance, in undisturbed naturally open habitats (*e.g.*, savanna), anthropogenic disturbance may have less severe consequences on ant communities compared to closed habitats (*e.g.*, tropical forest) (Andersen, 2018). Moreover, habitat openness can also interfere with ecological services provided by ants, such as changes in plant protection interactions against herbivory (Andersen, 2018). Then studies that reveal how each disturbance, individually, shapes the seed dispersal function by ants considering the natural openness of the habitats where the disturbance occurs would be carried out. This kind of information could help in a deeper understanding of the relationship between seed dispersal by ants and anthropogenic disturbances, analyzing other relevant aspects of this function (*e.g.*, seed germination, removal distance, quality of the removing by ant species).

We found a 38% and 19% decline on diaspore removal by ants in temperate and tropical regions, respectively. It is well known that temperate regions presented some climatic limitations (*e.g.*, extreme temperature and seasonality), with consequently, a low plant diversity and reduced attractive resources for soil fauna (Willig et al., 2003). Despite this, temperate ecosystems have an expressive diversity of myrmecochorous plants, where myrmecochory particularly and many other plant-animal interactions probably shaped communities of temperate plants (Jia et al., 2018; Lengyel et al., 2009). Our findings demonstrate the severity of anthropogenic disturbances on these regions, since a 38% decrease in diaspores removal by ants can considerably reduce the probability of seeds being deposited in suitable locations. This can be very harmful for plant communities in these ecosystems that naturally present low species diversity. In contrast to temperate regions, tropical regions have more favorable climatic conditions for high floristic diversity and high heterogeneity of habitats and resources for fauna (Willig et al., 2003). This may explain the lower impact of disturbances in tropical regions when compared to temperate ones. Even so, a 19% decrease in diaspore removal by ants in these regions is expressive. This is because tropical regions are increasingly threatened by the intensification of human use of natural landscapes (Bradshaw et al., 2009). Thus, the drastic loss of large dispersers (Gardner et al., 2019; Traveset et al., 2012) associated with the decrease in diaspore removal by ants may indicate the impairment of seed dispersal process in tropical forests under anthropogenic influence. Our results show that anthropogenic disturbances can severely impair the natural regeneration processes in both temperate and tropical ecosystems by reducing the quantitative contribution of ants to seed dispersal.

The overall negative effect of fragmentation (*i.e.*, not fragmentation *per se*; Please, see Table 1) on diaspore removal by ants (24% decrease) is possibly related to the fact that habitat fragmentation reduces the local ant diversity and changes the average body size of remaining ant communities (Bieber et al., 2014; Carvalho and Vasconcelos, 1999; Gibb et al., 2018; Leal et al., 2012). This is because disturbed environments tend to present a predominance of smaller ants, which are less likely to remove diaspores in general (Gibb et al., 2018; Ness et al., 2004). In addition, the functional composition of ants is also modified by reducing specialist ants, with as a consequence, the reduction of diaspore-removing ants in forests (Leal et al., 2012). In fact, isolation between forest habitats hinders the movement of ants, since some of these organisms have limited dispersal capacity, and different surrounding barriers can be a filter for some of species (Gascon et al., 1999). In addition, the edges in remaining forests directly affect communities of insects that forage predominantly on the ground, such as ants (Caitano et al., 2020). This is because these organisms have a narrower niche and the conditions in these locations (*e.g.*, temperature, humidity, reduced food resources) make them highly vulnerable to edge effects (Caitano et al., 2020). Any change in ant communities may directly affect the diaspore removal by ants, since changes in abundance of main dispersers (*i.e.*, dominant dispersers) can cause a decrease in removal rates (Zhu and Wang, 2018).

Mining-related disturbances induce an 83% decline on diaspore removal by ants. Integral removal of the topsoil in areas subjected to this type of disturbance has a drastic impact on ant assemblages (Arruda et al., 2020; Fernandes et al., 2018; Holec and Frouz, 2005; Rabello et al., 2015). In general, ground-nesting ants contribute significantly to diaspores removal (Oliveira et al., 2017). These ants tend to be the most affected by mining, since mining impacts the ground at severe levels (Arruda et al., 2020). In this case, the high reduction in ant richness in mining areas may explain the expressive decline in diaspores removal. Furthermore, the elimination of vegetation in the same places induces a strong reduction in arboreal ant diversity (Rabello et al., 2015). Despite the relatively low contribution of arboreal ants to seed dispersal, arboreal ants interact with fallen diaspores during occasional foraging in the soil (Raimundo et al., 2004). In environments of scarce diversity due to critical disturbances, such as mining, any loss of interaction between species is harmful to ecosystem maintenance. In addition, in these environments generalist ant species that are more tolerant to disturbances may occur (Majer et al., 2007), but the low abundance or lack of diaspores hampers ant-plant interactions. Our findings showed a high impact of mining activities and a considerable threat to natural regeneration or vegetation recovery on these ecosystems.

The weak evidence of a general effect of agricultural processes on diaspore removal by ants (0.9% decrease) was quite surprising but may be related to the combine effect of favoring specific group of ants, such as leaf-cutting and invasive ant species while decreasing specialist species, such as high-quality seed-disperser ants. In their range of distribution through Americas, leaf-cutting ants present a considerable increase in abundance and foraging activities, such as fallen fruits and seeds, on disturbed environments (Leal et al., 2014; Meyer et al., 2009; Siqueira et al., 2017; Vieira-Neto et al., 2016). Similarly, processes related to agriculture such as pastures and relatively open plantations promote the increase of invasive ant species with mass recruitment, which tends to increase rates of diaspore removal in impacted sites (Carney et al., 2003; Hoffmann et al., 1999; Ness et al., 2004). In general, ants that are favored by disturbances do not perform the role of seed dispersal with quality. Low-quality ants for diaspore removal harm the process of seed dispersal in impacted sites in the long term (Leal et al., 2014a). In this sense, the increase in diaspore removal rates promoted by these ant species does not benefit plant communities, and on the contrary, negatively impact natural seed dispersal (Knoechelmann et al., 2020; Leal et al., 2014a). On the other hand, there is a loss of key species considered to be of high quality for the diaspores removal (*e.g.*, *Ectatomma edentatum*) in disturbed environments, which tends to reduce removal rates in these sites (Fontenele and Schmidt, 2021; Leal et al., 2014a; Wilker et al., 2022). This combination of effects may explain our findings, since the replacement of ant species in disturbed environments can influence the ecosystem interactions. Thus, the lack of evidence of the negative effects of agricultural processes on ant-diaspore interactions found here, must be seen with caution. Studies evaluating other aspects of secondary dispersal by ants mainly those focused on the qualitative component of the seed dispersal effectiveness framework (*sensu* Schupp et al. 2010), such as dispersal distance, diaspore fate, germination rates and survival rates, are necessary to reveal the general trend of these interactions.

Yet diaspore removal is the first step of the seed dispersal process, and seed removal by ants is important to partially mitigate the negative anthropogenic effects on large seed dispersers in human-modified landscapes (Anjos et al., 2020). Studies using diaspore-removing ants can help monitoring not only the return of ant species, but also of essential ecological interactions for the functioning of terrestrial ecosystems. Generally, the contribution of disperser agents to plant reproductive success depends not only on quantitative factors, such as diaspore removal, but also on qualitative ones (*i.e.*, the diaspore manipulation during transport by disperser agent) (Jordano and Schupp, 2000; Schupp et al., 2010). Our findings suggest a consistent negative effect of anthropogenic disturbances on the quantitative contribution of ants to seed dispersal in impacted ecosystems. Thus, it is needed more efforts to reveal how anthropogenic disturbances influence the quality component of the seed dispersal effectiveness framework through other important aspects of seed dispersal by ants. The quality of seed-removing ants and/or their habitat specialty (see Leal et al. 2014a, 2014b; Vasconcelos et al. 2018; Fontenele and Schmidt 2021), for example, are important information less evaluated that should be better explored.

5. Conclusion

Our study demonstrated that anthropogenic disturbances contribute to an overall 26% decrease in frequency of diaspore removal by ants on a global scale. It reveals that these impacts occur in both temperate and tropical regions (38% and 19% decrease, respectively) and that processes related to fragmentation and mining have a strong influence on the decrease of removal events (24% and 83% decrease, respectively). In contrast, processes related to agriculture have presented not enough evidence to point out to negative effects of this type of disturbance (0.9% decrease). Our explanations and interpretations are based on a relatively low number of studies, despite this, it is possible to verify how negative the effects of anthropogenic disturbances in natural landscapes are on essential functions for the ecosystem. Thus, we emphasize the need for more efforts to fill knowledge gaps on this topic in more places around the globe. Although diaspore removal by ants is beneficial for plants on a small spatial scale, discreet interactions on the ecosystems can be the initial step that enables large roles to be performed. Thus, we emphasize the importance of conserving natural landscapes for the perpetuation of essential ecological processes carried out by ants.

6. Author contributions

KB, JHCD and EC developed the conceptual framework of this study; KB conducted the literature review and data processing; and KB wrote the paper with contributions from all authors.

7. Acknowledgments

We thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for scholarship to KB (Financing Code 001). JHCD and EC acknowledge their productivity research grant from CNPq (304629/2018-9, 311545/2021-1, respectively).

8. References

Adams, D.C., Gurevitch, J., Rosenberg, M.S., 1997. Resampling tests for meta-analysis of ecological data. Ecology 78, 1277–1283. https://doi.org/10.1890/0012-9658(1997)078[1277:RTFMAO]2.0.CO;2

Almeida, F.S., Mayhé-Nunes, A.J., Queiroz, J.M., 2013. The importance of poneromorph ants for seed dispersal in altered environments. Sociobiology 60, 229–235. https://doi.org/10.13102/sociobiology.v60i3.229-235

Alroy, J., 2017. Effects of habitat disturbance on tropical forest biodiversity. Proc. Natl. Acad. Sci. U. S. A. 114, 6056–6061. https://doi.org/10.1073/pnas.1611855114

Andersen, A.N., 2018. Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. J. Anim. Ecol. 88, 350–362. https://doi.org/10.1111/1365-2656.12907

Anjos, D. V., Leal, L.C., Jordano, P., Del-Claro, K., 2020. Ants as diaspore removers of non-myrmecochorous plants: a meta-analysis. Oikos 129, 775–786. https://doi.org/10.1111/oik.06940

Arnan, X., Rodrigo, A., Retana, J., 2006. Post-fire recovery of Mediterranean ground ant communities follows vegetation and dryness gradients. J. Biogeogr. 33, 1246–1258. https://doi.org/10.1111/j.1365-2699.2006.01506.x

Arruda, A.J., Costa, F. V., Guerra, T.J., Junqueira, P.A., Dayrell, R.L.C., Messeder, J.V.S., Rodrigues, H.T.S., Buisson, E., Silveira, F.A.O., 2020. Topsoil disturbance reshapes diaspore interactions with ground-foraging animals in a megadiverse grassland. J. Veg. Sci. 31, 1039–1052. https://doi.org/10.1111/jvs.12866

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R. Mac, Thomson, J.R., Ferraz, S.F.D.B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro De Castro Solar, R., Vieira, I.C.G., Araga??, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C.D.O., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-De-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. Nature 535, 144–147. https://doi.org/10.1038/nature18326

Bascompte, J., Jordano, P., 2007. Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. Annu. Rev. Ecol. Evol. Syst. 38, 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Beattie, A.J., 1985. The evolutionary ecology of ant–plant mutualisms. Cambridge University Press, New York. https://doi.org/10.1017/CBO9780511721878

Bieber, A.G.D., Silva, P.S.D., Sendoya, S.F., Oliveira, P.S., 2014. Assessing the impact of deforestation of the Atlantic rainforest on ant-fruit interactions: A field experiment using synthetic fruits. PLoS One 9, 1–9. https://doi.org/10.1371/journal.pone.0090369

Borenstein, M., Hedges, L. V., Higgins, J.P.T., Rothstein, H.R., 2009. Introduction to Meta-Analysis, Leadership and Organizational Outcomes: Meta-Analysis of Empirical Studies. John Wiley & Sons, Ltd, Chichester, UK. https://doi.org/10.1002/9780470743386

Bradshaw, C.J.A., Sodhi, N.S., Brook, B.W., 2009. Tropical turmoil: A biodiversity tragedy in progress. Front. Ecol. Environ. 7, 79–87. https://doi.org/10.1890/070193

Caitano, B., Chaves, T.P., Dodonov, P., Delabie, J.H.C., 2020. Edge effects on insects depend on life history traits: a global meta-analysis. J. Insect Conserv. 24, 233–240. https://doi.org/10.1007/s10841-020-00227-1

Carvalho, K.S., Vasconcelos, H.L., 1999. Forest fragmentation in central Amazonia and its effects on litter-dwelling ants. Biol. Conserv. 91, 151–157. https://doi.org/10.1016/S0006-3207(99)00079-8

Castro Pena, J.C., Goulart, F., Wilson Fernandes, G., Hoffmann, D., Leite, F.S.F., Britto dos Santos, N., Soares-Filho, B., Sobral-Souza, T., Humberto Vancine, M., Rodrigues, M., 2017. Impacts of mining activities on the potential geographic distribution of eastern Brazil mountaintop endemic species. Perspect. Ecol. Conserv. 15, 172–178. https://doi.org/10.1016/j.pecon.2017.07.005

Christianini, A. V., Mayhé-Nunes, A.J., Oliveira, P.S., 2007. The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a neotropical savanna. J. Trop. Ecol. 23, 343–351. https://doi.org/10.1017/S0266467407004087

Crist, T.O., 2009. Biodiversity, species interactions, and functional roles of ants (Hymenoptera: Formicidae) in fragmented landscapes: a review. Myrmecological News 12, 3–13.

Decaëns, T., Martins, M.B., Feijoo, A., Oszwald, J., Dolédec, S., Mathieu, J., Arnaud de Sartre, X., Bonilla, D., Brown, G.G., Cuellar Criollo, Y.A., Dubs, F., Furtado, I.S., Gond, V., Gordillo, E., Le Clec'h, S., Marichal, R., Mitja, D., de Souza, I.M., Praxedes, C., Rougerie, R., Ruiz, D.H., Otero, J.T., Sanabria, C., Velasquez, A., Zararte, L.E.M., Lavelle, P., 2018. Biodiversity loss along a gradient of deforestation in Amazonian agricultural landscapes. Conserv. Biol. 32, 1380–1391. https://doi.org/10.1111/cobi.13206

Dominguez-Haydar, Y., Armbrecht, I., 2011. Response of ants and their seed removal in rehabilitation areas and forests at El Cerrejón Coal Mine in Colombia. Restor. Ecol. 19, 178–184. https://doi.org/10.1111/j.1526-100X.2010.00735.x

Echeverría, C., Newton, A.C., Lara, A., Benayas, J.M.R., Coomes, D.A., 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. Glob. Ecol. Biogeogr. 16, 426–439. https://doi.org/10.1111/j.1466-8238.2007.00311.x

Egger, M., Smith, G.D., Schneider, M., Minder, C., 1997. Bias in meta-analysis detected by a simple, graphical test. Br. Med. J. 315, 629–634. https://doi.org/10.1136/bmj.315.7109.629

Farji-Brener, A.G., Werenkraut, V., 2017. The effects of ant nests on soil fertility and plant performance: a meta-analysis. J. Anim. Ecol. 86, 866–877. https://doi.org/10.1111/1365-2656.12672

Fernandes, G.W., Barbosa, N.P.U., Alberton, B., Barbieri, A., Dirzo, R., Goulart, F., Guerra, T.J., Morellato, L.P.C., Solar, R.R.C., 2018. The deadly route to collapse and the uncertain fate of Brazilian rupestrian grasslands. Biodivers. Conserv. 27, 2587–2603. https://doi.org/10.1007/s10531-018-1556-4

Fontenele, L.K., Schmidt, F.A., 2021. Forest-pasture shifting alters the assemblages of seed-removing ants in southwestern Brazilian Amazon. J. Insect Conserv. 25, 213–220. https://doi.org/10.1007/s10841-021-00295-x

Gardner, C.J., Bicknell, J.E., Baldwin-Cantello, W., Struebig, M.J., Davies, Z.G., 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. Nat. Commun. 10, 1–7. https://doi.org/10.1038/s41467-019-12539-1

Gascon, C., Lovejoy, T.E., Bierregaard Jr., R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurance, W.F., Zimmerman, B., Tocher, M., Borges, S., 1999. Matrix habitat and species richness in tropical forest remnants. Biol. Conserv. 91, 223–229. https://doi.org/10.1016/S0006-3207(99)00080-4

Gibb, H., Sanders, N.J., Dunn, R.R., Arnan, X., Vasconcelos, H.L., Donoso, D.A., Andersen, A.N., Silva, R.R., Bishop, T.R., Gomez, C., Grossman, B.F., Yusah, K.M., Luke, S.H., Pacheco, R., Pearce-Duvet, J., Retana, J., Tista, M., Parr, C.L., 2018. Habitat disturbance selects against both small and large species across varying climates. Ecography (Cop.). 41, 1184–1193. https://doi.org/10.1111/ecog.03244

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–381. https://doi.org/10.1038/nature10425

Griffiths, H.M., Ashton, L.A., Walker, A.E., Hasan, F., Evans, T.A., Eggleton, P., Parr, C.L., 2018. Ants are the major agents of resource removal from tropical rainforests. J. Anim. Ecol. 87, 293–300. https://doi.org/10.1111/1365-2656.12728

Guimarães, P.R., Cogni, R., 2002. Seed cleaning of Cupania vernalis (Sapindaceae) by ants: Edge effect in a highland forest in south-east Brazil. J. Trop. Ecol. 18, 303–307. https://doi.org/10.1017/S0266467402002213

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052. https://doi.org/10.1126/sciadv.1500052

Higgins, J.P.T., Thompson, S.G., Deeks, J.J., Altman, D.G., 2003. Measuring inconsistency in meta-analyses. BMJ 327, 557–560. https://doi.org/10.1136/bmj.327.7414.557

Hoffmann, B.D., Andersen, A.N., 2003. Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecol. 28, 444–464. https://doi.org/10.1046/j.1442-9993.2003.01301.x

Holec, M., Frouz, J., 2005. Ant (Hymenoptera: Formicidae) communities in reclaimed and unreclaimed brown coal mining spoil dumps in the Czech Republic. Pedobiologia (Jena). 49, 345–357. https://doi.org/10.1016/j.pedobi.2005.03.001

Howe, F., Smallwood, J., 1982. Ecology of seed dispersal. Annu. Rev. Ecol. Syst. Vol. 13 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Howe, H.F., Miriti, M.N., 2004. When seed dispersal matters. Bioscience 54, 651–660. https://doi.org/10.1641/0006-3568(2004)054[0651:WSDM]2.0.CO;2

Jia, S., Wang, X., Yuan, Z., Lin, F., Ye, J., Hao, Z., Luskin, M.S., 2018. Global signal of top-down control of terrestrial plant communities by herbivores. Proc. Natl. Acad. Sci. U. S. A. 115, 6237–6242. https://doi.org/10.1073/pnas.1707984115

Jordano, P., Schupp, E.W., 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for Prunus mahaleb. Ecol. Monogr. 70, 591–615. https://doi.org/10.1890/0012-9615(2000)070[0591:sdetqc]2.0.co;2

Knoechelmann, C.M., Oliveira, F.M.P., Siqueira, F.F.S., Wirth, R., Tabarelli, M., Leal, I.R., 2020. Leaf-cutting ants negatively impact the regeneration of the Caatinga dry forest across abandoned pastures. Biotropica 52, 686–696. https://doi.org/10.1111/btp.12782

Kuate, A.F., Hanna, R., Tindo, M., Nanga, S., Nagel, P., 2015. Ant Diversity in Dominant Vegetation Types of Southern Cameroon. Biotropica 47, 94–100. https://doi.org/10.1111/btp.12182

Lach, L., Parr, C., Abbott, K., 2010a. Ant Ecology. Oxford University Press, New York.

Lach, L., Parr, C., Abbott, K., 2010b. Ant conservation: Current status and a call to action, in: Ant Ecology. Oxford University Press Inc., New York, pp. 137–156.

Leal, I.R., Filgueiras, B.K.C., Gomes, J.P., Iannuzzi, L., Andersen, A.N., 2012. Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodivers. Conserv. 21, 1687–1701. https://doi.org/10.1007/s10531-012-0271-9

Leal, I.R., Leal, L.C., Andersen, A.N., 2015. The benefits of myrmecochory: A matter of stature. Biotropica 47, 281–285. https://doi.org/10.1111/btp.12213

Leal, I.R., Wirth, R., Tabarelli, M., 2014. The multiple impacts of leaf-cutting ants and their novel ecological role in human-modified Neotropical forests. Biotropica 46, 516–528. https://doi.org/10.1111/btp.12126

Leal, L.C., Andersen, A.N., Leal, I.R., 2014a. Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the Brazilian Caatinga. Oecologia 174, 173–181. https://doi.org/10.1007/s00442-013-2740-6

Leal, L.C., Neto, M.C.L., de Oliveira, A.F.M., Andersen, A.N., Leal, I.R., 2014b. Myrmecochores can target high-quality disperser ants: Variation in elaiosome traits and ant preferences for myrmecochorous Euphorbiaceae in Brazilian Caatinga. Oecologia 174, 493–500. https://doi.org/10.1007/s00442-013-2789-2

Lengyel, S., Gove, A.D., Latimer, A.M., Majer, J.D., Dunn, R.R., 2009. Ants sow the seeds of global diversification in flowering plants. PLoS One 4, 1–6. https://doi.org/10.1371/journal.pone.0005480

Majer, J.D., Brennan, K.E.C., Moir, M.L., 2007. Invertebrates and the restoration of a forest ecosystem: 30 years of research following bauxite mining in Western Australia. Restor. Ecol. 15, 104–115. https://doi.org/10.1111/j.1526-100X.2007.00298.x

McConkey, K.R., Prasad, S., Corlett, R.T., Campos-Arceiz, A., Brodie, J.F., Rogers, H., Santamaria, L., 2012. Seed dispersal in changing landscapes. Biol. Conserv. 146, 1–13. https://doi.org/10.1016/j.biocon.2011.09.018

McKinney, M.L., 2008. Effects of urbanization on species richness: A review of plants and animals. Urban Ecosyst. 11, 161–176. https://doi.org/10.1007/s11252-007-0045-4

McLaughlin, A., Mineau, P., 1995. The impact of agricultural practices on biodiversity. Agric. Ecosyst. Environ. 55, 201–212. https://doi.org/10.1016/0167-8809(95)00609-V

Meyer, S.T., Leal, I.R., Wirth, R., 2009. Persisting hyper-abundance of leaf-cutting ants (Atta spp.) at the edge of an old Atlantic Forest fragment. Biotropica 41, 711–716. https://doi.org/10.1111/j.1744-7429.2009.00531.x

Munguía-Rosas, M.A., Jácome-Flores, M.E., Sosa, V.J., Quiroz-Cerón, L.M., 2009. Removal of Pilosocereus leucocephalus (Cactaceae, tribe Cereeae) seeds by ants and their potential role as primary seed dispersers. J. Arid Environ. 73, 578–581. https://doi.org/10.1016/j.jaridenv.2008.12.017

Naeem, S., Bunker, D.E., Hector, A., 2009. Biodiversity, ecosystem functioning, and human wellbeing: An ecological and economic perspective, Biodiversity, Ecosystem Functioning, and Human Wellbeing. Oxford University Press, New York.

