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ISABELLE LEITE DE HOLANDA SILVA

AVALIAÇÃO DOS IMPACTOS DA URBANIZAÇÃO NA COMUNIDADE DE FORMIGAS E NA PROVISÃO DE SERVIÇOS ECOSSISTÊMICOS

Recife
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Tese apresentada ao Programa de Pós-Graduação em Biologia vegetal da Universidade Federal de Pernambuco, como requisito para obtenção do título de doutora em Biologia vegetal. Área de concentração: Ecologia e conservação

Orientador (a): Inara Roberta Leal

Coorientador (a): Xavier Arnan

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BANCA EXAMINADORA

_____
Prof(a). Dr(a). Inara Roberta Leal (Orientador(a))
UFPE

_____
Prof(a). Dr(a). CARLA RODRIGUES RIBAS (Examinador(a) Externo(a))
UFRPE

_____
Dr. ANDERSON DANTAS LEAL (Examinador(a) Externo(a))
UFPE

_____
Prof(a). Dr(a). FERNANDA MARIA PEREIRA DE OLIVEIRA (Examinador(a) Interno(a))
UFPE

_____
Dr. RONALD NOUTCHEU (Examinador(a) Interno(a))
UFPE

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RESUMO

A urbanização transforma paisagens naturais, introduzindo filtros ambientais que afetam a biodiversidade, a estrutura das comunidades biológicas e os serviços ecossistêmicos. Nesta tese, investiguei os padrões de diversidade das comunidades de formigas ao longo de um gradiente de urbanização e suas consequências para a dispersão de sementes. O estudo foi conduzido na Região Metropolitana do Recife, onde coletamos formigas utilizando armadilhas, analisamos sua tolerância térmica máxima e mensuramos atributos morfológicos. Também avaliamos a taxa de remoção de sementes como medida do serviço ecossistêmico. Os resultados indicaram que, apesar da riqueza e abundância de formigas permanecerem constantes ao longo do gradiente, a composição taxonômica e funcional mudou. Generalistas, como onívoros epigéicos e Attini cortadeiras, tornaram-se dominantes em áreas urbanizadas, enquanto especialistas, como predadores epigéicos e onívoros crípticos, reduziram-se. A descoberta de recursos alimentares foi mais rápida em ambientes altamente urbanizados, sugerindo ajustes no comportamento de forrageamento. Com relação aos traços funcionais, a tolerância térmica máxima foi conservada entre as espécies. Os atributos morfológicos permaneceram estáveis, mas houve uma redução no tamanho da perna e mandíbula de *Atta sexdens* em ambientes urbanizados. A dispersão de sementes por formigas também foi impactada. Registramos 443 indivíduos de 29 espécies interagindo com 2.705 sementes artificiais, das quais 26,4% foram removidas e 73,6% apenas limpas. A taxa de remoção de sementes diminuiu com o aumento da urbanização, enquanto a limpeza das sementes aumentou, sugerindo impactos na regeneração vegetal nesses ambientes. Os resultados evidenciam que a urbanização altera a estrutura das comunidades de formigas e seus papéis ecológicos, favorecendo espécies generalistas e modificando interações ecológicas essenciais. Além disso, a substituição de dispersores eficientes por espécies de baixa qualidade pode comprometer a dinâmica de regeneração vegetal em ecossistemas urbanos. A compreensão dessas mudanças é fundamental para avaliar os impactos da urbanização sobre a biodiversidade e os serviços ecossistêmicos, subsidiando estratégias de conservação em cidades.

Palavras-chave: Formigas urbanas, Gradiente urbano, Remoção de sementes, Traços funcionais

ABSTRACT

Urbanization transforms natural landscapes, introducing environmental filters that affect biodiversity, the structure of biological communities, and ecosystem services. In this thesis, I investigated the diversity patterns of ant communities along an urbanization gradient and their consequences for seed dispersal. The study was conducted in the Metropolitan Region of Recife, where we collected ants using traps, analyzed their maximum thermal tolerance, and measured morphological attributes. We also assessed seed removal rates as a measure of ecosystem service provision. The results indicated that, although ant richness and abundance remained constant along the gradient, taxonomic and functional composition changed. Generalists, such as epigaeic omnivores and leaf-cutting Attini, became dominant in urbanized areas, while specialists, such as epigaeic predators and cryptic omnivores, declined. Resource discovery was faster in highly urbanized environments, suggesting adjustments in foraging behavior. Regarding functional traits, maximum thermal tolerance was conserved among species. Morphological attributes remained stable overall, but *Atta sexdens* showed reduced leg and mandible size in urban environments. Seed dispersal by ants was also affected. We recorded 443 individuals from 29 species interacting with 2,705 artificial seeds, of which 26.4% were removed and 73.6% were only cleaned. Seed removal rates decreased with increasing urbanization, while seed cleaning increased, suggesting potential impacts on plant regeneration in these environments. The results highlight that urbanization alters ant community structure and their ecological roles, favoring generalist species and modifying essential ecological interactions. Moreover, the replacement of efficient seed dispersers by lower-quality species may compromise plant regeneration dynamics in urban ecosystems. Understanding these changes is crucial for assessing the impacts of urbanization on biodiversity and ecosystem services, supporting conservation strategies in cities.

Keywords: Urban ants, Urban gradient, Seed removal, Functional traits

SUMÁRIO

1 APRESENTAÇÃO

A urbanização é um dos processos mais significativos que moldam os ambientes terrestres, especialmente diante do aumento acelerado da população humana (MCKINNEY, 2008). Esse processo promove a diminuição da cobertura vegetal e a impermeabilização do solo, que potencializam os efeitos da temperatura nos habitats, como o fenômeno das ilhas de calor urbano. Esses filtros ambientais modificam os padrões de distribuição e afetam a composição e a estrutura das comunidades biológicas (FERRANTE et al., 2014; BENINDE et al., 2015; CASALEGNO et al., 2017). Essas mudanças limitam não apenas a distribuição das espécies (DIAMOND et al., 2012), mas também a vulnerabilidade dos organismos e os serviços ecossistêmicos que eles promovem (ARNAN et al., 2015). As cidades, embora frequentemente vistas como espaços hostis à biodiversidade, podem ser compreendidas como ecossistemas com habitats de diferentes qualidades, capazes de abrigar comunidades com composições variadas de espécies. Dentre os organismos afetados por essas mudanças, as formigas desempenham um papel fundamental nos ecossistemas urbanos, participando de diversos processos ecológicos.

A compreensão do papel das formigas em ecossistemas urbanos é particularmente importante, pois elas desempenham funções ecológicas essenciais servindo de serviços ecossistêmicos, como a dispersão de sementes. Nesse contexto, a literatura existente ainda carece de um entendimento mais profundo sobre como as mudanças nos padrões de urbanização influenciam a adaptação das formigas, suas interações ecológicas e, consequentemente, a prestação desses serviços. Embora se saiba que as formigas são organismos altamente adaptáveis a ambientes urbanos, as respostas específicas de diferentes espécies a variações na urbanização e como isso afeta sua função nos ecossistemas urbanos ainda são pouco exploradas.

Esta tese busca preencher essa lacuna, oferecendo uma análise detalhada dos efeitos da urbanização sobre as comunidades de formigas e seus serviços ecossistêmicos, com foco particular na dispersão de sementes. Ao longo de três capítulos principais, esta pesquisa aborda a estrutura taxonômica e funcional das comunidades de formigas, os traços funcionais que explicam suas respostas à

urbanização e as interações das formigas como serviços ecológicos. O primeiro capítulo investiga como as comunidades de formigas se distribuem ao longo de um gradiente de urbanização, enquanto o segundo capítulo explora os traços funcionais das formigas, como a tolerância térmica e os atributos morfológicos, que podem explicar suas adaptações aos ambientes urbanos. O terceiro capítulo examina a função ecológica das formigas na dispersão de sementes, essencial para a regeneração das plantas urbanas.

A relevância desta pesquisa está na necessidade urgente de entender os impactos da urbanização sobre as comunidades biológicas e seus serviços ecossistêmicos. Compreender como as formigas se adaptam às pressões urbanas e o impacto disso na prestação de serviços ecológicos pode orientar estratégias de conservação mais eficazes. Em particular, destaca-se a importância de preservar "reservatórios de biodiversidade" em habitats urbanos, a fim de garantir que os serviços ecossistêmicos oferecidos por esses organismos sejam mantidos, contribuindo para um desenvolvimento urbano mais sustentável e equilibrado.

2 FUNDAMENTAÇÃO TEÓRICA

2.1- A Urbanização e seus impactos na biodiversidade

A urbanização é um processo multidimensional que se manifesta por meio de rápidas transformações na população e na cobertura do solo. A expansão das cidades resulta da combinação de quatro fatores principais: crescimento populacional, migração rural-urbana, deslocamentos em massa causados por eventos extremos e redefinições de limites administrativos (ELMQVIST et al., 2013). Trata-se de um fenômeno em contínua expansão, mais duradouro do que outras formas de perda de habitat, que leva à homogeneização biótica e à redução da singularidade dos ecossistemas locais (BLAIR, 2001). Como consequência, impacta profundamente a biodiversidade e os serviços ecossistêmicos (ELMQVIST et al., 2013). A crescente extensão das áreas urbanas avança a um ritmo acelerado, exigindo a conversão de ecossistemas naturais em espaços urbanos para suprir a demanda da população humana e suas atividades (SETO et al., 2012). Esse

crescimento não apenas altera o uso da terra, mas também modifica o clima local e regional, criando ilhas de calor e alterando padrões de temperatura e precipitação (GRIMM et al., 2008), o que afeta funções ecológicas essenciais (SETO & PANDEY, 2019). Além disso, resulta no consumo intensivo de recursos naturais, como água e terras agrícolas, ameaçando habitats e a biodiversidade local (SETO et al., 2012).

A urbanização, quando analisada sob um viés espacial, é caracterizada pela distribuição de elementos construídos pelo homem, como estradas e edifícios, que são indicadores desse processo (WU, 2014). A diversidade biológica pode ser alterada e, diferentes níveis de urbanização, pois diferentes espécies respondem de formas distintas à proximidade com áreas urbanizadas. Algumas espécies prosperam em ambientes urbanos, enquanto outras são evitadas, criando uma dinâmica populacional complexa. Battin (2004) observa que as cidades podem funcionar como "fontes" ou "sumidouros" para determinadas espécies, dependendo da qualidade ambiental local. Em áreas de alta qualidade ecológica, as populações podem crescer, enquanto em locais degradados, as populações declinam, caracterizando "armadilhas ecológicas". Ademais, a abundância de espécies também é influenciada por fatores locais, como o "efeito de vizinhança" descrito por Dunning et al. (1992), que demonstra que a interação com áreas adjacentes, como fragmentos de vegetação remanescente, impacta diretamente a presença e a sobrevivência de espécies urbanas.

A biodiversidade desempenha um papel crucial na manutenção de diversos serviços ecossistêmicos essenciais para o bem-estar humano (FULLER et al . 2007). Recursos como alimentos, madeira para construção, água potável e combustíveis dependem diretamente da biodiversidade (BOLUND 1999). A fixação de nitrogênio realizada por plantas como as leguminosas é fundamental para a produtividade agrícola. Florestas preservadas próximas a cultivos, como os de café, proporcionam polinizadores que podem melhorar o rendimento das plantações em até 20% (MELILLO & SALA, 2008). Assim, a biodiversidade é essencial não apenas para a segurança alimentar e a saúde humana, mas também para a resiliência dos ecossistemas urbanos, auxiliando na adaptação às mudanças climáticas e promovendo a qualidade de vida (E.M.A, 2005). No entanto, a biodiversidade está em declínio, e pesquisadores identificaram um possível sexto grande evento de

extinção, impulsionado principalmente pelas atividades humanas (WILSON, 2005). As ações antrópicas estão alterando irreversivelmente a diversidade biológica do planeta, conforme descrito na Avaliação Ecossistêmica do Milênio (2005). As taxas de extinção continuam a aumentar, e o número de espécies ameaçadas segue crescendo (PIMM et al., 1995), demonstrando que a pressão da urbanização e de outras atividades humanas sobre os ecossistemas se intensifica.

A urbanização impacta a biodiversidade principalmente pela conversão do uso da terra e pelo desmatamento. Embora as áreas urbanas cubram cerca de 3% da superfície terrestre (MCGRANAHAN et al., 2006), sua influência ultrapassa esses limites (SCHNEIDER et al., 2009; SETO et al., 2010). A concentração da urbanização em regiões de alta biodiversidade amplia as ameaças a espécies raras e vulneráveis (SETO et al., 2010). Apesar de ocuparem uma pequena fração da superfície terrestre, as cidades abrigam a maior parte da população mundial e são centros dinâmicos de atividades humanas, com decisões urbanas influenciando a biodiversidade em diferentes escalas (PYŠEK & JAROŠÍK, 2005). Cidades maiores tendem a abrigar mais espécies exóticas do que localidades menores devido à maior complexidade das paisagens e à ampla disponibilidade de habitats, facilitando a introdução e permanência de espécies invasoras (PYŠEK et al., 2004). No entanto, a análise da biodiversidade urbana pode ser limitada por fatores como métodos de amostragem e variações nos limites urbanos e padrões de propriedade ao longo do tempo (van Heezik et al., 2012).

Diante dessas limitações, abordagens que consideram gradientes de urbanização são fundamentais para uma compreensão mais precisa dos impactos urbanos sobre a biodiversidade (MELÉNDEZ et al., 2023). Esse tipo de abordagem permite avaliar como diferentes níveis de urbanização afetam a composição e distribuição das espécies, identificando padrões que seriam invisíveis em estudos restritos a um único tipo de paisagem. Além disso, o uso de gradientes facilita a identificação de transições ecológicas e auxilia no planejamento de estratégias de conservação mais eficazes (MCDONNELL & HAHS, 2008).

2.2 – Respostas dos organismos a urbanização: Traços funcionais

A urbanização tem impactado as estruturas populacionais das espécies, alterando os filtros ambientais aos quais elas estão expostas (ARONSON et al., 2016). Para entender como essas espécies persistem frente a esses novos desafios, é fundamental analisar os traços funcionais que determinam sua capacidade de interagir e sobreviver nos ambientes urbanos (SANTINI et al., 2019). A ecologia funcional, que investiga essas plasticidades, desempenha um papel crucial na compreensão das respostas dos organismos frente as perturbações, especialmente em contextos fortemente influenciados pelas atividades humanas (CADOTTE, 2017). Os traços funcionais, que incluem características fisiológicas, morfológicas e comportamentais dos organismos, são determinantes cruciais para sua sobrevivência, reprodução e interações com o ambiente ao seu redor (VIOLLE et al., 2007). Algumas espécies podem se tornar mais tolerantes ao calor, à poluição do ar ou à escassez de alimentos, enquanto outras podem ter seus comportamentos alimentares alterados para se adaptar ao novo ambiente (ROTA 2018; KOTZE et al., 2022; CHEN & NEOH 2023).

Em ambientes urbanos onde as espécies enfrentam condições muitas vezes extremas, como aumento da temperatura, poluição, presença de espécies invasoras e fragmentação de habitats (MCDONNELL & HAHS, 2015). Como resultado, as adaptações relacionadas aos traços funcionais das espécies se tornam ainda mais evidentes, refletindo a capacidade desses organismos de lidar com os desafios impostos pela urbanização (ALBERTI et al., 2017). Por exemplo, estudos indicam que aves urbanas podem apresentar cérebros relativamente maiores, possivelmente para lidar com a complexidade do ambiente urbano (MAKLAKOV et al., 2011). Além disso, algumas espécies de anuros, exibem redução no tamanho corporal e alterações no canto em áreas urbanas, influenciadas por fatores como aumento da temperatura, menor umidade e maior nível de ruído (CAVALCANTE-PINTO et al., 2020). Insetos também apresentam mudanças na tolerância térmica e modificações morfológicas associadas à urbanização, embora os efeitos variem entre grupos taxonômicos (MARTINSON & RAUPP, 2013; MERCKX et al., 2018; BISHOP et al., 2017; BUCHHOLZ et al., 2020).

A temperatura é um dos principais fatores que influenciam a reestruturação da biota em ambientes urbanos, variando espacial e temporalmente nos habitats dos

organismos (DIAMOND et al., 2012). A urbanização, ao remover a vegetação e impermeabilizar o solo, intensifica os efeitos térmicos, restringindo a distribuição das espécies e alterando suas interações ecológicas (URBAN et al., 2024). As mudanças térmicas em habitats urbanos afetam diretamente a biologia das espécies, influenciando seu desempenho, vulnerabilidade e as interações com os serviços ecossistêmicos (JANZEN 1967; GASTON 2000; ARNAN & BLÜTHGEN 2015). A tolerância térmica máxima (TTM), ou "Ctmáx", é um traço fisiológico fundamental que indica a temperatura na qual os organismos perdem a capacidade locomotora ou sofrem mortalidade diante de aumentos rápidos de temperatura (DIAMOND et al., 2012). Esse limite fisiológico determina o desempenho, a atividade e o comportamento das espécies (STEVENS 1992; CAMARA et al., 2024). Por exemplo, em formigas, diferenças na TTM influenciam a coexistência de espécies dominantes e subordinadas em diversos ecossistemas (CERDÁ et al., 1997; 1998; BESTELMEYER 2000; LESSARD et al., 2009). Além de definir a ocupação dos habitats, esses limites térmicos moldam os períodos de atividade e as interações ao longo do dia e do ano, impactando a qualidade dos serviços ecossistêmicos que as formigas promovem (ARNAN et al., 2015; TAMASHIRO et al., 2019).

Outro fator relevante que determina as respostas das comunidades de formigas e de outros insetos é o tamanho do corpo (GIBB et al., 2018). Uma meta-análise de 23 estudos indicou que Hymenoptera, Hemiptera, Odonata e Orthoptera demonstram mudanças significativas em suas características morfológicas, principalmente relacionadas ao tamanho corporal e à dispersão (BAILEY et al., 2021). Em muitos casos, espécies urbanas apresentam aumento do tamanho corporal, o que pode ser favorecido pela necessidade de maior mobilidade para superar a fragmentação do habitat (BAILEY et al., 2021). Por outro lado, a seleção por fenótipo de dispersão pode influenciar a morfologia de diferentes formas, dependendo da ecologia da espécie e do grau de isolamento dos ambientes urbanos (MERCKX et al., 2018).

Esses traços são respostas às pressões seletivas impostas pelos ambientes urbanos, e podem ter efeitos em cascata nas interações ecológicas, afetando não apenas a sobrevivência e o sucesso reprodutivo das espécies, mas também o funcionamento dos ecossistemas urbanos (GOODNESS et al., 2016;

MCPHEARSON et al., 2016; THEODOROU et al., 2021). Podendo afetar a eficiência dos serviços ecossistêmicos associados, como a polinização, a decomposição e o controle de pragas (THEODOROU et al., 2021). Assim, a urbanização gera um contexto de mudanças rápidas e significativas que desafiam as espécies a se adaptarem aos novos cenários. A compreensão de como esses traços funcionais se modificam em resposta às pressões urbanas oferece uma visão crucial de como os organismos se ajustam e como esses ajustes influenciam a dinâmica ecológica nas cidades.

2.3 – Influência da urbanização na provisão de serviços ecossistêmicos

A urbanização tem gerado crescente atenção sobre os serviços ecossistêmicos urbanos, com um número cada vez maior de estudos avançando nossa compreensão sobre as diferentes dimensões desses serviços. Iniciativas importantes, como a Avaliação dos Ecossistemas do Milênio (EMA, 2005) e a Economia dos Ecossistemas e da Biodiversidade (TEEB, 2011), destacaram a relevância dos serviços ecossistêmicos urbanos no debate sobre sustentabilidade. Apesar disso, o foco nos ecossistemas urbanos ainda é modesto em comparação com outros ecossistemas naturais, mesmo com mais da metade da população mundial vivendo atualmente em áreas urbanas (ELIZALDE et al., 2020). Os serviços ecossistêmicos são classificados em quatro grandes categorias: provisão, regulação, habitat e culturais/amenidades (MA, 2005). Os serviços de provisão englobam produtos materiais, como alimentos e água doce, enquanto os serviços reguladores envolvem benefícios como a regulação do clima e da água. Os serviços culturais são não materiais, como experiências espirituais, recreativas e estéticas, e os serviços de habitat incluem funções essenciais para o equilíbrio dos ecossistemas, como a produção de biomassa e o ciclo de nutrientes (MA, 2005).

Os ecossistemas urbanos desempenham um papel crucial ao fornecer serviços diretamente ligados à saúde humana, como a purificação do ar, redução de ruídos e a mitigação de escoamento, com a relevância desses serviços variando conforme as características ambientais e socioeconômicas de cada região (MACE et al. 2012). Pesquisas consideráveis demonstraram que a urbanização é uma das principais

forças motrizes para a mudança dos serviços ecossistêmicos (GARCÍA-NIETO et al., 2018; B. LI et al., 2016; ZHOU et al., 2018). Um exemplo claro do impacto da urbanização sobre a biodiversidade é a perda de espécies frugívoras de aves em regiões urbanas, comprometendo a capacidade de dispersão de sementes e a colonização de novos ambientes pelas plantas (MORANTE-FILHO et al., 2015). Os processos de urbanização afetam particularmente os parceiros mutualistas essenciais, como polinizadores e dispersores de sementes, que frequentemente são mais especializados e suscetíveis a perturbações antrópicas (THEODOROU et al., 2016; OLIVEIRA et al., 2019; ELIZALDE et al., 2020; SILVA et al., 2020). O aumento da urbanização está associado a alterações ambientais que reduzem a riqueza de organismos chaves, resultando em uma perda potencial de serviços ecossistêmicos nas áreas urbanas (MITCHELL & DEVISSCHER, 2022; PAL et al., 2019). A polinização, a regulação de pragas e a dispersão de sementes são processos essenciais para a diversidade funcional dos ecossistemas urbanos e podem desempenhar um papel crítico em sua durabilidade a longo prazo (ANDERSSON et al., 2007; HOHLENWERGER et al., 2021). Esses serviços, no entanto, estão cada vez mais ameaçados pela perda de habitats e pela fragmentação causadas pelo crescimento urbano (HOHLENWERGER et al., 2021). Em resposta, espaços verdes urbanos, como jardins comunitários, jardins privados e outros pequenos refúgios de vegetação, têm se mostrado cruciais para o suporte desses serviços essenciais (AHRNÉ et al., 2009).

Os artrópodes são excelentes candidatos para estudar os efeitos da urbanização porque desempenham uma ampla gama de serviços ecossistêmicos e servem como importantes bioindicadores de mudanças ecológicas (NIEMELÄ, 1999; MCINTYRE, 2000; BURKMAN & GARDINER, 2014). As formigas, em particular, são importantes porque representam uma variedade de níveis tróficos, têm tempos de geração relativamente curtos e, portanto, respondem rapidamente às mudanças ambientais, além de serem consideradas bioindicadoras importantes de habitats alterados pelo homem (MAJER, 1983, ANDERSEN, 1997, HOFFMANN & ANDERSEN, 2003, 2004; LÓPEZ-MORENO et al., 2003, LESSARD & BUDDLE, 2005; ZARA et al., 2021). A capacidade de adaptação das formigas aos ambientes urbanos é amplamente documentada, com algumas espécies estabelecendo populações estáveis mesmo em habitats densamente urbanizados (MAJER &

BROWN, 1986; LÓPEZ-MORENO & DÍAZ-BETANCOURT, 1995). Suas interações com outros organismos, especialmente as plantas (ZARA et al., 2021). Além de desempenharem um papel central na dispersão de sementes, protegendo-as contra predadores e contribuindo para a regeneração vegetal (LEAL et al., 2007; ELIZALDE et al., 2020; ZARA et al., 2021), que são essenciais para a manutenção dos ecossistemas urbanos. Também foi documentado que sua atividade subterrânea melhora a qualidade do solo, promovendo a infiltração de água e redistribuindo matéria orgânica e inorgânica, favorecendo ainda mais o crescimento da vegetação, e consequentemente aumenta a heterogeneidade do habitat (FOLGARAIT, 1998; NKEM et al., 2000; STREITBERGER & FARTMANN, 2015). Outro serviço ecossistêmico importante proporcionado pelas formigas é o controle biológico de pragas. Ao predarem insetos herbívoros, ajudam a reduzir os danos às plantas e a manter a estabilidade das comunidades vegetais (OLIVEIRA & FREITAS, 2004; TANAKA et al., 2009). A relevância dos estudos sobre serviços ecossistêmicos nas cidades é cada vez mais reconhecida, tanto para melhorar a saúde e o bem-estar dos residentes urbanos quanto para equilibrar o crescimento urbano com a conservação da biodiversidade (GASTON et al., 2013; ELIZALDE et al., 2020).

2.4 - Formigas em Ambientes Urbanos

As formigas são excelentes organismos para estudos de monitoramento ambiental devido à sua grande abundância, diversidade de espécies, presença contínua ao longo do ano e estabilidade dos ninhos (KOCH & VOHLAND, 2008). Além disso, elas ocupam uma ampla variedade de nichos alimentares, tanto no solo quanto na vegetação, o que resulta em uma diversidade local frequentemente superior à de outros insetos sociais na maioria dos habitats (HÖLLDOBLER & WILSON, 1990). Seu potencial como bioindicadoras tem sido cada vez mais reconhecido, tornando-se ferramentas valiosas para gestores ambientais na avaliação das condições dos ecossistemas (UNDERWOOD & FISHER, 2006; ALONSO & AGOSTI, 2000; ŚLIPIŃSKI et al., 2012; HETERICK et al., 2013). Adicionalmente formigas desempenham um papel essencial nos ecossistemas, contribuindo para o ciclo de nutrientes, a estruturação do solo e a manutenção da composição da vegetação (DEL TORO et al., 2012; SANFORD et al., 2009). Além

disso, são provedoras de importantes serviços ecossistêmicos, como a aeração do solo, proteção anti-herbivoria, dispersão de sementes (LEAL et al., 2003; RIBBONS & PELINI, 2012).

Apesar de sua importância, as formigas urbanas têm recebido pouca atenção científica, representando apenas 3,6% de todas as publicações sobre formigas (SANTOS, 2016). No entanto, os estudos existentes destacam hipóteses relevantes e fornecem implicações importantes para a compreensão da ecologia dos sistemas urbanos, justificando o interesse no papel das formigas nas cidades, áreas verdes e edificações (YAMAGUCHI, 2005; BUCZKOWSKI & RICHMOND, 2012). As pesquisas sobre formigas em ambientes urbanos abrangem temas variados dentro da ecologia e da biodiversidade, analisando a riqueza, diversidade e composição das espécies, bem como sua relação com fatores abióticos e bióticos (ESPADALER & LÓPEZ-SORIA, 1991; CEREJA, 2001; IVANOV & KEIPER, 2009; MUNHAE et al., 2009; SOUZA et al., 2012). Além disso, muitos trabalhos focam na presença de formigas invasoras, exóticas e nativas (OI et al., 1994; BUCZKOWSKI & BENNETT, 2006; HOLWAY & SUAREZ, 2006; SCHULTZ & BUSCH, 2009; SILVA et al., 2009; RODRIGUES et al., 2010), bem como no desenvolvimento e teste de métodos químicos e biológicos para controle e manejo de espécies consideradas pragas (OI et al., 1996; REY & ESPADALER, 2004; BRIGHTWELL et al., 2010; GUSMÃO et al., 2011). Além da importância ecológica, a relevância das formigas urbanas se estende às esferas social e econômica. Socialmente, a interação das formigas com seres humanos, outros animais e a flora local tem sido evidenciada, especialmente em pesquisas sobre saúde pública, uma vez que muitas formigas compartilham o mesmo espaço físico dos seres humanos, podendo causar prejuízos sanitários e econômicos (PESQUERO et al., 2008; BLIGHT et al., 2009). No aspecto econômico, diversos estudos têm sido direcionados ao controle de formigas-praga, com ênfase no uso de produtos químicos para manejo dessas populações (KLOTZ et al., 2010 Greenberg, L., Rust, M. K., Klotz, J. H., Haver, D., Kabashima, J. N., Bondarenko, S., & Gan, J. (2010). Impact of ant control technologies on insecticide runoff and efficacy. Pest management science, 66(9), 980-987.). Ecologicamente, os estudos demonstram resultados variados sobre a permanência de formigas nativas nos ecossistemas urbanos, relacionados ao nível de perturbação antrópica (LESSARD & BUDDLE, 2005; SANFORD et al., 2009; SANTOS, 2016).

A diversidade funcional das formigas também influencia sua resposta à perturbação, podendo ser uma ferramenta chave para o entendimento dos impactos da urbanização. Baseando se na classificação dos grupos funcionais de formigas (LEAL et al., 2012): espécies generalistas apresentam maior capacidade de colonizar pequenos fragmentos urbanos, pois possuem dietas variadas, toleram diferentes condições ambientais e recolonizam áreas degradadas rapidamente. Por outro lado, formigas especializadas, como predadores específicos, espécies crípticas e aquelas adaptadas a condições climáticas particulares, tendem a ser mais sensíveis à perturbação, pois dependem de recursos específicos e possuem menor flexibilidade ecológica. Esse padrão reflete uma tendência observada em diversos grupos biológicos, onde ambientes degradados favorecem espécies oportunistas e comuns em detrimento das raras e especializadas. Apesar das mudanças claras na composição das comunidades de formigas em áreas urbanas (GIBB & HOCHULI, 2002; YAMAGUCHI, 2004; LESSARD & BUDDLE, 2005; PACHECO & VASCONCELOS, 2007), ainda há pouco conhecimento sobre como esses insetos diferem entre os diversos tipos de espaços verdes dentro das cidades. Dada sua diversidade ecológica e suas interações complexas com o ambiente, as formigas representam um excelente modelo para avaliar os impactos da urbanização na biodiversidade e para monitorar a persistência da fauna em paisagens tropicais modificadas.

2.5 - Dispersão de sementes por formigas

A dispersão de sementes por formigas (mirmecocoria) é um método amplamente distribuído, envolvendo 11.000 espécies de angiospermas de 77 famílias botânicas (LEAL et al., 2007; LENGYEL et al., 2010; PENN & CRIST, 2018). As plantas mirmecocóricas são particularmente abundantes e diversas em habitats como as florestas temperadas do Hemisfério Norte e os arbustos esclerofilos em climas mediterrâneos, como na África do Sul, Austrália, sul da Europa e América do Sul (BERG, 1975; BEATTIE, 1985; BOND & SLINGSBY, 1983; WESTOBY et al., 1991; LENGYEL et al., 2009; LEAL et al., 2007). As formigas são atraídas pelos diásporos que caem ao chão e removem o elaiossomo, um processo que pode facilitar a quebra da dormência e aumentar o sucesso da germinação (HUGHES &

WESTOBY, 1992; CANNER et al., 2012; PACINI, 1990; LOBSTEIN & ROCKWOOD, 1993). Além disso, ao transportar as sementes para seus ninhos, as formigas reduzem a predação sob a planta-mãe (HORVITZ, 1981; HOWE & SMALLWOOD, 1982) e a competição entre as plântulas (WESTOBY et al., 1982), ao mesmo tempo em que as depositam em locais ricos em nutrientes favoráveis para a germinação (RISSING, 1986). A remoção do elaiossomo também pode diminuir os ataques fúngicos, contribuindo para o estabelecimento bem-sucedido das plântulas (OLIVEIRA et al., 1995; LEAL & OLIVEIRA, 1998). A distância média de dispersão e a forma da curva de dispersão desempenham papéis cruciais nas taxas de colonização de propágulos em novos locais (PORTNOY & WILLSON, 1993). Após o transporte inicial até o ninho, as sementes podem ser descartadas em locais distantes por meio de dispersão secundária (BEAUMONT et al., 2012).

As formigas respondem ao tamanho das sementes e dos elaiossomos; geralmente, preferem coletar sementes maiores e com elaiossomos maiores, provavelmente porque isso aumenta a recompensa alimentar em relação ao custo de mover a semente (GUNTHER & LANZA, 1989; GORB & GORB, 2003). Embora diversas espécies de formigas estejam envolvidas na limpeza e remoção de sementes, a dispersão mais eficaz é frequentemente realizada por um pequeno grupo de espécies-chave (ANDERSEN, 1988; GOVE et al., 2007; ZELIKOVA & RATCHFORD, 2008). Serviços de dispersão de sementes de alta qualidade são tipicamente fornecidos por formigas de maior porte, pois elas coletam sementes com facilidade e as transportam por grandes distâncias (ANDERSEN & MORRISON, 1998; LEAL et al., 2014). Dispersores de baixa qualidade (ou seja, espécies de formigas que limpam elaiossomos sem mover sementes ou que movem sementes apenas por curtas distâncias) não mostram preferências por elaiossomos ou massa de sementes (LEAL et al., 2014). Eventos de dispersão de longa distância, menos frequentes, e o comportamento de descartar sementes próximas aos montes de lixo das colônias de formigas, ampliam ainda mais o alcance desse serviço ecossistêmico, influenciando o destino e a distribuição das sementes (BERG, 1975; LUBERTAZZI et al., 2010). Embora poucas espécies de formigas sejam dispersores de alta qualidade, essas espécies dispersam um grande número de sementes, removendo rotineiramente mais de 75% das sementes oferecidas pelas plantas (WARREN & GILAD, 2014).

No entanto, as formigas de grande porte são especialmente sensíveis a perturbações (GIBB et al., 2018; LEAL et al., 2014), o que pode resultar em reduções severas na qualidade dos serviços de dispersão de sementes em habitats perturbados (GOVE et al., 2007; LEAL et al., 2014; NESS et al., 2004). Embora formigas menores sejam consideradas mais sensíveis a altas temperaturas devido à dessecação (BAUDIER et al., 2015; KÜHSEL et al., 2017), estudos recentes descobriram que as formigas maiores são, na verdade, mais sensíveis às mudanças climáticas (ANDREW et al., 2019; GIBB et al., 2018). Isso pode ocorrer porque as formigas grandes exigem mais recursos e demoram mais para amadurecer, o que reduz sua capacidade adaptativa (GIBB et al., 2018; MCCAIN & KING, 2014; SAVAGE et al., 2004). A sensibilidade das formigas de grande porte à perturbação pode, portanto, ser exacerbada pelas mudanças climáticas, diminuindo ainda mais a perda dos serviços de dispersão de sementes fornecidos por essas formigas. Isso é particularmente relevante em ambientes urbanos, onde as pressões antrópicas influenciam significativamente a abundância, a frequência e a composição dos potenciais dispersores de sementes (SCHNEIBERG et al., 2020; TEIXIDO et al., 2022).

Em habitats degradados, a ausência de formigas dispersoras de sementes eficientes pode prejudicar a regeneração natural permitindo que as sementes sejam levadas a distâncias maiores (GALLEGOS et al., 2014). As formigas também são reconhecidas por sua capacidade de recuperação rápida após distúrbios (PIK et al., 2002; LUKE et al., 2007), sendo algumas das primeiras espécies a recolonizar áreas afetadas, desempenhando um papel vital na regeneração de ambientes perturbados ao iniciar a remoção de sementes. De acordo com Carpanezzi et al. (1990), ambientes degradados são aqueles que passaram por distúrbios e perderam seus mecanismos de regeneração biótica, exibindo baixa resiliência, o que pode resultar em um retorno lento ou até impossível ao estado original. Estudos indicam que distúrbios antrópicos, como mineração (VAN HAMBURG et al., 2004), conversão de habitats naturais (Queiroz et al., 2017), urbanização (SANTIAGO et al., 2018) e fogo (VASCONCELOS et al., 2017), alteram de forma significativa o ambiente, afetando tanto a fauna quanto a flora, além de comprometer o funcionamento ecológico.

ARTIGO DO PRIMEIRO CAPITULO

Increased urbanization promotes winner-loser species replacement and shifts in foraging behavior among ant species in a large neotropical metropolis

Isabelle Leite de Holanda Silva[1], Diego Centeno-Alvarado[1], João Carlos Pena[2], Xavier Arnan[3], Inara Roberta Leal[1,4*]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[2]Araucária Sustainability and Innovation Lab (LASI), Environmental Studies Center (CEA),, São Paulo State University, Rio Claro, São Paulo, Brazil

[3]Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

[4]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

***Corresponding author:** inara.leal@ufpe.br; Departamento de Botânica, Universidade Federal de Pernambuco, Av. Professor Moraes Rego, s/n, Cidade Universitária, Recife, Pernambuco, Brazil – 50670-091.

Email: isabelleholanda_@hotmail.com (I. L. H. Silva). centenoalvaradodiego@gmail.com (D. Centeno-Alvarado), joaocpena@gmail.com (J. C. Pena), xavier.arnan@upe.br (X. Arnan), inara.leal@ufpe.br (I. R. Leal).

ORCID:

Isabelle Leite de Holanda Silva: https://orcid.org/0000-0001-7832-4433

Diego Centeno-Alvarado: https://orcid.org/0000-0003-0273-8538

João Carlos Pena: https://orcid.org/0000-0003-1368-1805

Xavier Arnan: https://orcid.org/0000-0002-9904-274X

Inara Roberta Leal: https://orcid.org/0000-0002-8125-2191

Abstract

Urbanization introduces novel environmental filters that can reshape species behavior, distribution, and community structure. Ants, a dominant and ecologically significant group in urban environments, frequently thrive under such conditions. However, urbanization-driven changes in resource availability may lead to shifts in community composition, resulting in winner-loser dynamics that significantly impact community interactions and behaviors. In this study, we investigated the influence of urbanization intensity on ant community structure (i.e., species richness, abundance, and both taxonomic and functional group composition) and foraging behavior (i.e. food resource use and discovery time) in the city of Recife, northeastern Brazil. We sampled ants using two different types of bait (carbohydrate-based and protein-based) at 22 urban sites representing a wide gradient of urbanization intensity (measured as urban land cover). We recorded 42 ant species across the urbanization gradient. Ant species richness and abundance were similar across the entire gradient. Nevertheless, ant taxonomic and functional group composition changed with urbanization intensity, reflecting unique community assemblages across the gradient. Notably, generalists (winners), such as epigaeic omnivores and leaf-cutting Attini, increasingly replaced specialists (losers), including epigaeic predators and cryptic omnivores, along the gradient. Bait discovery time by ants decreased in highly urbanized sites potentially reducing risks such as predation and thermal stress during foraging in urban environments. These changes involve quicker assessments of resources availability or more efficient foraging tactics, allowing ant communities to optimize their resource acquisition in response to urban pressures. Our findings underscore the transformative effect of urbanization on ant communities, including winner-loser dynamics and altered foraging behaviors. These insights are critical for understanding the broader ecological consequences of urbanization on biological communities and ecosystem processes.

Keywords: Atlantic Forest; Hymenoptera; Streetscape; Urban ecology; Urban ecosystems.

Introduction

Over the last few decades, significant land-use transformations have become evident (Ellis, 2021). Urbanization, particularly the conversion of natural areas to urban land cover, is one of the most impactful anthropogenic changes currently shaping environments (McKinney, 2008). With the rapid and continuous growth of human populations, urbanization has intensified to accommodate human activities (Gaston et al., 2013). In urban environments, original vegetation is often replaced, either partially or entirely, by impermeable surfaces such as roads, sidewalks, and buildings (Heterick et al., 2013). As a result, urbanization creates homogeneous, highly managed landscapes that force native species to exhibit plasticity in response to significantly altered environments, allowing them to cope with new environmental filters (Elizalde et al., 2020; Santangelo et al 2022); otherwise, they may face local extinction. These filters include altered microclimatic conditions, such as higher temperatures from urban heat islands, reduced habitat complexity, and shifts in resource availability (Aronson et al., 2014; Penick et al., 2015; Diamond et al., 2017; Diamond et al., 2018). The creation of new habitats through urban modifications can directly or indirectly reduce or alter the availability of crucial resources necessary for the biodiversity survival in these areas (Aronson et al., 2014). As a result, urban conditions favor the establishment and dominance of generalist species ('winners'), which can alter abiotic conditions and resource availability, ultimately contributing to biotic homogenization (Gaertner et al., 2017). This process leads to the decline of specialist species ('losers'), exemplifying winner-loser replacement (*sensu* Filgueiras et al., 2021; see Smart et al., 2006). Numerous studies have demonstrated the impact of urbanization on species distributions, resulting in changes in community composition and diversity, including taxonomic, phylogenetic, and functional alterations (e.g., Magura et al., 2010; Simkin, 2022; Aoki-Gonçalves et al., 2023; Dylewski et al., 2023; Pena et al., 2023; Szabó et al., 2023).