Ness, J.H., 2004. Forest edges and fire ants alter the seed shadow of an ant-dispersed plant.

Oecologia 138, 448–454. https://doi.org/10.1007/s00442-003-1440-z

Ness, J.H., Bronstein, J.L., Andersen, A.N., Holland, J.N., 2004. Ant body size predicts dispersal distance of ant-adapted seeds: Implications of small-ant invasions. Ecology 85, 1244–1250. https://doi.org/10.1890/03-0364

Oliveira, P.S., Christianini, A. V., Bieber, A.G.D., Pizo, M.A., 2017. Anthropogenic Disturbances Affect the Interactions between Ants and Fleshy Fruits in Two Neotropical Biodiversity Hotspots, in: Oliveira, P.S., Koptur, S. (Eds.), Ant-Plant Interactions. Cambridge University Press, Cambridge, pp. 133–156. https://doi.org/10.1017/9781316671825.008

Parr, C.L., Gibb, H., 2009. Competition and the Role of Dominant Ants, in: Ant Ecology. Oxford University Press, pp. 77–96. https://doi.org/10.1093/acprof:oso/9780199544639.003.0005

Passos, L., Oliveira, P.S., 2002. Ants affect the distribution and performance of seedlings of Clusia criuva, a primarily bird-dispersed rain forest tree. J. Ecol. 90, 517–528. https://doi.org/10.1046/j.1365-2745.2002.00687.x

Philpott, S.M., Perfecto, I., Armbrecht, I., Parr, C.L., 2009. Ant Diversity and Function in Disturbed and Changing Habitats, in: Ant Ecology. Oxford University Press, pp. 137–156. https://doi.org/10.1093/acprof:oso/9780199544639.003.0008

Queiroz, A.C.M., Rabello, A.M., Braga, D.L., Santiago, G.S., Zurlo, L.F., Philpott, S.M., Ribas, C.R., 2017. Cerrado vegetation types determine how land use impacts ant biodiversity. Biodivers. Conserv. 29, 2017–2034. https://doi.org/10.1007/s10531-017-1379-8

R Core Team, 2020. R: A Language and environment for statistical computing (No. 3.4.3), R Foundation for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

Rabello, A.M., Queiroz, A.C.M., Lasmar, C.J., Cuissi, R.G., Canedo-Júnior, E.O., Schmidt, F.A., Ribas, C.R., 2015. When is the best period to sample ants in tropical areas impacted by mining and in rehabilitation process? Insectes Soc. 62, 227–236. https://doi.org/10.1007/s00040-015-0398-2

Raimundo, R.L.G., Guimarães, P.R., Almeida-Neto, M., Pizo, M.A., 2004. The influence of fruit morphology and habitat structure on ant-seed interactions: A study with artificial fruits. Sociobiology 44, 261–270.

Rico-Gray, V., Oliveira, P.S., 2007. The ecology and evolution of ant-plant interactions.

University of Chicago Press, Chicago.

Rocha-Santos, L., Pessoa, M.S., Cassano, C.R., Talora, D.C., Orihuela, R.L.L., Mariano-Neto, E., Morante-Filho, J.C., Faria, D., Cazetta, E., 2016. The shrinkage of a forest: Landscape-scale deforestation leading to overall changes in local forest structure. Biol. Conserv. 196, 1–9. https://doi.org/10.1016/j.biocon.2016.01.028

Rosenthal, R., 1991. Meta-Analytic procedures for social research, Meta-Analytic Procedures for Social Research. SAGE Publications, Inc., California. https://doi.org/10.4135/9781412984997

Santana, F.D., Cazetta, E., Delabie, J.H.C., 2013. Interactions between ants and non-myrmecochorous diaspores in a tropical wet forest in southern Bahia, Brazil. J. Trop. Ecol. 29, 71–80. https://doi.org/10.1017/S0266467412000715

Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytol. 188, 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Silva, P.D., Leal, I.R., Wirth, R., Tabarelli, M., 2007. Harvesting of Protium heptaphyllum (Aubl.) March. seeds (Burseraceae) by the leaf-cutting ant Atta sexdens L. promotes seed aggregation and seedling mortality. Rev. Bras. Bot. 30, 553–560. https://doi.org/10.1590/S0100-84042007000300019

Siqueira, F.F.S., Ribeiro-Neto, J.D., Tabarelli, M., Andersen, A.N., Wirth, R., Leal, I.R., 2017. Leaf-cutting ant populations profit from human disturbances in tropical dry forest in Brazil. J. Trop. Ecol. 33, 337–344. https://doi.org/10.1017/S0266467417000311

Solar, R.R. de C., Barlow, J., Andersen, A.N., Schoereder, J.H., Berenguer, E., Ferreira, J.N., Gardner, T.A., 2016. Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. Biol. Conserv. 197, 98–107. https://doi.org/10.1016/j.biocon.2016.03.005

Steffen, W., Grinevald, J., Crutzen, P., Mcneill, J., 2011. The Anthropocene: Conceptual and historical perspectives. Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 369, 842–867. https://doi.org/10.1098/rsta.2010.0327

Symstad, A.J., Tilman, D., Willson, J., Knops, J.M.H., 2006. Species loss and ecosystem functioning: Effects of species identity and community composition. Oikos 81, 389. https://doi.org/10.2307/3547058

Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L., Castro, J., Choi, C.Y., Cobb, T., Donato, D.C., Durska, E., Fontaine, J.B., Gauthier, S., Hebert, C., Hothorn, T., Hutto, R.L., Lee, E.J., Leverkus, A.B., Lindenmayer, D.B., Obrist, M.K., Rost, J., Seibold, S., Seidl, R., Thom, D., Waldron, K., Wermelinger, B., Winter, M.B., Zmihorski, M., Müller, J., 2018. Impacts of salvage logging on biodiversity: A meta-analysis. J. Appl. Ecol. 55, 279–289. https://doi.org/10.1111/1365-2664.12945

Traveset, A., González-Varo, J.P., Valido, A., 2012. Long-term demographic consequences of a seed dispersal disruption. Proc. R. Soc. B Biol. Sci. 279, 3298–3303. https://doi.org/10.1098/rspb.2012.0535

Tummers, B., 2006. DataThief III manual v. 1.1. Manual 1–52.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11, 1351–1363. https://doi.org/10.1111/j.1461-0248.2008.01250.x

Van der Pijl, L., 1982. Principles of dispersal in higher plants. Springer Berlin Heidelberg, Berlin, Heidelberg.

Vander Wall, S.B., Longland, W.S., 2004. Diplochory: Are two seed dispersers better than one? Trends Ecol. Evol. 19, 155–161. https://doi.org/10.1016/j.tree.2003.12.004

Vasconcelos, H.L., Maravalhas, J.B., Feitosa, R.M., Pacheco, R., Neves, K.C., Andersen, A.N., 2018. Neotropical savanna ants show a reversed latitudinal gradient of species richness, with climatic drivers reflecting the forest origin of the fauna. J. Biogeogr. 45, 248–258. https://doi.org/10.1111/jbi.13113

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Hermy, M., 2006. Extinction debt of forest plants presists for more than a century following habitat fragmentation. Ecology 87, 542–548. https://doi.org/10.1890/05-1182

Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor. J. Stat. Softw. 36, 1–48. https://doi.org/10.18637/jss.v036.i03

Vieira-Neto, E.H.M., Vasconcelos, H.L., Bruna, E.M., 2016. Roads increase population growth rates of a native leaf-cutter ant in Neotropical savannahs. J. Appl. Ecol. 53, 983–992. https://doi.org/10.1111/1365-2664.12651

Wilker, I., Rabelo, M.A., Angotti, M.A., Ribas, C.R., 2022. Ant species that remove diaspores alone are more efficient removers. Sociobiology 69, e8308. https://doi.org/10.13102/sociobiology.v69i3.8308

Willig, M.R., Kaufman, D.M., Stevens, R.D., 2003. Latitudinal gradients of biodiversity: Pattern, process, scale, and synthesis. Annu. Rev. Ecol. Evol. Syst. 34, 273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032

Zhu, Y., Wang, D., 2018. Response of ants to human-altered habitats with reference to seed dispersal of the myrmecochore Corydalis giraldii Fedde (Papaveraceae). Nord. J. Bot. 36, 1–7. https://doi.org/10.1111/njb.01882

Supplementary Material

Effects of anthropogenic disturbances on diaspore removal by ants: a meta-analysis

Bona, Ketlen[1,2]*, Delabie, Jacques H.C.[2,3] and Cazetta, Eliana[1,4]

[1]Applied Ecology and Conservation Lab, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Ilhéus, BA, Brazil.
[2]Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, CEPLAC, Ilhéus, BA, Brazil.
[3]Universidade Estadual de Santa Cruz, Departamento de Ciências Agrárias e Ambientais, Ilhéus, BA, Brazil.
[4]Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, BA, Brazil.

*Corresponding author. E-mail address: bonaketlen@gmail.com

ORCID ID

Ketlen Bona (0000-0002-8874-2919)
Jacques H.C. Delabie (0000-0002-2695-1061)
Eliana Cazetta (0000-0002-2209-2554)

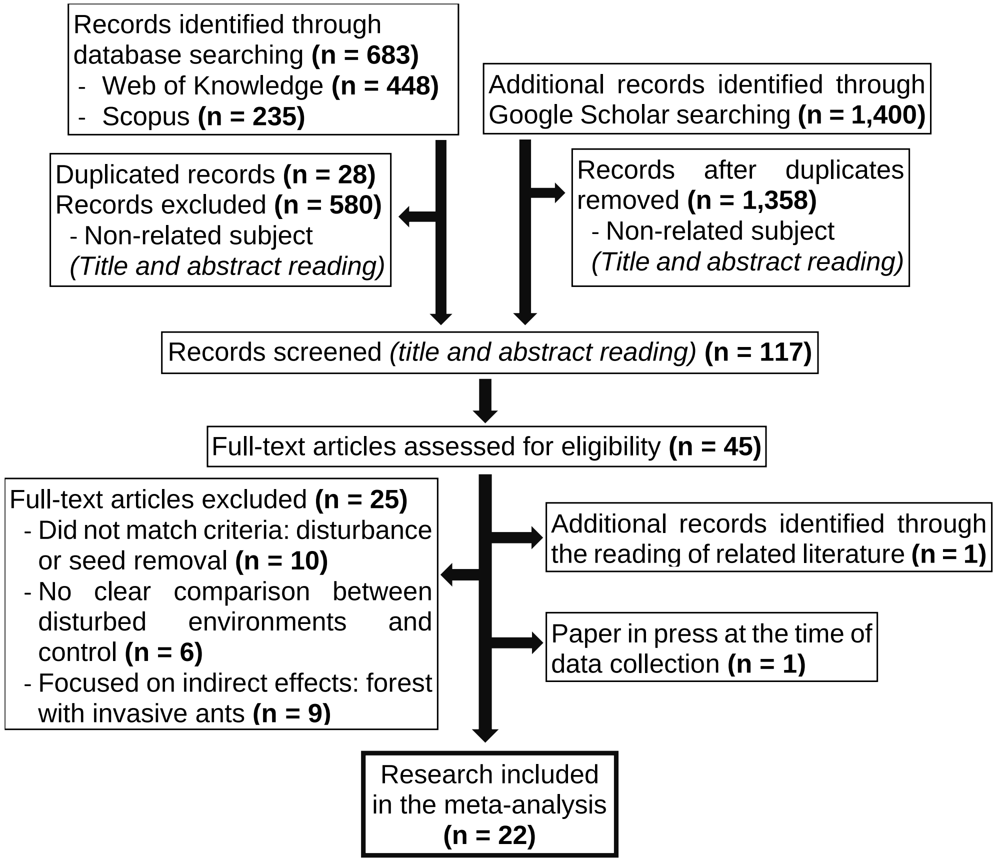


Figure S1. Flow of information of systematic review performed in dataset selection process of our study.

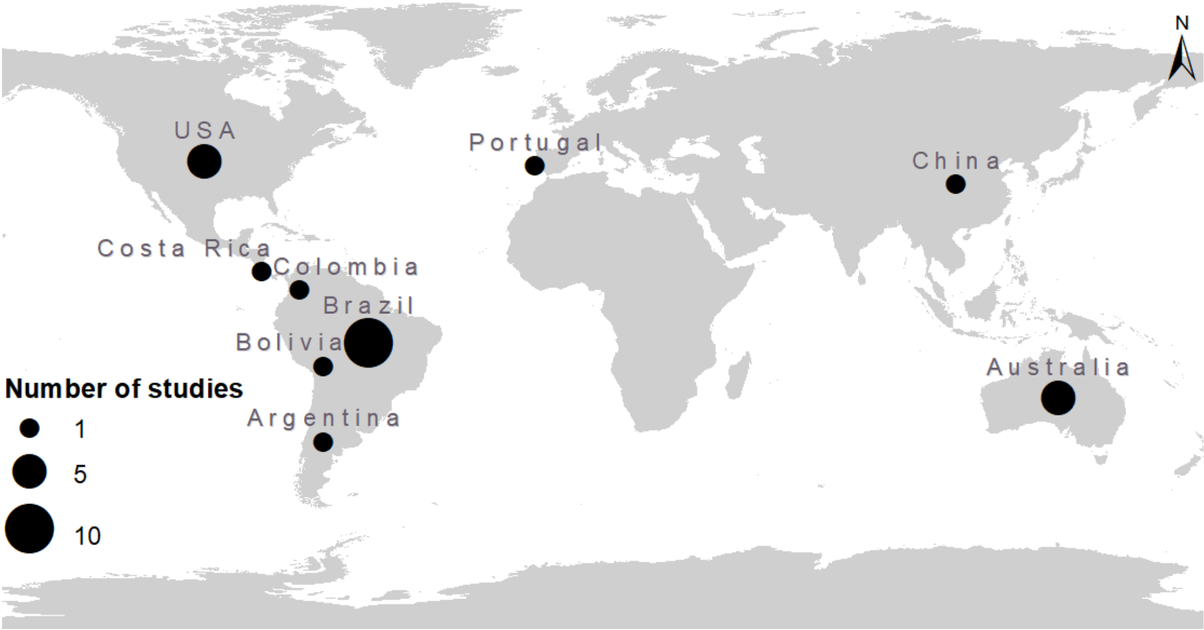


Figure S2. Global distribution of the number of studies per country used in the meta-analysis.

Table S1. Studies with their respective country, climatic region, type of anthropogenic disturbance and number of comparisons of each study used in the meta-analysis.

Reference	Country	Region	Disturbance	Number of comparisons
Almeida et al. 2013	Brazil	Tropical	Pasture	3
Andersen and Morrison 1998	Australia	Tropical	Mining	2
Angotti et al. 2018	Brazil	Tropical	Multiple agricultural disturbances	2
Arruda et al. 2020	Brazil	Tropical	Road	3
Bieber et al. 2014	Brazil	Tropical	Fragmentation	4
Christianini and Oliveira 2013	Brazil	Tropical	Edge effects	1
Dominguez-Haydar and Armbrecht 2011	Colombia	Tropical	Open-pit coal mining	6
Fontenele and Schmidt 2021*	Brazil	Tropical	Pasture	1
Gallegos et al. 2014	Bolivia	Tropical	Mining	6
Leal et al. 2014	Brazil	Tropical	Chronic human disturbances	3
Majer 1985	Australia	Temperate	Mining	3
Ness and Morin 2008	USA	Temperate	Edge effects	1

Ness 2004	USA	Temperate	Edge effects	2
Palfi et al. 2017	Australia	Temperate	Road	1
Palfi et al. 2020	Australia	Temperate	Road	2
Pirk and Lopez de Casenave 2017	Argentina	Temperate	Road	5
Rabello et al. 2018	Brazil	Tropical	Monoculture	6
Rocha-Ortega et al. 2017	Brazil	Tropical	Monoculture	5
Timóteo et al. 2016	Portugal	Temperate	Agro-sylvo-pastoral system	2
Zelikova and Breed 2008	Costa Rica	Tropical	Fragmentation	3
Zhu and Wang 2018	China	Temperate	Road	2
Zhu and Wang 2019	China	Temperate	Edge effects	2

*Paper in press at the time of data collection

Table S2. List of diaspore-removing ant species, plant species used in the studies and type of habitat which the ants were collected.

Study	Type of disturbance	Ant species how published	Plant species	Undisturbed	Disturbed
Almeida et al. 2013	Agriculture	*Ectatomma edentatum*	*Carica papaya*	X	
		Odontomachus chelifer		X	
		Pachycondyla striata		X	
		Pheidole fallax			X
		Pheidole gertrudae		X	
		Pheidole radoszkowskii			X
		Pheidole sp. 52		X	
		Solenopsis sp. 12			X
Andersen and Morrison 1998	Mining	*Bothroponera* sp. 3	*Acacia holosericea*	X	
		Iridomyrmex (anceps gp) sp. 2		X	
		Iridomyrmex pallidus		X	X
		Iridomyrmex sanguineus		X	X
		Meranoplus (mjobergi gp) sp. 4		X	
		Monomorium (nigrius gp, 2 spp.)		X	X
		Monomorium (rothsteini gp) sp. 1			X
		Oecophylla smaragdina		X	
		Papyrius sp. 1		X	
		Paratrechina longicornis			X
		Pheidole (4 spp)		X	X
		Rhytidoponera (2 spp.)		X	X
		Rhytidoponera (turneri gp) sp. 3		X	X
		Rhytidoponera aurata		X	X
		Rhytidoponera trachypyx		X	X

		Tetramorium (striolatum gp, 2 spp)		X	X
Arruda et al. 2020	Fragmentation	*Atta laevigata*	*Byrsonima vacciniifolia* *Davilla elliptica* *Miconia irwinii*	X	X
		Brachymyrmex cordemoyi			X
		Brachymyrmex pictus		X	
		Camponotus crassus		X	X
		Camponotus rufipes		X	
		Camponotus sp. 1		X	
		Camponotus trapeziceps		X	X
		Crematogaster sp. 1		X	
		Dolichoderinae preta			X
		Dorymyrmex pyramicus		X	X
		Dorymyrmex sp. 1		X	X
		Ectatomma permagnum		X	X
		Ectatomma tuberculatum			X
		Gnamptogenys sp. 1		X	X
		Pheidole oxyops			X
		Pheidole triconstricta			X
		Pseudomyrmex termitarius			X
Bieber et al. 2014	Fragmentation	*Acromyrmex rugosus*	Synthetic diaspore	X	
		Brachymyrmex sp. 1		X	
		Heteroponera inermis			X
		Megalomyrmex iheringi			X
		Odontomachus chelifer		X	
		Pachycondyla striata		X	X
		Pheidole sp. 19		X	X
		Pheidole sp. 20		X	X

		Pheidole sp. 27		X	X
		Pheidole sp. 7		X	
		Pheidole sp. 8		X	X
		Solenopsis sp. 11		X	
Christianini and Oliveira 2013	Fragmentation	*Atta sexdens*	*Erythroxylum pelleterianum*	X	
		Azteca sp. 2		X	
		Azteca sp. 3		X	
		Camponotus rengerii		X	
		Camponotus rufipes		X	
		Camponotus sp.		X	
		Cephalotes sp. 2		X	
		Dinoponera australis		X	
		Mycocepurus sp.			X
		Neoponera villosa		X	
		Odontomachus chelifer		X	X
		Pachycondyla striata		X	X
		Pheidole sp. 1		X	
		Pheidole sp. 15			X
		Pheidole sp. 17		X	X
		Pheidole sp. 2		X	X
		Pheidole sp. 4		X	X
		Pheidole sp. 5		X	X
		Pheidole sp. 7		X	
		Solenopsis sp. 1			X
		Solenopsis sp. 2		X	
		Wasmannia auropunctata		X	X

Dominguez-Haydar and Armbrecht 2011	Mining	*Acromyrmex octospinosus*	*Guazuma ulmifolia* *Capparis sp.* *Seguieria sp.*	X	
		Crematogaster sp. 1			X
		Ectatomma ruidum		X	X
		Labidus coecus		X	
		Odontomachus bauri			X
		Pheidole sp. 4		X	X
		Solenopsis geminata		X	X
		Solenopsis sp. 8		X	
Fontenele and Schmidt 2021	Agriculture	*Atta* sp. 1	Synthetic diaspore		X
		Dorymymex brunneus			X
		Ectatomma brunneum		X	X
		Ectatomma edentatum		X	
		Ectatomma lugens		X	
		Gigantiops destructor		X	
		Mayaponera constricta		X	
		Megalomyrmex ayri		X	
		Megalomyrmex balzani		X	
		Neoponera obscuricornis		X	
		Neoponera verenae		X	
		Nylanderia sp. 1			X
		Odontomachus haematodus		X	X
		Odontomachus laticeps		X	
		Odontomachus meinerti		X	
		Pachycondyla crassinoda		X	
		Pachycondyla harpax		X	
		Pheidole astur		X	
		Pheidole fissiceps		X	

		Pheidole gertrudae			X
		Pheidole jelskii			X
		Pheidole pr. paraensis		X	
		Pheidole scolioceps		X	
		Pheidole sp. 1		X	
		Pheidole sp. 10		X	
		Pheidole sp. 12		X	
		Pheidole sp. 14		X	
		Pheidole sp. 15		X	
		Pheidole sp. 18		X	
		Pheidole sp. 23		X	
		Pheidole subarmata			X
		Pheidole vorax		X	
		Pogonomyrmex naegeli			X
		Solenopsis invicta			X
		Solenopsis saevissima			X
Gallegos et al. 2014	Mining	*Acromyrmex* sp. 1	*Clusia trochiformis*	X	X
		Camponotus sp. 1			X
		Linepithema sp. 1		X	X
		Odontomachus sp. 1			X
		Pheidole socrates			X
		Pheidole sp. 2		X	
		Pheidole sp. 3		X	X
		Pheidole sp. 6		X	X
		Pheidole sp. 8		X	
		Pseudomyrmex sp. 1		X	

Leal et al. 2014	Agriculture	*Acromyrmex rugosus*	*Croton sonderianus* *Jatropha mollissima*		X
		Camponotus crassus		X	
		Crematogaster sp.			X
		Dinoponera quadriceps		X	
		Ectatomma muticum		X	
		Pheidole sp. 1			X
		Pheidole sp. 2			X
		Pheidole sp. 3			X
		Solenopsis sp. 1			X
		Solenopsis sp. 2			X
		Solenopsis sp. 3			X
Ness 2004	Fragmentation	*Aphaenogaster* spp.	*Sanguinaria canadensis*	X	X
		Camponotus castaneus			X
		Crematogaster ashmeadi		X	X
		Formica schaufussi			X
		Formica subsericea		X	X
		Solenopsis invicta		X	X
Palfi et al. 2017	Fragmentation	*Camponotus aeneopilosus*	*Acacia pycnantha*	X	X
		Camponotus obriger		X	X
		Camponotus sp. 1		X	X
		Camponotus sp. A (claripes group)		X	
		Crematogaster sp. A		X	X
		Iridomyrmex purpureus		X	X
		Iridomyrmex rufoniger		X	X
		Melophorus bruneus		X	X
		Melophorus sp. B (aeneovirens group)		X	X

		Meranoplus sp. A (group D)		X	
		Monomorium sp. A (sordidum group)		X	X
		Monomorium sp. B (rothsteini group)		X	X
		Notoncus ectatommoides		X	X
		Pheidole sp. A		X	X
		Pheidole sp. B		X	
		Rhytidoponera cristata		X	X
		Rhytidoponera metallica		X	X
		Rhytidoponera sp. A (convexa group)		X	X
Pirk and Lopez de Casenave 2017	Fragmentation	*Acromyrmex lobicornis*	*Carduus thoermeri* *Pappostipa speciosa*		X
		Dorymyrmex antarcticus		X	
		Dorymyrmex minutus		X	
		Dorymyrmex tener		X	X
		Dorymyrmex wolffhuegeli			X
		Lasiophanes valdiviensis		X	
		Pheidole spininodis			X
		Pogonomyrmex carbonarius		X	X
		Solenopsis richteri		X	
		Solenopsis sp.		X	
Rabello et al. 2018	Agriculture	*Acromyrmex crassispinus*	*Croton floribundus*		X
		Atta sp. 1		X	X
		Atta sp. 2		X	X
		Atta sp. 3		X	X
		Atta sp. 4		X	X
		Camponotus rufipes		X	X
		Crematogaster obscurata		X	X

Cyphomyrmex sp. 1		X
Dorymyrmex sp. 1		X
Ectatomma brunneum	X	X
Ectatomma edentatum	X	
Ectatomma lugens	X	X
Linepithema micans		X
Mycetarotes parallelus	X	
Mycetomoellerius kempfi	X	
Mycocepurus sp. 1	X	
Neoporena verenae	X	X
Odontomachus bauri	X	X
Odontomachus chelifer	X	
Pachycondyla striata	X	
Pheidole oxyops	X	X
Pheidole radoszkowskii	X	X
Pheidole sp. 1	X	X
Pheidole sp. 10		X
Pheidole sp. 11	X	
Pheidole sp. 12		X
Pheidole sp. 2	X	X
Pheidole sp. 3	X	
Pheidole sp. 4	X	
Pheidole sp. 6	X	X
Pheidole sp. 7	X	X
Pheidole sp. 8		X
Pheidole sp. 9		X
Pheidole subarmata	X	X
Solenopsis sp. 1		X

		Solenopsis sp. 2		X	X
		Trachymyrmex sp. 1		X	
		Wasmannia sp. 1		X	
Timóteo et al. 2016*	Agriculture	*Aphaenogaster senilis*	*Aegilops* sp. *Bromus tectorum* *Trifolium subterraneum* *Ornithopus compressus* *Ornithopus sativus* *Holcus lanatus*	X	X
		Messor barbarus		X	X
		Messor bouvieri		X	X
		Messor capitatus		X	X
		Messor hispanicus		X	X
		Messor lusitanicus		X	X
		Messor marocanus		X	
		Messor structor		X	X
		Messor celiae			X
		Camponatus cruentatus			X
		Tetramorium hispanicum			
Zelikova and Breed 2008	Fragmentation	*Acromyrmex echinatior*	*Acacia collinsii* *Carica papaya*		X
		Ectatomma ruidum		X	X
		Neoponera theresiae		X	X
		Odontomachus bauri			X
		Pachycondyla harpax		X	
		Pheidole fallax		X	X
		Pheidole pugnax			X
		Pheidole sp. 2			X
		Pheidole sp. 3		X	
		Pheidole subarnata			X
Zhu and Wang 2018	Fragmentation	*Aphaenogaster smythiesii*	*Corydalis giraldii*	X	X

	Camponotus sp. 1		X
	Camponotus sp. 2		X
	Crematogaster sp.		X
	Formica fusca		X
	Formica polyctena		X
	Lasius alienus	X	X
	Lasius flavus	X	
	Myrmica sp.	X	X
	Nylanderia flavipes	X	X
	Pachycondyla sp.	X	X
	Pheidole nietneri	X	X
	Tetramorium caespitum	X	X

*The main plant species. Complete list of plant species used in this study can be found in Supplementary Material of article online at http://dx.doi.org/10.1016/j.cub.2016.01.046

Table S3. List of plant species used in the studies for the diaspore removal experiments by ants and type of each diaspore species.

Study	**Plant species**	**Type of diaspore**
Almeida et al. 2013	*Carica papaya*	Non-myrmecochorous
Andersen and Morrison 1998	*Acacia holosericea*	Non-myrmecochorous
Angotti et al. 2018	*Croton floribundus*	Non-myrmecochorous
	Synthetic diaspore	Non-myrmecochorous#
Arruda et al. 2020	*Byrsonima vacciniifolia*	Non-myrmecochorous
	Davilla elliptica	Non-myrmecochorous
	Miconia irwinii	Non-myrmecochorous
Bieber et al. 2014	Synthetic diaspore	Non-myrmecochorous#
Christianini and Oliveira 2013	*Erythroxylum pelleterianum*	Non-myrmecochorous
Dominguez-Haydar and Armbrecht 2011	*Capparis* sp.	Non-myrmecochorous
	Guazuma ulmifolia	Non-myrmecochorous

	Seguieria sp.	Non-myrmecochorous
Fontenele and Schmidt 2021	Synthetic diaspore	Non-myrmecochorous[#]
Gallegos et al. 2014	*Clusia trochiformis*	Non-myrmecochorous
Leal et al. 2014	*Croton sonderianus*	Myrmecochorous
	Jatropha mollissima	Myrmecochorous
Majer 1985	*Acacia concurrens*	Myrmecochorous
	Allocasuarina littoralis	No information
	Allocasuarina torulosa	No information
	Banksia aemula	No information
	Banksia serrata	No information
	Eucalyptus intermedia	No information
	Eucalyptus pilularis	No information
	Eucalyptus signata	No information
	Tristania conferta	No information
	Xanthorrhoea johnsonii	Non-myrmecochorous

Ness and Morin 2008	*Sanguinaria canadensis*	Myrmecochorous
Ness 2004	*Sanguinaria canadensis*	Myrmecochorous
Palfi et al. 2017	*Acacia pycnantha*	Non-myrmecochorous
Palfi et al. 2020	*Acacia pycnantha*	Non-myrmecochorous
Pirk and Lopez de Casenave 2017	*Carduus thoermeri*	Non-myrmecochorous
	Pappostipa speciosa	Non-myrmecochorous
Rabello et al. 2018	*Croton floribundus*	Non-myrmecochorous
Rocha-Ortega et al. 2017	*Matayba guianensis*	Non-myrmecochorous
	Siparuna guianensis	Non-myrmecochorous
	Solanum lycocarpum	Non-myrmecochorous
	Tapirira guianensis	Non-myrmecochorous
	Xylopia aromatica	Non-myrmecochorous

Timóteo et al. 2016*	*Aegilops* sp.	No information
	Bromus tectorum	No information
	Trifolium subterraneum	No information
	Ornithopus compressus	No information
	Ornithopus sativus	No information
	Holcus lanatus	No information
Zelikova and Breed 2008	*Acacia collinsii*	Non-myrmecochorous
	Carica papaya	Non-myrmecochorous
Zhu and Wang 2018	*Corydalis giraldii*	Myrmecochorous
Zhu and Wang 2019	*Epimedium pubescens*	Myrmecochorous
	Helleborus thibetanus	Myrmecochorous

[#] The chemical formula used to produce artificial diaspores does not mimic elaiosome, but the fatty part of an arylated seed. Therefore, we consider them as non-myrmecochoric diaspores.

*The main plant species. Complete list of plant species used in this study can be found in Supplementary Material of article online at http://dx.doi.org/10.1016/j.cub.2016.01.046

References

Almeida, F.S., Mayhé-Nunes, A.J., Queiroz, J.M., 2013. The importance of poneromorph ants for seed dispersal in altered environments. Sociobiology 60, 229–235. https://doi.org/10.13102/sociobiology.v60i3.229-235

Andersen, A.N., Morrison, S.C., 1998. Myrmecochory in Australia’s seasonal tropics: Effects of disturbance on distance dispersal. Austral Ecol. 23, 483–491. https://doi.org/10.1111/j.1442-9993.1998.tb00756.x

Angotti, M.A., Rabello, A.M., Santiago, G.S., Ribas, C.R., 2018. Seed removal by ants in Brazilian savanna: optimizing fieldwork. Sociobiology 65, 155–161. https://doi.org/10.13102/sociobiology.v65i2.1938

Arruda, A.J., Costa, F. V., Guerra, T.J., Junqueira, P.A., Dayrell, R.L.C., Messeder, J.V.S., Rodrigues, H.T.S., Buisson, E., Silveira, F.A.O., 2020. Topsoil disturbance reshapes diaspore interactions with ground-foraging animals in a megadiverse grassland. J. Veg. Sci. 31, 1039–1052. https://doi.org/10.1111/jvs.12866

Bieber, A.G.D., Silva, P.S.D., Sendoya, S.F., Oliveira, P.S., 2014. Assessing the impact of deforestation of the Atlantic rainforest on ant-fruit interactions: A field experiment using synthetic fruits. PLoS One 9, 1–9. https://doi.org/10.1371/journal.pone.0090369

Christianini, A. V., Oliveira, P.S., 2013. Edge effects decrease ant-derived benefits to seedlings in a neotropical savanna. Arthropod. Plant. Interact. 7, 191–199. https://doi.org/10.1007/s11829-012-9229-9

Dominguez-Haydar, Y., Armbrecht, I., 2011. Response of ants and their seed removal in rehabilitation areas and forests at El Cerrejón Coal Mine in Colombia. Restor. Ecol. 19, 178–184. https://doi.org/10.1111/j.1526-100X.2010.00735.x

Fontenele, L.K., Schmidt, F.A., 2021. Forest-pasture shifting alters the assemblages of seed-removing ants in southwestern Brazilian Amazon. J. Insect Conserv. 25, 213–220. https://doi.org/10.1007/s10841-021-00295-x

Gallegos, S.C., Hensen, I., Schleuning, M., 2014. Secondary dispersal by ants promotes forest regeneration after deforestation. J. Ecol. 102, 659–666. https://doi.org/10.1111/1365-2745.12226

Leal, L.C., Andersen, A.N., Leal, I.R., 2014. Anthropogenic disturbance reduces seed-dispersal services for myrmecochorous plants in the

Brazilian Caatinga. Oecologia 174, 173–181. https://doi.org/10.1007/s00442-013-2740-6

Majer, J.D., 1985. Recolonization by ants of rehabilitated mineral sand mines on North Stradbroke Island, Queensland, with particular reference to seed removal. Aust. J. Ecol. 10, 31–48. https://doi.org/10.1111/j.1442-9993.1985.tb00861.x

Ness, J.H., 2004. Forest edges and fire ants alter the seed shadow of an ant-dispersed plant. Oecologia 138, 448–454. https://doi.org/10.1007/s00442-003-1440-z

Ness, J.H., Morin, D.F., 2008. Forest edges and landscape history shape interactions between plants, seed-dispersing ants and seed predators. Biol. Conserv. 141, 838–847. https://doi.org/10.1016/j.biocon.2007.12.029

Palfi, Z., Robinson, W., Spooner, P.G., 2020. Cheaters and removalists: the influence of soil disturbance on ant–seed interactions in roadside vegetation. Insectes Soc. 67, 429–438. https://doi.org/10.1007/s00040-020-00778-1

Palfi, Z., Spooner, P.G., Robinson, W., 2017. Seed dispersal distances by ants increase in response to anthropogenic disturbances in Australian roadside environments. Front. Ecol. Evol. 5, 1–9. https://doi.org/10.3389/fevo.2017.00132

Pirk, G.I., Lopez de Casenave, J., 2017. Ant interactions with native and exotic seeds in the Patagonian steppe: Influence of seed traits, disturbance levels and ant assemblage. Plant Ecol. 218, 1255–1268. https://doi.org/10.1007/s11258-017-0764-4

Rabello, A.M., Parr, C.L., Queiroz, A.C.M., Braga, D.L., Santiago, G.S., Ribas, C.R., 2018. Habitat attribute similarities reduce impacts of land-use conversion on seed removal. Biotropica 50, 39–49. https://doi.org/10.1111/btp.12506

Rocha-Ortega, M., Bartimachi, A., Neves, J., Bruna, E.M., Vasconcelos, H.L., 2017. Seed removal patterns of pioneer trees in an agricultural landscape. Plant Ecol. 218, 737–748. https://doi.org/10.1007/s11258-017-0725-y

Timóteo, S., Ramos, J.A., Vaughan, I.P., Memmott, J., 2016. High Resilience of Seed Dispersal Webs Highlighted by the Experimental Removal of the Dominant Disperser. Curr. Biol. 26, 910–915. https://doi.org/10.1016/j.cub.2016.01.046

Zelikova, T.J., Breed, M.D., 2008. Effects of habitat disturbance on ant community composition and seed dispersal by ants in a tropical dry forest in Costa Rica. J. Trop. Ecol. 24, 309–316. https://doi.org/10.1017/S0266467408004999

Zhu, Y., Wang, D., 2019. Effect of neighboring seeds associated with habitats on the seed removal of two coexisting myrmecochorous plants in central China. Basic Appl. Ecol. 40, 12–18. https://doi.org/10.1016/j.baae.2019.07.004

Zhu, Y., Wang, D., 2018. Response of ants to human-altered habitats with reference to seed dispersal of the myrmecochore Corydalis giraldii Fedde (Papaveraceae). Nord. J. Bot. 36, 1–7. https://doi.org/10.1111/njb.01882

APÊNDICE

Apêndice I. Esquema de divulgação do artigo nas redes sociais do Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade.

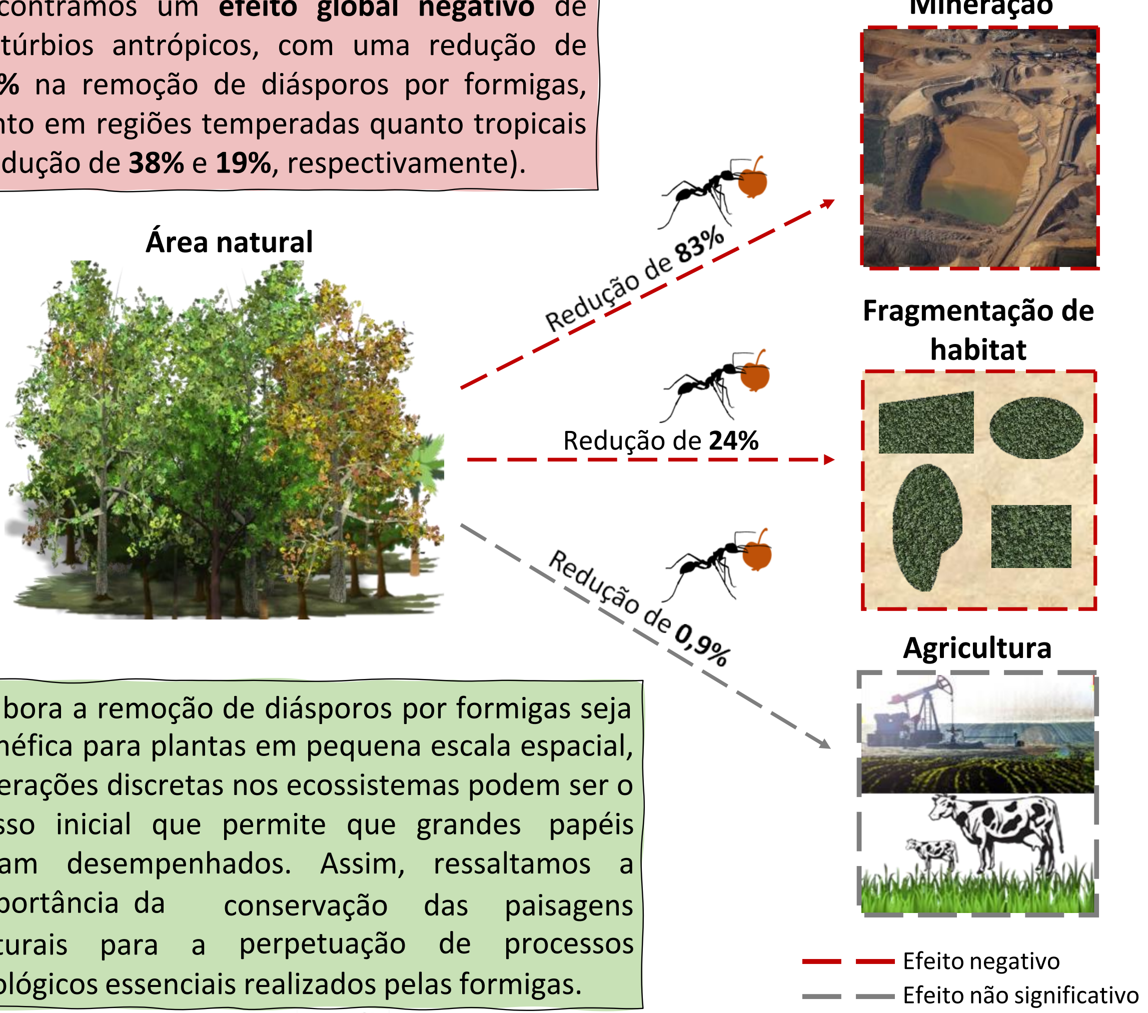
Efeitos de distúrbios antrópicos sobre a remoção de diásporos por formigas: uma meta-análise

Ketlen Bona, Jacques H. C. Delabie e Eliana Cazetta

Veja o artigo completo em: https://doi.org/10.1016/j.actao.2023.103893

Nesta pesquisa, conduzimos uma meta-análise global de 22 estudos (65 comparações) comparando a remoção de diásporos por formigas em áreas perturbadas *versus* áreas preservadas para investigar tendências gerais para diferentes distúrbios antrópicos.

Encontramos um **efeito global negativo** de distúrbios antrópicos, com uma redução de **26%** na remoção de diásporos por formigas, tanto em regiões temperadas quanto tropicais (redução de **38%** e **19%**, respectivamente).



Embora a remoção de diásporos por formigas seja benéfica para plantas em pequena escala espacial, interações discretas nos ecossistemas podem ser o passo inicial que permite que grandes papéis sejam desempenhados. Assim, ressaltamos a importância da conservação das paisagens naturais para a perpetuação de processos ecológicos essenciais realizados pelas formigas.

CAPÍTULO II

INTERACTIONS BETWEEN ANTS AND DIASPORES IN ATLANTIC FOREST: AN OVERVIEW OF TRENDS AND GAPS IN THE LITERATURE

Manuscrito será submetido à revista *Perspectives in Ecology and Conservation*.

Interactions between ants and diaspores in Atlantic Forest: an overview of trends and gaps in the literature

Ketlen Bona[1,2]*, Jacques H.C. Delabie[2,3], Luane K. Fontenele[4], Felipe Martello[5] e Eliana Cazetta[1,6]

[1]Laboratório de Ecologia Aplicada à Conservação, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Ilhéus, BA, Brasil.
[2]Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, CEPLAC, Ilhéus, BA, Brasil.
[3]Universidade Estadual de Santa Cruz, Departamento de Ciências Agrárias e Ambientais, Ilhéus, BA, Brasil.
[4]Laboratório de Ecologia de Formigas, Universidade Federal de Lavras, Lavras, MG, Brasil.
[5]Universidade Estadual Paulista Júlio de Mesquita Filho, São Paulo, SP, Brasil.
[6]Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, BA, Brasil.

*Corresponding author. E-mail: bonaketlen@gmail.com

ORCID ID
Ketlen Bona (0000-0002-8874-2919)
Luane K. Fontenele (0000-0002-4854-4539)
Jacques H.C. Delabie (0000-0002-2695-1061)
Felipe Martello (0000-0003-1243-9750)
Eliana Cazetta (0000-0002-2209-2554)

Abstract

Ants are present throughout almost the entire globe and participate in diverse ecological interactions that result in essential ecosystem functions, such as seed dispersal. In these interactions, ants collect fruits and seeds, move them to safe sites, preventing the proliferation of pathogens by cleaning the seeds and can increase the chances of seedling establishment. Furthermore, some ant species make a key contribution to ant-diaspore interactions, which increase the efficiency of the seed dispersal in areas where these species occur. However, the significant species loss due to changes in land use has considerably threatened these interactions and the performance of this important ecosystem function. The Atlantic Forest is among the most critically endangered hotspots in the world, which makes studies that actively help plan conservation strategies urgent. In this sense, we compiled 26 years of research on the ant-diaspore interactions in the Atlantic Forest to reveal the current and, thus, direct future research. We discovered that the vast majority of studies focus on three Brazilian states, which highlights large gaps in several regions of the Atlantic Forest. Furthermore, we found that most studies only evaluate quantitative component of seed dispersal by ants. We identified ant species that play a key role in removing and cleaning diaspores and discovered that the size and lipid content of diaspores can determine the type of interaction. Finally, we point out priority locations for future sampling based on environmental characteristics, including the ecoregions of the Brazilian Atlantic Forest. All this information is crucial to boost the discussion about ant species and their ecological interactions in the Atlantic Forest and direct efforts for future research on the role of ants in seed dispersal.