Understanding how species respond to urbanization has led to significant research on community composition and behavioral strategies enabling their persistence in these disturbed habitats (e.g., Kondratyeva et al., 2020; Ruas et al., 2022). Ants are a notable example of organisms thriving in urban environments due to their ability to utilize a wide range of food

54 resources and exhibit diverse nesting behaviors (Hölldobler & Wilson, 1990; Blüthgen &
55 Feldhaar, 2009; Pećarević et al., 2010). This adaptability reflects their increased tolerance to
56 challenging environmental conditions (e.g., heat islands; Diamond et al., 2017; Diamond et al.,
57 2018). However, local biological communities in urban environments generally represent only a
58 fraction of the species diversity present in the surrounding regional ecosystem (Shen et al., 2017),
59 primarily due to reduced vegetation cover, which leads to species loss, particularly among forest-
60 dwelling ants (Bestelmeyer & Wiens, 2001). The remaining species in urban environments are
61 typically habitat generalists, capable of adapting to various environmental conditions (Uno et al.,
62 2010; Buczkowski & Richmond, 2012; Cuautle et al., 2016; Melliger et al., 2018). Thus,
63 urbanization tends to promote winner-loser replacement even within ant communities (Ślipiński
64 et al., 2012; Heterick et al., 2013). Moreover, prior research has shown that the effects of
65 urbanization on ant functional composition can vary depending on the landscape within which
66 urban environments are embedded (Leal et al., 2012; Santiago et al., 2018). For instance, arboreal
67 ants are more negatively affected by isolation and fragment size within urban areas than within
68 forest environments (Santiago et al., 2018). In contrast, epigaeic ants appear to be unaffected by
69 both isolation and fragment size in urban environments (Santiago et al., 2018). Disturbances such
70 as land-use changes (e.g., conversion of natural habitats due to the expansion of cities), can reduce
71 critical resources, including food and nesting sites, for ants with specialized habits, including
72 cryptic species and specialist predators (Leal et al., 2012; Brooks et al., 2023). In contrast to
73 generalist species, specialized ants lack the flexibility to adjust their diets or rapidly recolonize
74 disturbed habitats (Andersen, 1995; Philpott & Foster, 2005; Campos et al., 2007; Leal et al.,
75 2012; Brooks et al., 2023). Moreover, despite increasing urbanization, the presence of scattered
76 and diverse trees can still enhance the likelihood of occupancy by tree-specialist species (Estrada
77 et al., 2014; Mendonça-Santos et al., 2023).

78 Beyond community composition, urbanization may also influence behavioral dynamics,
79 particularly foraging strategies. Changes in resource availability (e.g., higher availability of
80 protein-rich resources) due to urbanization are expected to shape ant foraging behavior, as
81 reflected in both the frequency of resource use and the timing of resource discovery (e.g., Sorvari

& Eeva, 2010; Penick et al., 2015; Foti et al., 2017; Jacquier et al., 2021; Barbee & Pinter-Wollman, 2023). Urban environments often alter the availability, distribution, and accessibility of food resources by depleting natural food sources and introducing unconventional ones, such as discarded human food and waste, which often have distinct nutritional compositions compared to natural sources (Bai et al., 2017; Stahlschmidt & Johnson, 2018). These changes can affect how ants utilize or prefer different food resources and alter foraging strategies accordingly (Bol & Pflieger 2002; Penick et al., 2015; Barbee & Pinter-Wollman, 2023). For instance, a study conducted in New York showed that urban ants modify their diets to focus on the resources that are most readily available, rather than sticking to their traditional food sources (Penick et al., 2015). However, previous studies have shown divergent results regarding preferences for protein or carbohydrates. Specifically, on the one hand, with the higher availability of protein-rich resources in urban environments (e.g., Penick et al., 2015), ants tend prioritize these over carbohydrate-rich resources, exploiting them more rapidly (Pearce-Duvet & Feener Jr., 2010). This pattern may, however, vary along the urbanization gradient, as the availability of protein-rich resources is unlikely to increase uniformly, potentially leading to shifts in resource prioritization depending on local conditions and urbanization intensity. On the other hand, in high-risk urban environments, where predation and resource constraints are prevalent, ants may prioritize foraging for carbohydrates to quickly replenish energy reserves, despite the greater accessibility of protein-rich waste due to increased human consumption of animal products (Barbee & Pinter-Wollman, 2023; Bol & Pflieger, 2002; Penick et al., 2015). Additionally, ants often modify their foraging strategies to minimize the risks of energetically costly encounters and attacks (Mitchell et al., 1990; Ydenberg et al., 1986). This general strategy involves deploying more scouts to cover larger areas and discover resources more quickly (Holway & Case, 2001; Roulston & Silverman, 2002), ultimately reducing discovery times.

In this study, we investigated the effects of urbanization intensity on ant community structure and foraging behavior in the city of Recife, northeastern Brazil. While previous research has largely confirmed trends such as shifts toward generalist species and changes in foraging behavior due to urbanization, results have been inconsistent, particularly regarding the specific

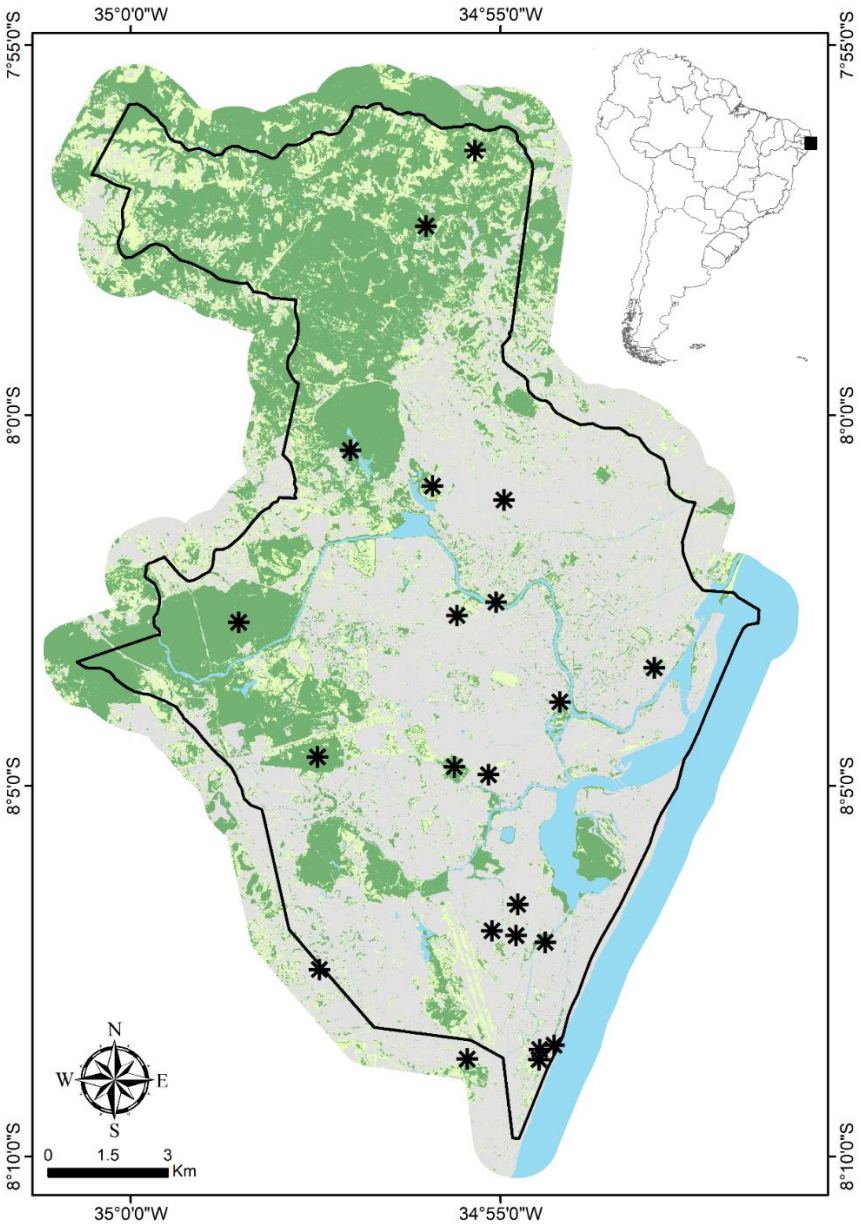
impacts on different ant functional groups and resource preferences (e.g., Bol & Pflieger, 2002; Pearce-Duvet & Feener Jr., 2010; Ślipiński et al., 2012; Heterick et al., 2013; Penick et al., 2015; Barbee & Pinter-Wollman, 2023). We tested the hypothesis that urbanization intensity shapes ant community structure (i.e., species richness, abundance, and both taxonomic and functional group composition), as well as ant foraging behavior (i.e. food resource use and discovery time), due to habitat modifications, changes in the availability of different food resources and the increased risks, such as predation and mortality from elevated temperatures, associated with foraging in urban environments. We predicted that, with increasing urbanization intensity: (1) species richness and abundance would reduce; (2) there would be shifts in taxonomic and functional group composition, favoring generalist species and functional groups at the expense of specialist species and functional groups; (3) species would prioritize carbohydrate baits over protein baits due to the potentially increased availability of protein resources as urbanization intensity increases; (4) consequently, bait discovery time would be reduced, particularly for carbohydrate-based baits.

Materials and methods

Study area and urbanization gradient

The study was conducted in the city of Recife, Pernambuco, northeastern Brazil (34.8780° – 34.9757°S, 7.9405° – 8.1450°W; Fig. 1). Recife stands out not only as the third most densely populated city in Brazil (IBGE, 2021) but also as one of the most deforested regions of the Brazilian Atlantic Forest (Bernard et al., 2023). The city experiences an average annual temperature of 27.7 °C and receives approximately 2200 mm of rainfall annually (APAC, 2017). Within the region, we selected 22 sites to capture a gradient of urbanization intensity ranging from the city center to southwestern suburban areas closer to rural regions. Each sampling point was placed in a representative location within each selected site, ensuring that the diversity of urban environments was effectively captured. The sites were spaced at least 2 km apart. Urbanization intensity was assessed by calculating the proportion of urban cover at each site. To obtain this information, we conducted a supervised classification of Planet Scope satellite imagery

with a resolution of 3m and four spectral bands, acquired in August 2021 (Planet Labs PBC, 2021). Three primary land cover classes were identified: woody vegetation, herbaceous vegetation, and urban cover. Buffers of various sizes (50, 100, 200, and 500 m radius) were defined around each site, and the proportion of urban cover within each buffer was determined (Table S1 – Supplementary Material). We then performed Spearman rank correlations to assess the correlation between the proportion of urban cover across all buffers. Since they all were highly correlated (Spearman $\rho > 0.7$), we used only the 500 m radius buffer in further analyses (Table S2 – Supplementary Material) as it is representative of the landscape area that directly influences ant habitat availability, resource distribution, and ecosystem dynamics (e.g., Cordonnier et al., 2019, 2020; Korányi et al., 2021). The proportion of urban cover within the 500 m radius buffers represents a wide gradient of urbanization intensity ranging from 0 to 95%. (Table S1 – Supplementary Material).



150

151 **Figure 1**. Land cover map of Recife (Pernambuco, Brazil). The black line shows Recife's political
152 boundary. Asterisks highlight the sites where the study was developed. Dark green: woody cover;
153 light green: herbaceous cover; grey: urban land cover (e.g. paved streets, infrastructure); blue:
154 hydrography. The map in the top-right corner shows the political boundaries of the states in Brazil,
155 with the city of Recife highlighted by a black square in the state of Pernambuco.

156

157 *Ant sampling*

158 To sample ants, we conducted surveys between December 2022 and March 2023. At each
159 site, we placed 10 circular filter papers along two transects, with five papers per transect, each
160 spaced 5 m apart. These papers served as baits, with five containing 5 g of tuna (protein-based
161 food resource) and five containing 5 g of honey (carbohydrate-based food resource), alternated in
162 sequence. The simultaneous use of tuna and honey is widely employed in ant sampling, as it not
163 only captures ant assemblages across multiple vertical strata but also ensures higher sampling
164 efficiency by attracting species that are exclusively drawn to either bait type or both (Bestelmeyer
165 et al., 2000; Yanoviak & Kaspari, 2000; Brandão et al., 2012; Antoniazzi et al., 2020). Ground-
166 dwelling ants may have reduced access to carbohydrates, while canopy-dwelling ants often
167 experience protein limitations (Yanoviak & Kaspari, 2000; Brandão et al., 2012). Ant
168 observations were conducted during 20-minute continuous events per bait, during sunny weather
169 between 7:00–12:00 h and 13:00–18:00 h, totaling 200 minutes per site. Following each
170 observation period, at least one individual from each observed ant species was collected for
171 subsequent identification. All ant species were identified using identification keys (Baccaro et al.,
172 2015; Feitosa & Dias, 2024) when possible; otherwise, they were assigned a unique code specific
173 to this study. All specimens were later deposited in the ant collection of the *Laboratório de*
174 *Interação Planta-Animal* at the Federal University of Pernambuco.

175

176 *Data analysis*

177 Ant species richness, abundance, and community composition

178 Species richness was assessed for each bait type and site (Table S3 – Supplementary
179 Material). Due to the inherent difficulty in quantifying colonial organisms, we calculated the
180 relative frequency of species (i.e., the number of baits where the species occurred divided by the
181 total number of baits per bait type) as a measure of abundance per species (Leponce et al., 2004).
182 Furthermore, abundance per site was calculated by summing the frequency of each species per
183 site (Table S3 – Supplementary Material). Ant species were also classified into functional groups
184 for ongoing monitoring of biotic responses to forest conversion in human-modified landscapes

185 designed specifically for Atlantic Forest by Leal et al. (2012) (Table 1). Using this classification,
186 we calculated the proportion of individuals within each functional group, offering insights into
187 how their composition varies along the urbanization gradient. In addition, ant functional groups
188 were classified as specialists or generalists based on a Filgueiras et al. (2019) (modified from
189 Andersen, 1995, 2010; Delabie et al., 2000; Leal et al. 2012) (Table 1). Arboreal dominants,
190 arboreal subordinates, army ants, cryptic omnivores, cryptic predators, epigaeic predators, and
191 non-leaf-cutting Attini were classified as specialists, and epigaeic omnivores, and epigaeic
192 omnivores and opportunists were classified as generalists (Filgueiras et al., 2019). Although
193 Filgueiras et al. (2019) classified leaf-cutting Attini ants as specialists, we opted to categorize
194 them as generalists due to their foraging behavior. These ants feed exclusively on a symbiotic
195 fungus, indicating a highly specialized trophic relationship. However, this fungus is cultivated
196 using a wide range of plant species and parts— e.g. up to 50% of the local flora within their
197 foraging area (Wirth et al. 2003). This extensive use of plant material could suggest a generalist
198 feeding strategy if the fungus is considered an extension of the ant's digestive process (e.g., Jofré
199 et al., 2022). Using this classification, we calculated the generalist/specialist ratios based on both
200 species richness and abundance of each category at each site (Table S4 – Supplementary
201 Material). A ratio of 1 indicates an equal number of generalists and specialists, values greater than
202 1 indicate a predominance of generalists, and values less than 1 indicate a predominance of
203 specialists.
204
205 Ant foraging behavior
206 To evaluate the effect of urbanization intensity on ant foraging behavior, we measured:
207 1) bait occupancy index, based on species richness and abundance previously calculated, and 2)
208 bait discovery time. The bait occupancy index reflects the frequency of protein or carbohydrate
209 use within the ant community, while bait discovery time indicates the rate of resource discovery
210 for each species. For each type of bait (i.e., protein-based and carbohydrate-based), we calculated
211 the bait occupancy index using the following formula:

212 $$Bait\ occupancy\ index = \frac{oB_b}{nB_b} \times \frac{n_b}{N}$$

213 where: oB_b is the number of baits occupied by ants for each type of resource *b*(i.e., protein- or
214 carbohydrate-based); nB_b is the total number of baits for each type of resource *b*; n_b = total species
215 richness or ant abundance per bait type *b*; *N* = total species richness or ant abundance per site
216 (Table S5 – Supplementary Material). For bait discovery time, we recorded the time it took for
217 the first individual of each ant species to discover each bait, from the moment the bait was placed
218 until an ant made contact with the food resource (Table S6 – Supplementary Material).
219
220 *Statistical analyses*
221 Ant species richness, abundance, and community composition
222 To investigate how urbanization intensity affected ant community structure in the city of
223 Recife, we employed generalized linear mixed models (GLMMs), permutational multivariate
224 analysis of variance (PERMANOVA), and generalized linear models (GLMs), with urbanization
225 intensity as the sole explanatory variable. First, GLMMs were used to analyze species richness
226 and abundance. Species richness was modeled using a Poisson error distribution, while abundance
227 was modeled with a Gaussian error distribution. Site was included as a random factor in all models
228 to account for paired measurements across different bait types. However, since including site as
229 a random factor did not explain the variation in the effects of urbanization intensity on species
230 richness, we opted for a GLM instead of a GLMM. Second, we assessed taxonomic and functional
231 composition along the urbanization gradient using PERMANOVA, based on a Bray-Curtis
232 dissimilarity matrix of ant abundance, with site included as strata. Additionally, we conducted
233 threshold indicator taxa analysis (TITAN) to identify changes in species and functional groups
234 along the urbanization intensity gradient (Baker & King, 2010). Third, to examine shifts in
235 generalist/specialist replacement, we analyzed generalist/specialist ratios in terms of both species
236 richness and abundance using GLMs with a Gaussian error distribution.
237
238 Ant foraging behavior

Foraging behavior was analyzed using GLMMs, with urbanization intensity and its interaction with bait type as explanatory variables, and site as a random factor. The interaction was tested to gain insight into how resource availability varies along the urbanization gradient. Bait occupancy indices were modeled with a Gaussian error distribution. Bait discovery time was analyzed separately using GLMMs, with individual ants treated as replicates and species included as an additional random factor. However, since including site as a random factor did not explain the variation in the effects of urbanization intensity on bait occupancy indices, we opted for a GLMs instead of a GLMM.

Overdispersion was checked and found to be absent in all models. We also verified the absence of spatial autocorrelation by conducting Moran's I tests for the residuals of each global model, with all explanatory variables combined with the respective response variable (Table S7 – Supplementary Material). All analyses were performed in R (v. 4.1.3; R Core Team, 2022), using the *lme4* (v. 1.1-7; Bates et al., 2020) and *stats* (v. 4.4.0; R Core Team, 2022) packages for GLMMs and GLMs, respectively, the *vegan* package (v. 2.6-6.1; Oksanen et al., 2024) for PERMANOVA, and the *TITAN2* package (v. 2.4.3; Baker et al., 2023) for TITAN. Additionally, we used the R script *poncho* (Dambros, 2020) to visually represent species composition variations along the urbanization intensity gradient.

Results

Ant community structure (species richness, abundance, and taxonomic and functional group composition)

We recorded 42 ant species in the city of Recife (Fig. 2; Table S3 – Supplementary Material). We identified ten functional groups, categorized as generalists and specialists, comprising 24 and 18 species, respectively (Table 1). The generalist group consisted of 17 species of epigaeic omnivores, 5 opportunists, and 2 leaf-cutting Attini (Table 1). In contrast, the specialist group exhibited reduced diversity (i.e., in terms of species richness), including 6 species of arboreal subordinates, 5 cryptic omnivores, 2 arboreal dominants, 2 epigaeic predators, and

267 single representatives of army ants, cryptic predators, and non-leaf-cutting Attini (Table 1). In
268 general, the most abundant species were *Camponotus crassus* (unscaled relative frequency sum
269 = 16), *Odontomachus bauri* (7.4), *Solenopsis_saevissima* (6.4), *Crematogaster victima* (4.8),
270 *Solenopsis invicta* (4.2), *Wasmannia auropunctata* (4.2) (Fig. 2). All other species had unscaled
271 relative frequency sums of less than 4 (Fig. 2).

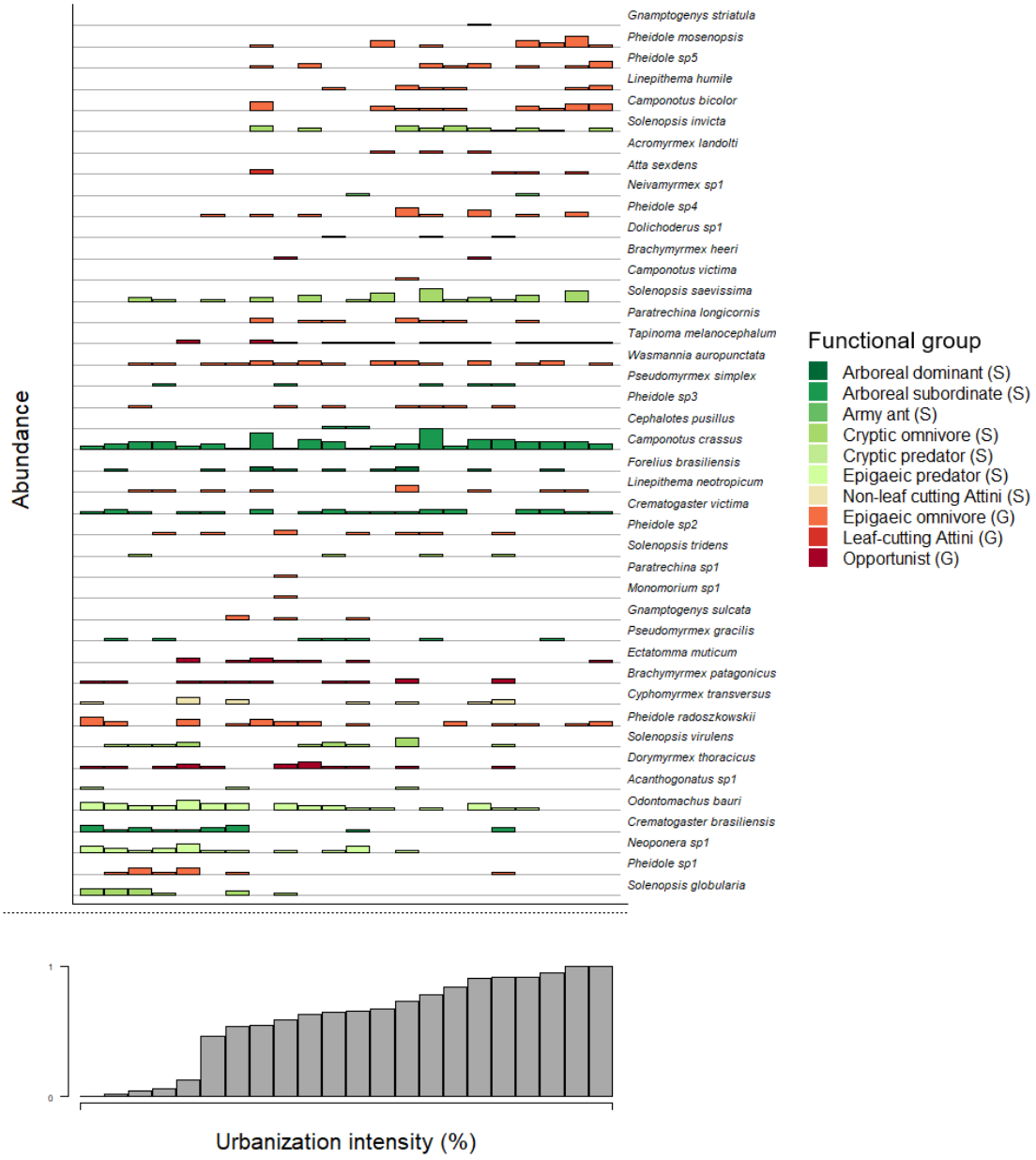
272 Ant richness and abundance were not affected by urbanization intensity [GLM; richness:
273 0.03 ± 0.16 (slope estimate ± SE), Z = 0.16, P = 0.87, Table S8 – Supplementary Material;
274 abundance: GLMM; 0.02 ± 0.45, t = 0.04, P = 0.97, Table S9 – Supplementary Material]. Ant
275 taxonomic community composition significantly varied with urbanization intensity
276 (PERMANOVA; R^2 = 0.37, F = 11.90, P = 0.001; Fig. 2) (Table S10 – Supplementary Material).
277 *Solenopsis invicta* (IndVal = 73.08), *Pheidole mosenopsis* (IndVal = 70.57), *Camponotus bicolor*
278 (IndVal = 64.62), *Pheidole* sp. 5 (IndVal = 64.62), *Tapinoma melanocephalum* (IndVal = 60.17),
279 and *Camponotus crassus* (IndVal = 60.09) were the species most strongly associated with higher
280 urbanization intensity (Fig. 2; Table S11 – Supplementary Material). Conversely, *Crematogaster*
281 *brasiliensis* (IndVal = 90.28), *Neoponera* sp. 1 (IndVal = 83.33), *Odontomachus bauri* (IndVal =
282 75.86), *Pheidole* sp. 1 (IndVal = 67.91), *Solenopsis globularia* (IndVal = 66.67), and *Dorymyrmex*
283 *thoracicus* (IndVal = 63.59) were most strongly associated with lower urbanization intensity (Fig.
284 2; Table S11 – Supplementary Material). Moving to functional group composition, community
285 composition also varied significantly with urbanization intensity (PERMANOVA; R^2 = 0.25, F =
286 6.74, P = 0.001; Fig. 3) (Table S12 – Supplementary Material). Epigaeic omnivores (generalists;
287 IndVal = 63.62) were most strongly associated with higher levels of urbanization intensity,
288 whereas epigaeic predators (specialists; IndVal = 78.45) showed the strongest association with
289 lower levels of urbanization intensity (Fig. 3; Table S13 – Supplementary Material). Moreover,
290 the replacement of specialist by generalist species, both in terms of species richness and
291 abundance, significantly increased with the intensity of urbanization (GLM; generalist/specialist
292 ratio of species richness: 1.04 ± 0.40, t = 2.59, P = 0.02, Fig. 4A, Table S14 – Supplementary
293 Material; GLM; generalist/specialist ratio of ant abundance: 0.69 ± 0.31, t = 2.23, P = 0.04, Fig.
294 4B, Table S15 – Supplementary Material).

295

296 *Ant foraging behavior*

297 Bait occupancy in terms of species richness ranged from 0.37 to 0.80 for protein-based
298 baits and from 0.10 to 0.92 for carbohydrate-based baits (Table S5 – Supplementary Material).
299 Meanwhile, bait occupancy in terms of ant abundance ranged from 0.35 to 0.74 for protein baits
300 and from 0.21 to 0.65 for carbohydrate baits (Table S5 – Supplementary Material). Bait
301 occupancy in terms of species richness was not significantly affected by urbanization intensity
302 [GLM; 0.08 ± 0.12 (slope estimate ± SE), t = 0.68, P = 0.50], bait type (GLM; 0.14 ± 0.11, t =
303 1.29, P = 0.20), or the interaction between both factors (GLM: -0.07 ± 0.17, t = -0.44, P = 0.67)
304 (Table S16 – Supplementary Material). In contrast, bait occupancy in terms of ant abundance was
305 significantly influenced by bait type (GLM; 0.17 ± 0.08, t = 2.22, P = 0.03): more ants visited the
306 protein-based baits than the carbohydrate-based baits (Fig. 5). However, abundance-based bait
307 occupancy was not significantly affected by urbanization intensity (GLM; 0.10 ± 0.08, t = 1.26,
308 P = 0.22) or by the interaction between urbanization intensity and bait type (GLM; -0.08 ± 0.12,
309 Z = -0.72, P = 0.48) (Table S17 – Supplementary Material). Interestingly, higher levels of
310 urbanization significantly reduced bait discovery time for the ant community (GLMM; -1.27 ±
311 0.33, Z = -3.90, P = <0.001, Fig. 4C, Table S18 – Supplementary Material). However, neither bait
312 type (GLMM; -0.08 ± 0.11, Z = -1.32, P = 0.29, Table S18 – Supplementary Material) nor the
313 interaction between urbanization intensity and bait type (GLMM; 0.06 ± 0.11, Z = -0.51, P = 0.61,
314 Table S14 – Supplementary Material) significantly influenced bait discovery time.

315



316

317 **Figure 2**. Ant species found in the city of Recife, northeastern Brazil. The size of the bars
318 represents abundance. The distribution of species is arranged with respect to their distribution
319 along urbanization intensity, with the species above being dominant in more urbanized areas and
320 the species below dominating in less urbanized areas. S = specialist; G = generalist.

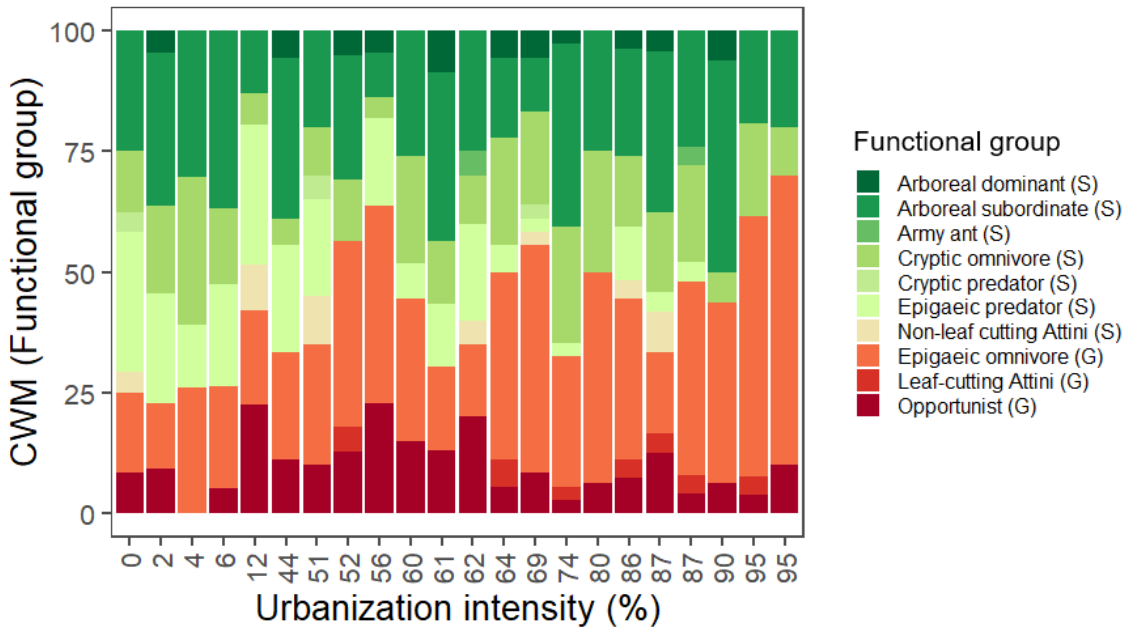
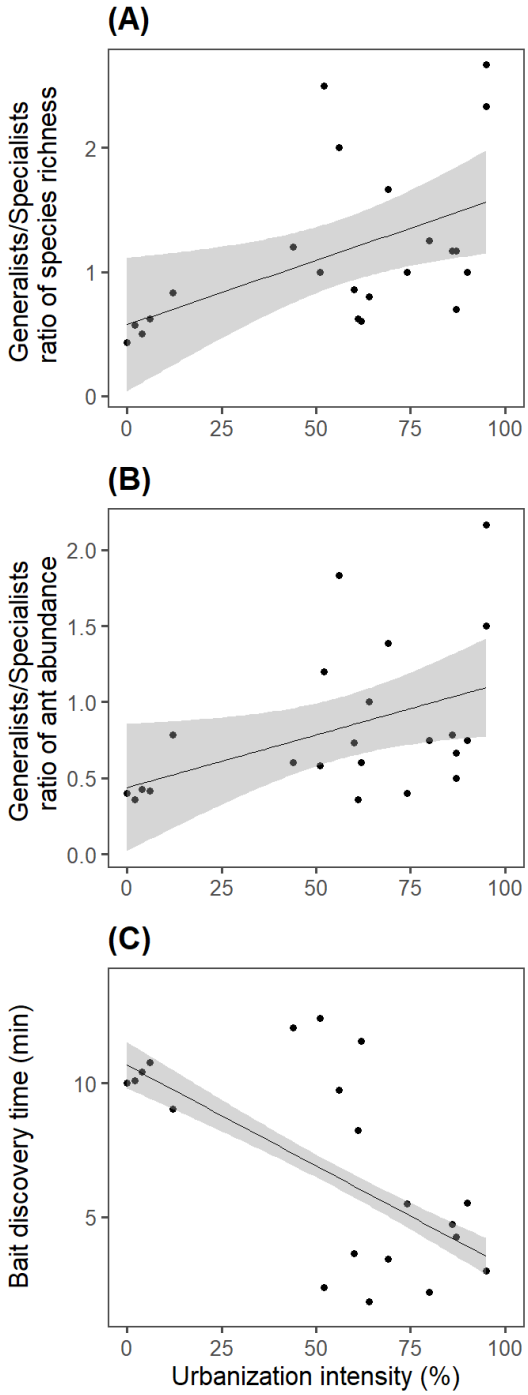


Figure 3. Relative abundance of ant functional groups considered in this study along the urbanization intensity gradient in Recife, northeastern Brazil. Abbreviations: S = specialist; G = generalist.



325

326 **Figure 4.** Significant effects of urbanization intensity on the generalist/specialist ratio in terms of
327 species richness (A) and ant abundance (B) and on bait discovery time by ants (C) in the city of
328 Recife, northeastern Brazil. The black dots represent mean values per sampling site; the black line
329 indicates the model fitted line; the gray-shaded area indicates the 95% confidence interval of the
330 model estimates**.**

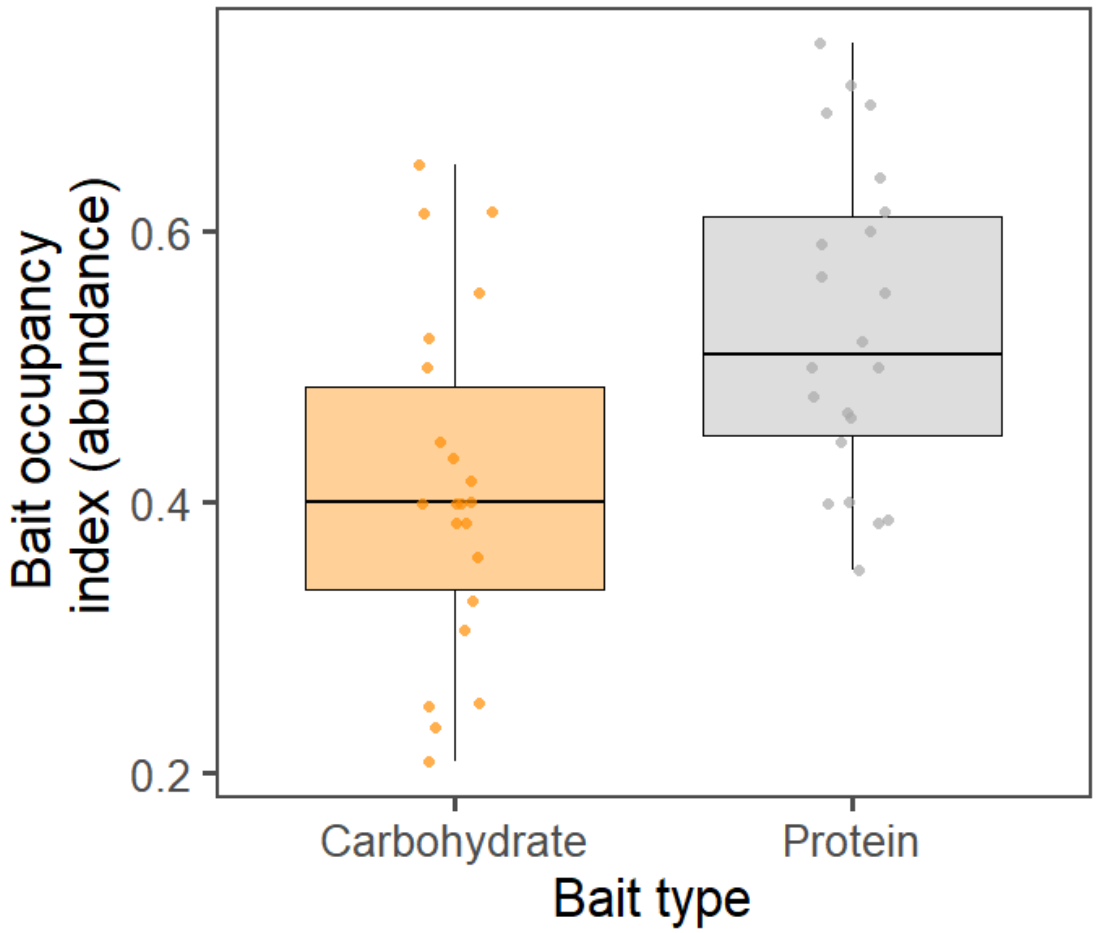


Figure 5. Significant effects of bait type on the bait occupancy index based on ant abundance in the city of Recife, northeastern Brazil. The black dots represent values per sampling site; the box in the plot represents the interquartile range; the line inside the box represents the median; whiskers represent the range of the data not considering outliers.

Discussion

We demonstrated that while increasing urbanization intensity does not significantly alter overall ant species richness or abundance, it drives substantial shifts in community composition and foraging behavior. As urbanization increases, ant communities shift towards a dominance of generalist species and functional groups such as epigaeic omnivores, while specialist species and functional groups as cryptic and epigaeic predators declined. This pattern reflects clear winner-loser dynamics in response to urban pressures, with generalist species emerging as the primary winners. Moreover, ant species in highly urbanized environments exhibit consistently shorter bait

345 discovery times, regardless of resource type. These results highlight the broader implications of
346 land-use change on biodiversity and suggest potential shifts in ant-mediated ecological processes
347 within urban ecosystems.

348 Numerous studies have demonstrated that urbanization primarily drives changes in ant
349 community composition (e.g., Bestelmeyer & Wiens, 2001; Wang et al., 2001; Thompson &
350 McLachlan, 2007; Ślipiński et al., 2012; Heterick et al., 2013; Estrada et al., 2014), a pattern
351 supported by our findings. Ultimately, higher urbanization intensity contributes to community
352 homogenization, leading to the decline of specialist species (the 'losers') while promoting the
353 expansion of generalist species (the ‘winners’). Moreover, previous studies have highlighted
354 opposing responses of ant species richness and abundance to different levels of urbanization
355 intensity (e.g., Miguelena & Baker, 2019; Santos et al., 2019; Brooks et al., 2023). These studies
356 have shown that the effects of urbanization on ant species richness and abundance differ across
357 regions, influenced by habitat characteristics (Santos et al., 2019) and species adaptability
358 (Miguelena & Baker, 2019). While some environments, such as tropical forests and deserts,
359 support higher diversity under specific conditions (Santos et al., 2019; Miguelena & Baker, 2019),
360 others, including temperate ecosystems, exhibit minimal changes due to the resilience of local
361 species or the dominance of generalists in urbanized areas (Brooks et al., 2023).

362 Our study revealed that increasing urbanization is associated with a notable decline in
363 both cryptic and epigaeic predator populations, while simultaneously driving a significant rise in
364 epigaeic omnivores. On the one hand, this trend supports the findings of Leal et al. (2012), who
365 highlighted the heightened sensitivity of specialist predators to habitat loss and fragmentation in
366 the Atlantic Forest of northeast Brazil. The decline is likely attributed to urbanization impacts on
367 predator habitat, such as continuous natural forests, and essential resources these predators depend
368 on, such as leaf litter, rotting logs, and prey like living arthropods and their eggs (Leal et al., 2012;
369 Heterick et al., 2013). Cryptic predators generally nest in environments such as leaf litter and
370 decaying logs, where they feed on living arthropods and their eggs (Leal et al., 2012). In contrast,
371 epigaeic predators forage on the litter surface, specializing in hunting other arthropods (Leal et
372 al., 2012). The existence of these specialist predators is closely tied to the availability of resources

consumed by their prey. Consequently, urbanization not only leads to the degradation of predator habitats (e.g., continuous natural forests) but also results in the loss of prey habitats, directly contributing to the decline of predator populations (Swihart et al., 2001; Ryall & Fahrig, 2006). Conversely, epigaeic omnivores, as generalist predators and scavengers (Leal et al., 2012), may capitalize on the novel resources (e.g., beef and chicken meat, and corn-based foods) introduced by urbanization (Aronson et al., 2014; Penick et al., 2015). Our findings also reveal that generalist native leaf-cutting ants can coexist with pioneer and/or exotic species and flourish in disturbed habitats, as has already been reported by other studies (e.g., Wirth et al., 2007, Meyer et al., 2009, Leal et al., 2014). Fragmentation, which often results from urbanization (Mitchell & Devisscher, 2022), can favor widespread generalist species. These unspecialized organisms can thrive in diverse habitats, exhibit flexible nesting requirements, and maintain broad dietary preferences (Andersen, 1995; Leal et al., 2012).

Contrary to our expectations and in contrast to previous studies (Barbee & Pinter-Wollman, 2023; Bol & Pflieger, 2002; Penick et al., 2015), but consistent with findings from Pearce-Duvet & Feener Jr. (2010), we found that ants preferentially foraged on protein-rich resources over carbohydrate-rich ones, regardless of the area or level of urbanization intensity. Similarly, as anticipated (e.g., Mitchell et al., 1990; Ydenberg et al., 1986), ants demonstrated faster resource discovery with increasing urbanization intensity. However, contrary to our expectations that ants would locate protein-rich resources more quickly than carbohydrate-rich ones (Kay, 2004; Bihn et al., 2008; Ness et al., 2009; Pearce-Duvet & Feener Jr., 2010), we found no significant differences between the two resource types. The observed patterns in bait occupancy and discovery times further illustrate how urbanization influences ant communities. These patterns can be attributed to the differing ecological roles that protein and carbohydrate baits play in attracting ants, as well as the impact of urbanization on foraging behaviors. Protein-based baits tend to attract more ants than carbohydrate-based baits regardless of the level of urbanization intensity, likely due to the greater availability of protein resources across the urban environments (e.g., Penick et al., 2015). This phenomenon can mainly be attributed to the dominance of epigaeic omnivores and opportunistic species along the entire gradient, which

exploit the more available resources because of their generalist foraging behaviors (Leal et al., 2012). Additionally, the finding that bait discovery time decreases in highly urbanized areas suggests that ants are adapting their foraging strategies, possibly due to the high risks such as predation and thermal stress associated with urban environments. Moreover, the finding that bait discovery time decreases in highly urbanized areas suggests that ants may be adapting their foraging strategies in response to urban pressures, such as predation risks and thermal stress. This could be related to the discovery-dominance trade-off (e.g., Fellers, 1987; Feener, 2000; Andersen, 2008), in which subordinate ants tend to discover resources more quickly than dominant ones, possibly due to their lower competitive abilities and need to locate food more rapidly. Given that urban environments could potentially host, due to altered community structures, more subordinate species, it is possible that more subordinate species dominate foraging in these areas, leading to faster resource discovery times. Further studies exploring the balance between species dominance and foraging efficiency in urbanized areas would be important to fully understand this dynamic.