Keywords

Atlantic Forest; Ecosystem functions; Ant-plant interactions; Seed removing ants; Secondary dispersal.

1. Introduction

Interactions between ants and plants play a significant role in tropical and temperate terrestrial ecosystems (Beattie, 1985). Studies suggest that ant-plant interactions emerged during the Cretaceous period and evolved into various mutualisms (Beattie, 1985; Rico-Gray and Oliveira, 2007). In these mutualistic relationships, ants provide crucial services to plants and are rewarded in various ways. For instance, ants can offer protection to plants against herbivores and other threats, in return for food resources (Passos and Leal, 2019) and nesting sites (Coley and Barone, 1996; Longino, 1991). Additionally, by using plants as foraging substrates and patrolling grounds, ants can pollinate some plants (Beattie, 1985). Ants also interact with fallen fruits on the ground, removing and using the lipid-rich arils as food (Miller et al., 2020; Passos and Oliveira, 2004; Pizo and Oliveira, 2001). Overall, ant behaviors are influenced by the quality of rewards offered by plants, which can result in one or several ecosystem services (Beattie, 1985; Levine et al., 2019). These mutualistic interactions are part of a network involving several species and ecological processes, making them essential for biodiversity maintenance and ecosystem functioning.

Seed dispersal by ants is one of the most extensively studied ant-plant interactions, given its pivotal role in ecosystems (Handel and Beattie, 1990; Penn and Crist, 2018). In this interaction, ants rapidly collect diaspores (i.e., dispersal units) and transport them to safe sites (e.g., nests), preventing seed exposure to predators (Beattie, 1985). Moreover, ant nests are microsites enriched with ant residues and crucial, often limiting, nutrients like nitrogen and phosphorus (Beattie, 1985; Frouz and Jilková, 2008). The diaspore dispersal away from the parent plant and parental seedlings prevents competition for resources and nutrients, potentially enhancing seed dispersal success (Van der Pijl, 1982). Ants also play a role in cleaning diaspores, preventing the proliferation of pathogens that could compromise the seeds (Beattie, 1985; Passos and Oliveira, 2002). Following the cleaning process, inside the nests, ants deposit the clean, intact seed in a refuse pile within or outside the nest, potentially increasing germination rates (Beattie, 1985). In contrast, very small ant species unable to move diaspores, may disrupt interactions by consuming the attractive part of the seeds on-site, reducing the chances of the seed being dispersed by other ants or alternative dispersal agents (Bronstein, 2001).

In general, ecosystems with high species richness exhibit high functional redundancy, promoting critical ecological functions performed by species (Fonseca and Ganade, 2001). However, there is limited discussion regarding the specific importance of certain species in mutualist interactions, that contribute to functions such as seed dispersal (Gove et al., 2007). For example, even though plant species may engage with multiple ant partner species, certain ant species have been identified as key species for seed dispersal (Fontenele and Schmidt, 2021; Gove et al., 2007; Heithaus et al., 2005; Horvitz and Beattie, 1980; Ness, 2004). In ant-diaspore interactions, a key ant species plays a more fundamental role than its density would suggest (Gove et al., 2007). This highlights the relevance of ants in contributing to seed dispersal, especially focal species that act more efficiently in plant species dynamics. However, ecosystems undergoing anthropogenic changes have experienced a decline in ant species playing a key role in seed dispersal (Fontenele and Schmidt, 2021), which can dramatically compromise the effectiveness of this critical ecological function.

With the increasing human exploitation of various natural habitats, species richness and their ecological interactions have become increasingly threatened (Haddad et al., 2015). In Brazil, a country that harbors the world’s largest and most diverse ant fauna (Feitosa et al., 2022), the rapid advance of deforestation has compromised entire biomes. An example of this is the Atlantic Forest, considered one of the world’s most threatened biodiversity hotspots, with less than 3% of its primary vegetation remaining due to the human population’s forest exploitation since the beginning of the European colonization in the XVI century (Joly et al., 2014; Myers et al., 2000; Rezende et al., 2018). The Atlantic Forest contributes significantly to global biodiversity due to its high diversity of flora and fauna (Joly et al., 2014). Additionally, it exhibits a high number of endemic species (Myers et al., 2000) and different terrestrial and aquatic environments that share common species and environmental conditions (i.e., geographical ecoregions (Olson et al., 2001)), making it a unique and vital ecosystem. However, anthropogenic alterations have reduced and drastically modified species richness and how species are organized, leading to consequences in how species interact within ecosystems. Empirical evidence points to the conversion of natural areas into different land uses as one of the precursors of ant biodiversity loss in the Atlantic Forest (Leal et al., 2012), which has resulted in a reduction of their contribution to seed dispersal (Queiroz et al., 2021; Rabello et al., 2018). This could interfere with ecosystem stability, as ants, in addition to seed dispersal, play an active role in several other ecological functions and interactions (e.g., nutrient cycling, predation, pollination, soil aeration, and plant defense against herbivores).

In the face of the escalating biodiversity loss and their ecological interactions, studies that actively assist in planning conservation strategies are urgently needed. Considering several years of research on the important interaction between ants and diaspores in the

Atlantic Forest, compiling this information is crucial. Revealing the knowledge obtained to the present is essential for identifying gaps and defining priority locations, which can better guide future studies. Furthermore, obtaining specific information on ant and diaspore species involved in seed dispersal in the Atlantic Forest can enhance our understanding of the factors that determine these interactions. All this information can be vital in directing strategies for species conservation and ecological interactions in ecosystems.

In this present study, we conducted a comprehensive survey of research focusing on the interactions between ants and diaspores, systematically compiling data for the Brazilian Atlantic Forest. Our objective was to provide a qualitative overview of the central aspects addressed in these studies. Initially, we described the main ant and plant interacting species in the Atlantic Forest and evaluated the predominant types of interactions (cleaning/removal) that are often observed or studied. We identified key ant species and related their behavior to diaspore characteristics to assess whether diaspore morphology and nutritional quality influence the type of interaction. Finally, we assessed gaps in research coverage across the Atlantic Forest, aiming to define priority areas for future sampling of ant-diaspore interaction.

2. Material and Methods

2.1. Literature review

In July 2021, we conducted a systematic literature review on studies investigating interactions between ants and diaspores (e.g., removal behaviors, cleaning, inspection, handling, or access to diaspores within nests) throughout the Brazilian Atlantic Forest. Searches were performed in the following databases: SCOPUS (http://www.scopus.com), ISI Web of Knowledge (https://www.webofknowledge), and Google Scholar (http://scholar.google.com.br) to complement the dataset with theses and dissertations. We used the following search terms: "ant + seed" OR "ant + diaspore" AND "Atlantic Forest"; and "formiga + semente" OR "formiga + diásporo" AND "Mata Atlântica". For database construction, we included studies that assessed ant communities or plant communities interacting, as well as those that focused on a single ant species or a single plant species. After the screening process, we ended up with 62 studies (Figure 1), including theses and dissertations, encompassing all regions of the Brazilian Atlantic Forest (Figure 2).

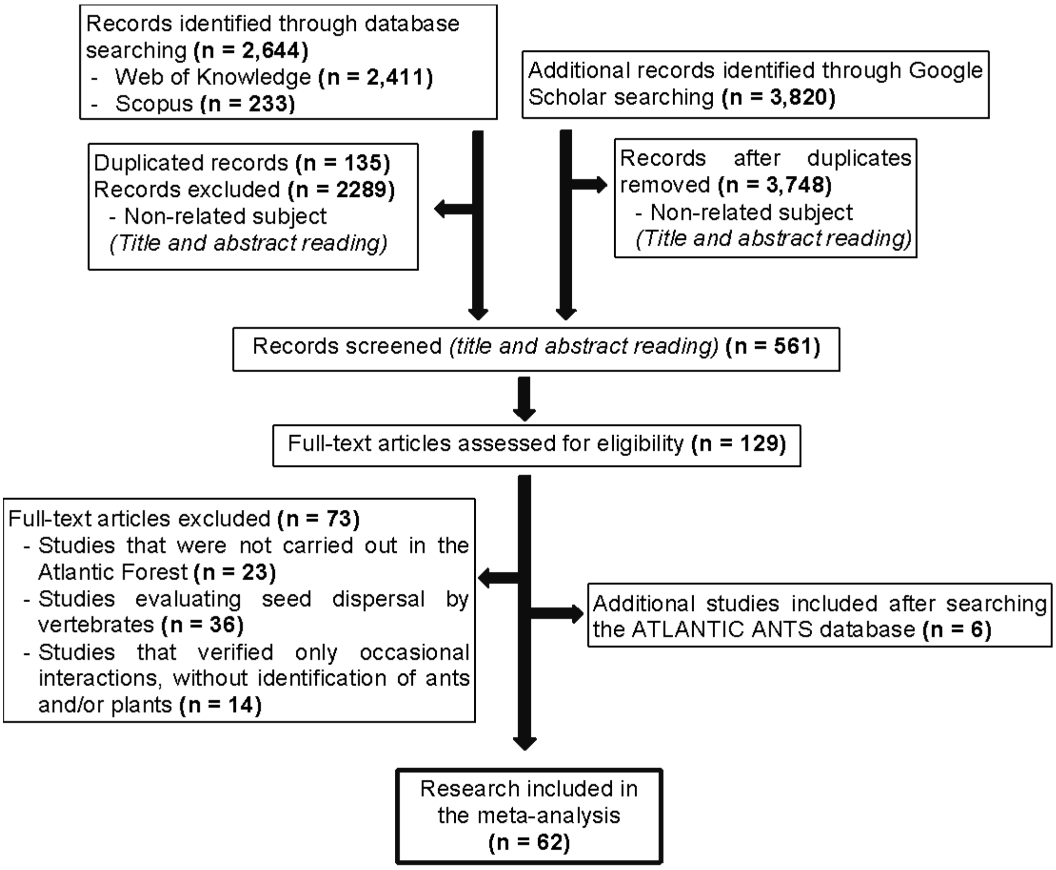


Figure 1. PRISMA flow diagram showing the selection procedure to identify studies to be included in the systematic review performed in the dataset selection process of our study.

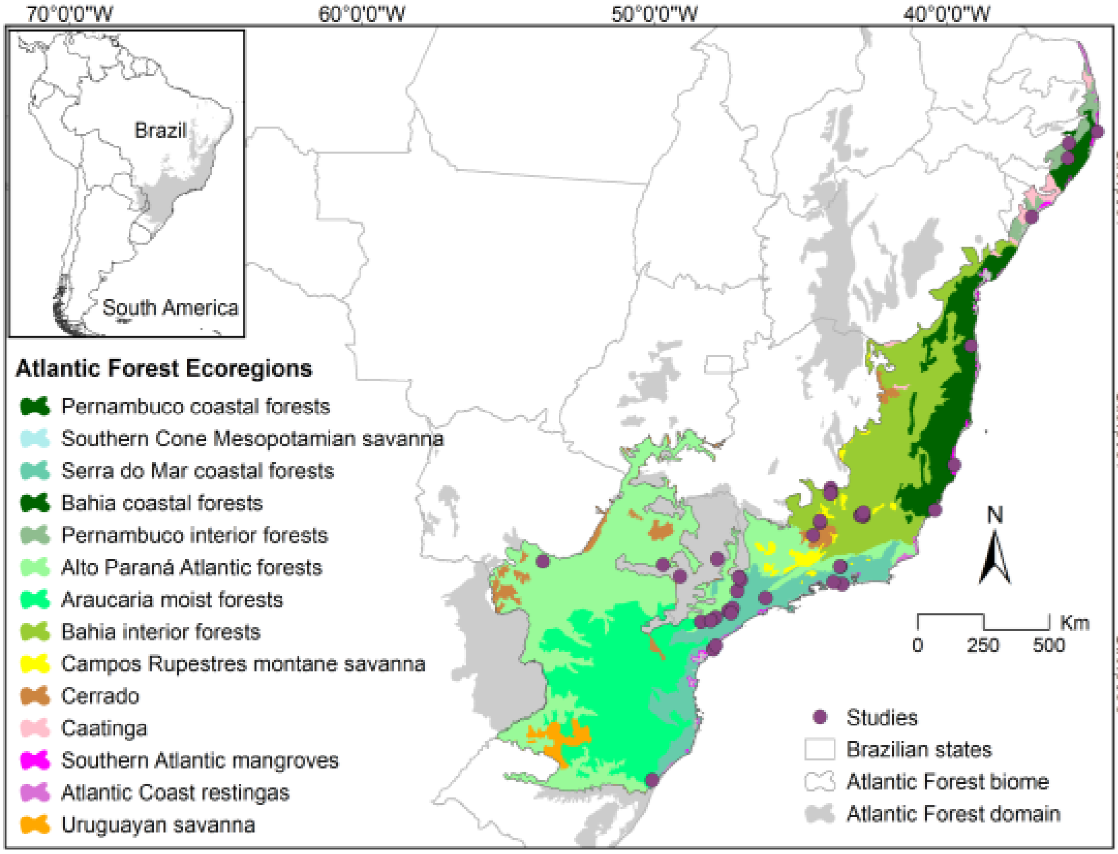


Figure 2. Geographic distribution of studies on ant-diaspore interactions in the Brazilian Atlantic Forest included in the systematic review. Geospatial information about the Atlantic Forest domain according to the ATLANTIC ANTS database (Silva et al., 2022). The ecoregions encompassing the Atlantic Forest biome are based on the Terrestrial Ecoregions of the World (TEOW) classification proposed by Olson et al., 2001.

2.2. Studies information

For each study, we extracted the following information: publication year, study type (published article or thesis/dissertation), journal, language, geographical coordinates, focus of the study (population or community study), and data collection method (laboratory or field study). Additionally, we gathered specific information on both ant and diaspore species, including species identification for ants and plants, the behavior exhibited by each ant species toward each diaspore species - to report the type of interaction investigated, morphological information, and, when available, chemical information for diaspores. To enhance our database on diaspore characteristics, we used data collected from studies covering a significant portion of plants that attract the fauna of the Atlantic Forest (Bello et al., 2017; Cazetta, 2008).

2.3. Classification of key ant species

To classify ant species, we focused only on those species involved in seed removal or cleaning, as these behaviors are the most well-studied in the context of ant-diaspore interactions. Identifying key species in ecosystems is crucial for a better understanding of the significance of certain species in ecological functions. A key species plays a fundamental role in the community's structure beyond what would be expected based on its abundance (Naeem et al., 2009; Power et al., 1996). In ecosystems, a key species can perform a function significantly, and its absence can compromise the maintenance of essential ecological processes (Naeem et al., 2009; Power et al., 1996).

To determine the existence of key ant species that remove or clean diaspores, we conducted Wilcoxon tests using the "wilcox.test" function from the stats R package (R Core Team, 2023). This test allows pairwise comparisons of different data generated from the same original dataset (Wilcoxon, 1946). To do this, we constructed two global matrices (original matrices) with the total frequency of ants that removed diaspores and ants that cleaned diaspores in each study. Subsequently, we subtracted from each global value (total frequency) the number of appearances of each ant species, without altering the values for locations where the species was absent. We performed this procedure for all ant species in each type of interaction (removal/cleaning). Thus, the global matrix, both for diaspore removal and cleaning, was compared to the matrix of the remaining frequency of each species in each study.

To determine whether diaspore traits determine the type of ant-diaspore interaction, we used diaspore length (mm) and lipid content (low, medium, and high) as predictor variables and the percentage of diaspore removal and/or cleaning in each study as response variables. To classify the lipid concentration of diaspores as low (0 to 10%), medium (> 10 to 20%), and high lipid concentration (> 20%), we followed Bello et al. (2017). Subsequently, we constructed Generalized Linear Mixed Models (GLMM (O'Connell, 1993)), where different types of interactions (i.e., removal and cleaning) were considered random variables since they showed differences in the number of events. To do this, we used the "glmmPQL" function from the MASS package (Ripley et al., 2023) in the R software (R Core Team, 2023). We employed a binomial error distribution and adjusted the distribution using the quasibinomial distribution to correct data overdispersion (Crawley, 2012).

2.4. Priority sites for future samplings

2.4.1. Spatial gap detection

In each 3 km^2 area of the Atlantic Forest, we assessed the sampling relevance for new studies on ant-diaspore interactions, using the geographical coordinates of each study. For this, we employed the environmental dissimilarity of locations already sampled in the literature, considering eight variables based on Schmidt et al. (2020). For environmental variables (categorical), we considered altitude and soil type, and for bioclimatic variables (continuous), we considered annual precipitation, precipitation in the wettest month, precipitation in the driest month, average annual temperature, maximum temperature in the hottest month, and minimum temperature in the coldest month (Schmidt et al., 2020). All these variables have raster layers available on the AmbData website [for soil types and altitude (Amaral et al., 2013)] and WorldClim [for bioclimatic variables (Fick and Hijmans, 2017)].

2.4.2. Ecogeographical gap detection

We investigated the presence of ecogeographical gaps in the Atlantic Forest using the dissimilarity of locations previously sampled in the literature. Ecoregions, defined as land units that exhibit distinct communities and species, with boundaries approximating the original extent of natural communities before significant land use changes (Olson et al., 2001). These biogeographic units are important for conservation planning as they may more accurately reflect species and community distributions (Olson et al., 2001). Therefore, we used the 14 different ecoregions of the Atlantic Forest (Olson et al., 2001; Figure 1) and altitude as categorical variables, along with the bioclimatic variables as continuous variables. To obtain the raster layer of Atlantic Forest ecoregions, we rasterized the shapefile available on the World Wildlife Fund (WWF) website (www.worldwildlife.org).

After obtaining all raster layers, we first standardized all continuous variables (bioclimatic variables) using z-scores. This procedure is essential to avoid biases from variables with larger values (Legendre and Legendre, 2012). Subsequently, we calculated the mean environmental dissimilarity of sampled locations for each 3 km^2 area throughout the Atlantic Forest biome, based on Gower’s distance (Legendre and Legendre, 2012). Finally, we normalized all values from 0 to 1 using Min-Max normalization (Patro and Sahu, 2015), so that values close to 0 represented environmentally similar areas, while values close to 1 represented environmentally different areas from where existing studies in the literature were sampled. This resulted in a raster containing a gradient of sampling relevance for ant-diaspore interactions in the Atlantic Forest biome. The same procedure was performed for ecoregions. For the analyses, we used the R software version 4.3.0 (R Core Team, 2023) with the 'vegan' (Oksanen et al., 2019), 'raster' (Hijmans et al., 2023), and 'rgdal' (Bivand et al., 2017) packages.

3. Results

3.1. General aspects of the literature

We found 62 studies that assessed various types of interactions between ants and diaspores in the Brazilian Atlantic Forest, spanning 26-years (1995-2021). The number of studies on ant-diaspore interactions in the Atlantic Forest has remained relatively consistent over time, indicating cumulative growth from 1995 to 2021 (Figure 3). Among these, 62 studies, 50 studies were published articles (80.6% of the total), five were theses (8.1%), and seven were dissertations (11.3%). The published studies were distributed across 24 journals, with Sociobiology (eight), Journal of Tropical Ecology (six), and Biotropica (six) being the most prominent (Figure S1). The theses and dissertations were accessible in five open-access academic repositories (Figure S2). Most of the studies were published in English (83.9%), with 16.1% in Portuguese. Geographically, the studies primarily focused on three states - São Paulo, Minas Gerais, and Rio de Janeiro, highlighting knowledge gaps in ant-diaspore interactions in specific regions of the Atlantic Forest (Figure S3).

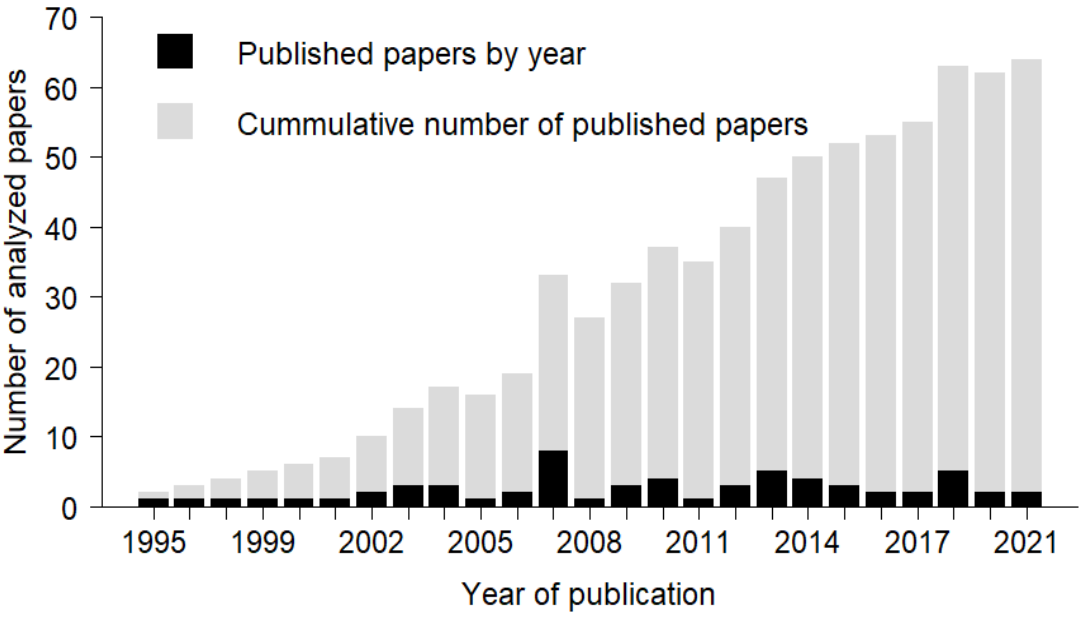


Figure 3. Number of published articles and cumulative number of published articles from 1995 to 2021 on ant-diaspore interactions in the Brazilian Atlantic Forest.

In general, the majority of studies used the method of actively collecting ants interacting with diaspores. Additionally, only 16.1% of the studies employed random active search for ant-diaspore interaction, while the remaining studies used predetermined diaspore species as bait for collection of the ant-diaspore interactions (Table 1). Regarding the focus of the studies, 19.4% specifically evaluated a single ant species interacting with diaspores, while 80.6% assessed ant communities (Table 1). Finally, 8.1% of the studies were conducted partially or entirely in a controlled laboratory environment, with the remaining taking place in the field.

Table 1. Number of studies according to the methodological approaches used.

		Number of studies
Method for ant-diaspore interactions collection	Active search on trails	10
	Diaspores as attraction traps	52
Level of biological organization	Ant population	12
	Ant community	50
Evaluated seed dispersal component	Quantitative component	44
	Qualitative component	18

3.2. Ant and diaspore species

In total, we recorded 356 ant species interacting with diaspores, distributed across eight subfamilies and 49 genera. Of this total, 140 (39.3%) ant species were identified at the species level, while 216 (60.7%) were identified at the genus level. The most abundant subfamily was Myrmicinae (Figure 4a), and the genera with the highest number of species were *Pheidole*, *Solenopsis,* and *Pachycondyla* (Figure 4b). Among the 15 ant genera with the highest number of species, morphospecies identifications exceeded nominal species in *Pheidole* (65 vs. 22), *Camponotus* (8 vs. 7), *Trachymyrmex* (9 vs. 5), *Solenopsis* (19 vs. 4), *Crematogaster* (9 vs. 4), and *Wasmannia* (4 vs. 3) (Figure S4).

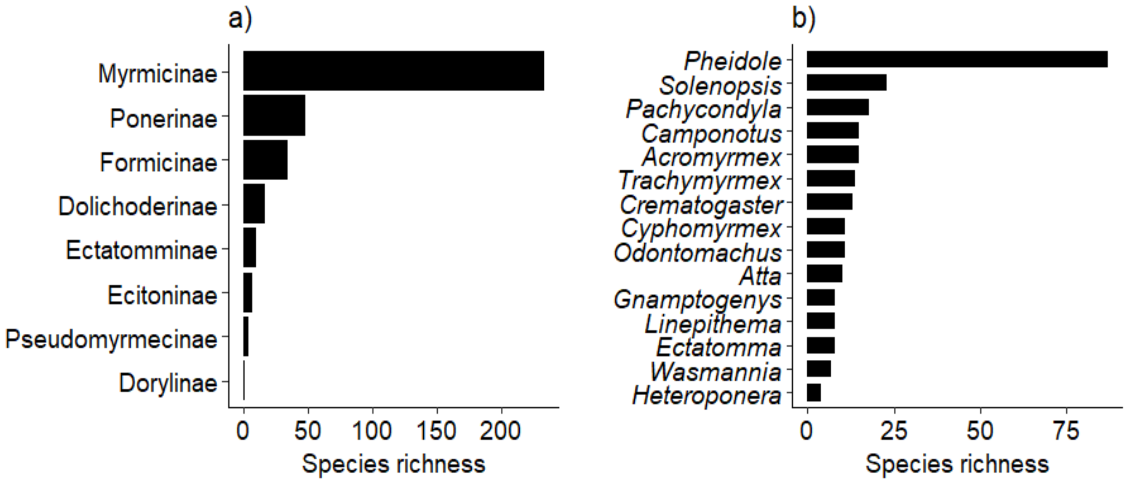


Figure 4. Subfamilies (a) and the top 15 ant genera (b) with the highest number of species found in studies on interactions between ants and diaspores in the Atlantic Forest.

Regarding diaspore species, we recorded 334 species distributed across 83 families and 181 genera. Among these, 248 (74.3%) were identified at the species level, 85 (25.4%) were identified at the genus level, and one (0.3%) at the family level (Sapotaceae). The most abundant family was Myrtaceae (Figure 5a), and the genera with the highest number of species were *Eugenia*, *Psychotria*, and *Myrcia* (Figure 5b). Among the 15 plant genera with the most species, morphospecies identifications exceeded nominal species only in *Ficus* (5 vs. 2) (Figure S5).

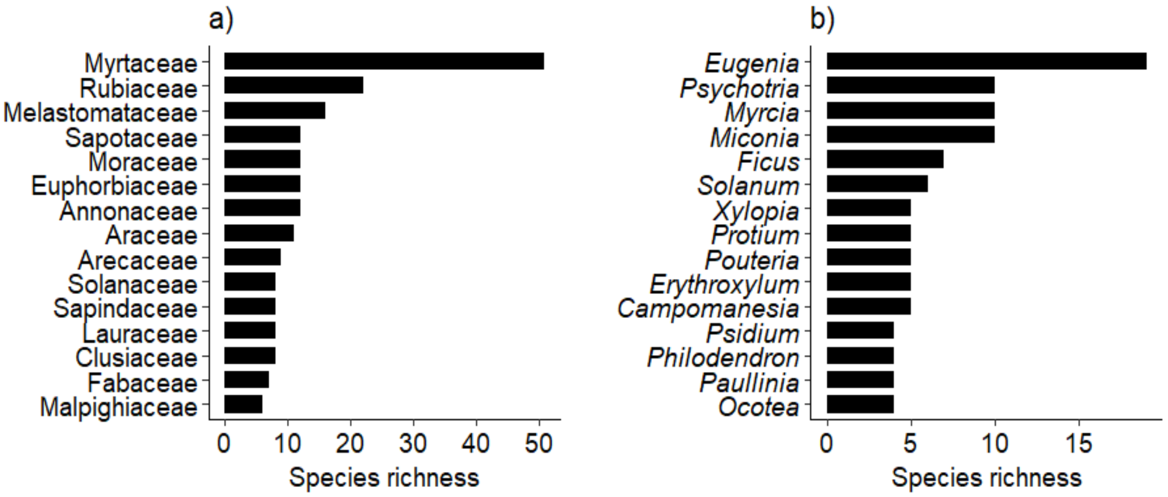


Figure 5. The top 15 plant families (a) and the top 15 plant genera (b) with the highest number of species found in studies on interactions between ants and diaspores in the Atlantic Forest.

3.3. Main objectives of the studies

The studies on ant-diaspore interactions exhibited diverse objectives. The studies primarily focused on the quantitative component of the seed dispersal framework (71% of the total), with a greater interest in quantifying removal and cleaning rates (63.6%), removal only (29.5%), or diaspore cleaning (6.8%) (Table 1). In contrast, fewer studies assessed the qualitative component of the seed dispersal framework (29% of the total) (Table 1). Among the qualitative components, diaspore dispersal distance and diaspores deposition in ant nests exhibited more studies (44.4% and 16.7%, respectively). Additionally, 16.7% examined the effects of ant nests on seedling establishment, evaluating the distance from the nest or the relationship of soil components around specific ant nests to plant seedling richness or abundance. Concerning seed germination, only 11.1% of studies were interested in assessing germination rates after ant manipulation. It is important to note that studies that consider manual removal of the pulp from the diaspore were excluded. Finally, 11.1% of the studies covered the entire process of diaspore dispersal by ants, from removal and cleaning to germination.

Regarding ant behavior towards diaspores, ants exhibited diverse responses upon encountering fallen diaspores on the ground. In addition to diaspore removal and cleaning, observed ant behaviors included worker recruitment, removal attempts, fluid collection from seed appendages, inspection, and instances where ant species ignored the diaspores. Notably, some studies did not specify ant behavior (four studies), while others only partially specified it (four studies).

3.5. Key ant species

Out of the 356 ant species recorded interactions with diaspores, 203 were observed removing the diaspores, while 183 were observed cleaning them. We identified 35 key ant species playing a crucial role in diaspore removal and 24 key species in the context of diaspore cleaning (Table S1 and S2). Overall, key ant species involved in removal and cleaning interacted with a wide diversity of diaspore species. Among the key diaspore-removing ant species, *Pachycondyla striata* (95 species), *Odontomachus chelifer* (59 species), and *Atta sexdens* (45 species) interacted with the highest number of diaspore species. As for key ant cleaning species, *Pheidole* sp. 1 (114 species), *Pheidole* sp. 3 (94 species), and *Solenopsis* sp. 1 (54 species) were the ants that interacted with the highest number of diaspore species.

We found that the type of interaction is influenced by both the diapore size (χ^2 = 5.2487, df = 1, p = 0.02196) and the lipid content (χ^2 = 17.144, df = 2, p = 0.0001893). We observed that the percentage of diaspore cleaning and removal by ants decreased with an increase in diaspore size (df = 173, t-value = -2.277941, p = 0.024) (Figure 7). Additionally, diaspores with high and medium lipid content were more frequently cleaned and removed by ants. At the same time, both types of interactions had a lower proportion of events with diaspores with low lipid concentration (df = 236, t-value = -3.776245, p = 0.0002) (Figure 8).

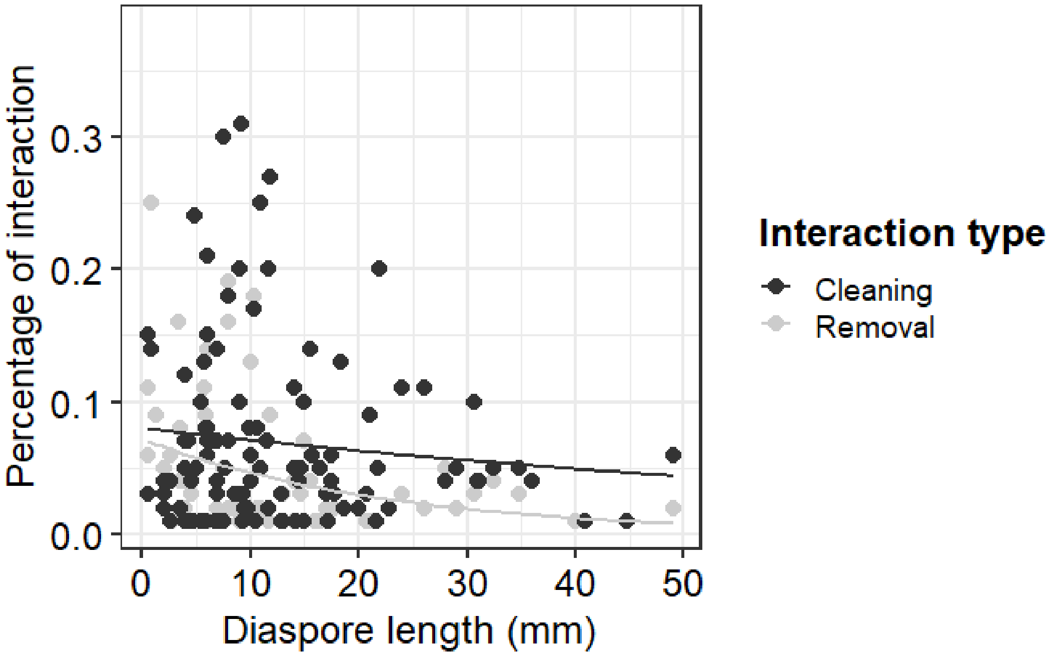


Figure 7. Percentages of removal and cleaning based on diaspore size in the Atlantic Forest.

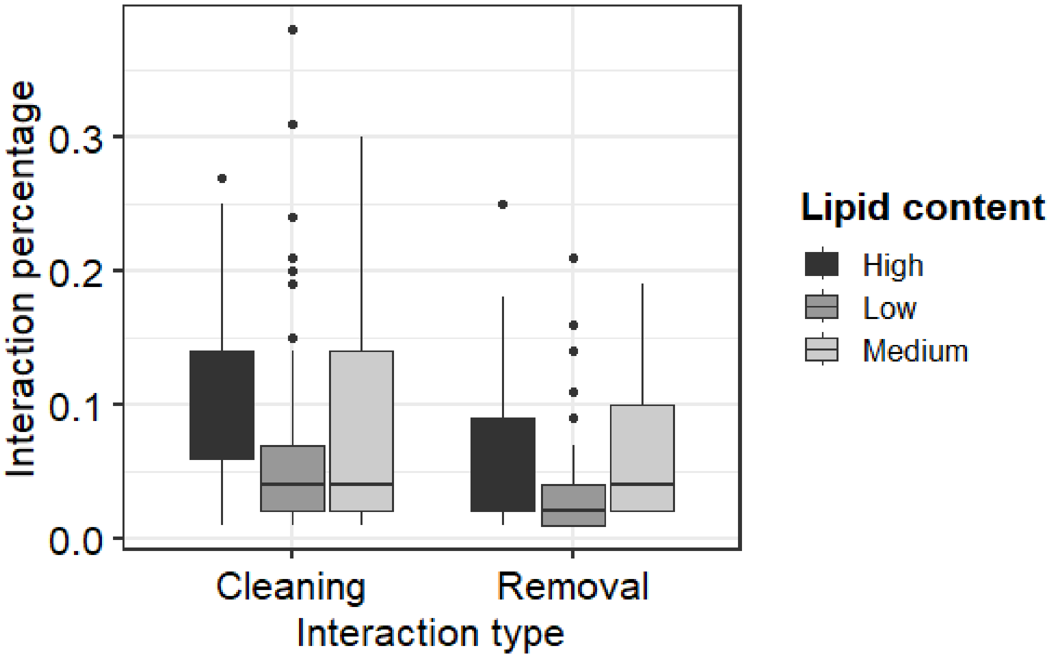


Figure 8. Percentages of removal and cleaning based on diaspore lipid content in the Atlantic Forest.

3.4. Relevance for future sampling of ant-diaspore interactions

The spatial analysis of environmental dissimilarity revealed several knowledge gaps regarding ant-diaspore interactions in the Atlantic Forest (Figure 9). A significant portion of the South and Southeast regions showed low relevance for future sampling (Figure 9). However, when we examined environmental dissimilarity based on information from Atlantic Forest ecoregions, it became possible to identify other priority locations for future studies (Figure 10). Most of the Atlantic Forest ecoregions exhibited dissimilarity values greater than 0.6, with some ecoregions having their entire extent or a majority of it highly relevant for future studies (e.g., Alto Paraná Atlantic forests, Pernambuco interior forests) (Figure 10).

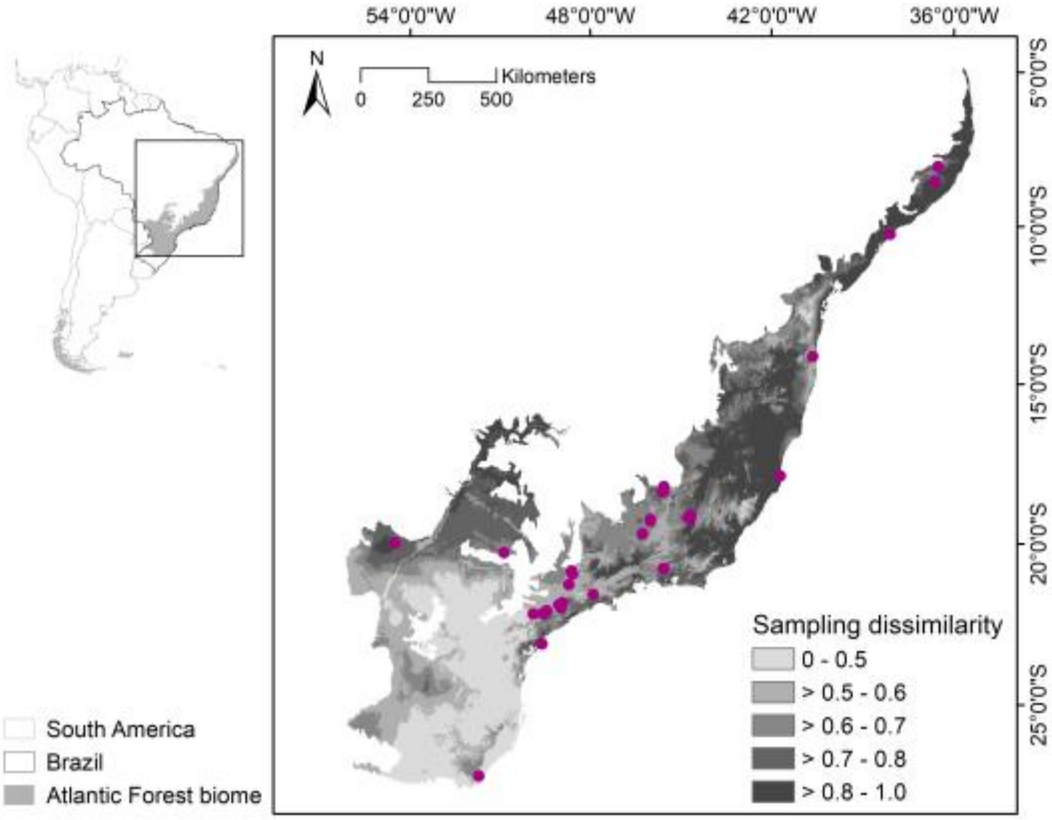


Figure 9. Map of relevance for future sampling of ant-diaspore interactions in the Atlantic Forest. Locations with values closer to 1 exhibit higher environmental dissimilarity from already sampled locations, indicating greater relevance for future studies.

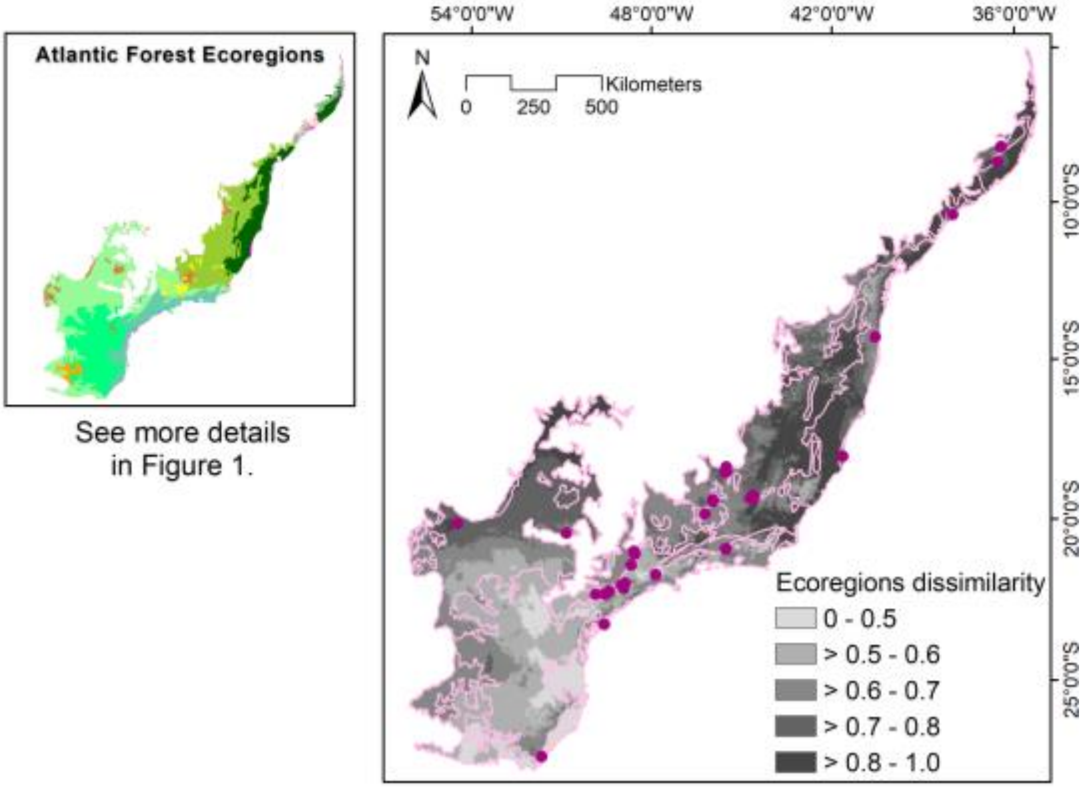


Figure 10. Map of relevance for future sampling of ant-diaspore interactions based on different Atlantic Forest ecoregions. Locations with values closer to 1 exhibit higher environmental dissimilarity from already sampled locations, indicating greater relevance for future studies.

4. Discussion

Our study provides detailed information on interactions between ants and diaspores throughout the Brazilian Atlantic Forest. After a thorough review of the literature from the past 26 years, we found that the vast majority of studies are concentrated in three Brazilian states, highlighting significant gaps in various regions of the Atlantic Forest. Furthermore, we revealed that the primary focus of ant-diaspore interaction studies in the Atlantic Forest is seed dispersal by ants. However, our results showed that the majority of these studies evaluate only the quantitative component of the seed dispersal framework. Additionally, we identified ant species that play a key role in diaspore removal and cleaning and found that diaspore size and lipid content can determine the type of interaction. Finally, we identified priority locations for future sampling based on environmental characteristics, including the ecoregions of the Brazilian Atlantic Forest. This information is crucial for advancing the discussion on ant species and their ecological interactions in the Atlantic Forest and guiding efforts for future research on the role of ants in seed dispersal.

4.1. General aspects of the literature

In 26 years of studies on ant-diaspore interactions, we found that most of them were published in journals accessible to the international scientific community. This is significant as it facilitates multidisciplinary discussions on ant-plant interactions. Our findings indicate a relatively consistent interest in ants and their interactions with diaspores in the Atlantic Forest over time, underscoring the relevance of the topic. However, most studies are concentrated in three Brazilian states, specifically near major research centers. This can be explained by the fact that these states are part of the southeastern region of Brazil, which exhibits higher socioeconomic development and, consequently, more investments in research centers (Schmidt et al., 2022). These trends underscore the importance of diversifying research efforts to encompass other regions of the Atlantic Forest, ensuring a more comprehensive understanding of ant-plant interactions within this ecosystem.

4.2. Ant species and diaspores

Less than half of the ant species found were identified to species level. Accurate identification of ant species is highly necessary for precise data interpretation and ecological pattern recognition (Feitosa et al., 2023). While genus-level identification is efficient in predicting variations in ant assembly structure (Souza et al., 2016), our findings highlight the great need for increased collaboration with taxonomists. Such collaboration, for both specimen identification and review of ants identified based on guides and keys, is extremely important for making results more robust and accurate (Feitosa et al., 2023).