The transition from specialist to generalist species in urbanized environments has significant implications for biological communities and the ecosystem services they provide (Filgueiras et al., 2021). Urbanization can alter ant assemblages, resulting in shifts in trait distributions that affect their ecosystem functions within urban environments (Chen & Neoh et al., 2023). Lastly, faster assessments of bait availability or more efficient foraging strategies may enable ant communities to optimize resource acquisition under urban pressures (Dáttilo & MacGregor-Fors, 2021), potentially influencing the provision of ecosystem services.

Data availability statement

The data that supports the findings of this study are openly available in Mendeley Data at link.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

ILHS: Conceptualization (equal); data curation (lead); investigation (lead); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **DC-A:** Conceptualization (equal); formal analysis (lead); methodology (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). **JCP:** Conceptualization (equal); data curation (supporting); methodology (equal); writing – review and editing (equal). **XA:** Conceptualization (equal); methodology (equal); supervision (supporting); validation (supporting); writing – review and editing (equal). **IRL:** Conceptualization (equal); funding acquisition (lead); methodology (equal); supervision (lead); validation (lead); writing – review and editing (equal).

References

Andersen AN (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. Journal of Biogeography, 22, 15–29. https://doi.org/10.2307/2846070

455 Andersen AN (2008) Not enough niches: non-equilibrial processes promoting species co-
456 existence in diverse ant communities. Austral Ecology, 33, 211–220.
457 https://doi.org/10.1111/j.1442-9993.2007.01810.x
458 Andersen AN (2010) Functional groups in ant community ecology. In: Lach L, Parr C, Abbott K
459 (eds) Ant ecology. Oxford University Press, Oxford, pp 142–144.
460 Antoniazzi R, Ahuatzin DA, Pelayo-Martínez J, Ortiz-Lozada L, Leponce M, Dáttilo W (2020)
461 On the effectiveness of hand collection to complement baits when studying and vertical
462 stratification in tropical rainforests. Sociobiology, 67(2), 213–222.
463 https://doi.org/10.13102/sociobiology.v67i2.4909
464 Aoki-Gonçalvez F, Pena JC, Toledo-Aceves T, MacGregor-Fors I (2023) Urban epiphytes:
465 Bromeliad diversity in a green cover gradient across a Neotropical streetscape. Urban Forestry
466 & Urban Greening 83, 127901. https://doi.org/10.1016/j.ufug.2023.127901
467 Agência Pernambucana de Águas e Clima (APAC) (2017) APAC - Agência Pernambucana de
468 Águas e Clima. Governo do Estado de Pernambuco. http://www.apac.pe.gov.br/
469 Aronson MFJ, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA et al. (2014) A global
470 analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic
471 drivers. Proceedings of the Royal Society of London B: Biological Sciences 281, 20133330.
472 https://doi.org/10.1098/rspb.2013.3330
473 Baccaro FB, Feitosa RM, Fernandez F, Fernandes IO, Izzo TJ, de Souza JLP, Solar R (2015) Guia
474 para os gêneros de formigas do Brasil. Editora INPA, Manaus.
475 Bai X, McPhearson T, Cleugh H, Nagendra H, Tong X, Zhu T, Zhu Y-G (2017) Linking
476 urbanization and the environmen: Conceptual and empirical advances. Annual Review of
477 Environment and Resources 42: 215–240. https://doi.org/10.1146/annurev-environ-102016-
478 061128
479 Baker ME, King RS, Kahle D (2023) TITAN2: Threshold Indicator Taxa Analysis (v. 2.4.3).
480 https://cran.r-project.org/web/packages/TITAN2/
481 Barbee B, Pinter-Wollman N (2023) Nutritional needs and mortality risk combine to shape
482 foraging decisions in ants. Current Zoology 69, 747–755. https://doi.org/10.1093/cz/zoac089

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01

Bernard E, Damasceno LTL, de Frias AVC, Hintze F (2023) Assessing the effects of urbanisation on bats in Recife area, Atlantic Forest of Brazil. In: Moretto L, Coleman JL, Davy CM, Fenton MB, Korine C, Patriquin KJ (eds) Urban bats: Biology, ecology, and human Dimensions. Springer International Publishing, Cham, pp 123-136.

Bestelmeyer BT, Agosti D, Alonso LE, Brandão CRF, Brown WL, Delabie JHC, Silvestre R (2000) Field techniques for the study of ground-dwelling ant: an overview, description, and evaluation. In Agosti D, Majer J, Alonso LE, Schultz TR (eds) Ants: Standard methods for measuring and monitoring biodiversity. Smithsonian Institution Press. Washington, pp. 122-144.

Bestelmeyer BT, Wiens JA (2001) Ant biodiversity in semiarid landscape mosaics: The consequences of grazing vs. natural heterogeneity. Ecological Applications 11: 1123–1140. https://doi.org/10.1890/1051-0761(2001)011[1123:ABISLM]2.0.CO;2

Bihn JH, Verhaagh M, Brandl R (2008) Ecological stoichiometry along a gradient of forest succession: bait preferences of litter ants. Biotropica, 40, 597–599. https://doi.org/10.1111/j.1744-7429.2008.00423.x

Blüthgen N, Feldhaar H (2009) Food and Shelter: How resources influence ant ecology. In: Lach L, Parr C, Abbott K (eds) Ant Ecology. Oxford Academic Press, Oxford, pp 115–136.

Bol R, Pflieger C (2002) Stable isotope (^{13}C, ^{15}N and ^{34}S) analysis of the hair of modern humans and their domestic animals. Rapid Communications in Mass Spectrometry, 16(23), 2195–2200. https://doi.org/10.1002/rcm.706

Brooks HB, Guzman-Hernandez I, Beasley DE (2023) Ant biodiversity in a temperate urban environment. BIOS, 93, 117–123. https://doi.org/10.1893/BIOS-D-20-00018

Buczkowski G, Richmond DS (2012) The effect of urbanization on ant abundance and diversity: A temporal examination of factors affecting biodiversity. PLoS ONE, 7(8). e41729. https://doi.org/10.1371/journal.pone.0041729

Campos RBF, Schoereder JH, Sperber CF (2007) Small-scale patch dynamics after disturbance in litter ant communities. Basic Applied Ecology, 8, 36–43. https://doi.org/10.1016/j.baae.2006.03.010

Cordonnier M, Bellec A, Escarguel G, Kaufmann B (2020) Effects of urbanization–climate interactions on range expansion in the invasive European pavement ant. Basic and Applied Ecology, 44, 46–54. https://doi.org/10.1016/j.baae.2020.02.003

Chen Y-H, Neoh K-B (2023) Urbanization causes shifts in the functional traits and foraging activity and alters food particle size preference and biomass removal of urban-dwelling ants. Frontiers in Ecology and Evolution, 11. https://doi.org/10.3389/fevo.2023.1044485

Cordonnier M, Gibert C, Bellec A, Kaufmann B, Escarguel G (2019) Multi-scale impacts of urbanization on species distribution within the genus *Tetramorium*. Landscape Ecology, 34, 1937–1948. https://doi.org/10.1007/s10980-019-00842-7

Cuautle M, Vergara CH, Badano EI (2016) Comparison of ant community diversity and functional group composition associated to land use change in a seasonally dry oak forest. Neotropical Entomology, 45, 170-179. https://doi.org/10.1007/s13744-015-0353-y

Dambros CS (2020) csdambros/R-functions: First release (v1.0). Zenodo. https://doi.org/10.5281/zenodo.3784397

Davidson DW (1997) The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. Biological Journal of the Linnean Society 61(2), 153–181. https://doi.org/10.1111/j.1095-8312.1997.tb01785.x

Davidson DW, Cook SC, Snelling RR (2004) Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. Oecologia 139, 255–266. https://doi.org/10.1007/s00442-004-1508-4

Dáttilo W, MacGregor-Fors I (2021) Ant social foraging strategies along a Neotropical gradient of urbanization. Scientific Reports, 11, 6119. https://doi.org/10.1038/s41598-021-85538-2

Delabie JHC, Agosti D, Nascimento I (2000) Litter ant communities of the Brazilian Atlantic rain forest region. In: Agosti D, Majer J, Alonso L, Schultz TR (eds) Sampling ground-dwelling

ants: case studies from the world's rain forests. Curtin University of Technology School of Environmental Biology Bulletin No. 18, Perth, pp 1–17.

Diamond SE, Chick L, Perez A, Strickler SA, Martin RA (2017) Rapid evolution of ant thermal tolerance across an urban-rural temperature cline. Biological Journal of the Linnean Society 121 (2), 248–257. https://doi.org/10.1093/biolinnean/blw047

Diamond SE, Chick LD, Perez A, Strickler SA, Zhao C (2018) Evolution of plasticity in the city: urban acorn ants can better tolerate more rapid increases in environmental temperature. Conservation Physiology 6 (1), coy030. https://doi.org/10.1093/conphys/coy030

Dylewski Ł, Banaszak-Cibicka W, Maćkowiak Ł., Dyderski MK (2023) How do urbanization and alien species affect the plant taxonomic, functional, and phylogenetic diversity in different types of urban green areas? Environmental Science Pollution Research 30, 92390–92403. https://doi.org/10.1007/s11356-023-28808-y

Elizalde L, Arbetman M, Arnan X, Eggleton P, Leal IR, Lescano NM, Saez A, Werenkraut V, Pirk IG (2020) The ecosystem services provided by social insects: traits, management tools and knowledge gaps. Biologicals Reviews 95(5), 1418–1441. https://doi.org/10.1111/brv.12616

Estrada MA, Coriolano RE, Santos NT, Caixeira LR, Vargas AB, Almeida FS (2014) Influência de áreas verdes urbanas sobre a mirmecofauna. Floresta e Ambiente, 21(2), 162-169. http://doi.org/10.4322/floram.2014.035

Ellis EC (2021) Land use and ecological change: A 12,000-year history. Annual Review of Environment and Resources 46, 1–33. https://doi.org/10.1146/annurev-environ-012220-010822.

Feitosa RM, Dias AM (2024) An illustrated guide for the identification of ant subfamilies and genera in Brazil. Insect Systematics & Evolution, 2024, 1–121. https://doi.org/10.1163/1876312X-bja10062

Fellers JH (1987) Interference and exploitation in a guild of woodland ants. Ecology, 68, 1466–1478. https://doi.org/10.2307/1939230

564 Feener Jr DH, Orr MR, Wackford KM, Longo JM, Benson WW, Gilbert LE (2008) Geographic
565 variation in resource dominance-discovery in Brazilian ant communities. Ecology, 89, 1824–
566 1836. https://doi.org/10.1890/07-0659.1
567 Filgueiras BKC, Melo DHA, Andersen AN, Tabarelli M, Leal IR (2019) Cross-taxon congruence
568 in insect responses to fragmentation of Brazilian Atlantic Forest. Ecological Indicators, 98,
569 523–530. https://doi.org/10.1016/j.ecolind.2018.11.036
570 Filgueiras BKC, Peres CA, Melo FPL, Leal IR, Tabarelli M (2021) Winner-loser species
571 replacements in human-modified landscapes. Trends in Ecology & Evolution, 36, 545-555.
572 https://doi.org/10.1016/j.tree.2021.02.006
573 Foti L, Dubs F, Gignoux J, Lata J-C, Lerch TZ, Mathieu J, Nold F, Nunan N, Raynaud X, Abbadie
574 L, Barot S (2017) Trace element concentrations along a gradient of urban pressure in forest
575 and lawn soils of the Paris region (France). Science of the Total Environment, 598(2017),
576 938–948. https://doi.org/10.1016/j.scitotenv.2017.04.111
577 Gaertner M, Wilson JRU, Cadotte MW, MacIvor S, Zenni RD, Richardson DM (2017) Non-
578 native species in urban environments: patterns, processes, impacts and challenges. Biological
579 Invasions, 19, 3461–3469. https://doi.org/10.1007/s10530-017-1598-7
580 Gaston KJ, Bennie J, Davies TW, Hopkins J (2013) The ecological impacts of nighttime light
581 pollution: A mechanistic appraisal. Biological Reviews 88(4), 912–927.
582 https://doi.org/10.1111/brv.12036
583 Heterick BE, Lythe M, Smithyman C (2013) Urbanisation factors impacting on ant
584 (Hymenoptera: Formicidae) biodiversity in the Perth metropolitan area, Western Australia:
585 two case studies. Urban Ecosystems 16, 145–173. https://doi.org/10.1007/s11252-012-0257-
586 0
587 Hoffmann BD, Andersen AN (2003) Responses of ants to disturbance in Australia, with particular
588 reference to functional groups. Austral Ecology, 28, 444–464. https://doi.org/10.1046/j.1442-
589 9993.2003.01301.x
590 Holway DA, Case T (2001) Effects of colony-level variation on competitive ability in the invasive
591 Argentine ant. Animal Behaviour, 61, 1181–1192. https://doi.org/10.1006/anbe.2000.1698

592 Jacquier L, Doums C, Four-Chaboussant A, Peronnet R, Tirard C, Molet M (2021) Urban colonies
593 are more resistant to a trace metal than their forest counterparts in the ant *Temnothorax*
594 *nylanderi*. Urban Ecosystems, 24(3), 561–570. https://doi.org/10.1007/s11252-020-01060-9
595 Jofré LE, Curth MT, Farji-Brener AG (2022) Unexpected costs of extended phenotypes: nest
596 features determine the effect of fires on leaf cutter ant's demography. Proceedings of the Royal
597 Society B, 289, 202133333. https://doi.org/10.1098/rspb.2021.2333
598 Kuate AF, Hanna R, Tindo M, Nanga S, Nagel P (2015) Ant diversity in dominant vegetation
599 types of southern Cameroon. Biotropica, 47, 94–100. https://doi.org/10.1111/btp.12182
600 Kay A (2004) The relative availabilities of complementary resources affect the feeding
601 preferences of ant colonies. Behavioral Ecology, 15, 63–70.
602 https://doi.org/10.1093/beheco/arg106
603 Kondratyeva A, Knapp S, Durka W, Kühn I, Vallet J, Machon N, Martin G, Motard E, Grandcolas
604 P, Pavoine S (2020) Urbanization effects on biodiversity revealed by a two-scale analysis of
605 species functional uniqueness vs. redundancy. Frontiers in Ecology and Evolution, Sec. Urban
606 Ecology 24, 00073. https://doi.org/10.3389/fevo.2020.00073
607 Korányi D, Szigeti V, Mezőfi L, Kondorosy E, Markó V (2021) Urbanization alters the abundance
608 and composition of predator communities and leads to aphid outbreaks on urban trees. Urban
609 Ecosystems, 24, 571–586. https://doi.org/10.1007/s11252-020-01061-8
610 Leal IR, Filgueiras BKC, Gomes JP, Ianuzzi L, Andersen AN (2012) Effects of habitat
611 fragmentation on ant richness and functional composition in Brazilian Atlantic Forest.
612 Biodiversity and Conservation, 21, 1687-1701. https://doi.org/10.1007/s10531-012-0271-9
613 Leal IR, Wirth R, Tabarelli M (2014) The multiple impacts of leaf-cutting ants and their novel
614 ecological role in human-modified Neotropical forests. Biotropica, 46, 516-528.
615 https://doi.org/10.1111/btp.12126
616 Leponce M, Thenus L, Delabie JHC, Roisin Y (2004) Scale dependence of diversity measures in
617 leaf-litter ant assemblage. Ecography 27, 129-267. https://doi.org/10.1111/j.0906-
618 7590.2004.03715.x

MacGregor-Fors I (2011) Misconceptions or misunderstandings? On the standardization of basic terms and definitions in urban ecology. Landscape and Urban Planning 100, 347–349. https://doi.org/10.1016/j.landurbplan.2011.01.013

Magura T, Lövei GL, Tóthmérész B (2010) Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? Global Ecology and Biogeography 19(1), 16–26. https://doi.org/10.1111/j.1466-8238.2009.00499.x

McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems, 11(2), 161–176. https://doi.org/10.1007/s11252-007-0045-4

Mendonça-Santos RG, Antoniazzi R, Camarota F, Reis YT, Viana-Junior AB (2023) Scattered trees as crucial elements in maintaining urban diversity: A case study with canopy ants in a biodiversity hotspot. Acta Oecologica, 118, 103894. https://doi.org/10.1016/j.actao.2023.103894

Meyer ST, Leal IR, 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

McKinney ML (2008) Effects of urbanization on species richness: A review of plants and animals. Urban Ecosystems, 11(2), 161–176. https://doi.org/10.1007/s11252-007-0045-4

Melliger RL, Braschler B, Rusterholz H-P, Baur B (2018) Diverse effects of degree of urbanization and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. PLoS ONE, 13(6), e0199245. https://doi.org/10.1371/journal.pone.0199245

Miguelena JG, Baker PB (2019) Effects of urbanization on the diversity, abundance, and composition of ant assemblages in an arid city. Environmental Entomology 48(4), 836–846. https://doi.org/10.1093/ee/nvz069

Mitchell MGE, Devisscher T (2022) Strong relationships between urbanization, landscape structure, and ecosystem service multifunctionality in urban forest fragments. Landscaoe and Urban Planning, 228, 104548. https://doi.org/10.1016/j.landurbplan.2022.104548

Mitchell WA, Abramsky Z, Kotler BP, Pinshow B, Brown JS (1990) The effect of competition on foraging activity in desert rodents: theory and experiments. Ecology, 71, 844–854. https://doi.org/10.2307/1937356

Ness JH, Morris WF, Bronstein JL (2009) For ant-protected plants, the best defense is a hungry offense. Ecology 90, 2823–2831. https://doi.org/10.1890/08-1580.1

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR et al. (2024) vegan: Community Ecology Package (v. 2.6-6.1). https://cran.r-project.org/web/packages/vegan/

Pearce-Duvet JMC, Feener Jr. DH (2010) Resource discovery in ant communities: do food type and quantity matter? Ecological Entomology, 35(5), 549–556. https://doi.org/10.1111/j.1365-2311.2010.01214.x

Pećarević M, Danoff-Burg J, Dunn RR (2010) Biodiversity on Broadway – Enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. PLoS One 5, e13222. https://doi.org/10.1371/journal.pone.0013222

Pena JC, Aoki-Gonçalves F, Dáttilo W, Ribeiro MC, MacGregor-Fors I (2021) Caterpillars' natural enemies and attack probability in an urbanization intensity gradient across a Neotropical streetscape. Ecological Indicators 128, 107851. https://doi.org/10.1016/j.ecolind.2021.107851

Pena JC, Ovaskainen O, MacGregor-Fors I, Teixeira CP, Ribeiro MC (2023) The relationships between urbanization and bird functional traits across the streetscape. Landscape and Urban Planning, 232, 104685. https://doi.org/10.1016/j.landurbplan.2023.104685

Penick CA, Savage AM, Dunn RR (2015) Stable isotopes reveal links between human food inputs and urban ant diets. Proceedings of the Royal Society B, 282, 20142608. http://doi.org/10.1098/rspb.2014.2608

Philpott SM, Foster PF (2005) Nest-site limitation in coffee agroecosystems: artificial nests maintain diversity of arboreal ants. Ecological Applications, 15, 1478–1485. https://doi.org/10.1890/04-1496

Planet Labs PBC (2021) Planet Application Program Interface: In space for life on Earth. https://api.planet.com

R Core Team (2022) The R '*stats*' package (v.4.4.0). The R Project for Statistical Computing. https://stat.ethz.ch/R-manual/R-devel/library/stats

R Core Team (2022) The R Project for Statistical Computing (v. 4.1.3). The R Project for Statistical Computing. https://www.r-project.org/

Roulston TAH, Silverman J (2002) The effect of food size and dispersion pattern on retrieval rate by the Argentine ant, *Linepithema humile* (Hymenoptera: Formicidae). Journal of Insect Behavior, 15, 633–648 https://doi.org/10.1023/A:1020791705673

Ruas RB, Costa LMS, Bered F (2022) Urbanization driving changes in plant species and communities – A global view. Global Ecology and Conservation 38, e02243. https://doi.org/10.1016/j.gecco.2022.e02243

Ryall KL, Fahrig L (2006) Response of predators to loss and fragmentation of prey habitat: a review of theory. Ecology, 87, 1086–1093. https://doi.org/10.1890/0012-9658(2006)87[1086:ROPTLA]2.0.CO;2

Santangelo JS, Ness RW, Cohan B, Fitzpatrick CR, Innes SG, Koch S et al. (2022) Global urban environmental change drives adaptation in white clover. Science 375, 1275–1281. https://doi.org/10.1126/science.abk0989

Santiago GS, Camps RBF, Ribas CR (2018) How does landscape anthropization affect the myrmecofauna of urban forest fragments. Sociobiologu, 65(3), 441–448. https://doi.org/10.13102/sociobiology.v65i3.3042

Santos MN, Delabie JHC, Queiroz JM (2019) Biodiversity conservation in urban parks: a study of ground-dwelling ants (Hymenoptera: Formicidae) in Rio de Janeiro City. Urban Ecosystems 22, 927–942. https://doi.org/10.1007/s11252-019-00872-8

Shen T-J, Chen Y, Chen Y-F (2017) Estimating species pools for a single ecological assemblage. BMC Ecology 17, 45. https://doi.org/10.1186/s12898-017-0155-7

Simkin RD, Seto KC, McDonald RI, Jetz W (2022) Biodiversity impacts and conservation implications of urban land expansion projected to 2050. PNAS 119(12), e2117297119. https://doi.org/10.1073/pnas.2117297119

Siqueira FFS, Ribeiro-Neto JD, Tabarelli M, Andersen AN, Wirth R, Leal IR (2017) Leaf-cutting ant populations profit from human disturbances in tropical dry forest in Brazil. Journal of Tropical Ecology, 33, 337–344. https://doi.org/10.1017/S0266467417000311

Siqueira FFS, Ribeiro-Neto JD, Tabarelli M, Andersen AN, Wirth R, Leal IR (2018) Human disturbance promotes herbivory by leaf-cutting ants in the Caatinga dry forest. Biotropica, 50, 779–788. https://doi.org/10.1111/btp.12599

Ślipiński P, Żmihorski M, Czechowski W (2012) Species diversity and nestedness of ant assemblages in an urban environment. European Journal of Entomology 109, 197–206. https://doi.org/10.14411/eje.2012.026

Smart SM, Thompson K, Marss RH, Duc MGL, Maskell LC, Firbank LG (2006) Biotic homogenization and changes in species diversity across human-modified ecosystems. Proceedings of the Royal Society B 273(1601), 2659–2665. https://doi.org/10.1098/rspb.2006.3630

Sorvari J, Eeva T (2010) Pollution diminishes intra-specific aggressiveness between wood ant colonies. Science of the Total Environment, 408(16), 3189–3192. https://doi.org/10.1016/j.scitotenv.2010.04.008

Stahlschmidt ZR, Johnson D (2018) Moving targets: determinants of nutritional preferences and habitat use in an urban ant community. Urban Ecosystems 21, 1151–1158. https://doi.org/10.1007/s11252-018-0796-0

Swihart RK, Feng Z, Slade NA, Mason DM, Gehring TM (2001) Effects of habitat destruction and resource supplementation in a predator–prey metapopulation model. Journal of Theoretical Biology, 210, 287–303. https://doi.org/10.1006/jtbi.2001.2304

Szabó B, Korányi D, Gallé R, Lövei GL, Bakonyi G, Batáry P (2023) Urbanization decreases species richness, and increases abundance in dry climates whereas decreases in wet climates: A global meta-analysis. Science of the Total Environment 859(1), 160145. https://doi.org/10.1016/j.scitotenv.2022.160145

727 Tabarelli M, Peres CA, Melo FPL (2012) The 'few winners and many losers' paradigm revisited:
728 Emerging prospects for tropical forest biodiversity. Biological Conservation, 155, 136–140.
729 http://dx.doi.org/10.1016/j.biocon.2012.06.020
730 Thompson B, McLachlan S (2007) The effects of urbanization on ant communities and
731 myrmecochory in Manitoba, Canada. Urban Ecosystems 10, 43-52.
732 https://doi.org/10.1007/s11252-006-0013-4
733 Uhey DA, Hofstetter RW, Remke M, Vissa S, Haubensak KA (2020) Climate and vegetation
734 structure shape ant communities along elevational gradients on the Colorado Plateau. Ecology
735 and Evolution 10(15), 813–8322. https://doi.org/10.1002/ece3.6538
736 Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in
737 urban green spaces. Urban Ecosystems, 13, 425–441. https://doi.org/10.1007/s11252-010-
738 0136-5
739 Wan HY, Cushman SA, Ganey JL (2018) Habitat fragmentation reduces genetic diversity and
740 connectivity of the Mexican spotted owl: A simulation study using empirical resistance
741 models. Genes 9(8), 403. https://doi.org/0.3390/genes9080403.
742 Wang C, Strazanac JS, Butler L (2001) Association between ants (Hymenoptera: Formicidae) and
743 habitat characteristics in oak-dominated mixed forests. Environmental Entomology 30, 842–
744 847. https://doi.org/10.1603/0046-225X-30.5.842
745 Wilson EO (2003) *Pheidole* in the New World: A dominant, hyperdiverse ant genus, vol. 1.
746 Harvard University Press, Cambridge.
747 Wirth R., Meyer ST, Almeida, WR, Araújo MV, Barbosa VS, Leal IR (2007) Increasing densities
748 of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic Forest.
749 Journal of Tropical Ecology, 23, 501–505. https://doi.org/10.1017/S0266467407004221
750 Yanoviak SP, Kaspari M (2000) Community structure and the habitat templet: Ants in the tropical
751 forest canopy and litter. Oikos, 89(2), 259–266. https://doi.org/10.1034/j.1600-0706.
752 2000.890206.x

753 Ydenberg RC, Giraldeau LA, Kramer DL (1986) Interference competition, payoff asymmetries,
754 and the social relationships of central place foragers. Theoretical Population Biology, 30, 26–
755 44. https://doi.org/10.1016/0040-5809(86)90023-7

Table 1. Specialist-Generalist classification of ant species in the city of Recife, northeastern Brazil, following Leal et al. (2012) and Filgueiras et al. (2019).

No	Species	Functional group	Generalist/Specialist
1	*Acanthogonatus* sp. 1	Cryptic predator	Specialist
2	*Camponotus crassus*	Arboreal subordinate	Specialist
3	*Cephalotes pusillus*	Arboreal subordinate	Specialist
4	*Crematogaster brasiliensis*	Arboreal subordinate	Specialist
5	*Crematogaster victima*	Arboreal subordinate	Specialist
6	*Cyphomyrmex transversus*	Non-leaf-cutting Attini	Specialist
7	*Dolichoderus* sp. 1	Arboreal dominant	Specialist
8	*Forelius brasiliensis*	Arboreal dominant	Specialist
9	*Neivamyrmex* sp. 1	Army ant	Specialist
10	*Neoponera* sp. 1	Epigaeic predator	Specialist
11	*Odontomachus bauri*	Epigaeic predator	Specialist
12	*Pseudomyrmex gracilis*	Arboreal subordinate	Specialist
13	*Pseudomyrmex simplex*	Arboreal subordinate	Specialist
14	*Solenopsis globularia*	Cryptic omnivore	Specialist
15	*Solenopsis invicta*	Cryptic omnivore	Specialist
16	*Solenopsis saevissima*	Cryptic omnivore	Specialist
17	*Solenopsis tridens*	Cryptic omnivore	Specialist
18	*Solenopsis virulens*	Cryptic omnivore	Specialist
19	*Atta sexdens*	Leaf-cutting Attini	Generalist
20	*Acromyrmex landolti*	Leaf-cutting Attini	Generalist
21	*Brachymyrmex heeri*	Opportunist	Generalist
22	*Brachymyrmex patagonicus*	Opportunist	Generalist
23	*Camponotus bicolor*	Epigaeic omnivore	Generalist

24	*Camponotus victima*	Epigaeic omnivore	Generalist
25	*Dorymyrmex thoracicus*	Opportunist	Generalist
26	*Ectatomma muticum*	Opportunist	Generalist
27	*Gnamptogenys striatula*	Epigaeic omnivore	Generalist
28	*Gnamptogenys sulcata*	Epigaeic omnivore	Generalist
29	*Linepithema humile*	Epigaeic omnivore	Generalist
30	*Linepithema neotropicum*	Epigaeic omnivore	Generalist
31	*Monomorium* sp. 1	Epigaeic omnivore	Generalist
32	*Paratrechina longicornis*	Epigaeic omnivore	Generalist
33	*Paratrechina* sp. 1	Epigaeic omnivore	Generalist
34	*Pheidole mosenopsis*	Epigaeic omnivore	Generalist
35	*Pheidole radoszkowskii*	Epigaeic omnivore	Generalist
36	*Pheidole* sp. 1	Epigaeic omnivore	Generalist
37	*Pheidole* sp. 2	Epigaeic omnivore	Generalist
38	*Pheidole* sp. 3	Epigaeic omnivore	Generalist
39	*Pheidole* sp. 4	Epigaeic omnivore	Generalist
40	*Pheidole* sp.5	Epigaeic omnivore	Generalist
41	*Tapinoma melanocephalum*	Opportunist	Generalist
42	*Wasmannia auropunctata*	Epigaeic omnivore	Generalist

SUPPLEMENTARY MATERIAL

Increased urbanization promotes winner-loser species replacement and shifts in foraging behavior among ant species in a large neotropical metropolis

Isabelle Leite de Holanda Silva[1], Diego Centeno-Alvarado[2], João Carlos Pena[3], Xavier Arnan[2,4], Inara Roberta Leal[1,5*]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[2]Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Recife, Pernambuco, Brazil

[3]Spatial Ecology and Conservation Lab (LEEC), Department of Biodiversity, Instituto de Biociências, São Paulo State University, Rio Claro, São Paulo, Brazil

[4]Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

[5]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

***Corresponding author:** inara.leal@ufpe.br

This document contains 18 tables.

Table S1. Proportion of urban land cover per site in the city of Recife, northeastern Brazil.

Site	50 m buffer radius	100 m buffer radius	200 m buffer radius	500 m buffer radius
1	0	0	0	0
2	0	0	0	0.02
3	0	0	0.05	0.51
4	0	0	0	0.12
5	0.84	0.84	0.74	0.62
6	0.04	0.09	0.28	0.56
7	0.05	0.03	0.02	0.06
8	0.2	0.37	0.47	0.44
9	0.78	0.68	0.75	0.61
10	0.19	0.13	0.14	0.04
11	0.24	0.44	0.51	0.74
12	0.1	0.39	0.51	0.69
13	0.34	0.64	0.66	0.6
14	1	0.99	0.96	0.86
15	0.83	0.79	0.86	0.87
16	1	1	0.98	0.87
17	0.98	0.98	0.98	0.9
18	0.95	0.98	0.98	0.95
19	1	0.98	0.94	0.64
20	0.85	0.73	0.61	0.52
21	0.76	0.69	0.59	0.8
22	1	0.98	0.97	0.95

Table S2. Spearman rank correlation (ρ) between pairs of urbanization intensities across different buffer scales. Significant relationships are in bold ($P < 0.05$).

Variable 1	Variable 2	ρ	n	*P*
Urban land cover within a 50 m buffer radius	**Urban land cover within a 100 m buffer radius**	**0.98**	**22**	**<0.0001**
	Urban land cover within a 200 m buffer radius	**0.94**	**22**	**<0.0001**
	Urban land cover within a 500 m buffer radius	**0.79**	**22**	**<0.0001**
Urban land cover within a 100 m buffer radius	**Urban land cover within a 200 m buffer radius**	**0.96**	**22**	**<0.0001**
	Urban land cover within a 500 m buffer radius	**0.85**	**22**	**<0.0001**
Urban land cover within a 200 m buffer radius	**Urban land cover within a 500 m buffer radius**	**0.89**	**22**	**<0.0001**

Table S3. Occurrences of each ant species per station per site in the city of Recife, northeastern Brazil. Bait: CARB = carbohydrate-based and PRO = protein-based; "1" indicates presence and "0" indicates absence.

Site	Bait	Species	Station					Abundance (Relative frequency)	Total abundance	Richness
			1	2	3	4	5			
1	PRO	*Acanthogonatus* sp. 1	0	0	1	0	0	0.2	2.8	9
1	PRO	*Brachymyrmex patagonicus*	0	0	1	0	0	0.2		
1	PRO	*Camponotus crassus*	1	0	1	0	0	0.4		
1	PRO	*Cyphomyrmex transversus*	1	0	0	0	0	0.2		
1	PRO	*Dorymyrmex thoracicus*	1	0	0	0	0	0.2		
1	PRO	*Neoponera* sp. 1	0	1	0	0	0	0.2		
1	PRO	*Odontomachus bauri*	1	0	1	1	0	0.6		
1	PRO	*Pheidole radoszkowskii*	1	0	1	1	0	0.6		
1	PRO	*Solenopsis globularia*	0	1	0	0	0	0.2		
1	CARB	*Crematogaster brasiliensis*	0	1	1	0	1	0.6	2	6
1	CARB	*Crematogaster victima*	0	1	0	0	0	0.2		
1	CARB	*Neoponera* sp. 1	1	0	0	1	0	0.4		
1	CARB	*Odontomachus bauri*	1	0	0	0	0	0.2		
1	CARB	*Pheidole radoszkowskii*	1	0	0	0	0	0.2		
1	CARB	*Solenopsis globularia*	0	1	1	0	0	0.4		
2	PRO	*Brachymyrmex patagonicus*	0	0	0	1	0	0.2	2.6	10
2	PRO	*Camponotus crassus*	1	0	1	1	0	0.6		
2	PRO	*Crematogaster brasiliensis*	0	1	0	0	0	0.2		
2	PRO	*Dorymyrmex thoracicus*	0	0	1	0	0	0.2		

2	PRO	*Forelius brasiliensis*	0	1	0	0	0	0.2		
2	PRO	*Odontomachus bauri*	1	0	0	0	1	0.4		
2	PRO	*Pheidole radoszkowskii*	0	0	0	1	0	0.2		
2	PRO	*Pheidole* sp. 1	0	0	0	1	0	0.2		
2	PRO	*Pseudomyrmex gracilis*	0	0	0	1	0	0.2		
2	PRO	*Solenopsis virulens*	0	0	1	0	0	0.2		
2	CARB	*Crematogaster victima*	1	1	0	0	0	0.4	1.8	5
2	CARB	*Neoponera* sp. 1	1	0	0	1	0	0.4		
2	CARB	*Odontomachus bauri*	0	1	0	0	0	0.2		
2	CARB	*Pheidole radoszkowskii*	0	1	0	0	0	0.2		
2	CARB	*Solenopsis globularia*	0	1	0	1	1	0.6		
3	PRO	*Brachymyrmex patagonicus*	1	0	0	0	0	0.2	2.2	8
3	PRO	*Crematogaster brasiliensis*	0	1	0	0	0	0.2		
3	PRO	*Cyphomyrmex transversus*	0	0	0	1	1	0.4		
3	PRO	*Ectatomma muticum*	0	0	0	1	1	0.2		
3	PRO	*Gnamptogenys sulcata*	0	0	1	0	1	0.4		
3	PRO	*Odontomachus bauri*	0	0	0	0	1	0.2		
3	PRO	*Pheidole* sp. 1	0	0	0	1	0	0.2		
3	PRO	*Solenopsis globularia*	1	0	0	0	0	0.2		
3	CARB	*Acanthogonatus* sp. 1	0	0	0	0	1	0.2	2	8
3	CARB	*Camponotus crassus*	0	0	0	0	1	0.2		
3	CARB	*Crematogaster brasiliensis*	1	0	1	0	0	0.4		
3	CARB	*Neoponera* sp. 1	0	0	0	0	1	0.2		
3	CARB	*Odontomachus bauri*	1	0	0	1	0	0.4		

3	CARB	*Pheidole radoszkowskii*	1	0	0	0	0	0.2		
3	CARB	*Solenopsis globularia*	0	0	0	0	1	0.2		
3	CARB	*Wasmannia auropunctata*	0	0	0	0	1	0.2		
4	PRO	*Brachymyrmex patagonicus*	0	1	0	0	0	0.2	2.4	8
4	PRO	*Cyphomyrmex transversus*	0	0	0	1	1	0.4		
4	PRO	*Dorymyrmex thoracicus*	0	0	1	0	0	0.2		
4	PRO	*Ectatomma muticum*	0	1	0	0	0	0.2		
4	PRO	*Neoponera* sp. 1	0	0	1	0	0	0.2		
4	PRO	*Odontomachus bauri*	1	0	0	1	1	0.6		
4	PRO	*Pheidole radoszkowskii*	0	1	1	0	0	0.4		
4	PRO	*Pheidole* sp. 1	0	0	0	0	1	0.2		
4	CARB	*Camponotus crassus*	0	1	0	1	0	0.4	3.8	12
4	CARB	*Crematogaster brasiliensis*	1	0	0	0	0	0.2		
4	CARB	*Crematogaster victima*	0	0	1	0	0	0.2		
4	CARB	*Cyphomyrmex transversus*	0	0	0	1	0	0.2		
4	CARB	*Dorymyrmex thoracicus*	1	0	0	0	0	0.2		
4	CARB	*Ectatomma muticum*	0	1	0	0	0	0.2		
4	CARB	*Neoponera* sp. 1	1	0	1	1	0	0.6		
4	CARB	*Odontomachus bauri*	1	1	0	0	0	0.4		
4	CARB	*Pheidole radoszkowskii*	0	1	0	0	0	0.2		
4	CARB	*Pheidole* sp. 1	1	0	1	0	0	0.4		
4	CARB	*Solenopsis virulens*	0	1	1	0	0	0.4		
4	CARB	*Tapinoma melanocephalum*	0	0	2	0	0	0.4		
5	PRO	*Camponotus crassus*	1	0	0	0	0	0.2	2.4	11

5	PRO	*Cyphomyrmex transversus*	0	0	1	0	0	0.2		
5	PRO	*Dorymyrmex thoracicus*	0	0	0	0	1	0.2		
5	PRO	*Ectatomma muticum*	1	0	0	0	0	0.2		
5	PRO	*Neivamyrmex* sp. 1	0	0	1	0	0	0.2		
5	PRO	*Neoponera* sp.1	1	0	0	0	1	0.4		
5	PRO	*Odontomachus bauri*	0	1	0	0	0	0.2		
5	PRO	*Pheidole radoszkowskii*	0	0	1	0	0	0.2		
5	PRO	*Pheidole* sp. 2	0	0	1	0	0	0.2		
5	PRO	*Pseudomyrmex gracilis*	0	0	0	1	0	0.2		
5	PRO	*Solenopsis saevissima*	0	0	0	0	1	0.2		
5	CARB	*Brachymyrmex patagonicus*	1	0	0	0	0	0.2	1.6	8
5	CARB	*Cephalotes pusillus*	0	0	0	1	0	0.2		
5	CARB	*Crematogaster brasiliensis*	0	0	0	1	0	0.2		
5	CARB	*Crematogaster victima*	1	0	0	0	0	0.2		
5	CARB	*Gnamptogenys sulcata*	0	0	0	0	1	0.2		
5	CARB	*Neoponera* sp. 1	0	0	1	0	0	0.2		
5	CARB	*Solenopsis virulens*	1	0	0	0	0	0.2		
5	CARB	*Tapinoma melanocephalum*	0	0	1	0	0	0.2		
6	PRO	*Brachymyrmex heeri*	0	0	0	1	0	0.2	2.2	10
6	PRO	*Dorymyrmex thoracicus*	0	0	1	0	0	0.2		
6	PRO	*Forelius brasiliensis*	0	0	0	1	0	0.2		
6	PRO	*Gnamptogenys sulcata*	0	0	0	1	0	0.2		
6	PRO	*Neoponera* sp. 1	0	0	1	0	0	0.2		
6	PRO	*Odontomachus bauri*	1	0	0	0	0	0.2		