Most of the ant species found in the studies belong to the subfamilies Myrmicinae and Ponerinae. Indeed, ants from the subfamily Myrmicinae exhibit a high capacity to occupy all strata of tropical ecosystems, which is a pattern commonly observed in ant studies (Feitosa et al., 2022). Our findings support this pattern for ants interacting with diaspores in the Atlantic Forest, likely due to the highly generalist diet of these species. Similarly, the high number of ponerine ants encountered is not surprising, as fallen fruits and seeds on the ground are a primary resource for poneromorph ants in Brazil (Delabie et al., 2015). However, unlike myrmicines, ponerine ants are highly sensitive to habitat disturbances, highlighting the need for conservation plans for these seed-dispersing ant species.

Regarding diaspores, the most abundant families in ant-diaspore interactions consist of species primarily dispersed by other agents, especially birds (e.g., Myrtaceae (Bello et al., 2017)). These findings corroborate the contribution of ants to seed dispersal, which was previously dispersed by birds in the Atlantic Forest (Camargo et al., 2016; Christianini et al., 2007), potentially shaping the spatial distribution of seedlings. Furthermore, ants interacted primarily with diaspores from tree species, followed by shrubs (see more details about plant species in Table S3). All of this underscores the crucial role of ant-diaspore interactions in maintaining the functionality of terrestrial ecosystems in the Atlantic Forest.

4.3. Main objectives of studies

Our findings revealed that studies on ant-diaspore interactions in the Atlantic Forest primarily focused on assessing seed dispersal by ants. This is highly valuable, as the seed dispersal performed by ants (secondary or occasionally primary (Howe and Smallwood, 1982)) still has many knowledge gaps in tropical regions. Moreover, the substantial loss of large seed dispersers due to deforestation and defaunation in the Atlantic Forest (Gardner et al., 2019; Vellend et al., 2006) makes it increasingly necessary to understand the role of ants as potential mitigating agents (Anjos et al., 2020). Despite the progress in this field over 26 years of research, several aspects must be investigated and explored. For example, we found that the vast majority of studies only measure the quantitative component of the seed dispersal framework (sensu Schupp 1993) (e.g., removal and cleaning rates). While revealing quantitative patterns of seed dispersal aids in monitoring the initial phases of plant dynamics, the qualitative aspects need to be evaluated to uncover the effectiveness of the process (Schupp, 1993). Furthermore, evaluating qualitative aspects of seed dispersal can indicate how efficient the dispersal agents are for the seed dispersal function (Jordano and Schupp, 2000; Schupp et al., 2010). In this regard, behavioral and morphological characteristics of ants, diaspore fate, and the probability of a seed surviving and producing a new adult individual should be considered in future studies of seed dispersal by ants.

We revealed that studies typically use between one and five diaspore species as bait to attract ants, which can be attributed to the difficulty of assessing the ant and diaspore community in the complex and megadiverse Atlantic Forest. Additionally, for fruit and diaspore sampling to accurately represent the community, plant phenology must be taken into account, increasing the costs and time required for sampling. This lack of information on ant-diaspore interactions without using attractive baits (selected diaspores) can lead to important omissions regarding the plants that naturally attract ants in the Atlantic Forest. Moreover, information on the architecture of ant-diaspore interactions in the biome and how different anthropogenic impacts shape the structure of these interaction networks remains unknown (Laviski et al., 2021). Therefore, in addition to knowledge gaps in various states within the Brazilian Atlantic Forest, our findings point to data deficiencies that may be crucial for understanding ecological processes.

4.4. Key ant species for diaspore removal and cleaning

We found 35 key species of seed-removing ants for the Atlantic Forest. Our findings corroborate the importance of species like *Pachycondyla harpax* and *Ectatomma edentatum*, which contribute significantly to diaspore dispersal in other Brazilian biomes (i.e., Amazon and Cerrado, respectively) (Fontenele and Schmidt, 2021; Wilker et al., 2022). Several studies also highlight the substantial contribution of *Pachycondyla striata* and *Odontomachus chelifer*, both in diaspore removal and the benefits of their nests for seedling establishment (Bottcher and Oliveira, 2014; Camargo et al., 2019; Passos et al., 2002). In general, these ant species have a medium to large body size (> 4 mm), forage individually, and remove diaspores over long distances, characteristics that indicate high-quality seed dispersing ants (Leal et al., 2014). Therefore, we suggest that *P. striata* and *O. chelifer* are high-quality seed-dispersing ants in the Atlantic Forest (see maximum removal distances and body size in Figure S6). This information can be useful in developing conservation plans for areas where these ants occur since they are important seed dispersers.

Other species, such as *Atta sexdens*, *Atta laevigata*, and some species from the genera *Pheidole* and *Solenopsis*, were also identified as key species for diaspore removal in the Atlantic Forest. Several studies have revealed that these interactions offer no benefits due to the behavior of these species (e.g., mass recruitment, seed cleaning around nests, seed damage) (Carney et al., 2003; Knoechelmann et al., 2020). Moreover, these ant species exhibit characteristics indicating that they are low-quality seed dispersers (i.e., small body size (< 4 mm), mass recruitment behavior, and short-distance removal) (Leal et al., 2014). The presence of these ant species as key species may indicate low-quality performance in diaspore removal by ants in the Atlantic Forest, likely due to habitat loss in the biome and, consequently, favoring these ant species (Meyer et al., 2009). Regarding diaspore cleaning, 24 ant species in the Atlantic Forest were considered key species. All four observed genera (*Pheidole*, *Solenopsis*, *Crematogaster*, and *Paratrechina*) include small-bodied species that clean seeds without removing them far from the mother plant. Ants exhibiting this behavior are more associated with predation or cheating in mutualism by hindering the collection of diaspores by other ants (Bronstein, 2001). Together, these pieces of information can be useful in evaluating whether ant-diaspore interactions are closer to seed dispersal or seed predation, particularly in areas affected by some form of disturbance.

4.5. Influence of diaspore characteristics on the interaction type

The size and lipid content of diaspores influenced the number of ant-diaspore interactions (removal/cleaning). We found that both removal and cleaning of diaspores by key ants decreased with increasing diaspore size in the Atlantic Forest. Generally, in tropical environments, small-sized ants are responsible for the removal of the majority of diaspores (Pizo and Oliveira, 2001), which may explain their preference for smaller diaspores. Furthermore, due to the morphological limitations of ants, smaller diaspores have a higher probability of being removed (Anjos et al., 2020) and, as a result, being cleaned on-site after removal attempts. For example, larger diaspore species that exhibited both types of interactions (e.g., *Attalea dubia* (length 49.1 mm) and *Rollinea sericea* (length 34.82 mm)) were removed by large ponerines and cleaned by small myrmicines. However, some ant species tend to exhibit innate behavior rather than the consequence of diaspores being difficult to transport (Gove et al., 2007).

We found that diaspores with lower lipid concentration in their composition received lower removal and cleaning rates by ants. This pattern had previously been demonstrated for ant-diaspore interactions in some Atlantic Forest locations (Pizo and Oliveira, 2001; Santana et al., 2013). Our findings demonstrate that this pattern can be verified throughout the biome, considering both the removal and cleaning ant key species. Empirical evidence suggests that increased deforestation in the Atlantic Forest leads to a loss of functional plant diversity (Rocha-Santos et al., 2019), contributing to a reduction in the production, biomass, and nutritional quality of diaspores in these areas (Pessoa et al., 2017, 2016). Consequently, diaspores in deforested areas are nutritionally poorer (Pessoa et al., 2016). Therefore, ant-mediated seed dispersal may be compromised in areas under anthropogenic influence in the Atlantic Forest, as high-quality ants strongly prefer higher-quality diaspores (Kaspari, 1996; Leal et al., 2014).

4.6. Relevance for future ant-diaspore interaction sampling

Based on the environmental and bioclimatic differences between sampled and unsampled locations, we identified numerous knowledge gaps regarding ant-diaspore interactions in the Atlantic Forest. The Atlantic Forest has a significant number of ant species survey studies, with 10,071 records and a total of 657 species, making it the second richest biome in Brazil for ant species (Feitosa et al., 2022). This low urgency index for new ant fauna sampling, even in the face of high deforestation levels in the biome (Divieso et al., 2020). However, our findings demonstrated that this does not reflect the knowledge regarding ant-diaspore interactions. We found several relevant locations for future sampling, even in areas very close to previously sampled sites, a point made clearer when considering the different ecoregions of the Atlantic Forest.

Empirical evidence suggests that ecoregional scales play a crucial role in structuring ant assemblages in Brazil (Marques and Schoereder, 2014). This can be explained by the high number of completely distinct ecosystems with different degrees of environmental complexity and heterogeneity throughout the biome (Olson et al., 2001). Generally, differences in floristics, microclimates, and soil types are some of the environmental attributes that influence ant assemblage structures (Ribas et al., 2012; Schmidt et al., 2013). However, nothing is known about the role of the different ecoregions in the Atlantic Forest in ant-diaspore interactions. Therefore, we emphasize the importance of future research considering the classification of ecoregions, as it will enhance the understanding of the factors shaping these interactions, especially the seed dispersal function by ants. This will enable fine-scale spatial actions to assess the need for creating new protected areas within the Atlantic Forest, as ants serve as a surrogate taxon reflecting patterns of other groups (Paknia and Pfeiffer, 2011).

5. Conclusion

Our review of 26 years of research on ant-diaspore interactions in the Brazilian Atlantic Forest reveals that research tends to concentrate in regions with higher socioeconomic development and near major research centers. This underscores the critical need for financial investments and human resources to advance research in Brazil. Furthermore, we have shown that the primary focus of these studies is on seed dispersal by ants, indicating advancements in our understanding of the role of ants in this function in a scenario of other dispersal agents diminishing due to defaunation in the Atlantic Forest. However, we identify a substantial knowledge gap regarding the true role of ants in the dynamics of Atlantic Forest plants, as most studies only address the quantitative component of seed dispersal by ants. We have also identified 35 key ant species involved in diaspore removal and suggest that *Pachycondyla striata* and *Odontomachus chelifer* be classified as high-quality dispersers. Therefore, we emphasize the need to prioritize the conservation of areas in the Atlantic Forest where these species are present, as they significantly contribute to the maintenance of seed dispersal in these ecosystems. We also identify 24 key ant species involved in diaspore cleaning and find that these species are often characterized as mutualism cheaters, with their abundance generally favored by habitat disturbances. Furthermore, our research reveals that smaller diaspores with higher lipid concentrations are more frequently removed and cleaned by ants. Our findings will undoubtedly assist studies aimed at monitoring the role of ants in seed dispersal in both natural and anthropogenic landscapes. Lastly, our study underscores the importance of using ecoregion classification, as it allows for an understanding of ant-diaspore interactions considering the ecosystem attributes that shape the structure of ant assemblages in the Atlantic Forest. With this information, it will be possible to comprehend how each ecoregion maintains its unique identity (e.g., structural, and functional characteristics), facilitating the development of different strategies for the conservation of ant species and their interactions in the Atlantic Forest.

6. Acknowledgments

We thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for scholarship to KB and LKF (Financing Code 001). JHCD and EC acknowledge their productivity research grant from CNPq (304629/2018-9, 311545/2021-1, respectively).

7. References

Amaral, S., Costa, C.B., Arasato, L.S., Ximenes, C.D., Rennó, A. de C., 2013. AMBDATA: Variáveis ambientais para Modelos de Distribuição de Espécies (MDEs). An. XVI Simp. Bras. Sensoriamento Remoto - SBSR, Foz do Iguaçu d, 6917–6922.

Anjos, D. V., Leal, L.C., Jordano, P., Del-Claro, K., 2020. Ants as diaspore removers of non-myrmecochorous plants: a meta-analysis. Oikos 129, 775–786. https://doi.org/10.1111/oik.06940

Beattie, A.J., 1985. The evolutionary ecology of ant–plant mutualisms. Cambridge University Press, New York. https://doi.org/10.1017/CBO9780511721878

Bello, C., Galetti, M., Montan, D., Pizo, M.A., Mariguela, T.C., Culot, L., Bufalo, F., Labecca, F., Pedrosa, F., Constantini, R., Emer, C., Silva, W.R., da Silva, F.R., Ovaskainen, O., Jordano, P., 2017. Atlantic frugivory: a plant-frugivore interaction data set for the Atlantic Forest. Ecology 98, 1729–1729. https://doi.org/10.1002/ecy.1818

Bivand, R., Keitt, T., Rowlingson, B., Pebesma, E., Sumner, M., Hijmans, R., Rouault, E., 2017. Rgdal: Bindings for the “Geospatial” data abstraction library.

Bottcher, C., Oliveira, P.S., 2014. Consumption of lipid-rich seed arils improves larval development in a Neotropical primarily carnivorous ant, Odontomachus chelifer (Ponerinae). J. Trop. Ecol. 30, 621–624. https://doi.org/10.1017/S0266467414000479

Bronstein, J.L., 2001. The costs of mutualism. Am. Zool. 41, 825–839. https://doi.org/10.1093/icb/41.4.825

Camargo, P.H.S.A., Martins, M.M., Feitosa, R.M., Christianini, A. V., 2016. Bird and ant synergy increases the seed dispersal effectiveness of an ornithochoric shrub. Oecologia 181, 507–518. https://doi.org/10.1007/s00442-016-3571-z

Camargo, P.H.S.A., Rodrigues, S.B.M., Piratelli, A.J., Oliveira, P.S., Christianini, A. V., 2019. Interhabitat variation in diplochory: Seed dispersal effectiveness by birds and ants differs between tropical forest and savanna. Perspect. Plant Ecol. Evol. Syst. 38, 48–57. https://doi.org/10.1016/j.ppees.2019.04.002

Carney, S.E., Brooke Byerley, M., Holway, D.A., 2003. Invasive Argentine ants (Linepithema humile) do not replace native ants as seed dispersers of Dendromecon rigida (Papaveraceae) in California, USA. Oecologia 135, 576–582. https://doi.org/10.1007/s00442-003-1200-0

Cazetta, E., 2008. Variação morfológica e química dos frutos na escolha dos animais frugívoros da Mata Atlântica. Universidade Estadual Paulista.

Christianini, A. V., Mayhé-Nunes, A.J., Oliveira, P.S., 2007. The role of ants in the removal of non-myrmecochorous diaspores and seed germination in a neotropical savanna. J. Trop. Ecol. 23, 343–351. https://doi.org/10.1017/S0266467407004087

Coley, P.D., Barone, J.A., 1996. Herbivory and plant defenses in tropical forests. Annu. Rev. Ecol. Syst. 27, 305–335. https://doi.org/10.1146/annurev.ecolsys.27.1.305

Crawley, M.J., 2012. Generalized Linear Models, in: The R Book. John Wiley & Sons, Ltd, Chichester, UK, pp. 557–578. https://doi.org/10.4135/9781446251119.n40

Delabie, J.H.C., Feitosa, R.M., Serrão, J.E., Mariano, C.S.F., Majer, J.D., 2015. As formigas poneromorfas do Brasil, As formigas poneromorfas do Brasil. https://doi.org/10.7476/9788574554419

Divieso, R., Rorato, A., Feitosa, R.M., Meyer, A.L.S., Pie, M.R., 2020. How to prioritize areas for new ant surveys? Integrating historical data on species occurrence records and habitat loss. J. Insect Conserv. 24, 901–911. https://doi.org/10.1007/s10841-020-00262-y

Feitosa, R.M., Camacho, G.P., Silva, T.S.R., Ulysséa, M.A., Ladino, N., Oliveira, A.M., Albuquerque, E.Z., Schmidt, F.A., Ribas, C.R., Nogueira, A., Baccaro, F.B., Queiroz, A.C.M., Dáttilo, W., Silva, R.R., Santos, J.C., Rabello, A.M., Morini, M.S.D.C., Quinet, Y.P., Del-Claro, K., Harada, A.Y., Carvalho, K.S., Sobrinho, T.G., Moraes, A.B., Vargas, A.B., Torezan-Silingardi, H.M., Souza, J.L.P., Marques, T., Izzo, T., Lange, D., Santos, I.A., Nahas, L., Paolucci, L., Soares, S.A., Costa-Milanez, C.B., Diehl-Fleig, E., Campos, R.B.F., Solar, R., Frizzo, T., Darocha, W., 2022. Ants of Brazil: an overview based on 50 years of diversity studies. Syst. Biodivers. 20. https://doi.org/10.1080/14772000.2022.2089268

Feitosa, R.M., Silva, T.S.R., Camacho, G.P., Ulysséa, M.A., Ladino, N., Oliveira, A.M., De Albuquerque, E.Z., Ribas, C.R., Schmidt, F.A., Morini, M.S.D.C., Da Silva, R.R., Dáttilo, W., De Queiroz, A.C.M., Baccaro, F.B., Santos, J.C., Carvalho, K.S., Sobrinho, T.G., Quinet, Y.P., Moraes, A.B., Vargas, A.B., Torezan-Silingardi, H.M., Souza, J.L.P., Marques, T., Izzo, T., Lange, D., Dos Santos, I.A., Del-Claro, K., Nahas, L., Paolucci, L., Soares, S.A., Harada, A.Y., Rabello, A.M., Da Costa-Milanez, C.B., Diehl-Fleig, E., Campos, R.B.F., Solar, R., Frizzo, T., Darocha, W., Nogueira, A., 2023. From species descriptions to diversity patterns: The validation of taxonomic data as a keystone for ant diversity studies reproducibility and accuracy. R. Soc. Open Sci. 10. https://doi.org/10.1098/rsos.221170

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086

Fonseca, C.R., Ganade, G., 2001. Species functional redundancy, random extinctions and the stability of ecosystems. J. Ecol. 89, 118–125. https://doi.org/10.1046/j.1365-2745.2001.00528.x

Fontenele, L.K., Schmidt, F.A., 2021. Forest-pasture shifting alters the assemblages of seed-removing ants in southwestern Brazilian Amazon. J. Insect Conserv. 25, 213–220. https://doi.org/10.1007/s10841-021-00295-x

Frouz, J., Jilková, V., 2008. The effect of ants on soil properties and processes (Hymenoptera : Formicidae). Myrmecological News 11, 191–199.

Gardner, C.J., Bicknell, J.E., Baldwin-Cantello, W., Struebig, M.J., Davies, Z.G., 2019. Quantifying the impacts of defaunation on natural forest regeneration in a global meta-analysis. Nat. Commun. 10, 1–7. https://doi.org/10.1038/s41467-019-12539-1

Gove, A.D., Majer, J.D., Dunn, R.R., 2007. A keystone ant species promotes seed dispersal in a “diffuse” mutualism. Oecologia 153, 687–697. https://doi.org/10.1007/s00442-007-0756-5

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Sci. Adv. 1, e1500052. https://doi.org/10.1126/sciadv.1500052

Handel, S.N., Beattie, A.J., 1990. Seed Dispersal by Ants the insects to carry away its seeds without harming them. Sci. Am. 263, 76–83.

Heithaus, E.R., Heithaus, P.A., Liu, S.Y., 2005. Satiation in collection of myrmecochorous diaspores by colonies of Aphaenogaster rudis (Formicidae: Myrmicinae) in Central Ohio, USA. J. Insect Behav. 18, 827–846. https://doi.org/10.1007/s10905-005-8743-3

Hijmans, R.J., Etten, J. Van, Sumner, M., Cheng, J., Baston, D., Bevan, A., Bivand, R., Busetto, L., Canty, M., Fasoli, B., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J.A., Hiemstra, P., Hingee, K., Ilich, A., Karney, C., Mattiuzzi, M., Mosher, S., Naimi, B., Nowosad, J., Pebesma, E., Lamigueiro, O.P., Racine, E.B., Rowlingson, B., Shortridge, A., Venables, B., Wueest, R., 2023. Raster: Geographic data analysis and modeling.

Horvitz, C.C., Beattie, A.J., 1980. Ant Dispersal of Calathea (Marantaceae) Seeds by Carnivorous Ponerines (Formicidae) in a Tropical Rain Forest. Am. J. Bot. 67, 321. https://doi.org/10.2307/2442342

Howe, H.F., Smallwood, J., 1982. Ecology of Seed Dispersal. Annu. Rev. Ecol. Syst. 13, 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

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

Jordano, P., Schupp, E.W., 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for Prunus mahaleb. Ecol. Monogr. 70, 591–615. https://doi.org/10.1890/0012-9615(2000)070[0591:sdetqc]2.0.co;2

Kaspari, M., 1996. Worker size and seed size selection by harvester ants in a Neotropical forest. Oecologia 105, 397–404. https://doi.org/10.1007/BF00328743

Knoechelmann, C.M., Oliveira, F.M.P., Siqueira, F.F.S., Wirth, R., Tabarelli, M., Leal, I.R.,

2020. Leaf-cutting ants negatively impact the regeneration of the Caatinga dry forest across abandoned pastures. Biotropica 52, 686–696. https://doi.org/10.1111/btp.12782

Laviski, B.F.S., Mayhé-Nunes, A.J., Nunes-Freitas, A.F., 2021. Structure of ant-diaspore networks and their functional outcomes in a Brazilian Atlantic Forest. Sociobiology 68. https://doi.org/10.13102/SOCIOBIOLOGY.V68I3.7104

Leal, I.R., Filgueiras, B.K.C., Gomes, J.P., Iannuzzi, L., Andersen, A.N., 2012. Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodivers. Conserv. 21, 1687–1701. https://doi.org/10.1007/s10531-012-0271-9

Leal, L.C., Neto, M.C.L., de Oliveira, A.F.M., Andersen, A.N., Leal, I.R., 2014. Myrmecochores can target high-quality disperser ants: Variation in elaiosome traits and ant preferences for myrmecochorous Euphorbiaceae in Brazilian Caatinga. Oecologia 174, 493–500. https://doi.org/10.1007/s00442-013-2789-2

Legendre, P., Legendre, L.F.J., 2012. Numerical Ecology. Elsevier, Amsterdam.

Levine, N., Ben-Zvi, G., Seifan, M., Giladi, I., 2019. Investment in reward by ant-dispersed plants consistently selects for better partners along a geographic gradient. AoB Plants 11, 1–13. https://doi.org/10.1093/aobpla/plz027

Longino, J.T., 1991. Taxonomy of the cecropia-inhabiting azteca ants. J. Nat. Hist. 25, 1571–1602. https://doi.org/10.1080/00222939100770981

Marques, T., Schoereder, J.H., 2014. Ant diversity partitioning across spatial scales: Ecological processes and implications for conserving Tropical Dry Forests. Austral Ecol. 39, 72–82. https://doi.org/10.1111/aec.12046

Meyer, S.T., Leal, I.R., Wirth, R., 2009. Persisting hyper-abundance of leaf-cutting ants (Atta spp.) at the edge of an old Atlantic Forest fragment. Biotropica 41, 711–716. https://doi.org/10.1111/j.1744-7429.2009.00531.x

Miller, C.N., Whitehead, S.R., Kwit, C., 2020. Effects of seed morphology and elaiosome chemical composition on attractiveness of five Trillium species to seed-dispersing ants. Ecol. Evol. 10, 2860–2873. https://doi.org/10.1002/ece3.6101

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/468895a

Naeem, S., Bunker, D.E., Hector, A., Loreau, M., Perrings, C., 2009. Biodiversity, Ecosystem Functioning, and Human Wellbeing. Oxford University Press Inc., New York.

Ness, J.H., 2004. Forest edges and fire ants alter the seed shadow of an ant-dispersed plant.

Oecologia 138, 448–454. https://doi.org/10.1007/s00442-003-1440-z

O'Connell, M., 1993. Generalized Linear Mixed Models: A Pseudo-Likelihood Approach. J. Stat. Comput. Simul. 48, 233–243. https://doi.org/10.1080/00949659308811554

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Stevens, H.H.M., 2019. vegan: Community Ecology Package. R Packag. version 2.4-4.

Olson, D.M., Dinerstein, Eric Wikramanayake, Eric D. Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth. Bioscience 51, 933–938. https://doi.org/https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Paknia, O., Pfeiffer, M., 2011. Hierarchical partitioning of ant diversity: Implications for conservation of biogeographical diversity in arid and semi-arid areas. Divers. Distrib. 17, 122–131. https://doi.org/10.1111/j.1472-4642.2010.00719.x

Passos, F.C.S., Leal, L.C., 2019. Protein matters: Ants remove herbivores more frequently from extrafloral nectary-bearing plants when habitats are protein poor. Biol. J. Linn. Soc. 127, 407–416. https://doi.org/10.1093/biolinnean/blz033

Passos, L., Oliveira, P.S., 2004. Interaction between ants and fruits of Guapira opposita (Nyctaginaceae) in a Brazilian sandy plain rainforest: Ant effects on seeds and seedlings. Oecologia 139, 376–382. https://doi.org/10.1007/s00442-004-1531-5

Passos, L., Oliveira, P.S., 2002. Ants affect the distribution and performance of seedlings of Clusia criuva, a primarily bird-dispersed rain forest tree. J. Ecol. 90, 517–528. https://doi.org/10.1046/j.1365-2745.2002.00687.x

Passos, L., Oliveira, P.S., Passos, L., Oliveira, P.S., 2002. Ants Affect the Distribution and Performance of Seedlings of Clusia criuva , a Primarily Bird-Dispersed Rain Forest Tree Published by : British Ecological Society Linked references are available on JSTOR for this article : Ants affect the distribution and. J. Ecol. 90, 517–528.

Patro, S.G.K., Sahu, K.K., 2015. Normalization: A Preprocessing Stage. IARJSET 20–22. https://doi.org/10.17148/IARJSET.2015.2305

Penn, H.J., Crist, T.O., 2018. From dispersal to predation: A global synthesis of ant–seed interactions. Ecol. Evol. 8, 9122–9138. https://doi.org/10.1002/ece3.4377

Pessoa, M.S., Hambuckers, A., Benchimol, M., Rocha-Santos, L., Bomfim, J.A., Faria, D., Cazetta, E., 2017. Deforestation drives functional diversity and fruit quality changes in a tropical tree assemblage. Perspect. Plant Ecol. Evol. Syst. 28, 78–86. https://doi.org/10.1016/j.ppees.2017.09.001

Pessoa, M.S., Rocha-Santos, L., Talora, D.C., Faria, D., Mariano-Neto, E., Hambuckers, A., Cazetta, E., 2016. Fruit biomass availability along a forest cover gradient. Biotropica 49, 45–55. https://doi.org/10.1111/btp.12359

Pizo, M.A., Oliveira, P.S., 2001. Size and lipid content of nonmyrmecochorous diaspores: Effects on the interaction with litter-foraging ants in the Atlantic rain forest of Brazil. Plant Ecol. 157, 37–52. https://doi.org/10.1023/A:1013735305100

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J., Paine, R.T., 1996. Challenges in the Quest for Keystones. Bioscience 46, 609–620. https://doi.org/10.2307/1312990

Queiroz, A.C.M., Rabello, A.M., Lasmar, C.J., Cuissi, R.G., Canedo-Júnior, E.O., Schmidt, F.A., Ribas, C.R., 2021. Diaspore Removal by Ants Does Not Reflect the Same Patterns of Ant Assemblages in Mining and Rehabilitation Areas. Neotrop. Entomol. 50, 335–348. https://doi.org/10.1007/s13744-021-00861-7

R Core Team, 2023. R: A Language and Environment for Statistical Computing.

Rabello, A.M., Parr, C.L., Queiroz, A.C.M., Braga, D.L., Santiago, G.S., Ribas, C.R., 2018. Habitat attribute similarities reduce impacts of land-use conversion on seed removal. Biotropica 50, 39–49. https://doi.org/10.1111/btp.12506

Rezende, C.L., Scarano, F.R., Assad, E.D., Joly, C.A., Metzger, J.P., Strassburg, B.B.N., Tabarelli, M., Fonseca, G.A., Mittermeier, R.A., 2018. From hotspot to hopespot: An opportunity for the Brazilian Atlantic Forest. Perspect. Ecol. Conserv. 16, 208–214. https://doi.org/10.1016/j.pecon.2018.10.002

Ribas, C.R., Campos, R.B.F., Schmidt, F.A., Solar, R.R.C., 2012. Ants as indicators in Brazil: A review with suggestions to improve the use of ants in environmental monitoring programs. Psyche (Stuttg). 2012. https://doi.org/10.1155/2012/636749

Rico-Gray, V., Oliveira, P.S., 2007. The ecology and evolution of ant-plant interactions. University of Chicago Press, Chicago.

Ripley, B., Venables, B., Bates, D.M., Firth, D., 2023. Support Functions and Datasets for Venables and Ripley’s MASS.

Rocha-Santos, L., Mayfield, M.M., Lopes, A. V., Pessoa, M.S., Talora, D.C., Faria, D., Cazetta, E., 2019. The loss of functional diversity: A detrimental influence of landscape-scale deforestation on tree reproductive traits. J. Ecol. 108, 212–223.

https://doi.org/10.1111/1365-2745.13232

Santana, F.D., Cazetta, E., Delabie, J.H.C., 2013. Interactions between ants and non-myrmecochorous diaspores in a tropical wet forest in southern Bahia, Brazil. J. Trop. Ecol. 29, 71–80. https://doi.org/10.1017/S0266467412000715

Schmidt, F.A., Costa, M.M.S., Martello, F., De Oliveira, A.B., Menezes, A.S., Fontenele, Luane Karoline Morato, E.F.&, Oliveira, M.A., 2020. Ant diversity studies in Acre : what we know and what we could do to know more ? Estudos de diversidade de formigas no Acre : o que sabemos e o que devemos fazer para saber mais ? Bol. Mus. Para. Emílio Goeldi. Cienc. Nat. 15, 113–134.

Schmidt, F.A., Ribas, C.R., Feitosa, R.M., Baccaro, F.B., de Queiroz, A.C.M., Sobrinho, T.G., Quinet, Y., Carvalho, K.S., Izzo, T., de Castro Morini, M.S., Nogueira, A., Torezan-Silingardi, H.M., Souza, J.L.P., Ulysséa, M.A., Vargas, A.B., Dáttilo, W., Del-Claro, K., Marques, T., Moraes, A.B., Paolucci, L., Rabello, A.M., Santos, J.C., Solar, R., de Albuquerque, E.Z., Esteves, F., Campos, R.B.F., Lange, D., Nahas, L., dos Santos, I.A., Silva, R.R., Soares, S.A., Camacho, G.P., da Costa-Milanez, C.B., DaRocha, W., Diehl-Fleig, E., Frizzo, T., Harada, A.Y., Martello, F., 2022. Ant diversity studies in Brazil: an overview of the myrmecological research in a megadiverse country. Insectes Soc. 69, 105–121. https://doi.org/10.1007/s00040-022-00848-6

Schmidt, F.A., Ribas, C.R., Schoereder, J.H., 2013. How predictable is the response of ant assemblages to natural forest recovery? Implications for their use as bioindicators. Ecol. Indic. 24, 158–166. https://doi.org/10.1016/j.ecolind.2012.05.031

Schupp, E.W., 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107–108, 15–29. https://doi.org/10.1007/BF00052209

Schupp, E.W., Jordano, P., Gómez, J.M., 2010. Seed dispersal effectiveness revisited: a conceptual review. New Phytol. 188, 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Silva, R.R., Martello, F., Feitosa, R.M., Silva, O.G.M., do Prado, L.P., Brandão, C.R.F., de Albuquerque, E.Z., Morini, M.S.C., Delabie, J.H.C., dos Santos Monteiro, E.C., Emanuel Oliveira Alves, A., Wild, A.L., Christianini, A. V., Arnhold, A., Casadei Ferreira, A., Oliveira, A.M., Santos, A.D., Galbán, A., de Oliveira, A.A., Subtil, A.G.M., Dias, A.M., de Carvalho Campos, A.E., Waldschimidt, A.M., Freitas, A.V.L., Avalos, A.N., Meyer, A.L.S., Sánchez-Restrepo, A.F., Suarez, A. V., Souza, A.S., Queiroz, A.C.M., Mayhé-Nunes, A.J., da Cruz Reis, A., Lopes, B.C., Guénard, B., Trad, B.M., Caitano, B., Yagound, B., Pereira-Silva, B., Fisher, B.L., Tavares, B.L.P., Moraes, B.B., Filgueiras, B.K.C., Guarda, C., Ribas, C.R., Cereto, C.E., Esbérard, C.E.L., Schaefer, C.E.G.R., Paris, C.I., Bueno, C., Lasmar, C.J., da Costa-Milanez, C.B., Lutinski, C.J., Ortiz-Sepulveda, C.M., Wazema, C.T., Mariano, C.S.F., Barrera, C.A., Klunk, C.L., Santana, D.O., Larrea, D., Rother, D.C., Souza-Campana, D.R., Kayano, D.Y., Alves, D.L., Assis, D.S., Anjos, D., França, E.C.B., Santos, E.F., Silva, E.A., Santos, É.V., Koch, E.B., Siqueira, E.L.S., Almeida, É.A., Araujo, E.S., Villarreal, E., Becker, E., de Oliveira Canedo-Júnior, E., Santos-Neto, E.A., Economo, E.P., Araújo-Oliveira, É.S., Cuezzo, F., Magalhães, F.S., Neves, F.M., Rosumek, F.B., Dorneles, F.E., Noll, F.B., Arruda, F. V., Esteves, F.A., Ramos, F.N., Garcia, F.R.M., de Castro, F.S., Serna, F., Marcineiro, F.R., Neves, F.S., do Nascimento, G.B., de Figueiredo Jacintho, G., Camacho, G.P., Ribeiro, G.T., Lourenço, G.M., Soares, G.R., Castilho, G.A., Alves, G.P., Zurita, G.A., Machado Santos, G.H., Onody, H.C., Oliveira, H.S., Vasconcelos, H.L., Paulino-Neto, H.F., Brant, H., Rismo Coelho, I., de Melo Teles e Gomes, I.J., Leal, I.R., Dos Santos, I.A., Santos, I.C.S., Fernandes, I.O., Nascimento, I.C., Queiroz, J.M., Lattke, J.E., Majer, J., Schoereder, J.H., Dantas, J.O., Andrade-Silva, J., Díaz Guastavino, J.M., Silveira dos Santos, J., Filloy, J., Chaul, J.C.M., Lutinski, J.A., Carvalho, K.S., Ramos, K.S., Sampaio, K.L.S., Ribeiro, L.A.M., Sousa-Souto, L., Paolucci, L.N., Elizalde, L., Podgaiski, L.R., Chifflet, L., Carvalho-Leite, L.J., Calcaterra, L.A., Macedo-Reis, L.E., Magnago, L.F.S., Madureira, M.S., Silva, M.M., Pie, M.R., Uehara-Prado, M., Pizo, M.A., Pesquero, M.A., Carneiro, M.A.F., Busato, M.A., de Almeida, M.F.B., Bellocq, M.I., Tibcherani, M., Casimiro, M.S., Ronque, M.U.V., da Costa, M.M.S., Angotti, M.A., de Oliveira, M.V., Leponce, M., Imata, M.M.G., de Oliveira Martins, M.F., Antunes Ulysséa, M., do Espirito Santo, N.B., Ladino López, N.M., Balbino, N.S., da Silva, N.S., Safar, N.V.H., de Andrade, P.L., Camargo, P.H.S.A., Oliveira, P.S., Dodonov, P., Luna, P., Ward, P.S., Hanisch, P.E., Silva, P.S., Divieso, R., Carvalho, R.L., Campos, R.B.F., Antoniazzi, R., Vicente, R.E., Giovenardi, R., Campos, R.I., Solar, R.R.C., Fujihara, R.T., de Jesus Santos, R., Fagundes, R., Guerrero, R.J., Probst, R.S., de Jesus, R.S., Silvestre, R., López-Muñoz, R.A., de Souza Ferreira-Châline, R., Almeida, R.P.S., de Mello Pinto, S., Santoandré, S., Althoff, S.L., Ribeiro, S.P., Jory, T., Fernandes, T.T., de Oliveira Andrade, T., Pereira, T.P.L., Gonçalves-Souza, T., da Silva, T.S.R., Silva, V.N.G., Lopez, V.M., Tonetti, V.R., Nacagava, V.A.F., Oliveira, V.M., Dáttilo, W., DaRocha, W., Franco, W., Dröse, W., Antonialli, W., Ribeiro, M.C., 2022. ATLANTIC ANTS: a data set of ants in Atlantic Forests of South America. Ecology 103, 1–5. https://doi.org/10.1002/ecy.3580

Souza, J.L.P., Baccaro, F.B., Landeiro, V.L., Franklin, E., Magnusson, W.E., Pequeno, P.A.C.L., Fernandes, I.O., 2016. Taxonomic sufficiency and indicator taxa reduce sampling costs and increase monitoring effectiveness for ants. Divers. Distrib. 22, 111–122. https://doi.org/10.1111/ddi.12371

Van der Pijl, L., 1982. Principles of dispersal in higher plants. Springer Berlin Heidelberg, Berlin, Heidelberg.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., Van Calster, H., Peterken, G., Hermy, M., 2006. Extinction debt of forest plants presists for more than a century following habitat fragmentation. Ecology 87, 542–548. https://doi.org/10.1890/05-1182

Wilcoxon, F., 1946. Individual comparisons of grouped data by ranking methods. J. Econ. Entomol. 39, 269. https://doi.org/10.1093/jee/39.2.269

Wilker, I., Rabelo, M.A., Angotti, M.A., Ribas, C.R., 2022. Ant species that remove diaspores alone are more efficient removers. Sociobiology 69, e8308. https://doi.org/10.13102/sociobiology.v69i3.8308

Supplementary Material

Interactions between ants and diaspores in the Brazilian Atlantic Forest: an overview of trends and gaps in the literature

Ketlen Bona[1,2]*, Jacques H.C. Delabie[2,3], Luane K. Fontenele[4], Felipe Martello[5] e Eliana Cazetta[1,6]

[1]Laboratório de Ecologia Aplicada à Conservação, Programa de Pós-Graduação em Ecologia e Conservação da Biodiversidade, Ilhéus, BA, Brasil.
[2]Laboratório de Mirmecologia, Centro de Pesquisa do Cacau, CEPLAC, Ilhéus, BA, Brasil.
[3]Universidade Estadual de Santa Cruz, Departamento de Ciências Agrárias e Ambientais, Ilhéus, BA, Brasil.
[4]Laboratório de Ecologia de Formigas, Universidade Federal de Lavras, MG, Brasil.
[5]Informarções sobre Felipe.
[6]Universidade Estadual de Santa Cruz, Departamento de Ciências Biológicas, Ilhéus, BA, Brasil.

*Corresponding author. E-mail: bonaketlen@gmail.com

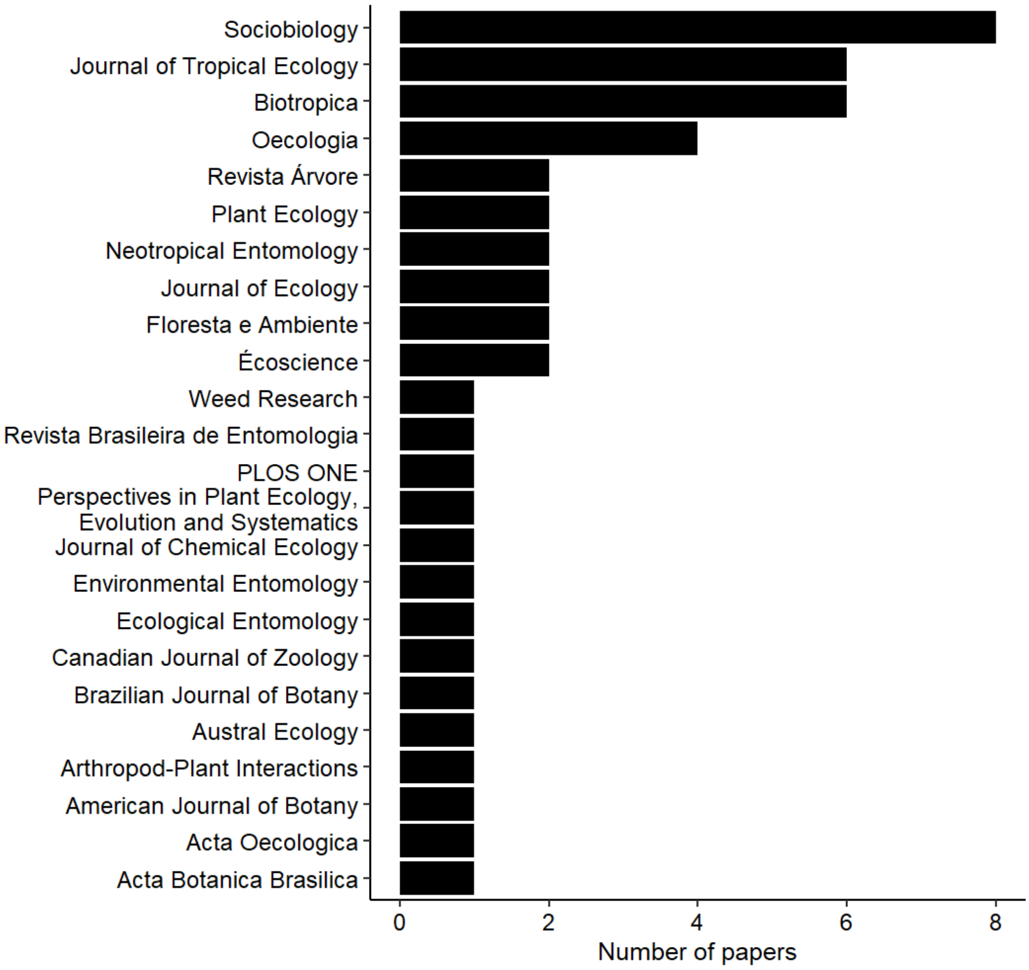


Figure S1. Journals and their respective publication numbers about interactions between ants and diaspores in the Brazilian Atlantic Forest.

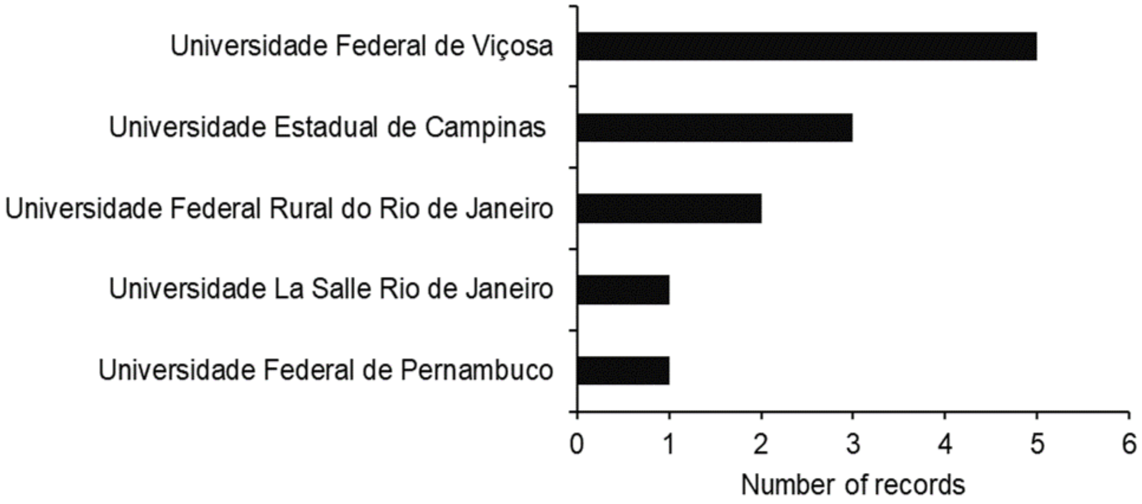


Figure S2. Number of studies (theses and dissertations) per academic repository found in the review.