6	PRO	*Paratrechina* sp. 1	0	1	0	0	0	0.2		
6	PRO	*Pheidole radoszkowskii*	1	0	0	0	0	0.2		
6	PRO	*Pheidole* sp. 2	1	0	0	1	0	0.4		
6	PRO	*Pheidole* sp. 3	0	0	0	1	0	0.2		
6	CARB	*Camponotus crassus*	0	0	0	0	1	0.2	2.2	10
6	CARB	*Dorymyrmex thoracicus*	0	0	0	0	1	0.2		
6	CARB	*Ectatomma muticum*	1	0	0	0	0	0.2		
6	CARB	*Monomorium* sp. 1	1	0	0	0	0	0.2		
6	CARB	*Odontomachus bauri*	0	1	0	0	1	0.4		
6	CARB	*Pheidole radoszkowskii*	0	0	0	0	1	0.2		
6	CARB	*Pseudomyrmex simplex*	0	0	0	1	0	0.2		
6	CARB	*Solenopsis globularia*	0	1	0	0	0	0.2		
6	CARB	*Tapinoma melanocephalum*	0	1	0	0	0	0.2		
6	CARB	*Wasmannia auropunctata*	0	0	0	1	0	0.2		
7	PRO	*Camponotus crassus*	0	1	1	0	1	0.6	2.2	7
7	PRO	*Linepithema neotropicum*	0	0	0	1	0	0.2		
7	PRO	*Neoponera* sp. 1	0	0	1	0	1	0.4		
7	PRO	*Odontomachus bauri*	0	0	1	0	1	0.4		
7	PRO	*Pheidole* sp. 2	0	0	0	1	0	0.2		
7	PRO	*Solenopsis globularia*	0	0	0	1	0	0.2		
7	PRO	*Solenopsis saevissima*	0	0	0	0	1	0.2		
7	CARB	*Camponotus crassus*	1	0	0	0	0	0.2	1.6	8
7	CARB	*Crematogaster brasiliensis*	1	0	0	0	0	0.2		
7	CARB	*Dorymyrmex thoracicus*	0	1	0	0	0	0.2		

7	CARB	*Pheidole* sp. 1	0	1	0	0	0	0.2		
7	CARB	*Pseudomyrmex gracilis*	0	0	0	1	0	0.2		
7	CARB	*Pseudomyrmex simplex*	1	0	0	0	0	0.2		
7	CARB	*Solenopsis virulens*	0	1	0	0	0	0.2		
7	CARB	*Wasmannia auropunctata*	0	1	0	0	0	0.2		
8	PRO	*Camponotus crassus*	1	1	1	0	0	0.6	1.8	6
8	PRO	*Crematogaster brasiliensis*	1	0	0	0	0	0.2		
8	PRO	*Forelius brasiliensis*	0	1	0	0	0	0.2		
8	PRO	*Odontomachus bauri*	1	0	1	0	0	0.4		
8	PRO	*Pheidole* sp. 4	1	0	0	0	0	0.2		
8	PRO	*Wasmannia auropunctata*	0	0	0	1	0	0.2		
8	CARB	*Brachymyrmex patagonicus*	0	0	0	1	0	0.2	1.8	9
8	CARB	*Crematogaster victima*	0	0	0	1	0	0.2		
8	CARB	*Crematogaster brasiliensis*	1	0	0	0	0	0.2		
8	CARB	*Dorymyrmex thoracicus*	0	0	0	1	0	0.2		
8	CARB	*Linepithema neotropicum*	0	0	1	0	0	0.2		
8	CARB	*Neoponera* sp. 1	0	0	1	0	0	0.2		
8	CARB	*Odontomachus bauri*	0	1	0	0	0	0.2		
8	CARB	*Pheidole* sp. 2	0	0	0	1	0	0.2		
8	CARB	*Solenopsis saevissima*	1	0	0	0	0	0.2		
9	PRO	*Camponotus crassus*	0	1	1	1	0	0.6	2.2	7
9	PRO	*Crematogaster victima*	1	0	0	0	0	0.2		
9	PRO	*Forelius brasiliensis*	1	0	0	0	0	0.2		
9	PRO	*Odontomachus bauri*	1	0	0	0	1	0.4		

9	PRO	*Pheidole* sp. 3	1	0	0	0	0	0.2		
9	PRO	*Solenopsis tridens*	0	0	1	0	0	0.2		
9	PRO	*Solenopsis virulens*	0	1	1	0	0	0.4		
9	CARB	*Brachymyrmex patagonicus*	0	0	0	1	0	0.2	2.4	12
9	CARB	*Camponotus crassus*	0	0	1	0	0	0.2		
9	CARB	*Cephalotes pusillus*	0	0	0	0	1	0.2		
9	CARB	*Crematogaster victima*	0	0	0	0	1	0.2		
9	CARB	*Dolichoderus* sp. 1	0	1	0	0	0	0.2		
9	CARB	*Dorymyrmex thoracicus*	1	0	0	0	0	0.2		
9	CARB	*Linepithema humile*	0	0	1	0	0	0.2		
9	CARB	*Neoponera* sp. 1	0	0	0	0	1	0.2		
9	CARB	*Paratrechina longicornis*	0	0	0	1	0	0.2		
9	CARB	*Pseudomyrmex gracilis*	1	0	0	0	0	0.2		
9	CARB	*Tapinoma melanocephalum*	0	0	1	0	0	0.2		
9	CARB	*Wasmannia auropunctata*	0	0	1	0	0	0.2		
10	PRO	*Camponotus crassus*	1	1	0	1	0	0.6	3	10
10	PRO	*Crematogaster brasiliensis*	1	0	1	0	0	0.4		
10	PRO	*Linepithema neotropicum*	0	0	0	0	1	0.2		
10	PRO	*Neoponera* sp. 1	0	1	0	0	0	0.2		
10	PRO	*Odontomachus bauri*	1	1	0	0	0	0.4		
10	PRO	*Pheidole* sp. 1	0	1	1	0	0	0.4		
10	PRO	*Solenopsis saevissima*	0	0	0	1	0	0.2		
10	PRO	*Solenopsis tridens*	1	0	0	0	0	0.2		
10	PRO	*Solenopsis virulens*	1	0	0	0	0	0.2		

10	PRO	*Wasmannia auropunctata*	0	0	0	1	0	0.2		
10	CARB	*Camponotus crassus*	0	0	1	0	0	0.2	1.6	7
10	CARB	*Crematogaster victima*	0	0	1	0	0	0.2		
10	CARB	*Oxyepoecus myops*	1	0	0	1	0	0.4		
10	CARB	*Pheidole* sp. 1	0	1	0	0	0	0.2		
10	CARB	*Pheidole* sp. 3	0	0	1	0	0	0.2		
10	CARB	*Solenopsis virulens*	0	1	0	0	0	0.2		
10	CARB	*Solenopsis saevissima*	0	0	0	1	0	0.2		
11	PRO	*Camponotus bicolor*	0	0	0	1	0	0.2	4	14
11	PRO	*Camponotus crassus*	1	1	1	1	1	1		
11	PRO	*Crematogaster victima*	0	0	0	0	1	0.2		
11	PRO	*Odontomachus bauri*	0	0	0	1	0	0.2		
11	PRO	*Paratrechina longicornis*	0	0	1	0	0	0.2		
11	PRO	*Pheidole mosenopsis*	0	0	0	0	1	0.2		
11	PRO	*Pheidole* sp. 2	1	0	0	0	0	0.2		
11	PRO	*Pheidole* sp. 4	0	0	1	0	0	0.2		
11	PRO	*Pheidole* sp. 5	0	0	1	0	1	0.4		
11	PRO	*Pseudomyrmex simplex*	0	0	0	0	1	0.2		
11	PRO	*Solenopsis saevissima*	0	0	1	1	0	0.4		
11	PRO	*Solenopsis tridens*	0	0	1	0	0	0.2		
11	PRO	*Solenopsis invicta*	0	0	0	0	1	0.2		
11	PRO	*Wasmannia auropunctata*	1	0	0	0	0	0.2		
11	CARB	*Acromyrmex landolti*	0	1	0	0	0	0.2	3.2	10
11	CARB	*Camponotus crassus*	1	1	0	1	1	0.8		

11	CARB	*Crematogaster victima*	0	0	1	0	0	0.2		
11	CARB	*Dolichoderus* sp. 1	0	0	0	0	1	0.2		
11	CARB	*Linepithema humile*	0	0	0	0	1	0.2		
11	CARB	*Pheidole* sp. 3	0	1	0	0	0	0.2		
11	CARB	*Pseudomyrmex gracilis*	0	0	0	1	0	0.2		
11	CARB	*Solenopsis saevissima*	1	1	0	1	1	0.8		
11	CARB	*Solenopsis invicta*	0	0	0	1	0	0.2		
11	CARB	*Tapinoma melanocephalum*	1	0	0	0	0	0.2		
12	PRO	*Acromyrmex landolti*	1	0	0	0	0	0.2	5	14
12	PRO	*Brachymyrmex patagonicus*	0	1	0	1	0	0.4		
12	PRO	*Camponotus bicolor*	1	0	0	0	0	0.2		
12	PRO	*Camponotus crassus*	0	0	1	0	1	0.4		
12	PRO	*Crematogaster victima*	1	0	0	0	0	0.2		
12	PRO	*Cyphomyrmex transversus*	0	1	0	0	0	0.2		
12	PRO	*Forelius brasiliensis*	0	1	0	0	1	0.4		
12	PRO	*Linepithema humile*	0	0	0	1	1	0.4		
12	PRO	*Linepithema neotropicum*	0	1	1	0	0	0.4		
12	PRO	*Paratrechina longicornis*	0	1	0	0	1	0.4		
12	PRO	*Pheidole* sp. 3	0	0	0	0	1	0.2		
12	PRO	*Pheidole* sp. 4	1	1	1	1	0	0.8		
12	PRO	*Solenopsis saevissima*	0	1	0	1	1	0.6		
12	PRO	*Wasmannia auropunctata*	0	1	0	0	0	0.2		
12	CARB	*Camponotus crassus*	1	0	0	0	0	0.2	2.2	8
12	CARB	*Crematogaster victima*	1	0	0	0	0	0.2		

12	CARB	*Dorymyrmex thoracicus*	0	0	1	0	0	0.2		
12	CARB	*Linepithema neotropicum*	1	0	0	0	0	0.2		
12	CARB	*Neoponera* sp. 1	0	0	0	0	1	0.2		
12	CARB	*Pheidole* sp. 2	1	0	0	0	0	0.2		
12	CARB	*Solenopsis virulens*	1	1	1	1	0	0.8		
12	CARB	*Wasmannia auropunctata*	0	1	0	0	0	0.2		
13	PRO	*Camponotus crassus*	1	0	1	0	1	0.6	2.6	7
13	PRO	*Dorymyrmex thoracicus*	0	0	1	1	0	0.4		
13	PRO	*Ectatomma muticum*	0	0	1	0	0	0.2		
13	PRO	*Odontomachus bauri*	1	1	0	0	0	0.4		
13	PRO	*Pheidole radoszkowskii*	1	0	0	0	0	0.2		
13	PRO	*Pheidole* sp. 5	0	1	0	0	1	0.4		
13	PRO	*Solenopsis invicta*	0	0	1	1	0	0.4		
13	CARB	*Camponotus crassus*	0	0	1	0	0	0.2	2.6	10
13	CARB	*Crematogaster victima*	1	0	0	0	0	0.2		
13	CARB	*Dorymyrmex thoracicus*	0	0	0	0	1	0.2		
13	CARB	*Paratrechina longicornis*	1	0	0	0	0	0.2		
13	CARB	*Pheidole* sp. 4	0	1	0	0	0	0.2		
13	CARB	*Pheidole radoszkowskii*	0	0	0	1	0	0.2		
13	CARB	*Pseudomyrmex gracilis*	0	0	0	1	0	0.2		
13	CARB	*Solenopsis saevissima*	0	1	1	0	1	0.6		
13	CARB	*Solenopsis virulens*	0	0	1	0	0	0.2		
13	CARB	*Wasmannia auropunctata*	1	0	1	0	0	0.4		
14	PRO	*Brachymyrmex heeri*	0	0	0	1	0	0.2	3	8

14	PRO	*Camponotus crassus*	0	1	1	1	1	0.8		
14	PRO	*Gnamptogenys striatula*	0	0	0	1	0	0.2		
14	PRO	*Linepithema neotropicum*	0	1	0	0	0	0.2		
14	PRO	*Odontomachus bauri*	1	0	1	0	1	0.6		
14	PRO	*Pheidole* sp. 5	0	1	0	1	0	0.4		
14	PRO	*Solenopsis invicta*	0	0	0	1	0	0.2		
14	PRO	*Wasmannia auropunctata*	0	0	1	1	0	0.4		
14	CARB	*Acromyrmex landolti*	0	0	0	1	0	0.2	2.4	9
14	CARB	*Camponotus crassus*	0	0	1	0	0	0.2		
14	CARB	*Cyphomyrmex transversus*	0	0	1	0	0	0.2		
14	CARB	*Forelius brasiliensis*	0	0	1	0	0	0.2		
14	CARB	*Pheidole* sp. 4	1	0	1	0	1	0.6		
14	CARB	*Pseudomyrmex simplex*	0	1	0	0	0	0.2		
14	CARB	*Solenopsis saevissima*	1	1	0	0	0	0.4		
14	CARB	*Solenopsis invicta*	0	0	0	1	0	0.2		
14	CARB	*Tapinoma melanocephalum*	1	0	0	0	0	0.2		
15	PRO	*Brachymyrmex patagonicus*	1	0	0	0	1	0.4	3.2	12
15	PRO	*Camponotus crassus*	1	0	0	1	0	0.4		
15	PRO	*Crematogaster brasiliensis*	1	0	0	1	0	0.4		
15	PRO	*Cyphomyrmex transversus*	0	0	1	0	1	0.4		
15	PRO	*Dolichoderus* sp. 1	0	1	0	0	0	0.2		
15	PRO	*Dorymyrmex thoracicus*	0	1	0	0	0	0.2		
15	PRO	*Pheidole radoszkowskii*	0	0	1	0	0	0.2		
15	PRO	*Pheidole* sp. 1	0	0	0	0	1	0.2		

15	PRO	*Pheidole* sp. 2	0	0	0	0	1	0.2		
15	PRO	*Pseudomyrmex simplex*	0	0	1	0	0	0.2		
15	PRO	*Solenopsis virulens*	0	0	1	0	0	0.2		
15	PRO	*Solenopsis invicta*	0	1	0	0	0	0.2		
15	CARB	*Atta sexdens*	0	0	0	1	0	0.2	1.4	6
15	CARB	*Camponotus crassus*	1	1	0	0	0	0.4		
15	CARB	*Odontomachus bauri*	0	1	0	0	0	0.2		
15	CARB	*Pheidole* sp. 3	0	0	0	1	0	0.2		
15	CARB	*Solenopsis saevissima*	0	0	1	0	0	0.2		
15	CARB	*Solenopsis tridens*	0	0	0	1	0	0.2		
16	PRO	*Camponotus bicolor*	1	0	0	1	0	0.4	3.2	11
16	PRO	*Camponotus crassus*	0	1	0	0	1	0.4		
16	PRO	*Crematogaster victima*	0	0	0	0	1	0.2		
16	PRO	*Neivamyrmex* sp. 1	0	1	0	0	0	0.2		
16	PRO	*Odontomachus bauri*	0	0	0	0	1	0.2		
16	PRO	*Paratrechina longicornis*	0	0	1	0	0	0.2		
16	PRO	*Pheidole mosenopsis*	0	1	0	1	0	0.4		
16	PRO	*Pheidole* sp. 4	0	1	0	0	0	0.2		
16	PRO	*Pheidole radoszkowskii*	0	1	0	0	0	0.2		
16	PRO	*Solenopsis saevissima*	0	1	1	1	0	0.6		
16	PRO	*Wasmannia auropunctata*	0	1	0	0	0	0.2		
16	CARB	*Atta sexdens*	1	0	0	0	0	0.2	1.8	7
16	CARB	*Camponotus crassus*	0	1	1	0	0	0.4		
16	CARB	*Crematogaster victima*	1	0	0	0	0	0.2		

16	CARB	*Pheidole mosenopsis*	1	0	0	0	0	0.2		
16	CARB	*Pheidole* sp. 5	0	0	0	0	1	0.2		
16	CARB	*Solenopsis invicta*	0	1	0	1	0	0.4		
16	CARB	*Tapinoma melanocephalum*	1	0	0	0	0	0.2		
17	PRO	*Camponotus bicolor*	0	0	1	0	0	0.2	2.2	8
17	PRO	*Camponotus crassus*	0	1	1	0	0	0.4		
17	PRO	*Crematogaster victima*	0	0	0	0	1	0.2		
17	PRO	*Forelius brasiliensis*	1	0	0	0	0	0.2		
17	PRO	*Linepithema neotropicum*	1	0	0	0	0	0.2		
17	PRO	*Pheidole mosenopsis*	1	0	0	1	0	0.4		
17	PRO	*Solenopsis invicta*	0	0	0	0	1	0.2		
17	PRO	*Wasmannia auropunctata*	0	1	0	0	1	0.4		
17	CARB	*Camponotus crassus*	0	1	1	0	0	0.4	1	4
17	CARB	*Crematogaster victima*	1	0	0	0	0	0.2		
17	CARB	*Pseudomyrmex gracilis*	1	0	0	0	0	0.2		
17	CARB	*Tapinoma melanocephalum*	0	0	0	0	1	0.2		
18	PRO	*Camponotus bicolor*	0	0	0	0	1	0.2	2	5
18	PRO	*Camponotus crassus*	1	0	0	0	1	0.4		
18	PRO	*Pheidole* sp. 4	1	0	1	0	0	0.4		
18	PRO	*Pheidole mosenopsis*	0	1	1	1	1	0.8		
18	PRO	*Solenopsis saevissima*	0	0	0	1	0	0.2		
18	CARB	*Atta sexdens*	0	1	0	0	0	0.2	3.2	11
18	CARB	*Camponotus bicolor*	0	1	1	0	0	0.4		
18	CARB	*Camponotus crassus*	0	1	1	0	0	0.4		

18	CARB	*Crematogaster victima*	1	0	0	0	0	0.2		
18	CARB	*Linepithema neotropicum*	0	0	1	0	0	0.2		
18	CARB	*Linepithema humile*	0	0	0	0	1	0.2		
18	CARB	*Pheidole radoszkowskii*	0	0	0	0	1	0.2		
18	CARB	*Pheidole* sp. 5	0	0	0	1	0	0.2		
18	CARB	*Pheidole mosenopsis*	0	0	0	1	0	0.2		
18	CARB	*Solenopsis saevissima*	1	1	1	1	0	0.8		
18	CARB	*Tapinoma melanocephalum*	0	0	1	0	0	0.2		
19	PRO	*Acromyrmex landolti*	0	1	0	0	0	0.2	1.6	7
19	PRO	*Camponotus bicolor*	0	0	0	0	1	0.2		
19	PRO	*Camponotus crassus*	0	0	0	1	0	0.2		
19	PRO	*Crematogaster victima*	0	0	0	1	0	0.2		
19	PRO	*Odontomachus bauri*	1	0	0	0	0	0.2		
19	PRO	*Pheidole mosenopsis*	1	0	0	0	0	0.2		
19	PRO	*Solenopsis saevissima*	0	1	1	0	0	0.4		
19	CARB	*Camponotus bicolor*	1	0	0	0	0	0.2	2	7
19	CARB	*Camponotus crassus*	1	0	0	0	0	0.2		
19	CARB	*Forelius brasiliensis*	0	0	1	0	0	0.2		
19	CARB	*Pheidole mosenopsis*	0	1	0	0	1	0.4		
19	CARB	*Solenopsis saevissima*	0	1	0	1	0	0.4		
19	CARB	*Tapinoma melanocephalum*	0	0	0	1	0	0.2		
19	CARB	*Wasmannia auropunctata*	0	0	1	0	1	0.4		
20	PRO	*Camponotus bicolor*	1	1	0	1	0	0.6	5	13
20	PRO	*Camponotus crassus*	1	1	1	1	0	0.8		

20	PRO	*Crematogaster victima*	0	0	0	0	1	0.2		
20	PRO	*Ectatomma muticum*	0	0	1	1	0	0.4		
20	PRO	*Forelius brasiliensis*	1	0	1	0	0	0.4		
20	PRO	*Linepithema neotropicum*	0	1	0	0	0	0.2		
20	PRO	*Pheidole radoszkowskii*	1	0	1	0	1	0.6		
20	PRO	*Pheidole* sp. 5	0	0	0	0	1	0.2		
20	PRO	*Pheidole mosenopsis*	1	0	0	0	0	0.2		
20	PRO	*Solenopsis saevissima*	0	0	0	1	1	0.2		
20	PRO	*Solenopsis invicta*	1	0	0	0	1	0.4		
20	PRO	*Tapinoma melanocephalum*	0	0	0	0	1	0.2		
20	PRO	*Wasmannia auropunctata*	0	1	0	0	1	0.4		
20	CARB	*Atta sexdens*	1	0	0	1	0	0.4	3	10
20	CARB	*Brachymyrmex patagonicus*	0	1	0	0	0	0.2		
20	CARB	*Camponotus bicolor*	0	0	0	0	1	0.2		
20	CARB	*Camponotus crassus*	0	1	1	1	1	0.8		
20	CARB	*Crematogaster victima*	1	0	0	0	0	0.2		
20	CARB	*Paratrechina longicornis*	0	1	1	0	0	0.4		
20	CARB	*Pheidole* sp. 4	1	0	0	0	0	0.2		
20	CARB	*Solenopsis invicta*	1	0	0	0	0	0.2		
20	CARB	*Solenopsis saevissima*	0	0	1	0	0	0.2		
20	CARB	*Tapinoma melanocephalum*	0	1	0	0	0	0.2		
21	PRO	*Camponotus bicolor*	0	0	1	0	0	0.2	1.6	6
21	PRO	*Camponotus crassus*	1	0	0	0	0	0.2		
21	PRO	*Crematogaster victima*	0	0	1	0	0	0.2		

21	PRO	*Pheidole* sp. 3	0	0	1	0	0	0.2		
21	PRO	*Pheidole radoszkowskii*	0	0	0	0	1	0.2		
21	PRO	*Solenopsis invicta*	1	1	0	1	0	0.6		
21	CARB	*Camponotus crassus*	0	0	0	0	1	0.2	1.6	8
21	CARB	*Crematogaster victima*	0	0	0	1	0	0.2		
21	CARB	*Linepithema humile*	0	1	0	0	0	0.2		
21	CARB	*Paratrechina longicornis*	0	0	0	0	1	0.2		
21	CARB	*Pheidole radoszkowskii*	0	0	0	0	1	0.2		
21	CARB	*Pheidole* sp. 5	1	0	0	0	0	0.2		
21	CARB	*Solenopsis saevissima*	0	1	0	0	0	0.2		
21	CARB	*Tapinoma melanocephalum*	0	0	1	0	0	0.2		
22	PRO	*Camponotus bicolor*	1	0	0	0	0	0.2	1.4	7
22	PRO	*Crematogaster victima*	0	0	1	0	0	0.2		
22	PRO	*Ectatomma muticum*	0	1	0	0	0	0.2		
22	PRO	*Pheidole* sp. 5	0	0	1	0	0	0.2		
22	PRO	*Pheidole mosenopsis*	0	0	0	1	0	0.2		
22	PRO	*Solenopsis invicta*	0	0	0	0	1	0.2		
22	PRO	*Wasmannia auropunctata*	0	1	0	0	0	0.2		
22	CARB	*Camponotus bicolor*	0	1	0	0	1	0.4	2.6	7
22	CARB	*Camponotus crassus*	1	1	0	1	0	0.6		
22	CARB	*Linepithema humile*	0	0	1	0	1	0.4		
22	CARB	*Pheidole radoszkowskii*	1	0	0	0	1	0.4		
22	CARB	*Pheidole* sp. 5	0	0	1	1	0	0.4		
22	CARB	*Solenopsis invicta*	0	0	1	0	0	0.2		

22	CARB	*Tapinoma melanocephalum*	0	0	1	0	0	0.2

Table S4. Generalist / specialists ratio of species richness and ant abundance per site in the city of Recife, northeastern Brazil.

Site	Generalist / specialist ratio	
	Richness	Abundance
1	0.43	0.40
2	0.57	0.36
3	1.00	0.58
4	0.83	0.79
5	0.60	0.60
6	2.00	1.83
7	0.63	0.42
8	1.20	0.60
9	0.63	0.36
10	0.50	0.43
11	1.00	0.40
12	1.67	1.38
13	0.86	0.73
14	1.17	0.79
15	0.70	0.50
16	1.17	0.67
17	1.00	0.75
18	2.67	1.50
19	0.80	1.00
20	2.50	1.20
21	1.25	0.75
22	2.33	2.17

Table S5. Protein- and carbohydrate-bait occupancy indices in the city of Recife, northeastern Brazil

Site	Bait occupancy index			
	Richness		Abundance	
	Protein	Carbohydrate	Protein	Carbohydrate
1	0.65	0.55	0.47	0.42
2	0.77	0.31	0.59	0.33
3	0.62	0.49	0.50	0.40
4	0.62	0.92	0.39	0.61
5	0.61	0.44	0.60	0.40
6	0.47	0.47	0.40	0.40
7	0.40	0.34	0.46	0.25
8	0.37	0.55	0.40	0.40
9	0.41	0.71	0.48	0.52
10	0.71	0.34	0.74	0.21
11	0.70	0.50	0.57	0.43
12	0.74	0.42	0.69	0.31
13	0.50	0.57	0.52	0.39
14	0.53	0.60	0.56	0.44
15	0.71	0.28	0.71	0.23
16	0.73	0.47	0.64	0.36
17	0.80	0.32	0.69	0.25
18	0.42	0.92	0.38	0.62
19	0.70	0.10	0.44	0.56
20	0.76	0.59	0.62	0.38
21	0.55	0.73	0.50	0.50
22	0.64	0.64	0.35	0.65

Table S6. Ant bait discovery time per station per site in the city of Recife, northeastern Brazil. Bait: CARB = carbohydrate-based and PRO = protein-based.

Site	Bait	Station	Species	Bait discovery time (min)
1	PRO	1	*Camponotus crassus*	15
1	PRO	1	*Cyphomyrmex transversus*	10
1	PRO	1	*Dorymyrmex thoracicus*	5
1	PRO	1	*Odontomachus bauri*	1
1	PRO	1	*Pheidole radoszkowskii*	5
1	PRO	2	*Neoponera* sp. 1	10
1	PRO	2	*Solenopsis virulens*	15
1	PRO	3	*Brachymyrmex patagonicus*	5
1	PRO	3	*Camponotus crassus*	2
1	PRO	3	*Odontomachus bauri*	11
1	PRO	3	*Pheidole radoszkowskii*	1
1	PRO	4	*Acanthogonatus* sp. 1	15
1	PRO	4	*Odontomachus bauri*	15
1	PRO	4	*Pheidole radoszkowskii*	20
1	CARB	1	*Neoponera* sp. 1	10
1	CARB	1	*Odontomachus bauri*	10
1	CARB	1	*Pheidole radoszkowskii*	15
1	CARB	2	*Crematogaster victima*	15
1	CARB	2	*Crematogaster brasiliensis*	5
1	CARB	2	*Pheidole* sp. 1	10
1	CARB	2	*Solenopsis virulens*	15
1	CARB	3	*Crematogaster brasiliensis*	20
1	CARB	3	*Solenopsis virulens*	5
1	CARB	4	*Neoponera* sp. 1	15
1	CARB	5	*Crematogaster brasiliensis*	5
1	CARB	5	*Pheidole* sp. 1	5
2	PRO	1	*Camponotus crassus*	5
2	PRO	1	*Odontomachus bauri*	15
2	PRO	1	*Pheidole* sp. 1	3
2	PRO	2	*Crematogaster brasiliensis*	10
2	PRO	2	*Forelius brasiliensis*	5
2	PRO	3	*Camponotus crassus*	15
2	PRO	3	*Dorymyrmex thoracicus*	1
2	PRO	3	*Solenopsis virulens*	15
2	PRO	4	*Brachymyrmex patagonicus*	10

2	PRO	4	*Camponotus crassus*	10
2	PRO	4	*Pheidole radoszkowskii*	10
2	PRO	4	*Pseudomyrmex gracilis*	10
2	PRO	5	*Odontomachus bauri*	10
2	CARB	1	*Crematogaster victima*	15
2	CARB	1	*Neoponera* sp. 1	5
2	CARB	2	*Crematogaster victima*	15
2	CARB	2	*Odontomachus bauri*	20
2	CARB	2	*Pheidole radoszkowskii*	15
2	CARB	2	*Solenopsis virulens*	5
2	CARB	4	*Neoponera* sp. 1	10
2	CARB	4	*Solenopsis virulens*	15
2	CARB	5	*Solenopsis virulens*	3
3	PRO	1	*Brachymyrmex patagonicus*	20
3	PRO	1	*Solenopsis virulens*	20
3	PRO	2	*Crematogaster brasiliensis*	20
3	PRO	3	*Gnamptogenys sulcata*	15
3	PRO	4	*Cyphomyrmex transversus*	15
3	PRO	4	*Ectatomma muticum*	15
3	PRO	4	*Pheidole* sp. 1	5
3	PRO	5	*Cyphomyrmex transversus*	15
3	PRO	5	*Ectatomma muticum*	15
3	PRO	5	*Gnamptogenys sulcata*	10
3	PRO	5	*Odontomachus bauri*	10
3	CARB	1	*Crematogaster brasiliensis*	1
3	CARB	1	*Odontomachus bauri*	15
3	CARB	1	*Pheidole radoszkowskii*	15
3	CARB	3	*Crematogaster brasiliensis*	1
3	CARB	4	*Neoponera* sp. 1	15
3	CARB	4	*Odontomachus bauri*	15
3	CARB	5	*Acanthogonatus* sp. 1	15
3	CARB	5	*Camponotus crassus*	15
3	CARB	5	*Neoponera* sp. 1	1
3	CARB	5	*Solenopsis virulens*	15
3	CARB	5	*Wasmannia auropunctata*	5
4	PRO	1	*Odontomachus bauri*	15
4	PRO	1	*Odontomachus bauri*	15
4	PRO	2	*Brachymyrmex patagonicus*	10
4	PRO	2	*Camponotus crassus*	1
4	PRO	2	*Ectatomma muticum*	3

4	PRO	2	*Odontomachus bauri*	5
4	PRO	2	*Pheidole radoszkowskii*	1
4	PRO	2	*Pheidole radoszkowskii*	5
4	PRO	3	*Dorymyrmex thoracicus*	15
4	PRO	3	*Neoponera* sp. 1	15
4	PRO	3	*Neoponera* sp. 1	5
4	PRO	3	*Pheidole radoszkowskii*	5
4	PRO	4	*Cyphomyrmex transversus*	5
4	PRO	4	*Cyphomyrmex transversus*	10
4	PRO	4	*Odontomachus bauri*	15
4	PRO	5	*Cyphomyrmex transversus*	5
4	PRO	5	*Odontomachus bauri*	5
4	PRO	5	*Pheidole* sp. 1	10
4	CARB	1	*Crematogaster victima*	5
4	CARB	1	*Crematogaster brasiliensis*	1
4	CARB	1	*Neoponera* sp. 1	3
4	CARB	1	*Solenopsis virulens*	15
4	CARB	2	*Ectatomma muticum*	5
4	CARB	2	*Neoponera* sp. 1	15
4	CARB	2	*Solenopsis virulens*	15
4	CARB	2	*Tapinoma melanocephalum*	15
4	CARB	3	*Crematogaster victima*	15
4	CARB	3	*Neoponera* sp. 1	15
4	CARB	3	*Pheidole* sp. 1	5
4	CARB	4	*Camponotus crassus*	15
4	CARB	5	*Crematogaster brasiliensis*	10
4	CARB	5	*Dorymyrmex thoracicus*	10
5	PRO	1	*Camponotus crassus*	20
5	PRO	1	*Ectatomma muticum*	2
5	PRO	1	*Neoponera* sp. 1	1
5	PRO	2	*Odontomachus bauri*	20
5	PRO	3	*Cyphomyrmex transversus*	15
5	PRO	3	*Neivamyrmex* sp. 1	10
5	PRO	3	*Pheidole radoszkowskii*	5
5	PRO	3	*Pheidole* sp. 2	15
5	PRO	4	*Pseudomyrmex gracilis*	20
5	PRO	5	*Dorymyrmex thoracicus*	20
5	PRO	5	*Neoponera* sp. 1	5
5	PRO	5	*Solenopsis saevissima*	15
5	CARB	1	*Crematogaster victima*	2

5	CARB	1	*Solenopsis virulens*	1
5	CARB	2	*Brachymyrmex patagonicus*	10
5	CARB	3	*Crematogaster brasiliensis*	15
5	CARB	3	*Neoponera* sp. 1	15
5	CARB	3	*Tapinoma melanocephalum*	15
5	CARB	4	*Cephalotes pusillus*	10
5	CARB	5	*Gnamptogenys sulcata*	15
6	PRO	1	*Odontomachus bauri*	5
6	PRO	1	*Pheidole radoszkowskii*	15
6	PRO	1	*Pheidole* sp. 2	5
6	PRO	2	*Paratrechina longicornis*	5
6	PRO	3	*Dorymyrmex thoracicus*	5
6	PRO	3	*Neoponera* sp. 1	5
6	PRO	4	*Brachymyrmex heeri*	5
6	PRO	4	*Forelius brasiliensis*	5
6	PRO	4	*Gnamptogenys sulcata*	5
6	PRO	4	*Pheidole* sp. 2	10
6	PRO	4	*Pheidole* sp. 3	15
6	CARB	1	*Ectatomma muticum*	15
6	CARB	1	*Monomorium* sp. 1	15
6	CARB	2	*Odontomachus bauri*	15
6	CARB	2	*Solenopsis virulens*	1
6	CARB	2	*Tapinoma melanocephalum*	10
6	CARB	4	*Pseudomyrmex simplex*	10
6	CARB	4	*Wasmannia auropunctata*	15
6	CARB	5	*Camponotus crassus*	15
6	CARB	5	*Dorymyrmex thoracicus*	20
6	CARB	5	*Odontomachus bauri*	15
6	CARB	5	*Pheidole radoszkowskii*	3
7	PRO	2	*Camponotus crassus*	2
7	PRO	3	*Neoponera* sp. 1	15
7	PRO	3	*Odontomachus bauri*	10
7	PRO	4	*Linepithema neotropicum*	15
7	PRO	4	*Pheidole* sp. 2	15
7	PRO	4	*Solenopsis virulens*	15
7	PRO	5	*Camponotus crassus*	5
7	PRO	5	*Neoponera* sp. 1	15
7	PRO	5	*Odontomachus bauri*	20
7	PRO	5	*Solenopsis saevissima*	20
7	CARB	1	*Camponotus crassus*	5

7	CARB	1	*Pseudomyrmex simplex*	10
7	CARB	2	*Crematogaster victima*	1
7	CARB	2	*Pheidole* sp. 1	5
7	CARB	2	*Solenopsis virulens*	5
7	CARB	2	*Wasmannia auropunctata*	1
7	CARB	4	*Dorymyrmex thoracicus*	15
7	CARB	4	*Pseudomyrmex gracilis*	20
8	PRO	1	*Camponotus crassus*	2
8	PRO	1	*Crematogaster victima*	10
8	PRO	1	*Odontomachus bauri*	15
8	PRO	1	*Pheidole* sp. 4	10
8	PRO	2	*Camponotus crassus*	10
8	PRO	2	*Forelius brasiliensis*	10
8	PRO	3	*Camponotus crassus*	10
8	PRO	3	*Odontomachus bauri*	5
8	PRO	4	*Wasmannia auropunctata*	10
8	CARB	1	*Crematogaster victima*	10
8	CARB	1	*Solenopsis saevissima*	20
8	CARB	2	*Odontomachus bauri*	15
8	CARB	3	*Linepithema neotropicum*	15
8	CARB	3	*Neoponera* sp. 1	15
8	CARB	4	*Brachymyrmex patagonicus*	15
8	CARB	4	*Crematogaster victima*	15
8	CARB	4	*Dorymyrmex thoracicus*	15
8	CARB	4	*Pheidole* sp. 2	15
9	PRO	1	*Crematogaster victima*	1
9	PRO	1	*Forelius brasiliensis*	5
9	PRO	1	*Odontomachus bauri*	5
9	PRO	1	*Pheidole* sp. 3	5
9	PRO	2	*Camponotus crassus*	5
9	PRO	2	*Solenopsis virulens*	1
9	PRO	3	*Camponotus crassus*	5
9	PRO	3	*Solenopsis virulens*	5
9	PRO	3	*Solenopsis tridens*	1
9	PRO	4	*Camponotus crassus*	1
9	PRO	5	*Odontomachus bauri*	15
9	CARB	1	*Dorymyrmex thoracicus*	10
9	CARB	1	*Pseudomyrmex gracilis*	10
9	CARB	2	*Dolichoderus* sp. 1	20
9	CARB	3	*Camponotus crassus*	15

9	CARB	3	*Linepithema humile*	15
9	CARB	3	*Tapinoma melanocephalum*	15
9	CARB	3	*Wasmannia auropunctata*	15
9	CARB	4	*Brachymyrmex patagonicus*	10
9	CARB	4	*Paratrechina longicornis*	15
9	CARB	5	*Cephalotes pusillus*	5
9	CARB	5	*Crematogaster victima*	5
9	CARB	5	*Neoponera* sp. 1	5
10	PRO	1	*Camponotus crassus*	5
10	PRO	1	*Crematogaster brasiliensis*	5
10	PRO	1	*Odontomachus bauri*	5
10	PRO	1	*Solenopsis virulens*	10
10	PRO	1	*Solenopsis tridens*	10
10	PRO	2	*Camponotus crassus*	15
10	PRO	2	*Neoponera* sp. 1	5
10	PRO	2	*Odontomachus bauri*	15
10	PRO	2	*Pheidole* sp. 1	15
10	PRO	3	*Crematogaster brasiliensis*	15
10	PRO	3	*Pheidole* sp. 1	20
10	PRO	4	*Camponotus crassus*	15
10	PRO	4	*Solenopsis saevissima*	15
10	PRO	4	*Wasmannia auropunctata*	15
10	PRO	5	*Linepithema neotropicum*	1
10	CARB	1	*Oxyepoecus myops*	15
10	CARB	2	*Pheidole* sp. 1	15
10	CARB	2	*Solenopsis virulens*	15
10	CARB	3	*Camponotus crassus*	2
10	CARB	3	*Crematogaster victima*	15
10	CARB	3	*Pheidole* sp. 3	15
10	CARB	4	*Oxyepoecus myops*	5
10	CARB	4	*Oxyepoecus myops*	1
10	CARB	4	*Solenopsis saevissima*	1
11	PRO	1	*Camponotus crassus*	15
11	PRO	1	*Pheidole* sp. 2	10
11	PRO	1	*Wasmannia auropunctata*	15
11	PRO	2	*Camponotus crassus*	15
11	PRO	3	*Paratrechina longicornis*	5
11	PRO	3	*Pheidole* sp. 4	15
11	PRO	3	*Pheidole* sp. 5	5
11	PRO	3	*Solenopsis saevissima*	5

11	PRO	3	*Solenopsis tridens*	10
11	PRO	4	*Camponotus bicolor*	5
11	PRO	4	*Camponotus crassus*	5
11	PRO	4	*Odontomachus bauri*	1
11	PRO	4	*Solenopsis saevissima*	1
11	PRO	5	*Camponotus crassus*	5
11	PRO	5	*Crematogaster victima*	1
11	PRO	5	*Pheidole* sp. 5	1
11	PRO	5	*Pheidole mosenopsis*	5
11	PRO	5	*Pseudomyrmex simplex*	5
11	PRO	5	*Solenopsis invicta*	10
11	CARB	1	*Camponotus crassus*	5
11	CARB	1	*Solenopsis saevissima*	5
11	CARB	1	*Tapinoma melanocephalum*	5
11	CARB	2	*Acromyrmex landolti*	2
11	CARB	2	*Camponotus crassus*	2
11	CARB	2	*Pheidole* sp. 3	5
11	CARB	2	*Solenopsis saevissima*	1
11	CARB	3	*Crematogaster victima*	5
11	CARB	4	*Camponotus crassus*	1
11	CARB	4	*Pseudomyrmex gracilis*	2
11	CARB	4	*Solenopsis invicta*	2
11	CARB	4	*Solenopsis saevissima*	5
11	CARB	5	*Camponotus crassus*	1
11	CARB	5	*Dolichoderus* sp. 1	2
11	CARB	5	*Linepithema humile*	10
11	CARB	5	*Solenopsis saevissima*	5
12	PRO	1	*Acromyrmex landolti*	2
12	PRO	1	*Camponotus bicolor*	2
12	PRO	1	*Crematogaster victima*	1
12	PRO	1	*Pheidole* sp. 4	4
12	PRO	2	*Brachymyrmex patagonicus*	5
12	PRO	2	*Cyphomyrmex transversus*	1
12	PRO	2	*Forelius brasiliensis*	1
12	PRO	2	*Linepithema neotropicum*	1
12	PRO	2	*Paratrechina longicornis*	1
12	PRO	2	*Pheidole* sp. 4	1
12	PRO	2	*Solenopsis saevissima*	1
12	PRO	2	*Wasmannia auropunctata*	5
12	PRO	3	*Camponotus crassus*	1

12	PRO	3	*Linepithema neotropicum*	1
12	PRO	3	*Pheidole* sp. 4	4
12	PRO	4	*Brachymyrmex patagonicus*	5
12	PRO	4	*Linepithema humile*	2
12	PRO	4	*Pheidole* sp. 4	10
12	PRO	4	*Solenopsis saevissima*	5
12	PRO	5	*Camponotus crassus*	5
12	PRO	5	*Forelius brasiliensis*	5
12	PRO	5	*Linepithema humile*	5
12	PRO	5	*Paratrechina longicornis*	5
12	PRO	5	*Pheidole* sp. 3	5
12	PRO	5	*Solenopsis saevissima*	5
12	CARB	1	*Camponotus crassus*	2
12	CARB	1	*Crematogaster victima*	5
12	CARB	1	*Linepithema neotropicum*	5
12	CARB	1	*Pheidole* sp. 2	5
12	CARB	1	*Solenopsis virulens*	5
12	CARB	2	*Solenopsis virulens*	2
12	CARB	2	*Wasmannia auropunctata*	2
12	CARB	3	*Dorymyrmex thoracicus*	5
12	CARB	3	*Solenopsis virulens*	2
12	CARB	4	*Solenopsis virulens*	2
12	CARB	5	*Neoponera* sp. 1	5
13	PRO	1	*Camponotus crassus*	2
13	PRO	1	*Odontomachus bauri*	1
13	PRO	1	*Pheidole radoszkowskii*	5
13	PRO	2	*Odontomachus bauri*	5
13	PRO	2	*Pheidole* sp. 5	5
13	PRO	3	*Camponotus crassus*	1
13	PRO	3	*Dorymyrmex thoracicus*	5
13	PRO	3	*Ectatomma muticum*	5
13	PRO	3	*Solenopsis invicta*	10
13	PRO	4	*Dorymyrmex thoracicus*	5
13	PRO	4	*Solenopsis invicta*	5
13	PRO	5	*Camponotus crassus*	5
13	PRO	5	*Pheidole* sp. 5	2
13	CARB	1	*Crematogaster victima*	1
13	CARB	1	*Paratrechina longicornis*	1
13	CARB	1	*Wasmannia auropunctata*	5
13	CARB	2	*Pheidole* sp. 4	1

13	CARB	2	*Solenopsis saevissima*	1
13	CARB	3	*Camponotus crassus*	1
13	CARB	3	*Pheidole radoszkowskii*	1
13	CARB	3	*Solenopsis virulens*	1
13	CARB	3	*Solenopsis saevissima*	10
13	CARB	3	*Wasmannia auropunctata*	1
13	CARB	4	*Dorymyrmex thoracicus*	5
13	CARB	4	*Pseudomyrmex gracilis*	5
13	CARB	4	*Solenopsis saevissima*	5
14	PRO	1	*Odontomachus bauri*	5
14	PRO	2	*Camponotus crassus*	5
14	PRO	2	*Linepithema neotropicum*	5
14	PRO	2	*Pheidole* sp. 5	5
14	PRO	3	*Odontomachus bauri*	10
14	PRO	3	*Wasmannia auropunctata*	5
14	PRO	4	*Brachymyrmex heeri*	5
14	PRO	4	*Camponotus crassus*	5
14	PRO	4	*Gnamptogenys striatula*	10
14	PRO	4	*Pheidole* sp. 5	1
14	PRO	4	*Solenopsis invicta*	5
14	PRO	4	*Wasmannia auropunctata*	5
14	PRO	5	*Camponotus crassus*	1
14	PRO	5	*Odontomachus bauri*	10
14	CARB	1	*Pheidole* sp. 4	5
14	CARB	1	*Solenopsis saevissima*	1
14	CARB	1	*Tapinoma melanocephalum*	5
14	CARB	2	*Pseudomyrmex simplex*	5
14	CARB	2	*Solenopsis saevissima*	1
14	CARB	3	*Camponotus crassus*	5
14	CARB	3	*Cyphomyrmex* transversus	10
14	CARB	3	*Forelius brasiliensis*	10
14	CARB	3	*Pheidole* sp. 4	1
14	CARB	4	*Acromyrmex landolti*	1
14	CARB	4	*Solenopsis invicta*	1
14	CARB	5	*Pheidole* sp. 4	1
15	PRO	1	*Brachymyrmex patagonicus*	1
15	PRO	1	*Camponotus crassus*	5
15	PRO	1	*Crematogaster brasiliensis*	5
15	PRO	2	*Dolichoderus* sp. 1	1
15	PRO	2	*Dorymyrmex thoracicus*	5

15	PRO	2	*Solenopsis invicta*	2
15	PRO	3	*Cyphomyrmex transversus*	5
15	PRO	3	*Pheidole radoszkowskii*	1
15	PRO	3	*Pseudomyrmex simplex*	1
15	PRO	3	*Solenopsis virulens*	5
15	PRO	4	*Camponotus crassus*	5
15	PRO	4	*Crematogaster brasiliensis*	2
15	PRO	5	*Brachymyrmex patagonicus*	2
15	PRO	5	*Cyphomyrmex transversus*	2
15	PRO	5	*Pheidole* sp. 1	2
15	PRO	5	*Pheidole* sp. 2	5
15	CARB	2	*Camponotus crassus*	1
15	CARB	3	*Odontomachus bauri*	5
15	CARB	4	*Solenopsis saevissima*	5
15	CARB	5	*Atta sexdens*	10
15	CARB	5	*Pheidole* sp. 3	2
15	CARB	5	*Solenopsis tridens*	5
16	PRO	1	*Camponotus bicolor*	5
16	PRO	2	*Camponotus crassus*	5
16	PRO	2	*Neivamyrmex* sp. 1	1
16	PRO	2	*Pheidole* sp. 4	5
16	PRO	2	*Pheidole radoszkowskii*	15
16	PRO	2	*Pheidole mosenopsis*	2
16	PRO	2	*Solenopsis saevissima*	5
16	PRO	2	*Wasmannia auropunctata*	1
16	PRO	3	*Camponotus bicolor*	5
16	PRO	3	*Paratrechina longicornis*	5
16	PRO	3	*Pheidole mosenopsis*	5
16	PRO	3	*Solenopsis saevissima*	5
16	PRO	4	*Camponotus bicolor*	5
16	PRO	4	*Pheidole mosenopsis*	5
16	PRO	4	*Solenopsis saevissima*	5
16	PRO	5	*Camponotus crassus*	5
16	PRO	5	*Crematogaster victima*	5
16	PRO	5	*Odontomachus bauri*	5
16	CARB	1	*Atta sexdens*	10
16	CARB	1	*Crematogaster victima*	5
16	CARB	1	*Pheidole mosenopsis*	5
16	CARB	1	*Tapinoma melanocephalum*	5
16	CARB	2	*Camponotus crassus*	5

16	CARB	2	*Solenopsis invicta*	5
16	CARB	3	*Camponotus crassus*	2
16	CARB	4	*Solenopsis invicta*	1
17	PRO	1	*Linepithema neotropicum*	5
17	PRO	1	*Pheidole mosenopsis*	5
17	PRO	2	*Camponotus crassus*	5
17	PRO	2	*Wasmannia auropunctata*	10
17	PRO	3	*Camponotus bicolor*	5
17	PRO	3	*Camponotus crassus*	5
17	PRO	4	*Pheidole mosenopsis*	5
17	PRO	5	*Crematogaster victima*	10
17	PRO	5	*Forelius brasiliensis*	10
17	PRO	5	*Solenopsis invicta*	2
17	PRO	5	*Wasmannia auropunctata*	5
17	CARB	1	*Pheidole* sp. 5	5
17	CARB	2	*Crematogaster victima*	2
17	CARB	2	*Pseudomyrmex gracilis*	5
17	CARB	3	*Camponotus crassus*	5
17	CARB	4	*Camponotus crassus*	5
17	CARB	5	*Tapinoma melanocephalum*	5
18	PRO	1	*Camponotus crassus*	5
18	PRO	1	*Pheidole* sp. 4	5
18	PRO	2	*Pheidole mosenopsis*	5
18	PRO	3	*Pheidole* sp. 4	1
18	PRO	3	*Pheidole mosenopsis*	5
18	PRO	4	*Pheidole mosenopsis*	1
18	PRO	4	*Solenopsis saevissima*	1
18	PRO	5	*Camponotus bicolor*	1
18	PRO	5	*Camponotus crassus*	1
18	PRO	5	*Pheidole mosenopsis*	1
18	CARB	1	*Crematogaster victima*	5
18	CARB	1	*Solenopsis saevissima*	5
18	CARB	2	*Atta sexdens*	5
18	CARB	2	*Camponotus bicolor*	5
18	CARB	2	*Camponotus crassus*	5
18	CARB	2	*Solenopsis saevissima*	1
18	CARB	3	*Camponotus bicolor*	2
18	CARB	3	*Linepithema neotropicum*	2
18	CARB	3	*Tapinoma melanocephalum*	2
18	CARB	4	*Camponotus crassus*	2

18	CARB	4	*Pheidole* sp. 5	10
18	CARB	4	*Pheidole mosenopsis*	2
18	CARB	4	*Solenopsis saevissima*	5
18	CARB	5	*Linepithema humile*	5
18	CARB	5	*Pheidole radoszkowskii*	2
19	PRO	1	*Crematogaster victima*	1
19	PRO	1	*Odontomachus bauri*	5
19	PRO	1	*Pheidole mosenopsis*	1
19	PRO	2	*Acromyrmex landolti*	1
19	PRO	2	*Solenopsis saevissima*	1
19	PRO	3	*Solenopsis saevissima*	1
19	PRO	4	*Camponotus crassus*	5
19	PRO	4	*Crematogaster victima*	1
19	PRO	5	*Camponotus bicolor*	2
19	CARB	1	*Camponotus bicolor*	5
19	CARB	1	*Camponotus crassus*	1
19	CARB	2	*Pheidole mosenopsis*	1
19	CARB	2	*Solenopsis saevissima*	1
19	CARB	3	*Forelius brasiliensis*	1
19	CARB	3	*Wasmannia auropunctata*	2
19	CARB	4	*Solenopsis saevissima*	2
19	CARB	4	*Tapinoma melanocephalum*	1
19	CARB	5	*Pheidole mosenopsis*	1
19	CARB	5	*Wasmannia auropunctata*	2
20	PRO	1	*Camponotus bicolor*	1
20	PRO	1	*Camponotus crassus*	1
20	PRO	1	*Ectatomma muticum*	1
20	PRO	2	*Crematogaster victima*	1
20	PRO	2	*Ectatomma muticum*	1
20	PRO	2	*Pheidole radoszkowskii*	1
20	PRO	2	*Solenopsis saevissima*	5
20	PRO	2	*Wasmannia auropunctata*	5
20	PRO	3	*Camponotus bicolor*	1
20	PRO	3	*Linepithema neotropicum*	1
20	PRO	3	*Pheidole radoszkowskii*	1
20	PRO	3	*Solenopsis invicta*	1
20	PRO	3	*Wasmannia auropunctata*	1
20	PRO	4	*Camponotus bicolor*	5
20	PRO	4	*Camponotus crassus*	1
20	PRO	4	*Forelius brasiliensis*	1

20	PRO	4	*Pheidole radoszkowskii*	1
20	PRO	5	*Camponotus crassus*	1
20	PRO	5	*Forelius brasiliensis*	1
20	PRO	5	*Pheidole radoszkowskii*	1
20	PRO	5	*Pheidole* sp. 5	1
20	PRO	5	*Pheidole mosenopsis*	1
20	PRO	5	*Solenopsis invicta*	1
20	PRO	5	*Solenopsis saevissima*	5
20	PRO	5	*Tapinoma melanocephalum*	5
20	CARB	1	*Camponotus crassus*	1
20	CARB	2	*Camponotus crassus*	1
20	CARB	3	*Atta sexdens*	5
20	CARB	3	*Brachymyrmex patagonicus*	1
20	CARB	3	*Crematogaster victima*	5
20	CARB	3	*Paratrechina longicornis*	5
20	CARB	3	*Pheidole* sp. 4	5
20	CARB	3	*Solenopsis invicta*	5
20	CARB	3	*Tapinoma melanocephalum*	5
20	CARB	4	*Atta sexdens*	5
20	CARB	4	*Paratrechina longicornis*	5
20	CARB	4	*Solenopsis saevissima*	1
20	CARB	5	*Camponotus bicolor*	1
20	CARB	5	*Camponotus crassus*	1
20	CARB	5	*Crematogaster victima*	5
20	CARB	5	*Solenopsis invicta*	1
21	PRO	1	*Camponotus crassus*	1
21	PRO	1	*Solenopsis invicta*	1
21	PRO	2	*Solenopsis invicta*	1
21	PRO	3	*Camponotus bicolor*	1
21	PRO	3	*Crematogaster victima*	1
21	PRO	3	*Pheidole* sp. 3	1
21	PRO	4	*Solenopsis invicta*	1
21	PRO	5	*Pheidole radoszkowskii*	1
21	CARB	1	*Pheidole* sp. 5	5
21	CARB	2	*Linepithema humile*	1
21	CARB	2	*Solenopsis saevissima*	2
21	CARB	3	*Tapinoma melanocephalum*	2
21	CARB	4	*Crematogaster victima*	5
21	CARB	5	*Camponotus crassus*	2
21	CARB	5	*Paratrechina longicornis*	5

21	CARB	5	*Pheidole radoszkowskii*	5
22	PRO	1	*Camponotus bicolor*	1
22	PRO	2	*Ectatomma muticum*	10
22	PRO	2	*Wasmannia auropunctata*	5
22	PRO	3	*Crematogaster victima*	5
22	PRO	3	*Pheidole radoszkowskii*	1
22	PRO	4	*Pheidole* sp. 5	1
22	PRO	4	*Pheidole mosenopsis*	1
22	PRO	5	*Solenopsis invicta*	1
22	CARB	1	*Camponotus crassus*	2
22	CARB	2	*Camponotus bicolor*	1
22	CARB	3	*Linepithema humile*	5
22	CARB	3	*Pheidole* sp. 5	1
22	CARB	3	*Solenopsis invicta*	1
22	CARB	3	*Tapinoma melanocephalum*	1
22	CARB	4	*Pheidole radoszkowskii*	1
22	CARB	4	*Pheidole* sp. 5	1
22	CARB	5	*Linepithema humile*	5
22	CARB	5	*Pheidole radoszkowskii*	1

Table S7. Moran's *I* autocorrelation test of model residuals. Values of observed and expected (assuming no spatial autocorrelation) Moran's *I* are shown. *P*-values (*P*) > 0.05 indicate lack of spatial autocorrelation.

Model ID (Response variable	Moran's *I* observed	Moran's *I* expected	*P*
Ant richness	-0.19	-0.02	0.86
Ant abundance	-0.20	-0.02	0.88
Generalist/specialist replacement of species richness	-0.74	-0.05	0.97
Generalist/specialist replacement of ant abundance	-0.08	-0.05	0.54
Bait discovery time	-0.03	-0.0	1
Bait occupancy index (based on species richness)	-0.37	-0.02	0.99
Bait occupancy index (based on ant abundance)	-0.53	-0.02	0.02

Table S8. Response of ant richness to urbanization intensity. The table presents estimates and standard errors (SE) from linear models assessing ant richness in response to urbanization intensity, with sites as random effects. Asterisks indicate significance (*P*<0.05).

Predictor	*Estimate*	*SE*	*Z*	*P*
Intercept	**2.14***	**0.11***	**20.16***	**<0.001***
Urbanization intensity	0.03	0.16	0.16	0.87

Table S9. Response of ant abundance to urbanization intensity. The table presents estimates and standard errors (SE) from mixed-effects models assessing ant abundance in response to urbanization intensity, with sites as random effects. Asterisks indicate significance (*P*<0.05).

Predictor	*Estimate*	*SE*	*t*	*P*
Intercept	**2.41***	**0.29***	**8.25***	**<0.001***
Urbanization intensity	0.02	0.45	0.04	0.97
Random effect variance				

Site	0.08
Fixed effect variance	<0.001
Number of sites	22
Number of observations	44
Marginal R^2	0
Conditional R^2	0.10

Table S10. Statistical outputs from the PERMANOVA analysis used to test the effects of urbanization intensity on ant taxonomic composition. Significant values are in bold (P<0.05); DF: degrees of freedom; SS: Sum of squares.

Variables	DF	SS	R^2	F	*P*
Urbanization intensity	**1**	**0.98**	**0.39**	**11.64**	**0.001***
Residuals	20	1.55	0.61		
Total	21	2.52	1		

Table S11. Threshold indicator taxa analysis (TITAN) of ant species in response to urbanization intensity.

Species	Threshold	Response	IndVal	*Z*
Crematogaster brasiliensis	0.52	Decrease	90.28	5.93
Neoponera sp. 1	0.28	Decrease	83.33	4.92
Odontomachus bauri	0.52	Decrease	75.86	3.82
Pheidole sp. 1	0.28	Decrease	67.91	5
Solenopsis globularia	0.28	Decrease	66.67	4.86
Dorymyrmex thoracicus	0.72	Decrease	63.49	3.29
Solenopsis virulens	0.28	Decrease	52.31	1.93
Pheidole radoszkowskii	0.61	Decrease	50.28	1.3
Brachymyrmex patagonicus	0.54	Decrease	47.62	1.57
Ectatomma muticum	0.63	Decrease	43.48	2.26
Forelius brasiliensis	0.72	Decrease	36	0.53
Cyphomyrmex transversus	0.52	Decrease	30.86	0.22
Pheidole sp. 2	0.77	Decrease	30.63	0.38
Pseudomyrmex gracilis	0.77	Decrease	29.47	0.34
Gnamptogenys sulcata	0.63	Decrease	25	1.5
Acanthogonatus sp. 1	0.52	Decrease	21.43	0.9
Solenopsis invicta	0.67	Increase	73.08	4.57

Pheidole mosenopsis	0.87	Increase	70.57	3.97
Camponotus bicolor	0.63	Increase	64.62	3.38
Pheidole sp. 5	0.72	Increase	64.02	3.79
Tapinoma melanocephalum	0.52	Increase	60.17	2.25
Camponotus crassus	0.72	Increase	60.09	1.21
Wasmannia auropunctata	0.28	Increase	56.32	1.23
Solenopsis saevissima	0.62	Increase	51.04	1.28
Atta sexdens	0.87	Increase	50.16	3.52
Linepithema humile	0.67	Increase	50	3.18
Crematogaster victima	0.58	Increase	49.13	0.3
Pheidole sp. 4	0.28	Increase	46.73	2.1
Paratrechina longicornis	0.52	Increase	46.67	2.07
Pheidole sp. 3	0.54	Increase	33.18	1.07
Linepithema neotropicum	0.67	Increase	30.41	0.2
Acromyrmex landolti	0.63	Increase	30	2.3
Pseudomyrmex simplex	0.72	Increase	27.16	0.68
Dolichoderus sp. 1	0.61	Increase	25	1.63
Solenopsis tridens	0.61	Increase	17.86	0.15

Table S12. Statistical outputs from the PERMANOVA analysis used to test the effects of urbanization intensity on ant functional composition. Significant values are in bold (P<0.05); DF: degrees of freedom; SS: Sum of squares.

Variables	DF	SS	R^2	F	*P*
Urbanization intensity	**1**	**0.29**	**0.25**	**6.74**	**0.001***
Residuals	20	0.85	0.74		
Total	21	1.14	1		

Table S13. Threshold indicator taxa analysis (TITAN) of ant functional groups in response to urbanization intensity.

Functional group	Threshold	Response	IndVal	*Z*
Epigaeic predator	0.63	Decrease	78.45	4.61
Opportunist	0.63	Decrease	59.7	1.3
Non-leaf-cutting Attini	0.52	Decrease	30.88	0.47
Cryptic predator	0.52	Decrease	25.03	1.02
Epigaeic omnivore	0.52	Increase	63.62	3.34
Cryptic omnivore	0.63	Increase	56.93	1.02

Arboreal subordinate	0.72	Increase	53.81	0.39
Leaf-cutting Attini	0.63	Increase	50.92	3.12
Arboreal dominant	0.28	Increase	45.32	0.74

Table S14. Response of generalist / specialist ratio of species richness to urbanization intensity. The table presents estimates and standard errors (SE) from linear models assessing generalist / specialist ratio of species richness in response to urbanization intensity. Asterisks indicate significance (P<0.05).

Predictor	*Estimate*	*SE*	*t*	*P*
Intercept	**0.57***	**0.26***	**2.24***	**0.04***
Urbanization intensity	**1.04***	**0.40***	**2.59***	**0.02***

Table S15. Response of generalist / specialist ratio of ant abundance to urbanization intensity. The table presents estimates and standard errors (SE) from linear models assessing generalist / specialist ratio of ant abundance in response to urbanization intensity. Asterisks indicate significance (P<0.05).

Predictor	*Estimate*	*SE*	*t*	*P*
Intercept	**0.44***	**0.20***	**2.20***	**0.04***
Urbanization intensity	**0.69***	**0.31***	**2.23***	**0.04***

Table S16. Response of bait occupancy index based on species richness to urbanization intensity. The table presents estimates and standard errors (SE) from linear models assessing protein-bait occupancy index in response to urbanization intensity, with sites as random effects. Asterisks indicate significance (P<0.05).

Predictor	*Estimate*	*SE*	*t*	*P*
Intercept	**0.47***	**0.08***	**6.19***	**<0.001***
Urbanization intensity	0.08	0.12	0.68	0.50
Bait type	0.14	0.11	1.29	0.20
Urbanization intensity:Bait type	-0.07	0.17	-0.44	0.67

Table S17. Response of bait occupancy index based on ant abundance to urbanization intensity. The table presents estimates and standard errors (SE) from linear models assessing carbohydrate-bait occupancy index in response to urbanization intensity, with sites as random effects. Asterisks indicate significance (P<0.05).

Predictor	*Estimate*	*SE*	*t*	*P*
Intercept	**0.35***	**0.05***	**6.64***	**<0.001***
Urbanization intensity	0.10	0.08	1.26	0.22
Bait type	**0.17***	**0.08***	**2.22***	**0.03***
Urbanization intensity:Bait type	-0.08	0.12	-0.72	0.48

Table S18. Response of ant bait discovery time to urbanization intensity. The table presents estimates and standard errors (SE) from mixed-effects models assessing ant bait discovery time in response to urbanization intensity, with sites as random effects. Asterisks indicate significance (P<0.05).

Predictor	*Estimate*	*SE*	*Z*	*P*
Intercept	**2.48***	**0.21***	**11.91***	**<0.001***
Urbanization intensity	**-1.27***	**0.33***	**-3.90***	**<0.001***
Bait type	-0.08	0.06	-1.31	0.19
Urbanization intensity:Bait type	0.06	0.11	-0.51	0.61
Random effect variance				
Site		0.22		
Fixed effect variance		0.15		
Number of sites		22		
Number of observations		534		
Marginal R^2		0.29		
Conditional R^2		0.73		

ARTIGO DO SEGUNDO CAPITULO

Ant physiological and morphological functional traits along an urbanization intensity gradient in the Atlantic Forest, northeastern Brazil

Isabelle Leite de Holanda Silva[1], Diego Centeno-Alvarado[1], Iago Monteiro da Costa Wäcker[2], João Carlos Pena[3], Xavier Arnan[4], Inara Roberta Leal[1,5*]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[2]Curso de Bacharelado em Ciências Biológicas, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[3]Araucária Sustainability and Innovation Lab (LASI), Environmental Studies Center (CEA), Universidade Estadual Paulista Julio de Mesquita Filho, Rio Claro, Brazil

[4]Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

[5]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

***Corresponding author:** inara.leal@ufpe.br; Departamento de Botânica, Universidade Federal de Pernambuco, Av. Professor Moraes Rego, s/n, Cidade Universitária, Recife, Pernambuco, Brazil – 50670-091.

Email: isabelleholanda_@hotmail.com (I. L. H. Silva). centenoalvaradodiego@gmail.com (D. Centeno-Alvarado), iago.wacker@ufpe.br (I. M. C. Wäcker), joaocpena@gmail.com (J. C. Pena), xavier.arnan@upe.br (X. Arnan), inara.leal@ufpe.br (I. R. Leal).

ORCID:

Isabelle Leite de Holanda Silva: https://orcid.org/0000-0001-7832-4433

Diego Centeno-Alvarado: https://orcid.org/0000-0003-0273-8538

Iago Monteiro da Costa Wäcker: https://orcid.org/0009-0008-3121-2985

João Carlos Pena: https://orcid.org/0000-0003-1368-1805

Xavier Arnan: https://orcid.org/0000-0002-9904-274X

Inara Roberta Leal: https://orcid.org/0000-0002-8125-2191

Abstract

Urbanization is a significant environmental change that might impact the functional attributes of plant and animal species, particularly among ectothermic organisms like ants. Alterations in the functional traits of ant species due to increasing urbanization can compromise the provision of ecosystem functions and services. This study investigates how urbanized areas affect the thermal maximum tolerance and morphological traits of eight common ant species along an urbanization gradient in the Metropolitan Region of Recife, Brazil. We selected 22 urban sites representing a wide gradient of urbanization intensity, measured as the percentage of urban land cover within 500 m radius buffers. In each area we collected 10 workers from the ant species using bait traps and used a dry bath machine to measure thermal maximum tolerance. The thermal tolerance amplitude across species varied between 30°C and 60°C. We also measured seven morphological attributes related to the ants' adaptive functions. Our results indicated that overall thermal tolerance remained largely conserved across the urban gradient, with no significant changes. Similarly, morphological traits did not exhibit changes associated with urbanization when analyzed across all species. However, when examining species individually, we observed a significant relationship between urbanization and certain morphological traits. *Atta sexdens* exhibited a reduction in relative mandible and leg length with increasing urbanization intensity. Additionally, this species showed a marginally significant trend of increasing head length in more urbanized areas. For *Camponotus crassus*, a marginally significant reduction in mandible size was observed, suggesting a subtle response in feeding habits due to urban pressures. These findings imply that while urban environments may not universally drive adaptations in thermal tolerance, specific species such as *A. sexdens* may develop morphological traits to better navigate urban challenges, with potential impacts on their role as herbivores. This underscores the need for further research into species-specific adaptations and the ecological implications of urbanization on ant communities, as well as the potential impacts on the ecosystem services and disservices provided by these organisms.

Keywords: Urban cover gradient, Urban ants, Critical thermal maximum, Morphological adaptations

Introduction

Human-induced modifications to ecosystems drive significant habitat loss and fragmentation, altering environmental gradients and depleting resources vital for biological communities (Curtis et al., 2018). While the impacts of these habitat changes on biodiversity are widely recognized, less attention has been given to the underlying ecological processes that govern population dynamics and community structure (Okie & Brown, 2009). In particular, understanding how populations and communities adjust to these alterations—reflected in their foraging behaviors, dietary preferences, and habitat choices—can be informed by examining their functional traits (Dehling et al., 2016; Pigot et al., 2020). These functional traits encompass a range of phenological, physiological, and behavioral attributes that enable organisms to respond to environmental changes (Tilman et al., 2001). Furthermore, these traits serve as proxies for the environmental conditions essential for survival, providing insights into the ecological niche dimensions pertinent to specific species or communities (Kearney et al., 2010; Pigot et al., 2016).

Urban areas represent one of the main landscapes that have been significantly transformed by human activity, featuring extensive infrastructure and a scarcity of natural habitats (Week, 2010). These modifications associated with urban development can result in alterations on plant and animal population size and distribution (McKinney, 2008; Liang et al., 2008), as well as affect the distribution of functional traits when transitioning from natural ecosystems to urbanized environments (Groffman et al., 2014). The rapid expansion of urban areas creates scenarios conducive to the manifestation of plastic phenotypic responses, which may become targets of natural selection (Diamond et al., 2018; Diamond & Martin, 2020; Levis & Pfennig, 2016; Santos et al., 2021; Santangelo et al., 2022). In this context, ants serve as an excellent model for studying how functional traits respond to urbanization, given that their physiology, morphology, and behavior are closely tied to environmental conditions (Menke et al., 2011). Additionally, while earlier studies have largely concentrated on the impact of urbanization on ant community composition (Ivanov & Keiper, 2010; Liu et al., 2019; Nooten et al., 2019; Savage et al., 2015; Uno et al., 2010), it remains plausible that ecosystem processes could be relatively

unaffected by changes in biodiversity (Naomi & Wright, 2003). Therefore, it is essential to evaluate functional traits related to species morphology, physiology and behaviour for anticipating how the distribution of organisms and the functioning of ecosystems will be altered in response to environmental changes (Arnan & Blüthgen, 2015; Arnan et al., 2015; Deutsch et al., 2008; Nascimento et al., 2024).

One of the most significant environmental changes associated with urbanization, which directly impacts ant functional traits, is the rise in temperature. Urbanization leads to the urban heat island effect, where cities experience higher temperatures due to the replacement of natural surfaces with impervious materials like concrete and asphalt (Grimmond, 2007; Oke, 1982; Arnfield, 2003; Diamond et al., 2012, 2017, 2018, 2020). This rise in temperature has significant implications for ectothermic species, such as ants, whose physiological functions are highly sensitive to their thermal environment (Angilletta, 2009). One of the key physiological traits affected by urbanization is the critical thermal maximum (CTMax), the temperature at which an organism experiences muscular spasms or death (Sinclair et al., 2016). These thermal limits are critical in shaping species distributions and abundance on both local and regional scales (Kearney & Porter, 2009; Diamond et al., 2012; Arnan & Blüthgen, 2015; Gardner et al., 2019; Nascimento et al., 2022). As urban areas warm, smaller, heat-tolerant species, including generalists and invasive ants, may thrive, while native and specialized species face the risk of migration or population declines (Diamond et al., 2012). Furthermore, Yilmaz et al. (2019) found that urban populations of *Temnothorax curvispinosus* (Myrmicinae) ants exhibited higher running speeds and metabolic rates than their rural counterparts, indicating adaptations to the hotter urban climate. Moreover, these urban ants showed greater thermal plasticity, with individuals tolerating higher CTMax temperatures than ants from rural areas (Diamond et al., 2018). This increased thermal tolerance reflects broader patterns in ant communities, where differences in species' abilities to cope with heat enable them to exploit varying thermal conditions within their habitats (Cerdá et al., 1997, 1998; Bestelmeyer, 2000; Lessard et al., 2009).

Alongside these physiological adaptations, urbanization can also influence the morphological traits of ants. Studies suggest that not all species are equally affected by urbanization in terms of their morphological traits. While some research demonstrates that larger-bodied ants can adapt to harsh urban environments and tolerate higher temperatures (Peng et al., 2020; Rajesh et al., 2022; Cerdá & Retana, 2000), other studies indicate that smaller ants also tend to thrive in highly urbanized areas (Bolger et al., 2000; Diamond et al., 2012; Egerer et al., 2017). Additionally, traits like leg length may also be influenced by urban conditions, with longer legs contributing to greater mobility (Weiser & Kaspari, 1999) and helping ants lift their bodies off the hot surfaces of urban environments during foraging, thus protecting them from heat (Angiletta et al., 2007; Yilmaz et al., 2019).

In this study, we investigated the morphological functional responses of eight widely distributed ant species along an urbanization intensity gradient in the city of Recife, northeastern Brazil, a large neotropical metropolis. We hypothesized that increasing urbanization intensity alters morphological traits (e.g., body size, relative eye length, relative scape length, relative mandible length, relative clypeus length, and relative leg length) as a result of plastic responses to habitat alterations associated with urban development. Specifically, we predicted that individuals inhabiting more urbanized areas would exhibit higher CTMax and smaller body sizes than those in contexts surrounded by higher proportions of woody cover, as these characteristics facilitate survival in warmer environments due to the urban heat island effect (Howard, 1833).

Materials and methods

Study area and urbanization levels

The study was conducted in the city of Recife, Pernambuco, northeastern Brazil (34.8780° – 34.9757°S, 7.9405° – 8.1450°W; Fig. 1). Recife is the third most densely populated metropolitan area in Brazil (IBGE, 2021) and is also recognized as one of the most deforested regions of the Brazilian Atlantic Forest (Bernard et al., 2023). The average annual temperature in

the region ranges from 25°C to 30°C, with humidity levels around 64% (APAC, 2017). We selected 22 sites within the metropolitan area to represent an urbanization gradient extending from the city center to suburban areas, located in the western and southern regions. Each site was situated at least 2 kilometers apart. The intensity of urbanization was assessed by calculating the proportion of urban cover at each site. This was achieved through a supervised classification of Planet Scope satellite imagery with a resolution of 3m and four spectral bands, acquired in August 2021 (Planet Labs PBC, 2021). Three primary land cover classes were identified: woody vegetation, herbaceous vegetation, hydrography and urban cover. Buffers of varying sizes (50, 100, 200, and 500 m radius) were defined around each site, and the proportion of urban cover within each buffer was calculated (Table S1 – Supplementary Material). We conducted Spearman rank correlations to evaluate the relationships between the proportion of urban cover across all buffers. Due to high correlations (Spearman $\rho > 0.7$), we used only the 500 m radius buffer in subsequent analyses, as it is representative of the landscape area that directly influences ant habitat availability, resource distribution, and ecosystem dynamics (e.g., Cordonnier et al., 2019, 2020; Korányi et al., 2021). The proportion of urban cover within the 500 m radius buffers represents a broad gradient of urbanization intensity ranging from 0 to 95% (Table S1 – Supplementary Material).

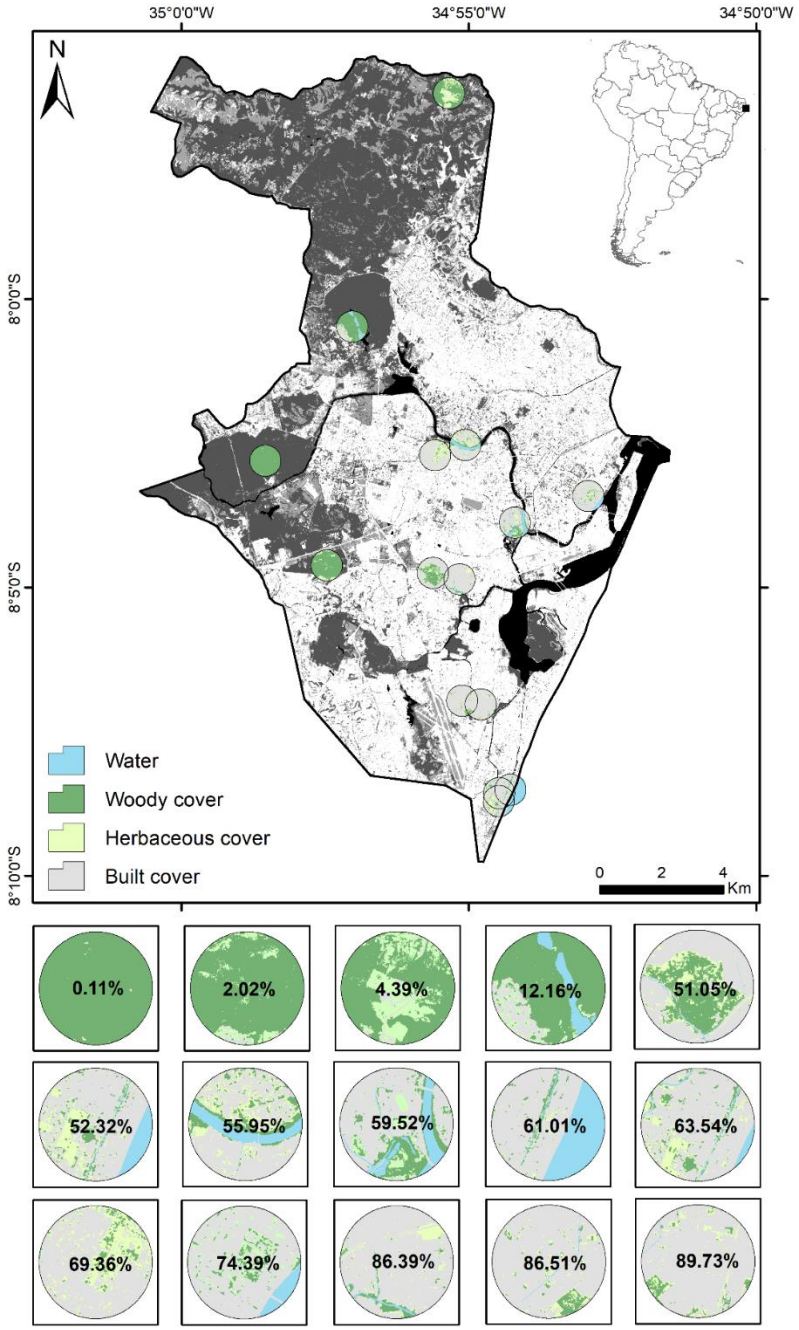

Figure 1. Land cover map of Recife (Pernambuco, Brazil) highlighted with asterisks the sites where the study was developed. Black line: political boundary of the city; dark green: woody cover; light green: herbaceous cover; grey: urban cover; blue: hydrography.

Ant species

We selected eight ant species [i.e., *Atta sexdens* L. (Myrmicinae), *Pheidole radoszkowskii* Mayr (Myrmicinae), *Solenopsis invicta* Buren (Myrmicinae),*Camponotus crassus* Mayr (Formicinae),*Tapinoma melanocephalum* (Fabricius) (Dolichoderinae), *Odontomachus bauri* Emery (Ponerinae), *Pseudomyrmex gracilis* (Fabricius) (Pseudomyrmecinae), *Ectatomma muticum* Mayr (Ectatomminae)] for this study based firstly on their distribution along the urban gradient (see Chapter 1 for more detail on ant distribution along the urbanization gradient). We chose species that occur across the entire urbanization gradient studied, ensuring a representative and consistent sampling across different levels of environmental impact. Additionally, we selected representatives from different ant subfamilies, providing a phylogenetically diverse approach. The chosen subfamilies include species that are phylogenetically distant from each other, which allows us to detect patterns of responses to urbanization across different evolutionary lineages. This phylogenetic approach enhances our understanding of the specific adaptations of each group and helps identify whether the impacts of urbanization manifest convergently or divergently in species that share similar functional traits. Among the represented subfamilies, we highlight Myrmicinae, the most diverse, with 149 genera, from which we included in this study the species *Atta sexdens*, *Pheidole radoszkowskii*, and *Solenopsis invicta*. The Formicinae subfamily, with 50 genera, included *Camponotus crassus*, while Dolichoderinae, with 48 genera, is represented by *Tapinoma melanocephalum*. The Ponerinae, with 47 genera, were included the species *Odontomachus bauri*, while the Ectatomminae, with a total of 12 genera, is represented in this study by *Ectatomma muticum*. Finally, the Pseudomyrmecinae subfamily, the least diverse subfamily, with only three genera, is represented by *Pseudomyrmex gracilis*.

Ant Sampling

We randomly sampled 20 workers from each species at each site along the urbanization gradient. Collections took place from June to September 2024, focusing on tree trunks, soil, and lawns within the designated radius for each area along the gradient. Sampling occurred both in the morning and afternoon. Carbohydrate- and protein-based baits were used to attract the ants when necessary; however, the baits were exclusively employed to lure the ants without being

consumed (Freires et al., 2023; Nascimento et al., 2024). Immediately after collection, the individuals were placed in 50 ml Falcon tubes, each containing a small cotton ball soaked in water to prevent desiccation of the ants. This methodology follows established protocols in entomological research, emphasizing the importance of maintaining specimen viability post-collection (López-Guerrero et al., 2020; Roulston & Goodell, 2011). Additionally, the use of attractants helps enhance sampling efficiency and ensures a more representative collection of species (Boulton et al., 2014).

Maximum Thermal Tolerance

We measured maximum thermal tolerance following established protocols used in various studies (e.g., Diamond et al., 2012). Thermal tolerance assays were conducted with a minimum of ten individuals from each species within four hours post-collection, with visibly injured ants excluded from the analyses. The individuals were placed in 1.5 ml microcentrifuge tubes (one individual per tube) sealed with cotton to prevent the ants from using the tube's end as a thermal refuge and to ensure they were exposed to the desired experimental temperature (Oberg et al., 2012). Each tube was randomly arranged in a slot of a pre-heated dry bath incubator set at 30°C. This temperature was chosen as the initial condition since preliminary analyses indicated that no species had a maximum thermal tolerance (CTmax) lower than this value. Although the rate of temperature increase can affect absolute CTmax (Roeder et al., 2021), this was not a concern in our study due to our focus on comparing workers subjected to the same protocol. The heating block temperature was raised by 1°C every 3 minutes (Arnan et al., 2022). At the end of each 3-minute interval, we assessed the ants' movement levels, recording either their mobility or mortality. Additionally, at least two individuals from each species were kept outside the device as controls to monitor for stress-induced mortality. The temperature at which an ant lost muscular coordination or succumbed was defined as its CTmax (Diamond et al., 2012). This methodology is crucial for understanding the thermal limits of species and can reveal potential adaptations to

urban environments where temperature extremes are more prevalent (Dáttilo et al., 2016; Riddell et al., 2020).