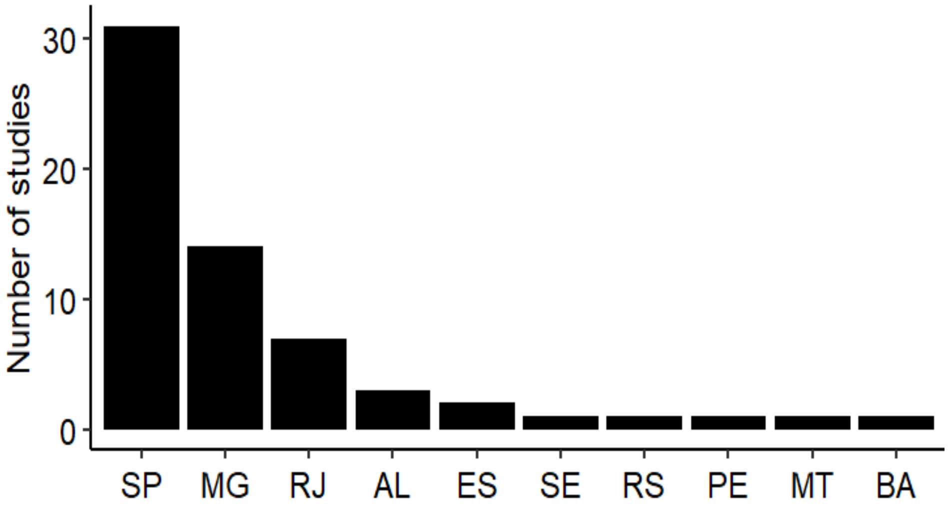


Figure S3. Number of studies per Brazilian state within the Atlantic Forest biome.

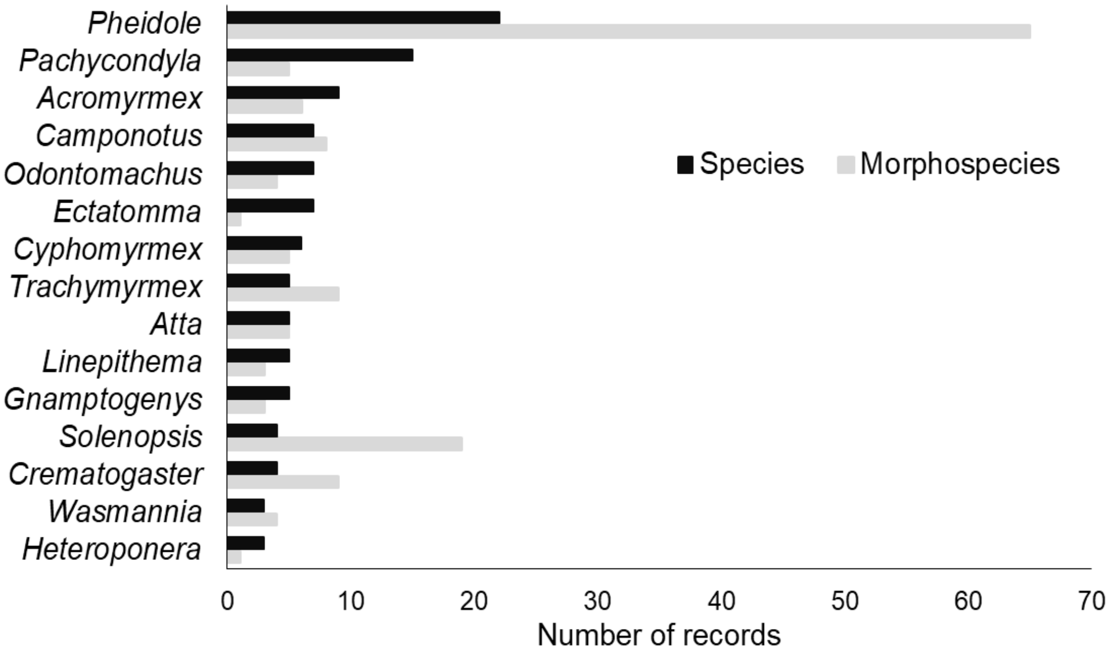


Figure S4. The top 15 most recorded species and morphospecies per ant genus in the review.

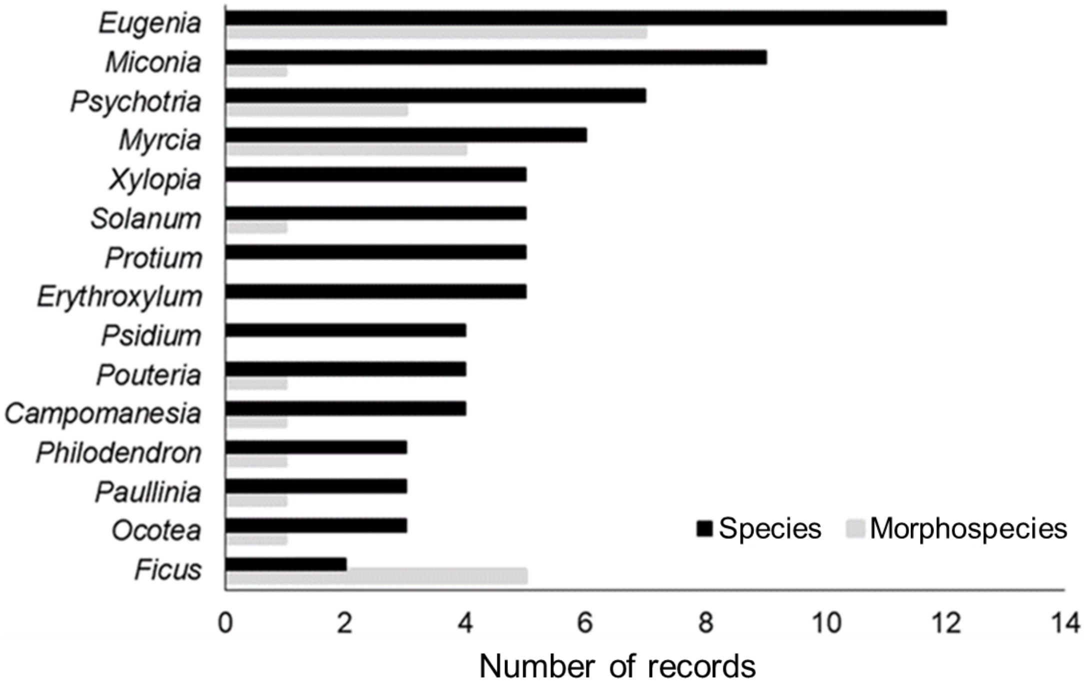


Figure S5. The top 15 most recorded species and morphospecies per plant genus in the review.

Table S1. Ant species identified by the Wilcoxon test as key species for diaspore removal in the Atlantic Forest.

Ant species	**p-value**
Atta sexdens	0.000
Ectatomma edentatum	0.000
Pachycondyla striata	0.001
Pheidole sp. 1	0.001
Acromyrmex subterraneus	0.002
Pheidole sp. 2	0.003
Pheidole sp. 7	0.004
Pheidole sp. 3	0.01
Pheidole sp. 8	0.01
Solenopsis sp. 1	0.012
Pheidole sp. 9	0.014
Atta laevigata	0.017
Pheidole sp. 4	0.02
Pheidole sp. 6	0.02
Gnamptogenys striatula	0.026
Camponotus rufipes	0.031
Odontomachus meinerti	0.031
Pheidole sp. 10	0.031
Pheidole sp. 15	0.031
Solenopsis sp. 2	0.033
Pachycondyla villosa	0.034
Pheidole sp. 5	0.034
Pachycondyla apicalis	0.036
Odontomachus chelifer	0.039
Linepithema micans	0.047
Cyphomyrmex sp.	0.054
Cyphomyrmex sp. 1	0.054
Ectatomma brunneum	0.054
Ectatomma opaciventre	0.054
Odontomachus sp.	0.054
Pachycondyla harpax	0.054
Pheidole sp. 11	0.054
Pheidole sp. 12	0.054
Pheidole sp. 13	0.054
Trachymyrmex sp. 1	0.054

Table S2. Ant species identified by the Wilcoxon test as key species for diaspore cleaning in the Atlantic Forest.

Ant species	**p-value**
Pheidole sp. 1	0.000
Pheidole sp. 3	0.000
Pheidole sp. 2	0.001
Pheidole sp. 4	0.001
Pheidole sp. 5	0.001
Solenopsis sp. 1	0.002
Pheidole sp. 6	0.003
Solenopsis sp. 4	0.007
Solenopsis sp. 5	0.007
Pheidole sp. 12	0.012
Crematogaster sp. 1	0.013
Pheidole sp. 11	0.013
Solenopsis sp. 2	0.013
Solenopsis sp. 3	0.013
Pheidole sp. 7	0.014
Pheidole sp. 8	0.014
Crematogaster sp. 2	0.034
Pheidole sp. 10	0.035
Pheidole sp. 14	0.035
Pheidole sp. 15	0.035
Pheidole sp. 9	0.035
Crematogaster sp.	0.047
Paratrechina sp. 2	0.047
Pheidole sp. 16	0.054

Table S3. Lipid content, plant life form, and length of diaspores used by key ant species in the Atlantic Forest (removal/cleaning).

Plant species	Lipid content	Plant form	Seed lenght (mm)
Abuta selloana	Low	Liana	NA
Aechmea nudicaulis	Low	Herb	15.6
Alchornea glandulosa	High	Tree	8
Alchornea triplinervia	High	Tree	5.8
Amaioua guianensis	Low	Tree	4.6
Andira fraxinifolia	Low	Tree	40.9
Annona cacans	Low	Tree	12.9
Annona crassiflora	Low	Tree	17.1
Annona neosericea	Low	Tree	8.7
Anthurium scandens	Low	Epiphyte	NA
Anthurium sellowianum	Low	Epiphyte	NA
Artocarpus heterophyllus	Low	Tree	32.5
Astrocaryum aculeatissimum	Medium	Palm	44.8
Attalea dubia	High	Palm	49.1
Bromelia balansae	Low	Herb	NA
Byrsonima ligustrifolia	Low	Tree	10.1
Byrsonima sericea	Low	Tree	6
Byrsonima stipulacea	Low	Tree	10.6
Cabralea canjerana	High	Tree	10
Calophyllum brasiliense	Low	Tree	20
Calyptranthes lucida	Low	Tree	3.9
Campomanesia neriifolia	Low	Tree	7.7
Campomanesia phaea	Low	Tree	7
Campomanesia xanthocarpa	Low	Tree	6
Carica papaya	Low	Tree	0.63
Casearia decandra	Medium	Tree	4.4
Casearia sylvestris	Medium	Tree	22.8
Cecropia glaziovii	Low	Tree	2
Cecropia pachystachya	Low	Tree	2
Chrysophyllum viride	Low	Tree	21.8
Citharexylum myrianthum	Low	Tree	11
Clidemia hirta	Low	Scrub	NA
Clusia criuva	High	Tree	10.3
Copaifera langsdorffii	Low	Tree	17
Copaifera trapezifolia	Low	Tree	18.3
Cryptocaria mandioccana	Medium	Tree	21.9
Cryptocarya moschata	Medium	Tree	11.5
Cupania oblongifolia	High	Tree	11.8
Cupania vernalis	High	Tree	11
Davilla elliptica	Low	Scrub	NA

Dialium guianense	Low	Tree	10.5
Diospyros hispida	Low	Tree	21.6
Diploon cuspidatum	Low	Tree	31
Duguetia lanceolata	Medium	Tree	17.5
Endlicheria paniculata	Medium	Tree	18.7
Erythroxylum ambiguum	Low	Scrub	0.93
Erythroxylum amplifolium	High	Scrub	7.48
Erythroxylum pelleterianum	High	NA	0.79
Erythroxylum pulchrum	Low	Scrub	14.1
Eschweilera ovata	Low	Tree	20.7
Eugenia cerasiflora	Low	Tree	14
Eugenia cuprea	Low	Tree	17.71
Eugenia melanogyna	Low	Tree	NA
Eugenia multicostata	Low	Tree	NA
Eugenia neoglomerata	Low	Tree	16.4
Eugenia oblongata	Low	Tree	NA
Eugenia punicifolia	Low	Tree	7.39
Eugenia stictosepala	Low	Tree	31.1
Eugenia uniflora	Low	Tree	16
Euterpe edulis	Medium	Palm	11.7
Ficus gomelleira	Low	Tree	0.5
Ficus insipida	Low	Tree	2.8
Garcinia gardneriana	Low	Tree	30.62
Gaylussacia brasiliensis	Low	Tree	2.7
Geonoma pauciflora	Medium	Palm	6.9
Geonoma schottiana	Medium	Palm	9.4
Gomidesia fenzliana	Low	Tree	6.78
Gomidesia spectabilis	Low	Tree	14.54
Guapira opposita	Low	Tree	6.1
Guarea guidonia	High	Tree	13
Guarea macrophylla	High	Tree	12.8
Guatteria australis	Low	Tree	10
Heisteria silviani	Low	Tree	15
Helicostylis tomentosa	Low	Tree	9.3
Henriettea succosa	Low	Scrub	15
Heteropsis oblongifolia	Low	Liana	NA
Hovenia dulcis	Low	Tree	NA
Hyeronima alchorneoides	Low	Tree	4
Hymenaea courbaril	Low	Tree	29
Ilex theezans	Low	Tree	3.5
Inga edulis	Low	Tree	21.3
Inga sessilis	Low	Tree	15
Manilkara salzmannii	Low	Tree	14

Manilkara subsericea	Medium	Tree	14.26
Marcgravia polyantha	Low	Liana	NA
Marlierea excoriata	Low	Tree	9.7
Marlierea tomentosa	Low	Tree	5.94
Maytenus aquifolia	Low	Tree	5.5
Maytenus robusta	Low	Scrub	9.04
Meliosma sellowii	Low	Tree	15
Mendoncia velloziana	Low	Liana	NA
Miconia albicans	Low	Scrub	NA
Miconia cabucu	Low	Scrub	2.6
Miconia calvescens	Low	Scrub	NA
Miconia hypoleuca	Low	Scrub	NA
Miconia minutiflora	Low	Scrub	NA
Miconia prasina	Low	Scrub	0.6
Miconia rubiginosa	Low	Scrub	NA
Monstera adansonii	Low	Liana	NA
Murraya paniculata	Low	Tree	NA
Myrceugenia myrcioides	Low	Tree	NA
Myrceugenia reitzii	Low	NA	NA
Myrcia bicarinata	Low	Tree	6.92
Myrcia pubipetala	Low	Tree	6.58
Myrcia rostrata	Low	Scrub	9.3
Myrcia spectabilis	Low	Tree	NA
Myrcia splendens	Low	Tree	6.1
Ocotea catharinensis	Medium	Tree	15.7
Ocotea pulchella	Medium	Tree	7
Parinari excelsa	Low	Tree	36
Paullinia micrantha	Low	Liana	NA
Paullinia seminuda	Low	Liana	NA
Pera glabrata	High	Tree	4
Persea willdenovii	Low	Tree	7.5
Philodendron appendiculatum	Low	Epiphyte	1.33
Philodendron corcovadense	Low	Epiphyte	3.41
Philodendron imbe	Low	Epiphyte	NA
Phoradendron crassifolium	Low	Epiphyte	NA
Piper caldense	Low	Scrub	NA
Posoqueria latifolia	Low	Tree	9.9
Pouroma guianensis	Low	Tree	17.5
Pouteria caimito	Low	Tree	40
Protium heptaphyllum	Low	Tree	9.23
Protium widgrenii	Low	Tree	NA
Prunus myrtifolia	Low	Tree	9
Psidium cattleianum	Low	Tree	4

Psidium guajava	Low	Tree	4.7
Psidium myrtoides	Low	Tree	7
Psittacanthus robustus	Low	Parasitic	NA
Psychotria leiocarpa	Low	Scrub	NA
Psychotria mapourioides	Low	Scrub	NA
Psychotria nuda	Low	Tree	NA
Psychotria suterella	Low	Tree	4.85
Quiina glaziovii	Low	Tree	NA
Rollinia sericea	High	Tree	34.82
Rudgea jasminoides	Low	Tree	NA
Rudgea villiflora	Low	Scrub	11.7
Schefflera morototonii	Low	Tree	5
Schinus terebinthifolius	Medium	Tree	3.5
Schlegelia parviflora	Low	NA	NA
Schwartzia brasiliensis	Low	Liana	NA
Siparuna guianensis	Low	Tree	5.8
Siphoneugenia guilfoyleiana	Low	NA	NA
Sloanea guianensis	High	Tree	NA
Solanum argenteum	Low	Tree	5.4
Solanum cinnamomeum	Low	Tree	NA
Solanum pseudoquina	Low	Tree	4.2
Sorocea hilarii	Low	Tree	NA
Syagrus romanzoffiana	Low	Palm	21
Symphonia globulifera	Low	Tree	28
Symplocos estrellensis	Low	Tree	NA
Symplocos laxiflora	Low	Tree	NA
Tabernaemontana flavicans	Low	Tree	6.9
Tapirira guianensis	Low	Tree	6.9
Ternstroemia brasiliensis	High	Scrub	5.89
Tetrastylidium grandifolium	High	Tree	NA
Tetrorchidium rubrivenium	High	Tree	6
Thyrsodium spruceanum	Low	NA	14.7
Tocoyena formosa	Low	Scrub	NA
Trema micrantha	Low	Tree	2
Vantanea compacta	Low	Tree	24
Virola bicuhyba	High	Tree	24
Virola gardneri	High	Tree	26
Virola oleifera	High	NA	NA
Xylopia aromatica	Medium	Tree	7.5
Xylopia langsdorfiana	Medium	Tree	8.6
Xylopia sericea	Medium	Tree	8

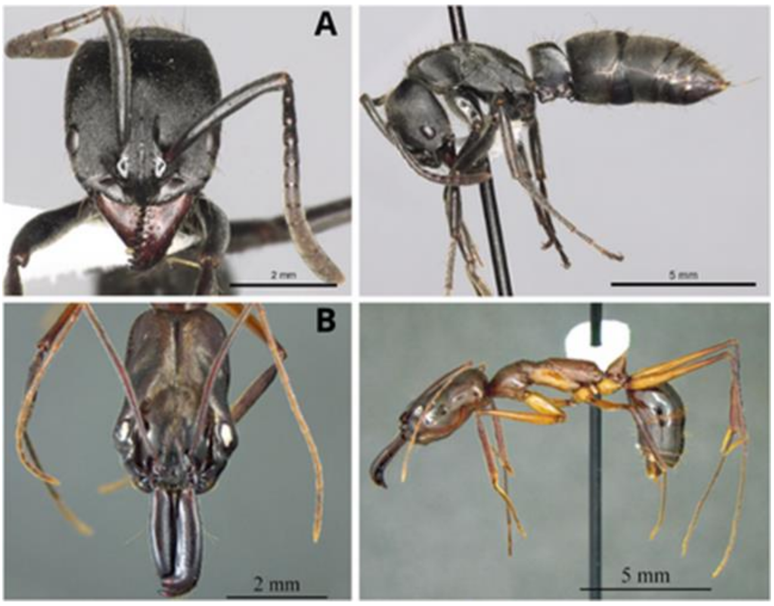


Figure S6. In frontal and lateral view, workers of two high quality ants for seed dispersal in Atlantic Forest. (A) *Pachycondyla striata* (CASENT0249158), (B) *Odontomachus chelifer* (ANTWEB1041409). Images by Ryan Perry and Juan Felipe Ortega, available from www.antweb.org. These two ant species played a key role in diaspore removal, which were considered key species for this interaction in the Atlantic Forest. The maximum diaspore removal distances by these two ant species recorded in our database were 12.54 m (A) and 5.2 m (B). Furthermore, these ants have a large body size (> 4 mm) and solitary foraging behavior, which characterizes high-quality ants for seed dispersal (see Leal et al 2014a in study references).

CONCLUSÕES GERAIS

Os resultados apresentados nesta tese contribuem para o avanço no conhecimento sobre as interações entre formigas e diásporos. A meta-análise global realizada no capítulo 1 elucidou resultados controversos encontrados na literatura sobre os efeitos de distúrbios antrópicos na remoção de diásporos por formigas. Aqui, demonstramos que a remoção de formiga é reduzida em 26% em locais submetidos a perturbações antrópicas. Esse impacto negativo de distúrbios antrópicos ocorre tanto em regiões temperadas (decréscimo de 38%) quanto tropicais (decréscimo de 19%). Além disso, mostramos que áreas submetidas a distúrbios relacionados à mineração reduzem a remoção de diásporos por formigas em 83% e fragmentação de habitats em 24%. No entanto, não encontramos evidências de efeitos em áreas submetidas a processos agrícolas (redução de 0,9%). Nossas descobertas demonstram a interferência negativa de distúrbios antrópicos em estágios iniciais cruciais para a regeneração natural dos ecossistemas, como a dispersão de sementes.

No capítulo 2 desta tese, compilamos 26 anos de pesquisa sobre interações entre formigas e diásporos na Mata Atlântica brasileira e apontamos lacunas de conhecimentos sobre aspectos qualitativos da dispersão de sementes. Surpreendentemente, demonstramos neste capítulo a grande escassez de estudos que avaliam os efeitos de distúrbios antrópicos nas interações formiga-diásporo nesse *hotspot* que está entre os mais criticamente ameaçados do mundo. Além disso, apontamos as espécies-chave de formigas para a remoção e para a limpeza de diásporos e propomos que as espécies *Pachycondyla striata* e *Odontomachus chelifer* sejam classificadas como dispersoras de alta qualidade. Com isso, sugerimos a priorização da conservação da Mata Atlântica em áreas de ocorrência dessas espécies, uma vez que são efetivas para a manutenção da dispersão de sementes nos ecossistemas. Também, mostramos que diásporos menores e com maiores concentrações de lipídios são mais removidos e limpos pelas formigas na Mata Atlântica. Por fim, demonstramos a necessidade da utilização de classificações baseadas em atributos ambientais mais refinados, como ecorregiões, em novos estudos sobre interações formigas-diásporos. Todas essas informações auxiliarão pesquisas posteriores e poderão subsidiar estratégias para a conservação das espécies de formigas e suas interações na Mata Atlântica.

Finalmente, todas as informações presentes nesta tese centralizam-se em um único consenso: formigas que dispersam sementes precisam ser preservadas para a manutenção da estabilidade de ecossistemas. Embora a dispersão de diásporos pelas formigas seja benéfica para plantas em escalas espaciais pequenas, essas interações aparentemente pequenas nos ecossistemas podem ser o ponto de partida para que grandes processos sejam concretizados. Assim, enfatizamos a necessidade da conservação de paisagens naturais para a perpetuação de processos ecológicos essenciais realizados pelas formigas.