Morphological Traits

We utilized ten workers per species from each site along the urbanization gradient to measure the morphological traits that may explain responses to environmental changes, particularly those related to temperature conditions (see Table 1 for more details on the implication to adaptation of each trait). The measurements were taken using a stereomicroscope and included: (1) head size as a representative measure of body size, and (2) relative leg size calculated as the ratio of leg length (femur + tibia) to head length. These traits provide insights into adaptations in foraging strategies influenced by rising temperatures, as they relate to the mobility capacity of the ants (Bihn et al., 2010; Kaspari & Weiser 1999). Additionally, we measured (3) clypeus size and (4) mandible size, as these metrics relate to water loss (Davidson et al., 2004; Weiser & Kaspari, 2006). The size of the (5) antennae and (6) eyes were also recorded, as they indicate sensory capabilities; larger antennae can increase the area available for sensory organs, while eye size reflects the foraging behavior of the ant (Bihn et al., 2010; Kaspari & Weiser 1999). Species with low thermal tolerance may prefer nocturnal foraging, typically associated with smaller eyes (Kaspari & Weiser 1999; Gordon, 2010). Finally, we assessed (7) eye positioning (distance between the eyes), which relates to predation, as greater eye separation is characteristic of visual predators (López-Guerrero et al., 2020; Hölldobler & Wilson, 1990; Cerdá et al., 1997). We standardized all trait measurements (except head length) by dividing each by the head length to limit correlations with body size. This comprehensive approach to measuring morphological attributes allows for a better understanding of how these traits may enable ants to adapt to the challenges posed by urban environments, particularly in relation to thermal stress and resource acquisition.

Statistical Analyses

To assess whether functional traits, including maximum thermal tolerance and morphological attributes (i.e., body size, relative eye length, relative scape length, relative mandible length, relative clypeus length, and relative leg length), varied in response to urbanization intensity, we performed both analyses for each species individually and across all species collectively using Generalized Linear Mixed Models (GLMMs) using a Gaussian error distribution. Site was included as a random effect in all models to account for repeated measurements of individuals, while species was also included as a random effect in the analysis of traits across all species collectively. We assessed the models for overdispersion, and when this assumption was violated, we log-transformed the response variables to meet the assumptions of normality and homoscedasticity of the data.. All analyses were conducted in R (v. 4.1.3; R Core Team, 2022). GLMMs were performed using the *lme4* (v. 1.1-7; Bates et al., 2020).

Results

Variation in maximal thermal tolerance and morphological attributes

Regarding the thermal tolerance of the ants collected along the urban gradient, we found that *Pheidole radoszkowskii* exhibited the greatest variation (93.8%), with a temperature range of 32°C to 62°C. This was followed by *Camponotus crassus*, with a variation of 68.8% (32°C to 54°C), *Tapinoma melanocephalum*, which showed a variation of 56.4% (39°C to 61°C), and *Solenopsis invicta*, who exhibited a variation of 50% (36°C to 54°C). *Atta sexdens* presented a variation of 38.9% (36°C to 50°C), while *Pseudomyrmex gracilis*, of 27.5% (40°C to 51°C), and *Ectatomma muticum*, of 14.6% (41°C to 47°C). Finally, *Odontomachus bauri* exhibited the smallest variation, at 9.5%, with a temperature range of 42°C to 46°C.

The variation in morphological traits among the ant species collected along the urban gradient revealed notable differences. Regarding leg length, *Atta sexdens* exhibited significantly greater variation than *Tapinoma melanocephalum*, with its legs increasing in size approximately

twice as much as those of the latter. Similarly, *Atta sexdens* showed the largest variation in head length, with an increase about five times greater than that observed in *Solenopsis invicta*. For eye distance, *Camponotus crassus* displayed a much more pronounced variation, around twice as great as the variation observed in *Solenopsis invicta*. Regarding eye length, Atta sexdens again exhibited the greatest variation, approximately five times greater than *Solenopsis invicta*. In terms of clypeus length, *Pheidole radoszkowskii* showed considerably larger variation, around four times greater than *Odontomachus bauri*. Mandible length presented an even more remarkable variation *in Pheidole radoszkowskii*, with an increase about ten times greater than that of *Ectatomma muticum*. Finally, in antenna length, *Atta sexdens* demonstrated a more pronounced variation, approximately 1.5 times greater than *Tapinoma melanocephalum*.

Variation of maximal thermal tolerance and morphological traits along the urbanization intensity gradient

The maximal thermal tolerance of each species showed no significant response to urbanization, even when considering all species collectively (Table 2). Similarly, the morphological traits did not show any variation related to urbanization intensity when analyzed all species collectively (Table 2). However, when analyzing species individually, a significant relationship between urbanization and morphological traits was observed for *Atta sexdens*, which exhibited reduced relative mandible and leg length with greater urbanization intensity (Table 2, Fig. 2). Additionally, a marginally significant positive effect of urbanization on head length was observed in *Atta sexdens*. None of the other relationships analyzed were significant (Table 2).

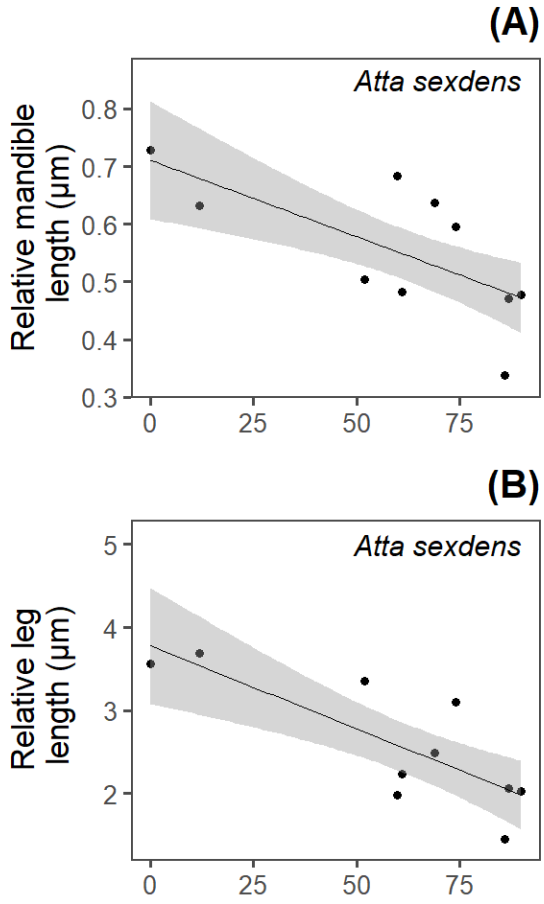

Figure 2. Significant effects of urbanization intensity on the relative mandible length (A), relative leg length (B) of *Atta sexdens* workers in the city of Recife, Pernambuco, northeastern Brazil. The black dots represent mean values per sampling site; the black line indicates the model fitted line; the gray-shaded area indicates the 95% confidence interval of the model estimates.

Discusion

In this study, we sought to understand how urban intensity influences the maximum thermal tolerance and several morphological traits related to eight ant species in Recife, northeastern Brazil. Initially, we hypothesized that ants in urban areas would exhibit higher thermal tolerance and smaller body sizes—traits that facilitate survival in warmer environments due to the urban heat island effect (Howard, 1833). However, our findings revealed no significant evidence of changes in thermal tolerance morphological traits along the urbanization intensity

gradient when analysing all species together and individually, except for *Atta sexdens* that exhibit reduce relative mandible and relative leg length with greater urbanization intensity. Our findings suggest that ants may rely on behavioral strategies, such as altering their foraging times or seeking cooler microhabitats, to mitigate the effects of elevated temperatures of urban areas.

Our results did not corroborate previous studies demonstrating that ants respond to environmental changes caused by urban intensification by alterating their thermal tolerance and/or morphological attributes (Angilletta et al., 2007; Kaspari & Weiser 2007; Diamond et al., 2018). With the sole exception of *Atta sexdens*, all focal species maintained the thermal tolerance and morphological attributes unalred across the urban intensity gradient. This leads us to propose that ants rely on behavioral strategies to cope with the environmental conditions altered by urbanization. Previous studies have documented such behavioral adjustments in ants (Silva et al., 2019; Esch et al., 2017), suggesting that these strategies may be as effective—or more so—than physiological adaptations. Regarding *Atta sexdens*, high plasticity in physiological, and behavioral attributes have been observed in previous studies (Snell-Rood, 2013; Bustamante, 2017; Bustamante & Amarillo-Suárez, 2019). For instance, colonies of *Atta sexdens* in the Atlantic Forest are able to identify highly preferred plant material as soon as it appears in their foraging areas and adjust their foraging networks accordingly (Silva et al 2012, 2013). Similarly, colonies of *Atta opaciceps* adjust the plant parts and species harvested across disturbance gradients in the Caatinga dry forest (Siqueira et al., 2018). Such high plasticity in foraging strategies has been proposed as a key factor enabling leaf-cutting ants to persist or even proliferate in human-modified landscapes, from dry forests to rainforests (Bueno, Campos & Morini, 2017).

The lack of significant alterations in physiological and morphological attributes across the urganization gradient reported for most focal species may reflect varying degrees of vulnerability and adaptive flexibility. Some species may already possess pre-adapted traits that confer resilience in urban environments, while others may face barriers to developing new traits (Alberti & Marzluff 2004). This dynamic supports the hypothesis that urbanization acts more as an environmental filter—favoring species with broader niches or superior acclimation

capacities—rather than inducing widespread phenotypic changes (Bueno, Campos & Morini, 2017). Beyond methodological considerations, our findings suggest that urbanization is not a universal driver of phenotypic change but rather a selective phenomenon that depends on species, environmental context, and the type of pressure exerted (Alberti, Marzluff, & Hunt, 2017). Another consideration is that urban environments, while generally warmer, are highly heterogeneous. The presence of shaded areas, moist soils, and built structures can provide thermal refuges, reducing the necessity for widespread physiological changes and then also explaining the lack of alteration in termal tolerance and morphological attributes for most species we evaluated. This variability might act as an "environmental buffer," allowing species to maintain relatively conserved physiological and morphological traits while exploiting diverse urban niches. The stability of thermal tolerance across all studied species, despite varying levels of urban intensity, also raises the hypothesis that this trait is inherently conservative. In other words, maximum thermal tolerance (CTmax) may be more tightly regulated by phylogenetic constraints than by immediate environmental pressures (Nascimento et al. 2022). Thus, urbanization might not exert a sufficiently strong selective force to alter this trait, especially in contexts like Recife, where the urban temperature gradient may be less pronounced compared to other global cities.

As an exception to the general patterns described here, *Atta sexdens* exhibited a significant reduction in the relative length of its mandibles and legs with increasing urban intensity (Table 2, Fig. 2), coupled with a marginally significant increase in head length. These findings diverge from our initial hypotheses, yet they may reflect specific functional adaptations to urban demands. The reduction in mandible and leg length could indicate shifts in foraging behavior and resource manipulation in urban settings, where spatial constraints and the availability of novel food resources might require different biomechanical strategies. In contrast, the marginal increase in head length may be associated with enhanced development of the muscular system—potentially improving food processing and defense capabilities. These morphological changes align with findings from studies on worker polymorphism in leaf-cutting ants (Wheeler, 1991; Muratore et al., 2023), where variations in traits such as the head, mandibles,

and legs have been linked to task performance. It was seen that in smaller workers, high levels of morphological integration facilitate the execution of complex, multifunctional tasks, whereas larger workers tend to exhibit greater modularity, allowing for specialized functions like efficient leaf cutting and fungal gardening (Muratore et al., 2023). Modifications in leg morphology may optimize the biomechanics of leaf cutting, where the legs act as anchors during a circular cutting motion (Roces and Hölldobler, 1994). However, the reduction in leg length observed in this study may indicate that ants in urban areas are altering their morphology or utilizing smaller workers to perform this task in a less intensive way or with different mechanics. Adjustments in head morphology may reflect increased investment in the musculature necessary for powerful bites (Gronenberg et al., 1997; Paul and Gronenberg, 1999). This plasticity may be a response to changes in the available resources or to the altered conditions of the urban habitat, which influence the need to perform leaf cutting as intensively as in natural areas.

It is important to note that the *Atta* genus is highly polymorphic (Wheeler, 1991), a characteristic that may underlie such adaptive morphological plasticity. Moreover, previous studies have documented that *Atta sexdens* not only proliferates in disturbed areas but also increases its consumption and herbivory rates in these habitats (Urbas et al., 2007; Siqueira et al., 2017, 2018). Thus, the morphological adjustments observed in our study raise intriguing questions about the role of phenotypic plasticity in the ecological success of leaf-cutting ants under urban pressures. Future studies should further explore how these shifts in integration and modularity among key morphological traits contribute to the functional efficiency and adaptability of *Atta sexdens* in increasingly urbanized landscapes.

In syntesis, our study reveals the complex nature of ants' responses to urbanization, indicating that adaptation to the urban environment may occur through mechanisms that go beyond changes in physiological and morphological traits. While we anticipated high plasticity of urban ant species, such as variation in thermal tolerance and morphological traits in response to the environmental changes of cities, the relative stability of these characteristics suggests that the urban environment studied may not be imposing a strong enough filter to drive significant

changes in these attributes. Additionally, alternative strategies such as behavioral flexibility, environmental acclimation, and selective adjustments in specific traits, may be more effective ways for ants to cope with urban stress, allowing some species to thrive despite challenging conditions. These insights emphasize the importance of considering a broader range of adaptive responses and the influence of the specific environment studied when trying to understand how species face the challenges of urbanized habitats.

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The authors have no relevant financial or non-financial interests to disclose.

References

Alberti, M., Marzluff, J., & Hunt, V. M. (2017). Phenotypic changes driven by cities: Empirical observations and theoretical implications for eco-evolutionary feedback. Philosophical Transactions of the Royal Society B: Biological Sciences, 372(1712), 20160029. https://doi.org/10.1098/rstb.2016.0029

Alberti, M., & Marzluff, J. M. (2004). Ecological resilience in urban ecosystems: Linking urban patterns to human and ecological functions. Urban ecosystems, 7, 241-265.

Allen, C. R., et al. (1994). Fire ants in Texas: Biology and control. Texas A&M University Press.

Andrew, N. R., Hart, R., & Dunn, R. R. (2013). Ants as indicators of ecosystem health. Ecosystem Services, 5, 1-9.

Angilletta Jr, M. J. (2009). Thermal adaptation: a theoretical and empirical synthesis.

Angilletta, M. J., Cooper, B. S., Schuler, M. S., & Boyles, J. G. (2007). The evolution of thermal physiology in endotherms. Functional Ecology, 21(4), 477-485.

Assis, V. C. B. D., Chagas, P. G., Marinho, C. G. S., Fadini, M. A. M., Delabie, J. H. C., & Mendes, S. M. (2018). Transgenic Bt maize does not affect the soil ant community. Pesquisa Agropecuária Brasileira, 53(02), 152-162.

Arnan, X., Blüthgen, N. (2015). Using ecophysiological traits to predict climatic and activity niches: lethal temperature and water loss in Mediterranean ants. Global Ecology and Biogeography, 24(12), 1454-1464.

399 Arnan, X., Cerdá, X., & Retana, J. (2012). Distinctive life traits and distribution along
400 environmental gradients of dominant and subordinate Mediterranean ant species. Oecologia, 170,
401 489-500.

402 Arnfield, A. J. (2003). Two decades of urban climate research: a review of turbulence, exchanges
403 of energy and water, and the urban heat island. International Journal of Climatology: a Journal of
404 the Royal Meteorological Society, 23(1), 1-26.

405 Bacci, M., V. F. de Almeida, F. H. da Silva, & H. G. Fowler. (2009). Phylogenetic relationships
406 among the leaf-cutting ant genera Atta and Acromyrmex (Hymenoptera: Formicidae) inferred
407 from molecular and morphological data. *Molecular Phylogenetics and Evolution*, 50(2), 264-274.

408 Benitez-Malvido, J., Dattilo, W., Martinez-Falcon, A. P., Duran-Barron, C., Valenzuela, J.,
409 Lopez, S., & Lombera, R. (2016). The multiple impacts of tropical forest fragmentation on
410 arthropod biodiversity and on their patterns of interactions with host plants. PloS one, 11(1),
411 e0146461.

412 Bestelmeyer, B. T. (2000). The contribution of ants to the diversity and structure of ecological
413 communities: A review. Insectes Sociaux, 47(4), 227-23

414 Bihn, J. H., Gebauer, G., & Brandl, R. (2010). Loss of functional diversity of ant assemblages in
415 secondary tropical forests. Ecology, 91(3), 782–792. https://doi.org/10.1890/08-1276.1

416 Bishop, T. R., Robertson, M. P., Van Rensburg, B. J., & Parr, C. L. (2017). Coping with the cold:
417 minimum temperatures and thermal tolerances dominate the ecology of mountain ants. Ecological
418 Entomology, 42(2), 105-114.

419 Blüthgen, N., & Feldhaar, H. (2010). Plant–ant interactions in a tropical rainforest: A quantitative
420 analysis. Ecology, 91(2), 481-490.

421 Bolger, D. T., Suarez, A. V., Crooks, K. R., Morrison, S. A., & Case, T. J. (2000). Arthropods in
422 urban habitat fragments in southern California: area, age, and edge effects. Ecological
423 Applications, 10(4), 1230-1248.

Bragard, C., Baptista, P., Chatzivassiliou, E., Di Serio, F., Gonthier, P., Jaques Miret, J. A., ... & MacLeod, A. (2023). Scientific Opinion on the pest categorisation of Solenopsis invicta. EFSA JOURNAL, 1-26.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. Ecology, 85(7), 1771-1789.

Buckley, L. B., Hurlbert, A. H., & Jetz, W. (2012). Broad-scale ecological implications of ectothermy and endothermy in changing environments. Global Ecology and Biogeography, 21, 873-885.

Bueno, O. C., Campos, A. E. D. C., & Morini, M. D. C. (2017). Formigas em ambientes urbanos no Brasil. Editora Canal, 6.

Bujan, J., Roeder, K. A., Yanoviak, S. P., & Kaspari, M. (2020). Seasonal plasticity of thermal tolerance in ants. Bulletin of the Ecological Society of America, 101(3), e01708. https://doi.org/10.1002/bes2.17082

Bustamante, S. (2017). Variação dos padrões de forrageamento de cefalotas Atta (Hymenoptera: Formicidae) em resposta a mudanças nas condições microclimáticas causadas por mudanças na cobertura da terra (Tesis de doctorado). Pontifícia Universidade Javeriana, Bogotá, Colômbia.

Bustamante, S., & Amarillo-Suárez, A. (2019). Foraging plasticity of Atta cephalotes (Hymenoptera: Formicidae) in response to temperature differences between forest and pasture. Revista de Biología Tropical, 67(4), 963-974.

Calixto, E. S., Lange, D., & Del-Claro, K. (2021). Benefícios líquidos de um mutualismo: Influência da qualidade do néctar extrafloral na aptidão da colônia de uma formiga mutualística. Biotropica, 53(3), 846-856.

Carlin, N. F., & Gladstein, D. (1989). Visual orientation in ants: comparison of visual capabilities of three species. Behavioral Ecology and Sociobiology, 25(4), 275-284

448 Casalegno, S., Anderson, K., Hancock, S., & Gaston, K. J. (2017). Improving models of urban
449 greenspace: from vegetation surface cover to volumetric survey, using waveform laser scanning.
450 Methods in Ecology and Evolution, 8(11), 1443-1452.

451 Cerdá, X., Retana, J., & Manzaneda, A. J. (1998). Ant community structure in relation to habitat
452 diversity in Mediterranean habitats. Oecologia, 117(1), 1-9

453 Cerdá, X., Retana, J., & Manzaneda, A. J. (1997). Habitat selection and community organization
454 in ants. Insectes Sociaux, 44(4), 393-406.

455 Chan, K. H., & Guénard, B. (2020). Ecological and socio-economic impacts of the red import fire
456 ant, Solenopsis invicta (Hymenoptera: Formicidae), on urban agricultural ecosystems. Urban
457 Ecosystems, 23(1), 1-12.

458 Chen, Y. H., & Neoh, K. B. (2023). Urbanization causes shifts in the functional traits and foraging
459 activity, and alters food particle size preference and biomass removal of urban-dwelling ants.
460 Frontiers in Ecology and Evolution, 11, 1044485.

461 Chown, S. L., Clarke, A., & Fraser, C. (2010). Physiological diversity in the Antarctic.
462 Biodiversity & Conservation, 19(6), 1833-1850.

463 Costa, A. N., Vasconcelos, H. L., Vieira-Neto, E. H., & Bruna, E. M. (2008). Do herbivores exert
464 top-down effects in Neotropical savannas? Estimates of biomass consumption by leaf-cutter ants.
465 Journal of vegetation science, 19(6), 849-854.

466 Cros, S., Cerdá, X., & Retana, J. (1997). Spatial and temporal variations in the activity patterns
467 of Mediterranean ant communities. Ecoscience, 4(3), 269-278.

468 Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying
469 drivers of global forest loss. Science, 361(6407), 1108-1111.

470 D. G., Haywood, J., Suarez, A. V., Tsutsui, N. D., ... & Gruber, M. A. (2018). Behavioural
471 variation and plasticity along an invasive ant introduction pathway. Journal of Animal Ecology,
472 87(6), 1653-1666.

da Silva Camargo, R., & Forti, L. C. (2015). What is the stimulus for the excavation of fungus chamber in leaf-cutting ants?. acta ethologica, 18, 31-35.

Davidson, D. W., Cook, S. C., & Snelling, R. R. (2004). Liquid-feeding performances of ants (Formicidae): ecological and evolutionary implications. Oecologia, 139, 255-266.

Davidson, D. W., & Stone, J. (1989). The role of ants in the ecology of the southeastern United States. Ecological Applications, 2(1), 12-16.

De La Mora, A., et al. (2008). Ants and their venom: a review of current knowledge. Journal of Insect Physiology, 54(5), 1039-1045.

Dehling, D. M., Jordano, P., Schaefer, H. M., Böhning-Gaese, K., & Schleuning, M. (2016). Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. Proceedings of the Royal Society B: Biological Sciences, 283(1823), 20152444.

Delabie, J. H. C. (1995). Ants in urban environments: A case study in southern Bahia, Brazil. Sociobiology, 26(1), 49-59.

Del-Claro, K., Lange, D., Fernandes, G. W., Rico-Gray, V., & Leal, I. R. (2019). Ant pollination of Paepalanthus lundii (Eriocaulaceae) in Brazilian savanna. Annals of Botany, 123(7), 1159-1165.

Denney, D. A., Jameel, M. I., Bemmels, J. B., Rochford, M. E., & Anderson, J. T. (2020). "Small spaces, big impacts: contributions of micro-environmental variation to population persistence under climate change." AoB PLANTS, 12(2), plaa005. https://doi.org/10.1093/aobpla/plaa005

Depner, H. (2023). Comparing mortality in response to simulated climate change in the harvester ant, Pogonomyrmex badius, and the fire ant, Solenopsis invicta (Master's thesis, University of South Florida).

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. Proceedings of the National Academy of Sciences, 105(18), 6668-6672.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., & Mouillot, D. (2007). Functional homogenization effect of urbanization on bird communities. Conservation Biology, 21(3), 741-751.

Diamond, S. E., & Martin, R. A. (2020). Evolutionary consequences of urbanization for animal populations. Biological Conservation, 242, 108376.

Diamond, S. E., Chick, L. D., Perez, A., Strickler, S. A., & Martin, R. A. (2018). Evolution of thermal tolerance and its fitness consequences: parallel and non-parallel responses to urban heat islands across three cities. Proceedings of the Royal Society B, 285(1882), 20180036.

Diamond, S. E., Chick, L., Perez, A. B. E., Strickler, S. A., & Martin, R. A. (2017). Rapid evolution of ant thermal tolerance across an urban-rural temperature cline. Biological Journal of the Linnean Society, 121(2), 248-257.

Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Toro, I. D., Hirsch, C., Oberg, E., & Dunn, R. R. (2012). Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. Global Change Biology, 18(2), 448-456.

Egerer, M. H., Arel, C., Otoshi, M. D., Quistberg, R. D., Bichier, P., & Philpott, S. M. (2017). Urban arthropods respond variably to changes in landscape context and spatial scale. Journal of Urban Ecology, 3(1), jux001.

Ehmer, B., & Hölldobler, B. (1995). The social organization of the ant Odontomachus bauri in the tropics. Insectes Sociaux, 42(3), 245-258.

Elizalde, L., Wenzel, J. W., & Clouse, R. M. (2020). The ecosystem services provided by social insects: traits, management tools and knowledge gaps. Biological Reviews, 95(5), 1418-1441.Fagundes, R., Lange, D., Anjos, D. V., de Lima, F. P., Nahas, L., Corro, E. J., ... & Dáttilo, W. (2018). Limited effects of fire disturbances on the species diversity and structure of ant-plant interaction networks in Brazilian Cerrado. Acta Oecologica, 93, 65-73.

Fernandez, F., Guerrero, R. J., & Sánchez-Restrepo, A. F. (2021). Sistemática e diversidade de formigas neotropicais. Revista Colombiana de Entomología, 47(1), 1-19.

Ferrante, M., Lo Cacciato, A., & Lövei, G. L. (2014). Quantifying predation pressure along an urbanisation gradient in Denmark using artificial caterpillars. European Journal of Entomology, 111(5).

Freires, M. E., Roeder, K., & Bujan, J. (2023). Critical thermal limits in ants and their implications under climate change. Biological Reviews.

Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity & Conservation, 7, 1221-1244.

Fowler, H. G., et al. (1993). Ants as indicators of environmental health in hospitals: the case of Tapinoma melanocephalum in Brazil. Environmental Monitoring and Assessment, 26(2), 167-176.

Fowler, H. G., Pereira, L. A., & Forti, L. C. (1991). Ecologia nutricional de formigas. Ecologia nutricional de insetos e suas implicações no manejo de pragas (pp. 131-223). Editora Manole Ltda.

Gardner, T. A., Barlow, J., & Peres, C. A. (2019). A multi-scale approach to understanding tropical forest degradation. Global Change Biology, 25(9), 2942-2955.

Gibbs, A. G., Pomonis, J. G., & Cripps, C. L. (2010). Cuticular lipids and water balance. In Insect hydrocarbons: biology, biochemistry, and chemical ecology (pp. 100-120).Global Biodiversity Information Facility (GBIF). (2020). GBIF Backbone Taxonomy. https://www.gbif.org

Gordon, D. M. (1991). Variation and change in behavioral ecology. Ecology, 72(4), 1196-1203.

Gotelli, N. J., & Arnett, A. E. (2000). Biotic interactions in the guild of invasive ants. Ecology Letters, 3(2), 137-146.

Grimmond, S. U. E. (2007). Urbanization and global environmental change: local effects of urban warming. The Geographical Journal, 173(1), 83-88.

547 Groffman, P. M., Cavender-Bares, J., Bettez, N. D., Grove, J. M., Hall, S. J., Heffernan, J. B., ...
548 & Steele, M. K. (2014). Ecological homogenization of urban USA. Frontiers in Ecology and the
549 Environment, 12(1), 74-81.

550 Hasegawa, E., & Taniguchi, Y. (1996). Predation and feeding behavior of the Japanese rat snake
551 (Elaphe climacophora). Ethology, 102(4), 345-354.

552 Hernando, A. M. (2012). The impact of solar radiation on the distribution of the red imported fire
553 ant, Solenopsis invicta (Hymenoptera: Formicidae). The University of Texas at El Paso.

554 Herz, H., Beyschlag, W., & Hölldobler, B. (2007). Herbivory rate of leaf-cutting ants in a tropical
555 moist forest in Panama at the population and ecosystem scales. Biotropica, 39(4), 482-488.

556 Heterick, B. E., Lythe, M., & Smithyman, C. (2013). Urbanisation factors impacting on ant
557 (Hymenoptera: Formicidae) biodiversity in the Perth metropolitan area, Western Australia: Two
558 case studies. Urban Ecosystems, 16, 145-173.

559 Hölldobler, B., & Wilson, E. O. (1990). The Ants. Cambridge, MA: Harvard University Press.

560 Holway, D. A., et al. (2002). The effects of the invasive Argentine ant on native ant species in the
561 United States. Conservation Biology, 16(5), 1150-1158.

562 Imhoff, M. L., Zhang, P., Wolfe, R. E., & Bounoua, L. (2010). Remote sensing of the urban heat
563 island effect across biomes in the continental USA. Remote sensing of environment, 114(3), 504-
564 513.

565 James S. Santangelo et al. ,Global urban environmental change drives adaptation in white
566 clover.Science375,1275-1281(2022).DOI:10.1126/science.abk0989

567 Janzen, D. H. (1966). Co-evolution of mutualism between ants and acacias in Central America.
568 Evolution, 20(3), 249-259.

569 Kamura, T., et al. (2007). Ants (Hymenoptera: Formicidae) of Brazilian hospitals: Species
570 richness and community structure. Braz. J. Biol., 67(4), 729-735.

571 Kaspari, M., & Weiser, M. D. (1999). The size-grain hypothesis and interspecific scaling in ants.
572 Functional Ecology, 13(4), 530–538. https://doi.org/10.1046/j.1365-2435.1999.00343

573 Kaspari, M., Clay, N. A., Lucas, J., Yanoviak, S. P., & Kay, A. (2015). Thermal adaptation
574 generates a diversity of thermal limits in a rainforest ant community. Global Change Biology,
575 21(3), 1092-1102.Kearney, M., Simpson, S. J., Raubenheimer, D., & Helmuth, B. (2010).
576 Modelling the ecological niche from functional traits. Philosophical Transactions of the Royal
577 Society B: Biological Sciences, 365(1557), 3469-3483.

578 Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: combining physiological and
579 spatial data to predict species' ranges. Ecology Letters, 12(4), 334-350.

580 Klotz, J. H., et al. (1995). Pest ants in the Greater Miami area. Florida Entomologist, 78(3), 441-
581 449.

582 Kramer, A., et al. (2017). Pseudomyrmex gracilis: The Role of Ants in Urban Ecosystems. Urban
583 Ecosystems, 20(2), 267-277.

584 Kübler, L. S., Kelber, C., & Kleineidam, C. J. (2010). Fenótipos distintos do lobo antenal na
585 formiga cortadeira (Atta vollenweideri). Journal of Comparative Neurology, 518(3), 352-365.

586 Langley, R. (1994). Predation and the evolution of high-speed strikes in mammals. Functional
587 Ecology, 8(4), 471-477.

588 Leal, I. R., Wirth, R., & Tabarelli, M. (2012). Seed dispersal by ants in the semi-arid Caatinga of
589 North-East Brazil. Annals of Botany, 110(2), 59-67.

590 Leal, I. R., Wirth, R., & Tabarelli, M. (2014). Os múltiplos impactos das formigas cortadeiras e
591 seu novo papel ecológico nas florestas neotropicais modificadas pelo homem. Biotropica, 46,
592 516-528.

593 Lessard, J. P., Gruner, D. S., & Dunn, R. R. (2009). The impact of environmental change on ant
594 communities: implications for ecological monitoring. Ecosystems, 12(1), 65-77.

595 Levis, N. A., & Pfennig, D. W. (2016). Phenotypic plasticity and the origins of novel phenotypes.
596 Nature Ecology & Evolution, 1(7), 0137.

597 Leong, M., Dunn, R. R., & Trautwein, M. D. (2019). The evolution of urban ants: evidence for
598 adaptation, historical contingency, and stochastic processes. Biodiversity and Conservation,
599 28(4), 847-866.

600 Liang, Y. Q., Li, J. W., Li, J., & Valimaki, S. K. (2008). Impact of urbanization on plant diversity:
601 a case study in built-up areas of Beijing. Forestry Studies in China, 10, 179-188.

602 Lofgren, C. S. (1986). Fire ants: Their biology and control. Florida Entomologist, 69(3), 492-498.

603 McKinney, M. L. (2002). Urbanization, biodiversity, and conservation: the impacts of
604 urbanization on native species are poorly studied, but educating a highly urbanized human
605 population about these impacts can greatly improve species conservation in all ecosystems.
606 Bioscience, 52(10), 883-890.

607 McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. Biological
608 conservation, 127(3), 247-260.

609 McKinney, M. L. (2008). Effects of urbanization on species richness: a review of plants and
610 animals. Urban ecosystems, 11, 161-176.

611 Mertl, A. L., Sorenson, M. D., & Traniello, J. F. A. (2010). Community-level interactions and
612 functional ecology of major workers in the hyperdiverse ground-foraging Pheidole
613 (Hymenoptera, Formicidae) of Amazonian Ecuador. Insectes Sociaux, 57, 441-452.

614 Menke, S. B., Santangelo, J. D., & Robinson, W. H. (2011). Urban ants: the role of ants in
615 ecological monitoring. Urban Ecosystems, 14(4), 617-628

616 Miranda, V. L. D., Koch, E. B. D. A., Oliveira, L. D. S., Nunes, J. D. J. M., Soares, M. R. A.,
617 Mariano, C. D. S. F., & Delabie, J. H. C. (2022). Seasonality effect on ant (Hymenoptera:
618 Formicidae) activity in an ecotonal environment in the state of Piauí, Brazil. Papéis Avulsos de
619 Zoologia, 62, e202262003.

Moreira, D., Morais, V. D., Vieira-da-Motta, O., Campos-Farinha, A. E. D. C., & Tonhasca Jr, A. (2005). Ants as carriers of antibiotic-resistant bacteria in hospitals. Neotropical Entomology, 34, 999-1006.

Morrison, L. W. (2002). The role of the fire ant in the ecological dynamics of the southeastern United States. Insectes Sociaux, 49(4), 394-401

Morris, R. F., & Steigman, D. (1993). Effects of imported fire ants on local ant communities in Louisiana. Oecologia, 96(4), 554-558.

Muratore, IB, Ilieş, I., Huzar, AK et al. Evolução morfológica e a organização comportamental da divisão agrícola do trabalho na formiga cortadeira Atta cephalotes . Behav Ecol Sociobiol 77 70 (2023). https://doi.org/10.1007/s00265-023-03344-4

Nascimento, G., Câmara, T., & Arnan, X. (2024). Critical thermal maxima in neotropical ants at colony, population, and community levels. Bulletin of Entomological Research, 1-10.

Nascimento, G., Câmara, T., & Arnan, X. (2022). Critical thermal limits in ants and their implications under climate change. Biological Reviews, 97(4), 1287-1305.

Narango, D. L., Tallamy, D. W., & Marra, P. P. (2018). Nonnative plants reduce population growth of an insectivorous bird. Proceedings of the National Academy of Sciences, 115(45), 11549-11554.

Nestel, D., & Dickschen, F. (1990). The foraging kinetics of ground ant communities in different Mexican coffee agroecosystems. Oecologia, 84, 58-63.

Nettel-Hernanz, A., Lachaud, J. P., Fresneau, D., López-Muñoz, R. A., & Poteaux, C. (2015). Biogeography, cryptic diversity, and queen dimorphism evolution of the Neotropical ant genus Ectatomma Smith, 1958 (Formicidae, Ectatomminae). Organisms Diversity & Evolution, 15, 543-553.Oke, T. R. (1982). The energetic basis of the urban heat island. Quarterly journal of the royal meteorological society, 108(455), 1-24.

644 Okie, J. G., & Brown, J. H. (2009). Niches, body sizes, and the disassembly of mammal
645 communities on the Sunda Shelf islands. Proceedings of the National Academy of Sciences,
646 106(supplement_2), 19679-19684.

647 Oliveira, F. M., Silva, L. L., Leal, I. R., & Arnan, X. (2022). Morphology of four common and
648 phylogenetically distant ant species varies along disturbance and aridity gradients in the Caatinga
649 dry forest. Biotropica, 54(1), 78-90.

650 Oliveira, P. S., & Hölldobler, B. (1989). The foraging behavior of the ant Odontomachus bauri in
651 relation to resource availability. Behavioral Ecology and Sociobiology, 25(3), 251-258.

652 Oms, C. S., Cerdá, X., & Boulay, R. (2017). Is phenotypic plasticity a key mechanism for
653 responding to thermal stress in ants?. The Science of Nature, 104(5), 42.

654 Peng, M. H., Hung, Y. C., Liu, K. L., & Neoh, K. B. (2020). Landscape configuration and habitat
655 complexity shape arthropod assemblage in urban parks. Scientific reports, 10(1), 16043.

656 Perfecto, I., & Philpott, S. M. (2023). Ants (Hymenoptera: Formicidae) and ecosystem functions
657 and services in urban areas: a reflection on a diverse literature. Myrmecological News, 33.

658 Perfecto, I., & Snelling, R. (1995). Biodiversity and the transformation of a tropical
659 agroecosystem: ants in coffee plantations. Ecological applications, 5(4), 1084-1097.

660 Perfecto I, (1991b) Dynamics of Solenopsis geminata in a tropical fallow field after ploughing.
661 Oikos 62: 139–144

662 Perfecto, I. (1991). Ants (Hymenoptera: Formicidae) as natural control agents of pests in irrigated
663 maize in Nicaragua. Journal of Economic Entomology, 84(1), 65-70.

664 Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., ... & Tobias, J.
665 A. (2020). Macroevolutionary convergence connects morphological form to ecological function
666 in birds. Nature Ecology & Evolution, 4(2), 230-239.

667 Pigot, A. L., Bregman, T., Sheard, C., Daly, B., Etienne, R. S., & Tobias, J. A. (2016). Quantifying
668 species contributions to ecosystem processes: a global assessment of functional trait and

669 phylogenetic metrics across avian seed-dispersal networks. Proceedings of the Royal Society B:
670 Biological Sciences, 283(1844), 20161597.

671 Porter, S. D., & Savignano, D. A. (1990). Invasion of polygyne fire ants decimates native ants in
672 Florida. Ecological Applications, 1(1), 23-31.

673 Rajesh, T. P., Manoj, K., Prashanth Ballullaya, U., Shibil, V. K., Asha, G., Varma, S., ... & Sinu,
674 P. A. (2022). Urban tropical forest islets as hotspots of ants in general and invasive ants in
675 particular. Scientific Reports, 12(1), 12003.

676 Retana, J., & Cerdá, X. (2000). Ants as indicators of biodiversity. Biodiversity & Conservation,
677 9(6), 927-942.

678 Rico-Gray, V., & Oliveira, P. S. (2007). The ecology of ant-plant interactions. In: Ants: Their
679 Structure, Development, and Behavior. Cambridge University Press, 282-301.

680 Ronque, M. U., Fourcassié, V., & Oliveira, P. S. (2018). Ecology and field biology of two
681 dominant Camponotus ants (Hymenoptera: Formicidae) in the Brazilian savannah. Journal of
682 Natural History, 52(3-4), 237-252.

683 Santamouris, M., Cartalis, C., Synnefa, A., & Kolokotsa, D. (2015). On the impact of urban heat
684 island and global warming on the power demand and electricity consumption of buildings—A
685 review. Energy and buildings, 98, 119-124.

686 Segev, U., & Foitzik, S. (2019). Ant personalities and behavioral plasticity along a climatic
687 gradient. Behavioral Ecology and Sociobiology, 73, 1-11.

688 Silva, I. L. H., Leal, I. R., Ribeiro-Neto, J. D., & Arnan, X. (2019). Spatiotemporal responses of
689 ant communities across a disturbance gradient: the role of behavioral traits. Insectes Sociaux,
690 66(4), 623-635.

691 Silva, P. S. D., Leal, I. R., Wirth, R., & Tabarelli, M. (2012). Spatial distribution and fruiting
692 phenology of Protium heptaphyllum (Burseraceae) determine the design of the underground

693 foraging system of *Atta sexdens* L. (Hymenoptera: Formicidae). Neotropical Entomology, 41(2),
694 257-262.

695 Silva, P. S. D., Bieber, A. G. D., Knoch, T. A., Tabarelli, M., Leal, I. R., & Wirth, R. (2013).
696 Foraging in highly dynamic environments: Leaf-cutting ants adjust foraging trail networks to
697 pioneer plant availability. Entomologia Experimentalis et Applicata, 147(2), 110-119.

698 Silvestre, R., Brandão, C. R. F., & da Silva, R. R. (2003). Capítulo 7 Grupos funcionales de
699 hormigas: el caso de los gremios del Cerrado. Introducción a las hormigas de la región
700 Neotropical, 1964, 101-136.

701 Sinclair, B. J., Williams, C. M., & Terblanche, J. S. (2016). Global warming and insect thermal
702 limits. Nature Climate Change, 6(3), 286-290.

703 Siqueira, F. F., Ribeiro-Neto, J. D., Tabarelli, M., Andersen, A. N., Wirth, R., & Leal, I. R. (2017).
704 Leaf-cutting ant populations profit from human disturbances in tropical dry forest in Brazil.
705 Journal of Tropical Ecology, 33(5), 337-344.

706 Siqueira, F. F., Ribeiro-Neto, J. D., Tabarelli, M., Andersen, A. N., Wirth, R., & Leal, I. R. (2018).
707 Human disturbance promotes herbivory by leaf-cutting ants in the Caatinga dry forest. Biotropica,
708 50(5), 779-788.

709 Snell-Rood, E. C. (2013). Uma visão geral das causas e consequências evolutivas da plasticidade
710 comportamental. Comportamento Animal, 85(5), 1004-1011. DOI:
711 10.1016/j.anbehav.2012.12.031

712 Sternberg, L. D. S., Pinzon, M. C., Moreira, M. Z., Moutinho, P., Rojas, E. I., & Herre, E. A.
713 (2007). Plants use macronutrients accumulated in leaf-cutting ant nests. Proceedings of the Royal
714 Society B: Biological Sciences, 274(1608), 315-321.

715 Swanson, A. C., Schwendenmann, L., Allen, M. F., Aronson, E. L., Artavia-León, A., Dierick,
716 D., ... & Zelikova, T. J. (2019). Welcome to the Atta world: A framework for understanding the
717 effects of leaf-cutter ants on ecosystem functions. Functional ecology, 33(8), 1386-1399.

718 Tavella, R. A., Reis, F. O., da Silva Bonifácio, A. et al. (2023). Efeito de fim de semana de
719 poluentes atmosféricos em uma metrópole tropical brasileira. Poluição do Solo do Ar da Água,
720 234, 521. https://doi.org/10.1007/s11270-023-06534-y

721 Tilman, D. (2001). Functional diversity. In Encyclopedia of Biodiversity: Second Edition (pp.
722 587-596). Elsevier Inc.

723 Uno, S., Cotton, J., & Philpott, S. M. (2010). Diversity, abundance, and species composition of
724 ants in urban green spaces. Urban Ecosystems, 13, 425-441.

725 Verble-Pearson, R. M., Henneman, C. A., & LaRue, C. T. (2015). Physiological responses of ants
726 to urbanization: evidence of plasticity and adaptation. Ecology and Evolution, 5(22), 5323-5334.

727 Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007).
728 Let the concept of trait be functional. Oikos, 116(5), 882-892.

729 Walther, G. R. (2010). Community and ecosystem responses to recent climate change.
730 Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1549), 2019-2024.

731 Ward, P. S., & Downie, D. A. (2005). Phylogeny and biogeography of the Pseudomyrmex ants.
732 Molecular Phylogenetics and Evolution, 35(2), 389-404.

733 Ward, P. S. (1991). The Evolution of Pseudomyrmex Ants: A Clade of Arboreal Ants in the New
734 World. Sociobiology, 19(1), 69-84.

735 Wang, C., et al. (2010). Economic impacts of the red imported fire ant in the United States.
736 Sociobiology, 55(1), 143-155.

737 Wehner, R., Marsh, A. C., & Wehner, S. (2019). Desert ants: pioneers of thermal ecology.
738 Frontiers in Behavioral Neuroscience, 13, 190.

739 Weiser, M. D., & Kaspari, M. (2006). Ecological morphospace of New World ants. Ecological
740 Entomology, 31(2), 131–142. https://doi.org/10.1111/j.0307-6946.2006.00768.x&#8203

741 Wetterer, J. K. (2009). Worldwide spread of the ghost ant, Tapinoma melanocephalum
742 (Hymenoptera: Formicidae). Myrmecological News, 12, 23-33.

743 Wetterer, J. K., Hill, J. G., MacGown, J. A., & Booher, D. B. (2022). Populations of the graceful
744 twig ant, Pseudomyrmex gracilis, now bridge the distribution gap between their native range in
745 Texas and non-native range in Florida, USA. Transactions of the American Entomological
746 Society, 148(1), 51-58.

747 Wheeler, D. E. (1991). The developmental basis of worker caste polymorphism in ants. The
748 American Naturalist, 138(5), 1218-1238.

749 Wilson, E. O. (2003). Pheidole in the New World: a dominant, hyperdiverse ant genus (Vol. 1).
750 Harvard University Press.

751 Wirth, R., Meyer, S. T., Almeida, W. R., Araújo, M. V., Barbosa, V. S., & Leal, I. R. (2007).
752 Increasing densities of leaf-cutting ants (Atta spp.) with proximity to the edge in a Brazilian
753 Atlantic forest. Journal of Tropical Ecology, 23(4), 501-505.

754 Wittman, S. E., Franks, N. R., & Gotelli, N. J. (2010). Behavioral and thermal constraints on ant
755 distribution in the eastern United States. Ecology, 91(7), 2024-2034.

756 Wong, B. B., & Candolin, U. (2015). Behavioral responses to changing environments. Behavioral
757 Ecology, 26(3), 665-673.

758 Wurm, Y., et al. (2011). The genome of the fire ant Solenopsis invicta. Proceedings of the
759 National Academy of Sciences, 108(14), 5679-5684.

760 Yates, M., & Andrew, N. R. (2011). Climate change and insect herbivory: implications for the
761 performance of insect herbivores along geographic gradients. Austral Ecology, 36(3), 336-344.

762 Yilmaz, M. O., Tekin, M., & Günther, D. (2019). Evolution of thermal performance curves and
763 fitness consequences: insights from urbanization. Functional Ecology, 33(12), 2310-2320.

764 Youngsteadt, E., Ernst, A. F., Dunn, R. R., & Frank, S. D. (2015). Responses of arthropod
765 populations to warming depend on latitude: evidence from urban heat islands. Global Change
766 Biology, 21(1), 322-333.

767 Zhang, F., Huang, G., Hou, Q., Liu, C., Zhang, Y., & Zhang, Q. (2019). Groundwater quality in
768 the Pearl River Delta after the rapid expansion of industrialization and urbanization: Distributions,
769 main impact indicators, and driving forces. Journal of Hydrology, 577, 124004.

770 Zhou, Y., Williams, A. P., Cook, B. I., & Iacobellis, S. (2020). Urban heat islands in the Los
771 Angeles metropolitan area: topography, local wind, and heat waves. Journal of Geophysical
772 Research: Atmospheres, 125(7), e2019JD031510.

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774

775 **Table 1.** Morphological traits measured in this study, along with the description, references and
776 implications for adaptation, which highlight how these characteristics contribute to the survival
777 and foraging strategies of ants, particularly in relation to environmental conditions.

778

Trait	Description	Reference	Implication for Adaptation
Head Size	Representative measure of body size. Measured by head length and width.	Kaspari & Weiser, 1999	Reflects overall body size, influencing the ability to withstand thermal stress.
Relative Leg Size	Ratio of leg length (femur + tibia) to head length.	Kaspari & Weiser, 1999; Bihn et al., 2010	Indicates mobility capacity for foraging strategies under rising temperatures.
Clypeus Size	Area at the front of the head. Measured by clypeus length and width.	Davidson et al., 2004	Related to water loss, important in hot and dry environments.
Mandible Size	Length of the mandibles.	Weiser & Kaspari, 2006	Contributes to the regulation of water loss during activities, especially in warm climates.
Antenna Size	Length of the antennae.	Weiser & Kaspari, 2006	Increases the area available for sensory organs, facilitating foraging in environments with varying urbanization.
Eye Size	Ratio of eye length and width.	Bihn et al., 2010	Reflects foraging behavior; species with low thermal tolerance tend to forage at night and have smaller eyes.
Eye Position	Distance between the eyes.	Bihn et al., 2010	Indicates sensory and adaptive capability to detect prey and threats in different light conditions.

779

780 **Table 2.** Effects of urbanization intensity on morphological functional traits of ants in the city of Recife, Pernambuco, northeastern Brazil. Significant *p*-values

781 are highlighted in bold; SE: Standard error; DF: Degrees of freedom.

Response	**Species**	**Transformation**	**Predictor**	**Estimate**	**SE**	**DF**	***t*-value**	***p*-value**
Body size [head length (μm)]	All species	Log (x + 1)	**Intercept**	**7.05**	**0.07**	**15.09**	**102.75**	**<0.001**
			Urbanization intensity	0.03	0.11	14.15	0.26	0.80
	Atta sexdens	Log (x + 1)	**Intercept**	**7.28**	**0.17**	**7.96**	**42.06**	**<0.001**
			Urbanization intensity	0.59	0.26	7.85	2.24	0.06
	Camponotus crassus	Log (x + 1)	**Intercept**	**7.47**	**0.34**	**5.00**	**21.83**	**<0.001**
			Urbanization intensity	-0.48	0.67	5.00	-0.72	0.50
	Ectatomma muticum	Log (x + 1)	**Intercept**	**7.82**	**0.05**	**13.00**	**157.99**	**<0.001**
			Urbanization intensity	-0.03	0.08	12.96	-0.33	0.75
	Odontomachus bauri	Log (x + 1)	**Intercept**	**7.41**	**0.09**	**13.10**	**85.45**	**<0.001**

			Urbanization intensity	0.06	0.15	13.08	0.43	0.68
	Pheidole radoszkowskii	Log (x + 1)	**Intercept**	**6.64**	**0.20**	**10.15**	**32.94**	**<0.001**
			Urbanization intensity	-0.17	0.31	10.14	-0.55	0.60
	Pseudomyrmex gracilis	Log (x + 1)	**Intercept**	**6.98**	**0.03**	**15.22**	**213.41**	**<0.001**
			Urbanization intensity	0.02	0.05	14.09	0.30	0.77
	Solenopsis invicta	Log (x + 1)	**Intercept**	**6.68**	**0.15**	**3.03**	**45.67**	**<0.001**
			Urbanization intensity	0.08	0.21	3.03	0.36	0.74
	Tapinoma melanocephalum	Log (x + 1)	**Intercept**	**5.98**	**0.06**	**12.25**	**99.96**	**<0.001**
			Urbanization intensity	0.05	0.10	12.35	0.47	0.65
Relative eye length (μm)	All species	–	**Intercept**	**0.23**	**0.03**	**13.32**	**7.52**	**<0.001**
			Urbanization intensity	0.02	0.05	13.06	0.32	0.75
	Atta sexdens	–	**Intercept**	**0.11**	**0.03**	**7.99**	**3.71**	**0.01**
			Urbanization intensity	0.01	0.04	7.90	0.25	0.81

Camponotus crassus	–	**Intercept**	**0.19**	**0.06**	**5.00**	**3.06**	**0.03**
		Urbanization intensity	0.02	0.12	5.01	0.13	0.90
Ectatomma muticum	–	**Intercept**	**0.26**	**0.02**	**13.03**	**15.04**	**<0.001**
		Urbanization intensity	0.02	0.03	12.98	0.69	0.50
Odontomachus bauri	–	**Intercept**	**0.23**	**0.04**	**13.11**	**5.22**	**<0.001**
		Urbanization intensity	-0.09	0.07	13.10	-1.24	0.24
Pheidole radoszkowskii	–	**Intercept**	**0.47**	**0.17**	**10.26**	**2.79**	**0.02**
		Urbanization intensity	-0.15	0.26	10.25	-0.57	0.58
Pseudomyrmex gracilis	–	**Intercept**	**0.22**	**0.06**	**13.32**	**3.73**	**0.002**
		Urbanization intensity	0.01	0.10	13.20	0.19	0.85
Solenopsis invicta	–	**Intercept**	**0.19**	**0.05**	**3.01**	**3.99**	**0.03**
		Urbanization intensity	0.07	0.07	3.01	0.96	0.41
Tapinoma melanocephalum	–	Intercept	0.17	0.10	11.98	1.73	0.11

			Urbanization intensity	0.21	0.17	11.99	1.24	0.24
Inter-ocular distance (µm)	All species	–	**Intercept**	**0.64**	**0.06**	**13.64**	**10.44**	**<0.001**
			Urbanization intensity	0.001	0.10	13.34	0.01	0.99
	Atta sexdens	–	**Intercept**	**0.79**	**0.13**	**7.94**	**5.96**	**<0.001**
			Urbanization intensity	-0.14	0.20	7.83	-0.67	0.52
	Camponotus crassus	–	Intercept	0.56	0.25	4.99	2.29	0.07
			Urbanization intensity	0.001	0.48	4.99	0.002	1
	Ectatomma muticum	–	**Intercept**	**0.68**	**0.04**	**13.01**	**16.65**	**<0.001**
			Urbanization intensity	0.04	0.07	12.98	0.57	0.58
	Odontomachus bauri	–	**Intercept**	**0.46**	**0.08**	**13.17**	**6.10**	**<0.001**
			Urbanization intensity	-0.17	0.13	13.16	-1.37	0.19
	Pheidole radoszkowskii	–	Intercept	0.91	0.43	10.17	2,11	0.06
			Urbanization intensity	-0.03	0.66	10.17	-0.04	0.97

	Pseudomyrmex gracilis	–	**Intercept**	**0.46**	**0.01**	**14.66**	**38.59**	**<0.001**
			Urbanization intensity	-0.02	0.02	12.87	-1.06	0.31
	Solenopsis invicta	–	Intercept	0.68	0.23	3.01	2.94	0.06
			Urbanization intensity	0.05	0.34	3.01	0.15	0.89
	Tapinoma melanocephalum	–	**Intercept**	**0.81**	**0.03**	**13.11**	**24.95**	**<0.001**
			Urbanization intensity	-0.003	0.05	13.47	-0.07	0.94
Relative mandible length (μm)	All species	–	**Intercept**	**0.67**	**0.08**	**13.08**	**8.16**	**<0.001**
			Urbanization intensity	-0.02	0.14	12.91	-0.18	0.86
	Atta sexdens	–	**Intercept**	**0.71**	**0.06**	**7.52**	**11.13**	**<0.001**
			Urbanization intensity	**-0.27**	**0.10**	**6.81**	**-2.79**	**0.03**
	Camponotus crassus	–	**Intercept**	**0.37**	**0.11**	**5.01**	**3.23**	**0.02**
			Urbanization intensity	-0.03	0.22	5.01	-0.14	0.89

Ectatomma muticum	–	**Intercept**	**0.80**	**0.05**	**13.01**	**16.44**	**<0.001**
		Urbanization intensity	0.04	0.08	12.97	0.53	0.60
Odontomachus bauri	–	**Intercept**	**0.90**	**0.07**	**13.14**	**12.05**	**<0.001**
		Urbanization intensity	-0.13	0.13	13.11	-0.99	0.34
Pheidole radoszkowskii	–	**Intercept**	**1.03**	**0.31**	**10.43**	**3.30**	**0.01**
		Urbanization intensity	-0.36	0.48	10.43	-0.74	0.48
Pseudomyrmex gracilis	–	**Intercept**	**0.39**	**0.03**	**19.25**	**13.44**	**<0.001**
		Urbanization intensity	-0.03	0.05	16.77	-0.70	0.49
Solenopsis invicta	–	**Intercept**	**0.49**	**0.08**	**3.03**	**6.28**	**0.01**
		Urbanization intensity	-0.09	0.11	3.03	-0.74	0.51
Tapinoma melanocephalum	–	**Intercept**	**0.58**	**0.21**	**12.04**	**2.78**	**0.02**
		Urbanization intensity	0.24	0.35	12.05	0.68	0.51

Relative clypeus length (µm)	All species	–	**Intercept**	**0.27**	**0.04**	**13.43**	**6.26**	**<0.001**
			Urbanization intensity	0.05	0.07	13.14	0.76	0.46
	Atta sexdens	–	**Intercept**	**0.14**	**0.03**	**7.91**	**4.26**	**0.003**
			Urbanization intensity	0.04	0.04	7.79	0.75	4.48
	Camponotus crassus	–	**Intercept**	**0.17**	**0.05**	**4.99**	**3.25**	**0.02**
			Urbanization intensity	0.03	0.10	5.01	0.31	0.77
	Ectatomma muticum	–	**Intercept**	**0.51**	**0.03**	**13.02**	**16.85**	**<0.001**
			Urbanization intensity	0.02	0.05	12.99	0.36	0.72
	Odontomachus bauri	–	**Intercept**	**0.08**	**0.01**	**13.18**	**10.10**	**<0.001**
			Urbanization intensity	0.01	0.01	13.13	0.64	0.53
	Pheidole radoszkowskii	–	Intercept	0.52	0.26	10.20	2.04	0.07
			Urbanization intensity	-0.04	0.40	10.20	-0.11	0.91

	Pseudomyrmex gracilis	–	**Intercept**	**0.25**	**0.02**	**15.62**	**11.03**	**<0.001**
			Urbanization intensity	-0.01	0.04	14.55	-0.22	0.83
	Solenopsis invicta	–	**Intercept**	**0.21**	**0.02**	**3.06**	**9.53**	**0.002**
			Urbanization intensity	0.05	0.03	3.07	1.65	0.20
	Tapinoma melanocephalum	–	Intercept	0.24	0.12	11.98	2.07	0.06
			Urbanization intensity	0.18	0.20	11.99	0.91	0.38
Relative antenna length (μm)	All species	–	**Intercept**	**1.11**	**0.12**	**13.79**	**9.27**	**<0.001**
			Urbanization intensity	0.30	0.20	13.27	1.52	0.15
	Atta sexdens	–	**Intercept**	**1.04**	**0.30**	**8.08**	**3.47**	**0.01**
			Urbanization intensity	-0.10	0.45	7.25	-0.23	0.82
	Camponotus crassus	–	**Intercept**	**0.96**	**0.32**	**5.02**	**3.05**	**0.03**
			Urbanization intensity	0.25	0.62	5.04	0.41	0.70

	Ectatomma muticum	–	**Intercept**	**1.03**	**0.06**	**13.02**	**16.94**	**<0.001**
			Urbanization intensity	0.04	0.10	12.98	0.35	0.73
	Odontomachus bauri	–	**Intercept**	**1.12**	**0.15**	**13.86**	**7.22**	**<0.001**
			Urbanization intensity	-0.09	0.26	13.82	-0.35	0.73
	Pheidole radoszkowskii	–	**Intercept**	**1.79**	**0.59**	**10.38**	**3.03**	**0.01**
			Urbanization intensity	0.97	0.91	10.38	1.06	0.31
	Pseudomyrmex gracilis	–	**Intercept**	**1.06**	**0.06**	**18.87**	**16.47**	**<0.001**
			Urbanization intensity	**-0.24**	**0.10**	**16.36**	**-2.30**	**0.04**
	Solenopsis invicta	–	Intercept	0.95	0.58	3.02	1.66	0.20
			Urbanization intensity	0.43	0.84	3.02	0.51	0.65
	Tapinoma melanocephalum	–	**Intercept**	**0.93**	**0.42**	**12.02**	**2.21**	**0.05**
			Urbanization intensity	0.68	0.71	12.04	0.96	0.36
Relative leg length (µm)	All species	–	**Intercept**	**2.32**	**0.27**	**19.60**	**8.54**	**<0.001**

		Urbanization intensity	-0.12	0.35	13.77	-0.35	0.73
Atta sexdens	–	**Intercept**	**3.78**	**0.35**	**107**	**10.74**	**<0.001**
		Urbanization intensity	**-1.99**	**0.51**	**107**	**-3.88**	**<0.001**
Camponotus crassus	–	**Intercept**	**2.39**	**0.43**	**5.00**	**5.61**	**<0.001**
		Urbanization intensity	0.37	0.83	5.02	0.44	0.68
Ectatomma muticum	–	**Intercept**	**2.31**	**0.12**	**13.00**	**18.61**	**<0.001**
		Urbanization intensity	0.08	0.21	12.95	0.37	0.72
Odontomachus bauri	–	**Intercept**	**1.82**	**0.15**	**13.25**	**12.44**	**<0.001**
		Urbanization intensity	-0.03	0.25	13.21	-0.14	0.90
Pheidole radoszkowskii	–	Intercept	2.84	1.14	10.24	2.50	0.03
		Urbanization intensity	0.41	1.76	10.24	0.23	0.82
Pseudomyrmex gracilis	–	**Intercept**	**1.47**	**0.23**	**14.60**	**6.43**	**<0.001**
		Urbanization intensity	0.05	0.38	13.73	0.13	0.90

	Solenopsis invicta	Log (x + 1)	Intercept	1.16	0.27	3.05	4.25	0.02
			Urbanization intensity	-0.05	0.40	3.06	-0.14	0.90
	Tapinoma melanocephalum	–	**Intercept**	**1.86**	**0.12**	**12.87**	**15.04**	**<0.001**
			Urbanization intensity	-0.06	0.21	13.05	-0.28	0.78
CTMax (°C)	All species	Log (x + 1)	**Intercept**	**3.84**	**0.02**	**18.74**	**181.66**	**<0.001**
			Urbanization intensity	0.004	0.03	13.52	0.16	0.88
	Atta sexdens	Log (x + 1)	**Intercept**	**3.87**	**0.02**	**9.06**	**233.36**	**<0.001**
			Urbanization intensity	-0.01	0.02	8.80	-0.45	0.66
	Camponotus crassus	Log (x + 1)	**Intercept**	**3.93**	**0.06**	**4.99**	**63.27**	**<0.001**
			Urbanization intensity	-0.18	0.12	4.99	-1.50	0.19
	Ectatomma muticum	Log (x + 1)	**Intercept**	**3.79**	**0.03**	**12.97**	**115.13**	**<0.001**
			Urbanization intensity	0.003	0.05	12.76	0.07	0.95
	Odontomachus bauri	Log (x + 1)	**Intercept**	**3.79**	**0.03**	**14.001**	**109.06**	**<0.001**

		Urbanization intensity	0.001	0.06	13.85	0.03	0.98
Pheidole radoszkowskii	Log (x + 1)	**Intercept**	**3.89**	**0.04**	**10.68**	**103.18**	**<0.001**
		Urbanization intensity	-0.07	0.06	10.73	-1.21	0.25
Pseudomyrmex gracilis	Log (x + 1)	**Intercept**	**3.78**	**0.02**	**13.77**	**192.12**	**<0.001**
		Urbanization intensity	0.06	0.03	13.51	1.71	0.11
Solenopsis invicta	Log (x + 1)	**Intercept**	**3.89**	**0.04**	**3.08**	**96.62**	**<0.001**
		Urbanization intensity	-0.003	0.06	3.10	-0.05	0.97
Tapinoma melanocephalum	Log (x + 1)	**Intercept**	**3.80**	**0.05**	**12.02**	**78.10**	**<0.001**
		Urbanization intensity	0.10	0.08	12.03	1.24	0.24

782

SUPPLEMENTARY MATERIAL

Ant physiological and morphological functional traits along an urbanization intensity gradient in the Atlantic Forest, northeastern Brazil

Isabelle Leite de Holanda Silva[1], Diego Centeno-Alvarado[1], Iago Monteiro da Costa Wäcker[2], João Carlos Pena[3], Xavier Arnan[4], Inara Roberta Leal[1,5*]

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[2]Curso de Bacharelado em Ciências Biológicas, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[3]Laboratório de Ecologia Espacial e Conservação, Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista Julio de Mesquita Filho, Rio Claro, Brazil

[4]Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

[5]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

***Corresponding author:** inara.leal@ufpe.br

Table S1. Characteristics and distribution of the ant species analyzed in the study, including their food preferences, environmental adaptations, and relevant references. The species include leaf-cutting ants, predatory ants, generalists, and specialists, with varying behaviors and relationships to urban and natural environments.

Species	Occurrence	Characteristics	Reference
Atta sexdens	Widely distributed in Brazil and the Neotropics.	Leaf-cutting ant considered generalist, uses plant material to cultivate fungi in its underground nests. Prefers open habitats, proliferating after anthropogenic disturbances.	Forti et al., 2020; Mehdiabadi et al., 2012; Wirth et al., 2007; Meyer et al., 2009; Dohm et al., 2011; Siqueira et al., 2018; Perfecto & Philpott, 2023; Swanson et al., 2019
Pheidole radoszkowskii	Distributed across Neotropical regions, especially in Brazil, Central and South America.	Epigaeic omnivore ant considered generalist, collects a variety of foods, including arthropods and plant exudates.	Benítez & Perfecto, 1990; Nestel & Dickschen, 1990; Assis et al., 2018; Mertl et al., 2010; Perfecto, 1991
Solenopsis invicta	Found in South America and various regions worldwide, including the United States.	Cryptic omnivore considered aggressive ant, forms large colonies and adapts to various environments, including urban and agricultural. It is known as an invasive species with negative impacts on health and agriculture.	Wurm et al., 2011; Bragard et al., 2023; Chan & Guénard, 2020; Holway et al., 2002; Adams, 1986; Wang et al., 2010
Camponotus crassus	Found in several regions of South America, including Brazil, Argentina, Colombia, Paraguay, and Peru.	Arboreal subordinate ants with castes varying in size and function. It has a mutualistic relationship with plants, protecting them from herbivores and helping control pests.	Leal et al., 2014; Fagundes et al., 2016; Câmara et al., 2018; Santos, 2016; Ronque et al., 2018
Tapinoma melanocephalum	Widely distributed worldwide, found in Brazil and other regions.	Opportunist ant considered generalist, with coloration that blends into backgrounds, commonly found in urban environments. Known for its potential to transmit pathogens, and is one of the most prevalent ants in hospitals.	Wetterer, 2009; Kamura et al., 2007; Fowler et al., 1993; Moreira et al., 2005
Odontomachus bauri	Found in Brazil and other tropical and subtropical regions of South America.	Epigaeic predator ants considered specialist with highly developed mandibles, used for capturing prey and defense. Forages individually, preying on arthropods and decomposing organic matter.	Hölldobler & Wilson, 1990; Oliveira & Hölldobler, 1989; Wetterer, 2010; Vogt et al., 2019

Species	Occurrence	Characteristics	Reference
Ectatomma muticum	Found in tropical and subtropical forests of South America.	Opportunist ant considered generalist, collects sugary exudates, and exhibits aggressive behavior. Can benefit from urban food sources like food scraps and garbage.	Nettel-Hernanz et al., 2015; Gómez et al., 2004; Fowler et al., 1991; Vogt et al., 2019
Pseudomyrmex gracilis	Distributed in tropical regions of the New World, especially in forests and savannas.	Arboreal subordinate ant considered specialist of plants with extrafloral nectaries, capable of preying on various insects. May be aggressive, damaging plants it protects.	Boulton et al., 2000; Hölldobler & Wilson, 1990; Fowler et al., 1991; Ward, 1985; Wetterer et al., 2022; Kramer et al., 2017

ARTIGO DO TERCEIRO CAPITULO

Urbanization intensity reduces the quality of seed dispersal service provided by ants in a metropolitan region in Northeastern Brazil

Isabelle Leite de Holanda Silva[1], Andreza Maria da Silva [2], Diego Centeno-Alvarado[3], João Carlos Pena[4], Xavier Arnan[3,5], Inara R. Leal[6*]

[1]Programa de Pós-Graduação em Biologia Vegetal, Departamento de Botânica, Universidade Federal de Pernambuco, Av. Professor Moraes Rego, s/n, Cidade Universitária, Recife, Pernambuco, Brazil – 50670-091

[2]Centro de Biociências, Universidade Federal de Pernambuco, Av. Professor Moraes Rego, s/n, Cidade Universitária, Recife, Pernambuco, Brazil – 50670-091

[3]Programa de Pós-Graduação em Etnobiologia e Conservação da Natureza, Universidade Federal Rural de Pernambuco, Rua Dom Manuel de Medeiros, s/n, Dois Irmãos, Recife, Pernambuco, Brazil – 52171-900

[4]Araucária Innovation and Sustainability Lab (LASI), Environmental Studies Center (CEA), São Paulo State University (UNESP), Rio Claro, Brazil – 13506-752

[5]Universidade de Pernambuco, Rua Cap. Pedro Rodrigues, São Jose, Garanhuns, Pernambuco, Brazil – 55294-902

[6]Departamento de Botânica, Universidade Federal de Pernambuco, Av. Professor Moraes Rego, s/n, Cidade Universitária, Recife, Pernambuco, Brazil – 50670-091

*** Corresponding author: inara.leal@ufpe.br**

ORCID:

I. L. H. Silva: https://orcid.org/0000-0001-7832-4433

X. Arnan: https://orcid.org/0000-0002-9904-274X

I.R. Leal: https://orcid.org/0000-0002-8125-2191

J.C Pena: https://orcid.org/0000-0003-1368-1805

A. M. Silva: https://orcid.org/0009-0009-0240-4045

Abstract

Ant-mediated seed dispersal is a critical ecological process that contributes to the maintenance and regeneration of plant communities. Urbanization can significantly alter these interactions via the reduction or even depletion of native ant dispersers, leading to shifts in biodiversity and ecosystem function. In this study, we assessed the effects of urbanization on seed dispersal by ants in the Metropolitan Region of Recife, Brazil. We established 22 sampling sites along an urbanization gradient, and offered artificial seeds to monitor interactions between ants and seeds. We recorded a total of 443 ants from 29 species and five subfamilies interacting with 2,705 artificial seeds. Of these, 26.4% were removed (≥5 cm displacement), while 73.6% were only cleaned (elaiosome consumed without seed transport). *Pheidole* was responsible for 47.6% of all interactions and removing 35.8% of the seeds. Species from genera such as *Ectatomma*, *Gnamptogenys*, *Neoponera*, and *Odontomachus* were restricted to less urbanized areas (<30% urban cover) and were characterized as high-quality dispersers. *Odontomachus bauri* was the most representative among these, removing 7.37% of seeds. On the other hand, *Pheidole*, *Camponotus*, and *Solenopsis*, were classified as low-quality dispersers and dominated more urbanized environments. Furthermore, these genera also exhibited the greatest mean removal distances (≈88 cm, 72.62 cm, and 64.83 cm, respectively). Overall, our results revealed a significant decrease in seed removal rate with increasing urbanization intensity, while seeds cleaned increased. While the composition of seed-dispersing ant communities shifted markedly along the gradient, dispersal distances and ant abundance and richness were not influenced by urbanization. These findings highlight the influence of urbanization on ant-mediated seed dispersal, with shifts in species composition and foraging behavior affecting dispersal efficiency and potential ecological functions.

Key-words: Artificial seeds; Urban ants; Removal seeds; Urban ecosystem

Introduction

Urbanization is one of the most significant global changes affecting ecosystems worldwide, deeply impacting biodiversity and the ecological interactions essential for ecosystem functioning (Fuller et al., 2010). It modifies local and regional climates through the urban heat island effect and alterations in precipitation patterns (Elmqvist et al., 2013). Furthermore, as urban populations grow, the demand for land and resources increases, while in some declining urban areas, abandoned spaces present both challenges and opportunities for biodiversity recovery (Elmqvist et al., 2013). Biodiversity recovery depends on a range of complex, interconnected natural processes that sustain life, such as suitable climatic conditions, water availability, nutrient cycling, organic matter decomposition, and the presence and abundance of ecological partners (Lal, 2004; Grimm et al., 2008; McKinney, 2006).

Although often considered secondary, other ecosystem functions related to biodiversity, such as pest control, pollination, and seed dispersal, also play crucial roles in maintaining the stability and functionality of ecosystems (Leal & Oliveira, 1998; Melathopoulos et al., 2015; Boesing et al., 2018; Vale et al., 2023). These processes often work together to ensure that ecological systems remain balanced and resilient in the face of change (Kiers et al., 2010). Among these ecosystem services, seed dispersal stands out as a fundamental process for plant regeneration and the maintenance of diversity, facilitating colonization of new environments and connectivity between habitats (Lengyel et al., 2010; Penn & Crist, 2018). This process not only sustains the continuity of plant populations but also contributes to the dynamics of ecological communities, especially in urban areas where natural processes are often altered or disrupted (Guerrero et al., 2016; McKinney, 2008).

In fact, urbanization can disrupt natural ecological processes due to habitat loss and fragmentation, as well as the introduction of exotic and/or invasive species, which can reduce the effectiveness of seed dispersal and negatively impact biodiversity recovery (Goddard et al., 2009; Shochat et al., 2006). Many animals participate in seed dispersal mutualisms, but diaspore traits can indicate the main dispersers for a given plant species (Valenta and Nevo, 2020). Fleshy fruits are generally dispersed by vertebrates. Brightly colored, thin-skinned fruits are associated with

bird dispersal, while dull, highly aromatic fruits are associated with mammal dispersal (Herrera, 1989, 2002; Sinnott-Armstrong et al., 2018). The presence of an elaiosome (a food body attached to a seed) indicates that the seed is primarily dispersed by ants (Jules, 1996). Elaiosomes are generally described as nutrient-rich food bodies attached to seeds that act as a food reward attracting and rewarding seed-dispersing ants (Karnish, 2024).

Seed dispersal by ants (myrmecochory) is a widely distributed strategy involving 11,000 species of angiosperms from 77 botanical families (Leal et al., 2007; Lengyel et al., 2010; Penn & Crist, 2018). Myrmecochorous plants are particularly abundant and diverse in habitats such as temperate forests of the Northern Hemisphere and sclerophyllous shrubs in Mediterranean climates of South Africa, Australia, southern Europe, and South America (Berg, 1975; Beattie, 1985; Bond & Slingsby, 1983; Westoby et al., 1991; Lengyel et al., 2009; Leal et al., 2007). Ants are attracted to diaspores that fall to the ground and remove the elaiosome, a process that may facilitate dormancy break and increase germination success (Hughes & Westoby, 1992; Canner et al., 2012; Pacini, 1990; Lobstein & Rockwood, 1993). Additionally, by transporting seeds to their nests, ants reduce predation beneath the mother plant (Horvitz, 1981; Howe & Smallwood, 1982) and competition among seedlings (Westoby et al., 1982), while depositing them in nutrient-rich sites favorable for germination (Rissing, 1986). The removal of the elaiosome may also decrease fungal attacks, contributing to successful seedling establishment (Oliveira et al., 1995; Leal & Oliveira, 1998). The average dispersal distance and the shape of the dispersal curve play crucial roles in the colonization rates of propagules at new sites (Portnoy & Willson, 1993). After the initial transport to the nest, seeds may be discarded in distant locations through secondary dispersal (Beaumont et al., 2012). Ants respond to seed and elaiosome size; generally, ants prefer to collect larger seeds and seeds with larger elaiosomes, likely because this increases the food reward relative to the cost of moving a seed (Gunther & Lanza, 1989; Gorb & Gorb, 2003). While numerous ant species are involved in seed cleaning and removal, the most effective dispersal is often carried out by a small group of key species (Andersen, 1988; Gove et al., 2007; Zelikova & Ratchford, 2008).

High-quality seed dispersal services are typically provided by larger ant species because they collect seeds readily and transport them over long distances (Andersen & Morrison, 1998; Leal et al., 2014). Low-quality dispersers (i.e., ant species that cleaned elaiosomes without moving seeds or move seeds only short distances; Andersen & Morrison, 1998) do not show preferences for elaiosome or seed mass (Leal et al., 2014). Less frequent long-distance dispersal events and the behavior of discarding seeds near ant colony waste piles further extend the reach of this ecosystem service, influencing the fate and distribution of seeds (Berg, 1975; Lubertazzi et al., 2010). Although few ant species are high-quality dispersers, these species disperse a large number of seeds, routinely removing over 75% of the seeds offered by plants (Warren & Giladi, 2014). However, large ant species are especially sensitive to disturbances (Gibb et al., 2018; Leal, Andersen, & Leal, 2014), which can result in severe reductions in the quality of seed dispersal services in disturbed habitats (Almeida et al., 2013; Gove, Majer, & Dunn, 2007; Leal, Andersen, & Leal, 2014; Ness, Bronstein, Andersen, & Holland, 2004). This is particularly relevant in urban environments, where anthropogenic pressures significantly influence the abundance, frequency, and composition of potential seed dispersers (Schneiberg et al., 2020; Teixido et al., 2022).

Urban ecosystems present unique conditions that influence ant behavior and seed dispersal dynamics. Physical barriers such as roads and buildings limit the movement of dispersers and alter natural vegetation regeneration patterns (McKinney, 2008; Ziter et al., 2019). Despite the limitations imposed by habitat fragmentation and degradation, ants exhibit significant ecological plasticity, which may help them persist in urban environments and continue to play functional roles in cities (Parr et al., 2007; Vissoto et al., 2023). Many urban ant species with generalist behavior persist or even benefit from simplified foraging landscapes and/or the availability of new types of food resources (Palfi & Robinson, 2017). However, the maintenance of ecosystem services provided by these species, such as seed dispersal, may be compromised by transformations imposed by urbanization. A recent review highlighted the need for integrative studies that address how these mutualisms respond to environmental changes, especially in urban landscapes where ecological interactions are often altered (Teixido et al., 2022).

In this context, this study is essential for understanding the vulnerability of plant-animal mutualisms in urban environments, evaluating how seed dispersal by ants can contribute to vegetation regeneration and ecological connectivity in cities (Harrison & Winfree, 2015; Seto et al., 2012; Palfi & Robinson, 2017). By filling this gap, it provides valuable insights for biodiversity conservation and the management of green spaces as reservoirs of ecosystem services (Thomson et al., 2010; Sorrells & Warren, 2011). We investigated the effects of urbanization intensity on seed dispersal provided by the ant community along a pre-established urbanization gradient in the Metropolitan Region of Recife, in Northeastern Brazil. We used artificial seeds to assess the potential seed dispersal service provided by ants. Our general hypothesis was that urbanization intensity reduces the quality of seed dispersal services due to a decrease in the ant disperser community, caused by habitat modifications, changes in the availability of different food resources, and increased risks associated with foraging as consequences of urbanization. We predicted that with increasing urbanization intensity, there will be (1) a reduction in removal rate, and (2) an increase in cleaned seeds.

Material and Methods

Study site

The study was carried out in the Metropolitan Region of Recife, Pernambuco, located in northeastern Brazil (34.8780° – 34.9757°S, 7.9405° – 8.1450°W; Fig. 1). Recife is known for being the third most densely populated metropolitan area in Brazil (IBGE, 2021) and one of the most deforested regions of the Brazilian Atlantic Forest (Bernard et al., 2023). The city has an average annual temperature of 27.7 °C and receives around 2200 mm of rainfall each year (APAC, 2017). The predominant vegetation in Recife is characteristic of the Atlantic Forest, specifically the Lowland Dense Ombrophilous Forest, which historically covered much of the region (Lima et al., 2019). However, urban expansion over time has led to significant fragmentation and degradation of this vegetation.

We selected 22 locations across the region to study urbanization influences on seed dispersal, ranging from the city center to suburban areas in the southwest near rural zones. Each

site was chosen based on the centroid of each grid cell, and experimental procedures were performed in sidewalks, small green spaces, or parks, to represent different urbanization contexts. To select these sites, we first applied a grid over the study area, then created buffers around each site and measured the amount of built cover as a proxy for urbanization intensity. For this, we used Planet Scope satellite images from August 2021, with a 3 m resolution and four spectral bands (Planet Labs PBC, 2021). We identified three main land cover types: woody vegetation, herbaceous vegetation, and built cover. We added the hydrography by merging the classified raster map with layers originally obtained in vector format at the Recife Municipal Government website (https://dados.recife.pe.gov.br/dataset/area-urbana/resource/47964772-09e5-4f6e-b9e3-3b829f475eec?inner_span=True).

We defined buffers of different sizes (50, 100, 200, and 500 meters) around each site and measured the built cover proportion within each buffer. Spearman rank correlations were used to check the relationship between built cover across all buffers. Since the correlations were high (Spearman $\rho > 0.7$), we focused on the 500-meter buffer in further analysis, as it best represents the area influencing ant habitat, resource distribution, and ecosystem dynamics (e.g., Cordonnier et al., 2019, 2020; Korányi et al., 2021). The built cover proportion within the 500-meter buffers represents a broad gradient of urbanization, ranging from 0 to 95%.

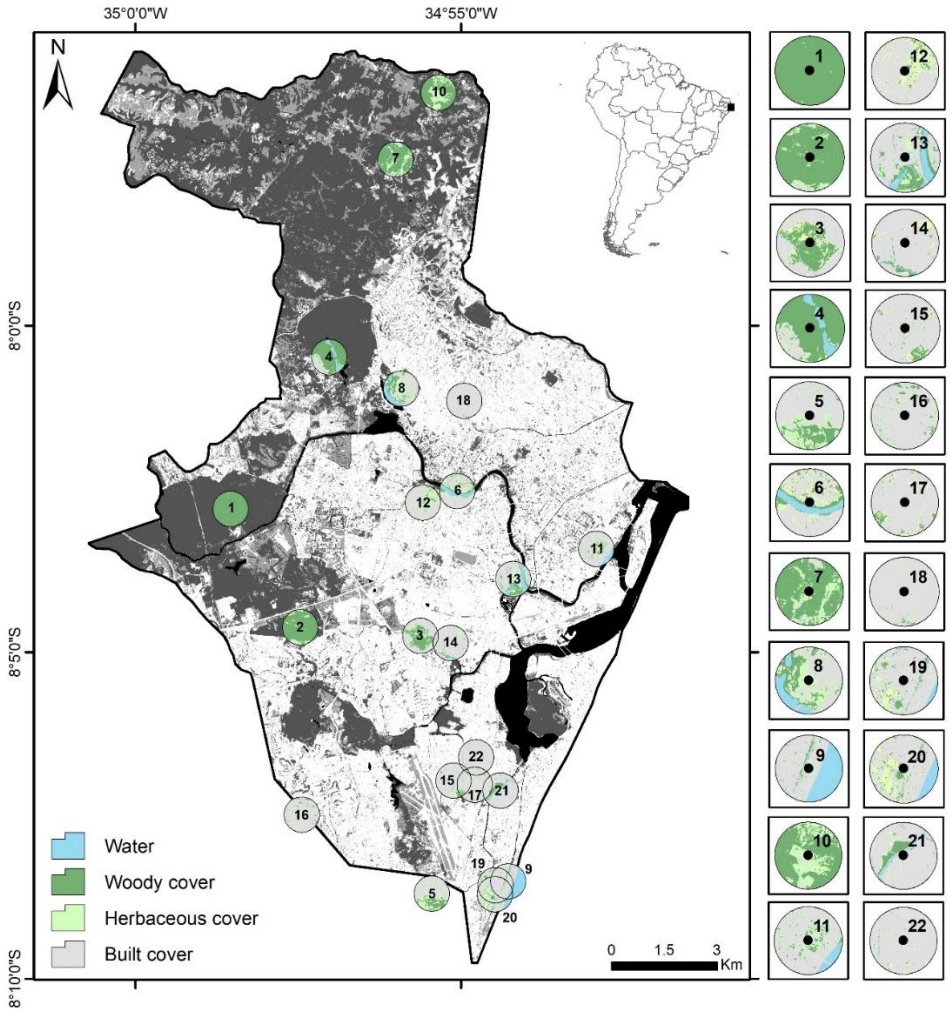


Figure 1. Land cover map of Recife (Pernambuco, Brazil) surrounded by its political boundary (black line) highlighting the sites were the study was developed and their surrounding 500m radius buffers.

Experimental procedure

We conducted seed dispersal experiments by ants at the 22 sites along the urbanization gradient (Fig. 1). Due to extensive anthropogenic management of vegetation in cities (gardens in squares, selection of plant types on sidewalks), we did not find a sufficient quantity of naturally occurring myrmecochorous seeds in the study region. Therefore, we used artificial seeds that exhibit characteristics similar to natural seeds for the seed removal experiments (Bieber et al. 2014; Fontenele & Schmidt, 2021). These artificial seeds were comprised by an orange bead (0.03

g, 2 mm diameter) involved by a hand-made pulp composed by vegetable fat (75%), fructose (4.8%), sucrose (0.5%), glucose (4.7%), casein (7%), calcium carbonate, and maltodextrin (5%) (Raimundo et al. 2004; Bieber et al. 2014; Rabello et al. 2014; Fontenele & Schmidt, 2021). At each sampling site, we placed 10 observation stations separated from each other by 10m to maintain independence (Leal et al. 2007). At each station, 20 artificial seeds were placed on a paper card, and the interaction of ants with the seeds was monitored and described within the period from 8 am to 12 pm. We recorded seed removals for 20 minutes at each sampling point and actively collected the ants that removed the seeds (Da Silva et al., 2020; Fontenele & Schmidt, 2021). During monitoring, we recorded the ant species identity and its behavior: (1) removal rate – i.e. the proportion of seeds that were removed by ants considering a removal event if the seed is moved > 5 cm outside the station, and (2) cleaned– in which case ants removed part of, or the whole, elaiosome. In the first case, the displacement distance of seed removal was measured as a proxy for dispersal quality. (Leal et al., 2007; Oliveira et al., 2019)

Statistical analysis

To investigate how urbanization intensity affects the quality of seed dispersal services provided by ants, we conducted generalized linear mixed models (GLMM), generalized linear models (GLM), permutational multivariate analysis of variance (PERMANOVA), and principal component analysis (PCA). We used GLMM to assess the influence of built cover on multiple aspects of ant-seed interactions (removal rate and cleaning), as well as on mean dispersal distances. We performed GLM to analyze the effects of built cover on the richness and total abundance (i.e., the sum of the relative frequency of all seed-dispersing ant species per site) of seed dispersers. For the number of interactions and species richness, we used a Poisson distribution; for seed removal rates, we used a binomial distribution (removal success vs. failure); for mean dispersal distances and abundance, we used a Gaussian distribution. All models were evaluated for overdispersion, and in cases where it was detected, a Poisson-lognormal model was employed (Harrison, 2014). We also performed a PERMANOVA using Bray-Curtis dissimilarity with 999 permutations to assess the impact of urban land cover on the species composition of the

seed-dispersing ant community. Additionally, PCA was used to visually represent changes in species composition along the urbanization gradient.

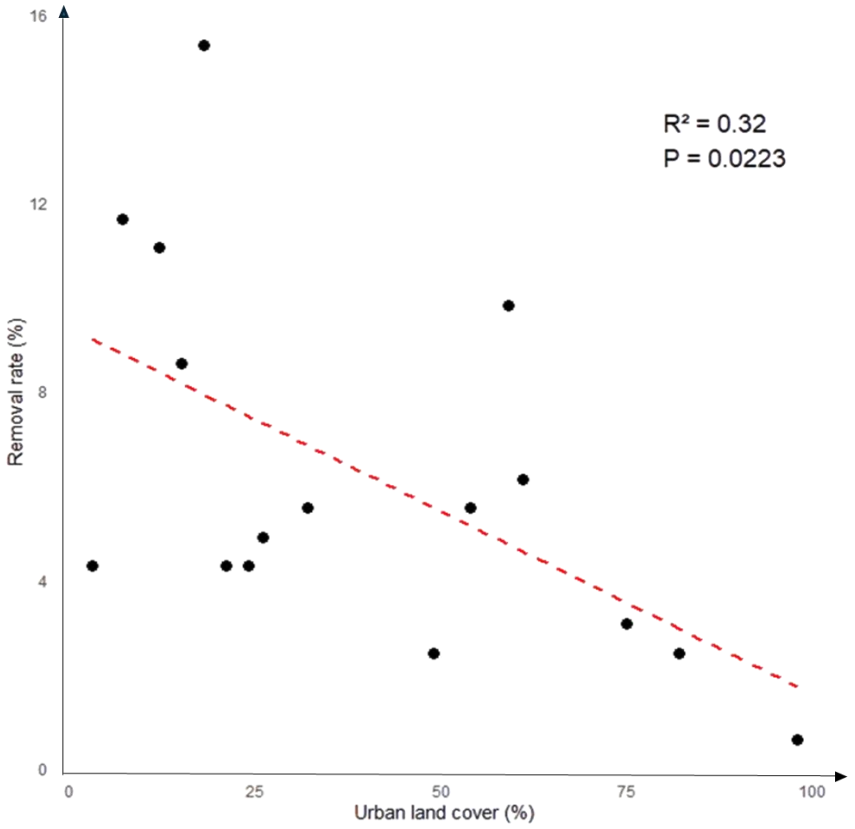
All analyses were performed in R (v. 4.1.3.; R Core Team, 2022). GLMM was conducted using the lme4 R package (v. 1.1-35.1; Bates et al., 2023), GLM was performed using the stats R package (v. 4.3.0; R Core Team, 2022), and the PERMANOVA and PCA analyses were conducted using the vegan (v. 2.6-2; Oksanen et al., 2022) and stats (v. 4.3.0; R Core Team, 2022) R packages.

Results

We recorded 443 ants from 29 different species and 5 subfamilies interacting with 2,705 artificial seeds (Table. S1). Of these, 312 seeds were removed (i.e. moved by ants for distances ≥ 5 cm), representing 26.4% of the total artificial seeds exposed to ants (Table. S1). The remaining 2,393 artificial seeds were cleaned (i.e., the elaiosome were without transporting the seeds), accounting for 73.6% of the total (Table. S1). Ant interactions with the seeds per area varied from 50 to 329 per area, maintaining a proportion pattern of 30% of seeds removed and 70% of seed cleaned (Table S1). The ants of the genus *Pheidole* (five species) were the most important group of ants interacting with seeds, accounting for 1,140 interactions, representing 47.6% of all interactions (Table S1). This genus removed most seeds (≈120), accounting for 35.8% of the removal events, as well as the most important seed cleaner, consuming the highest number of elaiosomes without removing the seeds in 1028 interactions (42.96%). Within this genus, *Pheidole radoszkowskii* was responsible for the highest number of seed removals (15.38%), and *Pheidole* sp. 3 for the highest number of seeds consumed (13.25%). *Camponotus* (four species) was the second most active genus, with 617 interactions, representing 25.8% of the overall number of interactions. Among these, 32 seeds were removed (10.20%) and 590 seeds were cleaned (24.66%). *Camponotus crassus* was the most representative species of this group, with the highest number of seeds removed (14) and cleaned (268), followed closely by *Camponotus bicolor* (7 and 233 seeds removed and cleaned, respectively). Notably, these species of *Camponotus* predominantly removed seeds in areas with medium levels of urbanization, between

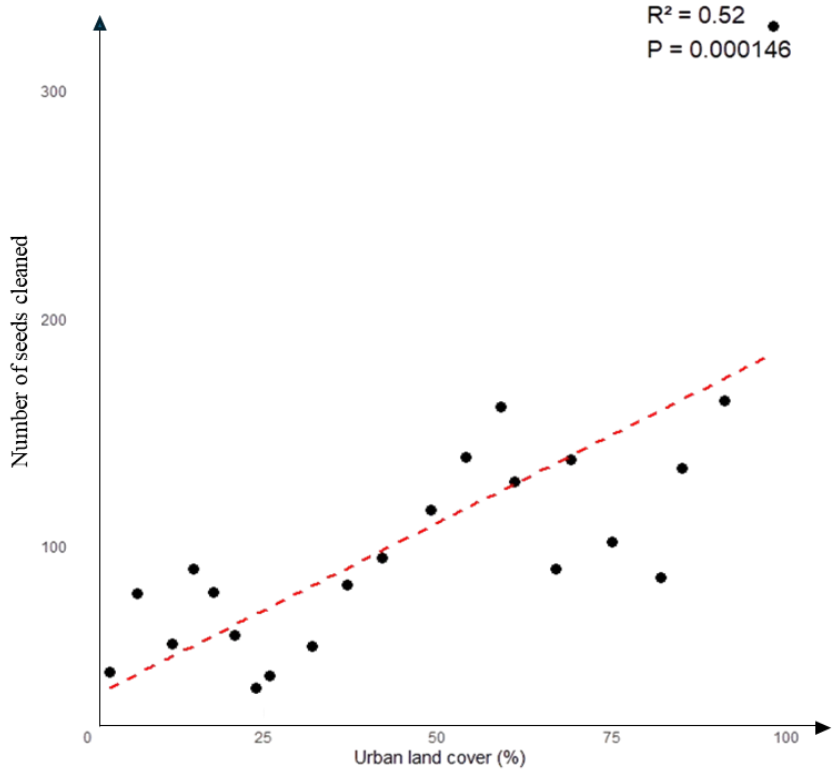
30% and 60%, while *Pheidole* removed throughout the entire urban gradient. The species that interacted with the seeds only in areas with a low percentage of urbanization (< 20% urbanized), such as *Ectatomma*, *Gnamptogenys*, *Neoponera*, and *Odontomachus*, were characterized as high-quality dispersers (Leal et al., 2014). *Odontomachus bauri* was the most representative species of this group, with the highest number of seeds removed (7.37%) and 2.72% of seeds consumed. Considering all 312 removed seed, removal distance varied from 10cm to 380cm (mean ± SD: 58,7 ± 88,9, Table S2). The genera presenting higher removal distance were *Pheidole*, *Camponotus*, and *Solenopsis* (mean≈88cm, 72.62cm, and 64.83cm respectively). *Pheidole* sp. 3 also recorded the greatest distance for seed removal, with a maximum of 380 cm, where the seed was lost among busy highways. For the species that removed seeds only in the less urbanized areas, the one that stood out with the greatest removal distance among these groups was *Neoponera* sp.1, with 190 cm.

The total number of interactions between ants and seeds showed a positive effect of urbanization (Estimate = 0.49, SE = 0.25, z-value = 2.01, p-value = 0.04, Table 1), suggesting that the frequency of these interactions tends to increase in urbanized areas. When we analyzed the number of seeds cleaned also showed a significant effect of urbanization (Estimate = 0.89, SE = 0.32, z-value = 2.8, p-value = 0.001, Table 1, Figure 2B), indicating that ants in more urbanized areas consume more seeds. However, the seed removal rate was negatively impacted by urbanization (Estimate = -0.64, SE = 0.2, z-value = -3.3, p-value = 0.02, Table 1, Figure 2A). The seed dispersal distance showed no significant effect of urbanization (Estimate = -2.86, SE = 3.48, z-value = -0.82, p-value = 0.41, Table 1), suggesting that urbanization does not directly influence this aspect of the seed dispersal ecosystem service.


R² = 0.32
P = 0.0223
Removal rate (%)
Urban land cover (%)
0
4
8
12
16
0
25
50
75
100

247

248


R² = 0.52
P = 0.000146
Number of seeds cleaned
Urban land cover (%)
0
100
200
300
0
25
50
75
100

249

Figure 2. Significant effects of urban land cover on (A) the removal rate and (B) number of seeds cleaned by ants in the Metropolitan Region of Recife, Northeastern Brazil. The red line indicates the fitted line of the model; black dots represent averages.

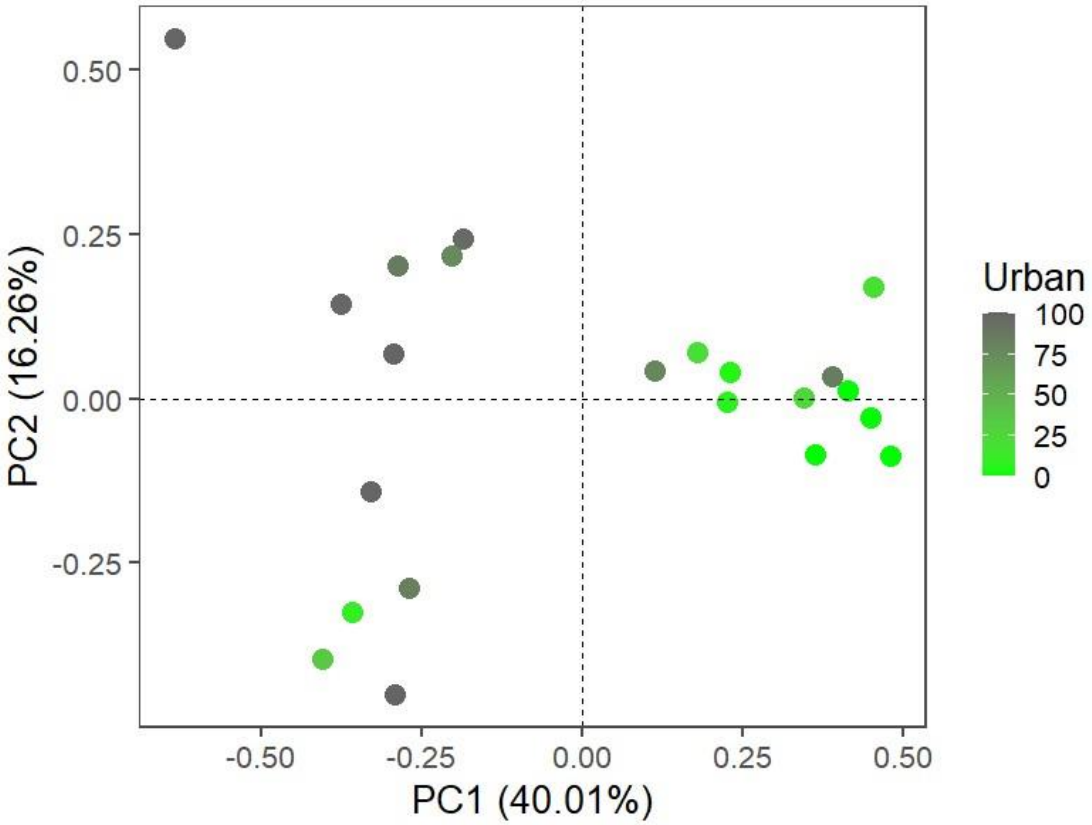


Figure 3. The principal component analysis (PCA; Axis 1 × Axis 2) of the seed-dispersing ant community in the Metropolitan Region of Recife, Northeastern Brazil. Points represent sites; the color gradient indicates the urban land cover percentage at each location, with greener points indicating lower proportion of urban cover and grayer points indicating higher urban cover.

Discussion

The results of this study show that the potential for seed dispersal by ants in urban ecosystems is significantly impacted by increasing urbanization, as seed removal rates decrease while seed cleaning increases. Furthermore, while species abundance and richness remain unchanged, the ant community composition is altered along the urbanization gradient. Low-

quality seed dispersers occur throughout the urbanization gradient, but there is a significant increasing in more urbanized areas. On the other hand, although the removal distance is not altered by urbanization, high-quality disperser ants were recorded interacting with seeds only in less urbanized environments. This result supports our hypothesis that increased urbanization compromises the quality of seed dispersal services due to changes in the ant disperser community structure. Therefore, urbanization, by altering the composition and functionality of the ant disperser community, impairs the maintenance of essential ecological processes for plant regeneration and the resilience of urban ecosystems.

Our findings align with previous research showing that anthropogenic activities negatively impact ant-mediated seed dispersal, reducing both removal rates and dispersal distances (Almeida et al., 2013; Leal et al., 2014a; Rocha-Ortega et al., 2017). In the broader context of anthropogenic disturbances, prior studies indicate that removals over distances greater than two meters are drastically reduced in highly disturbed environments, suggesting a significant loss in dispersal efficiency (Leal et al., 2014a; Queiroz et al., 2021; Fontenele & Schmidt, 2021). Ant genera considered high quality seed disperser in this study (i.e. *Ectatomma*, *Gnamptogenys*, *Neoponera*, and *Odontomachus*) were previously described as providing long distance dispersal events (Leal et al. 2007 and 2017A; Leal et al. 2014A and 2014B, Oliveira et al. 2022). The same pattern was observed for low quality seed dispersers, with *Pheidole* and *Camponotus* commonly observed in previous studies just cleaning the seeds locally without removal, also recorded in Recife (Leal et al. 2007 and 2017A; Leal et al. 2014A and 2014B; Queiroz et al., 2021; Oliveira et al. 2022).

Changes in the quality of seed dispersal services provided by ants are generally related to shifts in the composition of ant disperser species (Oliveira et al., 2019). Ants characterized by their large body size, predatory behavior, and specialized tendencies, are recognized as high-quality seed dispersers because of their ability to achieve higher seed removal rates and distances (Andersen & Morrison, 2006; Ness et al., 2004; Leal et al., 2014b, 2017; Oliveira et al., 2019). These large-bodied and specialized ant species are especially sensitive to disturbances (Gibb et al., 2018; Leal, Andersen, & Leal, 2014), which may result in severe reductions in seed dispersal

293 quality in disturbed habitats (Almeida et al., 2013; Gove, Majer, & Dunn, 2007; Leal, Andersen,
294 & Leal, 2014; Ness, Bronstein, Andersen, & Holland, 2004). On the other hand, generalist
295 species, such as those from the genera *Pheidole* and *Camponotus*, were present along the whole
296 urbanization gradient, but were abundant in more urbanized areas. These species are considered
297 low-quality dispersers, meaning they consume elaiosomes in situ without moving seeds or move
298 them only short distances (Anderson & Morrison, 1998; Leal et al. 2014A, 201B: Oliveira et al.
299 2020). This is consistent with the idea that human disturbances in general leads to a winner-loser
300 replacement (see Filgueiras et al. 2021), i.e. few generalist and disturbance-adapted species
301 proliferate while several specialist and disturbance sensitive species are lost (see also McKinney,
302 2008; Arnan et al., 2018). This same pattern was described in the first chapter of this thesis when
303 evaluating the whole ant community occurring across the urbanization gradient.

304 The favoring of generalist species over specialists as urbanization intensity increases
305 implicate in alteration in the type of services ants provide in urban ecosystems, reducing seed
306 dispersal and increasing the seed cleaning. But the simple consumption and removal of the
307 elaiosome by ants can directly benefit seed germination (Leal et al. 1998, 2007). By cleaning the
308 elaiosome, ants may inject saliva and perform scarifications that enhance the germination process
309 (Hughes & Westoby, 1992). The high degree of elaiosome cleaning observed in urban
310 environments, where nutritional resources tend to be scarcer, suggests that ants find an important
311 nutritional alternative in these areas, benefiting from this resource. Elaiosomes are calorie-dense
312 sources of proteins and fats, serving as a vital food source for ants, especially in environments
313 with limited access to other resources (Karnish, 2024). Although seed cleaning is often considered
314 an opportunistic interaction between ants and seeds (Bronstein 2001), it can also be viewed as a
315 form of mutualism. In this process, ants remove the elaiosome from the seeds, providing
316 themselves with an energy-rich food source, while simultaneously benefiting the plants by
317 enhancing seed dispersal and reducing predation. This mutualistic relationship, in which both
318 parties benefit from interaction, highlights the intricate ecological balance that persists even in
319 urban ecosystems.

In anthropogenic environments, where the presence of vertebrates is limited, ants can become key dispersers, favoring the persistence of certain plant species (Leal et al., 2014). Although most studies on ant-mediated seed dispersal focus on the negative impacts of generalist species, especially those acting as low-quality dispersers, it is crucial to expand the perspective and consider the various roles these ants can offer, particularly in more urbanized and disturbed environments. For example, *Pheidole*, although considered low-quality seed dispersers, seed predators, and "cheating" ants that hinder seed recruitment from higher-quality dispersers (Bronstein, 2001; Vasconcelos et al., 2018; Leal et al., 2014b; Ewers et al., 2015), was the genus recorded in this study as having removed the most seeds and covered the greatest removal distances. This behavior can be viewed as a significant aspect of this category, as these ants are often more abundant in disturbed habitats, where opportunities for other, more specialized species are limited. Therefore, understanding the multiple dimensions of the interaction between ants and seeds can provide a more comprehensive view of the services these organisms can provide.

Our study significantly contributes to understanding ant-seed interactions along an urban gradient, particularly given the lack of research that directly addresses urbanization as a disturbance and its impact on ecosystem services. Our findings revealed a decline in the quality of seed dispersal services provided by ants in more urbanized areas, along with an increase in seed cleaning. By focusing on the importance of maintaining these ecosystem services, particularly in an increasingly urbanized context, our study emphasizes the urgent need to adopt urban management strategies that favor biodiversity and promote the preservation of fundamental ecological interactions. Creating small, high-quality semi-urban fragments connected by green corridors can promote the dispersal and colonization of both flora and fauna (Sadler et al., 2010). Additionally, these spaces can foster the coexistence of specialist and generalist species, ensuring the maintenance of ecological interactions and associated ecosystem services, such as seed dispersal (Schwarz et al., 2017). These strategies may help to maintain or enhance seed dispersal services in cities, contributing to ecological resilience and long-term urban sustainability.

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

ILHS: Conceptualization (equal); data curation (lead); investigation (lead); methodology (equal); writing – original draft (equal); writing – review and editing (equal). DC-A: Conceptualization (equal); formal analysis (lead); methodology (equal); visualization (lead); writing – original draft (equal); writing – review and editing (equal). JCP: Conceptualization (equal); data curation (supporting); methodology (equal); writing – review and editing (equal). XA: Conceptualization (equal); methodology (equal); supervision (supporting); validation (supporting); writing – review and editing (equal). IRL: Conceptualization (equal); funding acquisition (lead); methodology (equal); supervision (lead); validation (lead); writing – review and editing (equal).

References

375 Arnan, X., Molowny-Horas, R., Rodrigo, A., & Retana, J. (2018). Ant functional responses along
376 environmental gradients: when the habitat tempts the ants. Journal of Insect Conservation, 22(3),
377 457-471.
378 Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M. et al. (2017). "Multiple successional
379 pathways in human-modified tropical landscapes: new insights from forest succession, forest
380 fragmentation and landscape ecology research". Biol Rev Camb Philos Soc, 92(1): 326-340.
381 Bates, Douglas, et al. "Models Using lme4." (2023): 10-01.
382 Bohm, M., Obergfell, D., & Vanbergen, A. J. (2018). The interplay between urbanization, host
383 plant phenology, and ant-mediated seed dispersal. Urban Ecosystems, 21(4), 759-769.
384 da Silva, G. S., Rabelo, M. A., de Oliveira Canedo-Júnior, E., & Ribas, C. R. (2020). Formigas
385 removedoras de sementes apresentam potencial para auxiliar na regeneração de áreas impactadas.
386 Revista Cientifica MG. Biota, 12(2), 44-54.
387 Dáttilo, Wesley, and Ian MacGregor-Fors. (2021) "Ant social foraging strategies along a
388 Neotropical gradient of urbanization." Scientific Reports 11.1: 6119.
389 Davidson, D. W. (1977). Foraging ecology and community organization in desert seed-eating
390 ants. Ecology, 58(4), 725-737.
391 Díaz-Castelazo, C., Ramírez-Amezcua, M., Rico-Gray, V., & Dáttilo, W. (2021). Seed dispersal
392 by ants in disturbed and undisturbed environments. Ecology and Evolution, 11(7), 3344-3353.
393 Diehl-Fleig, E. (2006). Formigas invasoras: O caso da formiga argentina Linepithema humile
394 (Mayr 1868). Acta Biológica Leopondensia, 28(1), 5-9.
395 Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P. J., McDonald, R. I., ... &
396 Wilkinson, C. (2013). Urbanization, biodiversity and ecosystem services: challenges and
397 opportunities: a global assessment (p. 755). Springer Nature.
398 Fontenele, L. K., & Schmidt, F. A. (2021). Forest-pasture shifting alters the assemblages of seed-
399 removing ants in southwestern Brazilian Amazon. Journal of Insect Conservation, 25(2), 213-
400 220.
401 Fresneau, D., & Dupuy, P. (1988). A study of polyethism in a ponerine ant: Neoponera apicalis
402 (Hymenoptera, Formicidae). Animal Behaviour, 36(5), 1389-1399.

Gómez, C., Ribbons, R. R., & Hölldobler, B. (2020). The role of ants in urban ecosystems. Journal of Urban Ecology, 6(1), 1-12.

Hansen, D. M., & Müller, C. B. (2017). Seed dispersal: its importance in flora and fauna communities structure and dynamics. Ecology Letters, 20*(5), 605-621.

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. PeerJ, 2, e616.

IBGE (2021): Instituto Brasileiro de Geografia e Estatística. "Censo Demográfico 2021." https://censo.ibge.gov.br/.

Leal, I. R., Wirth, R., & Tabarelli, M. (2007). Conservation of Brazil's northeastern Atlantic Forest. Conservation Biology, 21(4), 1041-1050.

Majer, J. D., Kitching, R. L., Heterick, B. E., Hurley, K., & Brennan, K. E. C. (2001). North—South Patterns within Arboreal Ant Assemblages from Rain Forests in Eastern Australia 1. Biotropica, 33(4), 643-661.

McIntosh, C. R., Díaz-Castelazo, C., Bustamante-Marin, A., & Rico-Gray, V. (2021). Urban ants: linking biodiversity and ecosystem services in cities. Frontiers in Ecology and Evolution, 9(45), 1-15.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. Biological Conservation, 127(3), 247-260.

McLean, P., Gallien, L., Wilson, J. R., Gaertner, M., & Richardson, D. M. (2017). Small urban centres as launching sites for plant invasions in natural areas: insights from South Africa. Biological invasions, 19(12), 3541-3555.

Melo, T. S., de Azevedo Koch, E. B., Rodrigues Santos de Andrade, A., Caitano, B., Lima Peres, M. C., Domingos Brescovit, A., & Hubert Charles Delabie, J. (2024). Ants (Hymenoptera: Formicidae) and spiders (Arachnida: Araneae) in different urban green areas: an analysis of their taxonomic and functional diversity. Studies on Neotropical Fauna and Environment, 59(3), 898-919.

Morales, C.L., Aizen, M.A. (2018). "Invasive mutualisms and the structure of plant–pollinator interactions in the temperate forests of north-west Patagonia, Argentina". J Ecol, 106(2): 1012-1024.

Lattke, J. E. (1995). Revision of the ant genus Gnamptogenys in the New World (Hymenoptera: Formicidae). Journal of Hymenoptera Research, 4(4), 137-193.

Leal, L.C., Tabarelli, M., Silva, J.M.C. et al. (2020). "Land-use-driven changes in forest communities promote the phylogenetic homogenization of neotropical palm assemblages". Perspect Plant Ecol Evol Syst, 43: 125-132.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... & Wagner, H. (2022). vegan: Community Ecology Package. R package version 2.5-7. 2020. Preprint at, 3-1./

Planet Labs PBC (2021): Planet Labs Public Benefit Corporation. https://www.planet.com/.

Rabello, A. M., de Oliveira Bernardi, L. F., & Ribas, C. R. (2014). Testing an artificial aril as a new ant-attractant. Revista Biociências, 20(1).

Raimundo, R. L., Gibert, J. P., Hembry, D. H., & Guimaraes Jr, P. R. (2014). Conflicting selection in the course of adaptive diversification: the interplay between mutualism and intraspecific competition. The American Naturalist, 183(3), 363-375.

R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rajesh, T. P., Ballullaya, U. P., Unni, A. P., Parvathy, S., & Sinu, P. A. (2020). Interactive effects of urbanization and year on invasive and native ant diversity of sacred groves of South India. Urban Ecosystems, 23(6), 1335-1348.

Ronque, M. U., Fourcassié, V., & Oliveira, P. S. (2018). Ecology and field biology of two dominant Camponotus ants (Hymenoptera: Formicidae) in the Brazilian savannah. Journal of natural history, 52(3-4), 237-252.

Sadler, J., Bates, A., Hale, J., & James, P. (2010). Dando vida às cidades: a importância dos espaços verdes urbanos para as pessoas e a biodiversidade. Ecologia urbana, 230-260.

456 Schwarz, N., Moretti, M., Bugalho, M. N., Davies, Z. G., Haase, D., Hack, J., ... & Knapp, S.
457 (2017). Understanding biodiversity-ecosystem service relationships in urban areas: A
458 comprehensive literature review. Ecosystem services, 27, 161-171.
459 Traveset, A., Nogales, M. (2017). "Ecological and societal impacts of introduced species: acacia
460 mearnsii in South Africa as a case study". In: Simberloff, D., Rejmánek, M. (eds). Encyclopedia
461 of Biological Invasions. Berkeley: University of California Press, pp. 489-496.
462 Wilson, E. O. (2003). Pheidole in the New World: a dominant, hyperdiverse ant genus (Vol. 1).
463 Harvard University Press

Table 1. Effects of built cover on the quality of the ant-mediated seed dispersal service in the Metropolitan Region of Recife, northeastern Brazil. Significant p-values are in bold; SE: Standard error.

Element	Variables	Estimate	SE	*z*-value	*p*-value
Number of interactions (Total)	Intercept	1.22	0.16	7.43	1.08×10^{-13}
	Built cover	0.49	0.25	2.01	**0.04**
Number of seeds cleaned	Intercept	0.53	0.22	2.40	0.02
	Built cover	0.89	0.32	2.8	**0.001**
Removal rate	Intercept	-3.6	0.26	-13.85	2×10^{-16}
	Built cover	-0.64	0.2	-3.3	**0.02**
Dispersal distance	Intercept	8.34	2.28	3.67	0.0003
	Built cover	-2.86	3.48	-0.82	0.41
Richness	Intercept	2.43	0.1	24.19	2×10^{-16}
	Built cover	-0.2	0.16	-1.22	0.22
Abundance	Intercept	1.89	0.19	9.84	4.13×10^{-9}
	Built cover	0.14	0.29	0.48	0.64

Table 2. Results of PERMANOVA analysis of the effects of built cover on the seed-dispersing ant community composition of the Metropolitan Region of Recife, northeastern Brazil. Significant values are in bold; DF: degrees of freedom; SS: Sum of squares.

Variables	DF	SS	R^2	F	*p*-value
Built cover	1	1.3	0.27	7.31	**0.001**
Residual	20	3.55	0.73		
Total	21	4.84	1		

SUPPLEMENTARY MATERIAL

Urbanization intensity reduces the quality of seed dispersal service provided by ants in a metropolitan region in Northeast Brazil

Isabelle Leite de Holanda Silva[1], Diego Centeno-Alvarado[2], João Carlos Pena[3], Xavier Arnan[2,4], Inara Roberta Leal[1,5]*

[1]Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[2]Curso de Bacharelado em Ciências Biológicas, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

[3]Laboratório de Ecologia Espacial e Conservação, Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista Julio de Mesquita Filho, Rio Claro, Brazil

[4]Universidade de Pernambuco, Garanhuns, Pernambuco, Brazil

[5]Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, Brazil

*__Corresponding author__: inara.leal@ufpe.br

Table S1. The table presents the interactions of ants with seeds in areas with different percentages of urban cover. The columns "Seeds consumed" and "Seeds removed" show the amount of seeds consumed or removed by different ant species in areas with urban cover ranging from 3% to 98% along the urbanization gradient in the city of Recife, PE

Urban land cover	Species ant	Seeds consumed	Seeds removed
3%	*Camponotus atriceps*	5	0
	Crematogaster sp.1	7	0
	Ectatomma muticum	5	0
	Gnaptogenys sp.1	1	3
	Neoponera sp.1	2	3
	Odontomachus baurii	5	0
	Pheidole radoszkowiskii	7	8
	Pheidole sp.3	11	2
	Pseudomyrmex gracilis	2	1
	Pseudomyrmex sp.2	5	0
	Solenopsis sp.1	0	4
7%	*Solenopsis sp.1*	0	2
	Pseudomyrmex gracilis	8	0
	Crematogaster sp.1	3	5
	Gnaptogenys sp.1	5	5
	Ectatomma muticum	5	0
	Camponotus atriceps	0	6
	Neoponera sp.1	4	6
	Pheidole radoszkowiskii	5	8
	Camponotus crassus	5	0
	Pseudomyrmex sp.2	5	0
12%	*Camponotus crassus*	1	1
	Cephalotes atratus	3	0

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Crematogaster brasiliensis	5	0
	Crematogaster sp.1	6	0
	Ectatomma muticum	5	0
	Neoponera sp.1	3	6
	Odontomachus baurii	0	2
	Pheidole	0	5
	Pheidole radoszkowiskii	8	0
	Pheidole sp.3	10	8
	Pseudomyrmex gracilis	1	0
	Pseudomyrmex sp.2	4	0
	Solenopsis sp.2	6	4
	Solenopsis sp.4	0	4
15%	*Crematogaster sp.1*	6	2
	Odontomachus baurii	10	2
	Odontomachus sp.2	0	3
	Pheidole	9	0
	Pheidole radoszkowiskii	3	0
	Pheidole sp.3	47	5
	Pheidole sp.4	6	0
	Pseudomyrmex gracilis	4	0
	Solenopsis sp.3	2	5
	Solenopsis trisden	9	5
18%	*Cephalotes atratus*	2	0
	Crematogaster brasiliensis	0	17
	Dorymyrmex thoracicus	13	0
	Ectatomma muticum	6	0
	Ectatomma sp.1	4	3

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Gnaptogenys sp.1	3	3
	Neoponera sp.1	0	2
	Odontomachus baurii	8	3
	Odontomachus sp.2	0	4
	Pheidole radoszkowiskii	8	0
	Pheidole sp.3	20	0
	Pseudomyrmex gracilis	2	0
	Solenopsis sp.2	18	0
21%	*Camponotus atriceps*	3	0
	Camponotus crassus	4	1
	Crematogaster	4	0
	Crematogaster sp.1	4	0
	Dorymyrmex thoracicus	5	0
	Ectatomma sp.1	8	8
	Odontomachus baurii	7	2
	Pheidole radoszkowiskii	9	2
	Pheidole sp.3	18	5
	Pheidole sp.4	9	2
	Solenopsis sp.1	8	2
	Solenopsis sp.2	0	5
24%	*Camponotus bicolor*	6	0
	Camponotus crassus	5	0
	Crematogaster sp.1	7	4
	Dorymyrmex thoracicus	0	2
	Ectatomma muticum	0	1
	Odontomachus baurii	8	0
	Pheidole radoszkowiskii	7	1

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Pheidole sp.3	0	4
	Solenopsis sp.3	5	0
26%	*Camponotus crassus*	6	0
	Crematogaster sp.1	3	4
	Dorymyrmex thotacicus	5	0
	Gnaptogenys sp.1	3	1
	Odontomachus baurii	8	4
	Pheidole radoszkowiskii	0	2
	Pheidole sp.2	0	2
	Pheidole sp.3	3	2
	Solenopsis sp.1	6	3
	Solenopsis trisden	8	0
	Wasmannia auropunctata	0	10
32%	*Camponotus bicolor*	10	0
	Camponotus crassus	5	0
	Ectatomma muticum	5	0
	Odontomachus baurii	5	0
	Pheidole radoszkowiskii	6	6
	Pheidole sp.3	10	3
	Pheidole sp.4	4	0
	Pseudomyrmex gracilis	2	0
	Solenopsis sp.3	5	0
	Wasmannia auropunctata	3	0
37%	*Atta sexdens*	2	0
	Camponotus bicolor	5	0
	Crematogaster sp.1	6	0
	Odontomachus baurii	6	3

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Pheidole sp.3	45	0
	Solenopsis trisden	1	3
	Wasmannia auropunctata	5	2
42%	*Camponotus bicolor*	10	0
	Crematogaster sp.1	9	0
	Pheidole radoszkowiskii	17	5
	Pheidole sp.3	52	0
	Wasmannia auropunctata	12	0
49%	*Camponotus atriceps*	2	0
	Camponotus bicolor	4	0
	Camponotus crassus	16	3
	Crematogaster brasiliensis	16	3
	Pheidole radoszkowiskii	18	0
	Pheidole sp.3	13	0
	Pheidole sp.4	17	6
	Solenopsis sp.3	24	0
	Solenopsis sp.4	2	1
	Solenopsis trisden	4	0
	Wasmannia auropunctata	5	0
54%	*Camponotus atriceps*	19	0
	Camponotus bicolor	15	0
	Camponotus crassus	26	5
	Crematogaster brasiliensis	9	0
	Crematogaster sp.1	2	0
	Pheidole radoszkowiskii	20	3
	Pheidole sp.3	2	0
	Pheidole sp.4	28	0

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Solenopsis sp.3	14	9
	Solenopsis sp.4	12	0
	Wasmannia auropunctata	5	0
59%	*Camponotus atriceps*	7	0
	Camponotus bicolor	15	0
	Camponotus crassus	21	5
	Crematogaster sp.1	16	0
	Dorymyrmex thoracicus	7	0
	Pheidole radoszkowiskii	37	4
	Pheidole sp.3	17	0
	Pheidole sp.4	1	7
	Solenopsis sp.3	24	0
	Solenopsis sp.4	8	0
	Solenopsis trisden	0	2
61%	*Atta sexdens*	8	0
	Camponotus atriceps	9	0
	Camponotus bicolor	1	5
	Camponotus crassus	7	0
	Crematogaster sp.1	21	0
	Pheidole radoszkowiskii	35	5
	Pheidole sp.3	5	0
	Pheidole sp.4	31	0
	Solenopsis sp.3	9	0
	Solenopsis sp.4	2	0
67%	*Atta sexdens*	9	0
	Camponotus bicolor	8	0
	Camponotus crassus	14	0

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Crematogaster sp.1	4	0
	Pheidole radoszkowiskii	18	0
	Pheidole sp.4	14	0
	Solenopsis sp.2	9	0
	Solenopsis sp.3	9	0
	Solenopsis sp.4	5	0
69%	*Camponotus bicolor*	54	0
	Camponotus crassus	21	0
	Pheidole radoszkowiskii	19	0
	Pheidole sp.4	17	0
	Solenopsis sp.3	5	0
	Solenopsis sp.4	19	0
	Wasmannia auropunctata	3	0
75%	*Atta sexdens*	5	0
	Camponotus bicolor	12	0
	Camponotus crassus	11	0
	Camponotus sp.3	5	5
	Crematogaster brasiliensis	4	0
	Pheidole radoszkowiskii	4	0
	Pheidole sp.4	24	0
	Pheidole sp.5	13	0
	Solenopsis sp.4	12	0
	Solenopsis trisden	3	0
	Wasmannia auropunctata	9	0
82%	*Camponotus bicolor*	8	0
	Camponotus crassus	24	0
	Pheidole radoszkowiskii	4	4

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Pheidole sp.4	17	0
	Pheidole sp.5	17	0
	Solenopsis sp.3	9	0
	Solenopsis sp.4	7	0
85%	*Camponotus bicolor*	8	0
	Camponotus crassus	31	0
	Camponotus sp.3	5	0
	Pheidole radoszkowiskii	25	0
	Pheidole sp.4	18	0
	Pheidole sp.5	29	0
	Solenopsis sp.3	18	0
91%	*Camponotus bicolor*	8	0
	Camponotus crassus	32	0
	Camponotus sp.3	28	0
	Crematogaster sp.1	4	0
	Pheidole radoszkowiskii	7	0
	Pheidole sp.4	14	0
	Pheidole sp.5	39	0
	Solenopsis sp.3	15	0
	Solenopsis sp.4	9	0
	Wasmannia auropunctata	8	0
98%	*Camponotus bicolor*	69	1
	Camponotus crassus	40	0
	Crematogaster sp.1	5	0
	Pheidole radoszkowiskii	14	0
	Pheidole sp.4	68	0
	Pheidole sp.5	55	0

Urban land cover	Species ant	Seeds consumed	Seeds removed
	Solenopsis sp.3	14	0
	Solenopsis trisden	31	0
	Wasmannia auropunctata	32	0

Table S2. Maximum distances (in cm) traveled by ants when removing seeds from the station. The values represent the greatest distance recorded for each ant species during the seed remove rate process.

Urban land cover	Ants	Distance max (cm)
	Pheidole radoszkowiskii	12
	Pheidole sp.3	39
	Pseudomyrmex gracilis	190
3%	*Solenopsis sp.1*	23
	Crematogaster sp.1	10
	Pheidole sp.3	79
	Camponotus atriceps	207
7%	*Gnaptogenys sp.1*	69
	Pheidole radoszkowiskii	88
	Solenopsis sp.3	85
	Pheidole sp.3	99
	Camponotus crassus	80
12%	*Neoponera sp.1*	190
	Solenopsis trisden	79
	Pheidole sp.3	81
	Odontomachus baurii	50
15%	*Crematogaster sp.1*	19
	Crematogaster brasiliensis	109
	Odontomachus sp.2	99
	Crematogaster sp.2	19
18%	*Odontomachus baurii*	22
	Solenopsis sp.2	39
	Camponotus crassus	44
21%	*Ectatomma sp.1*	43
	Pheidole sp.3	47
	Dorymyrmex thoracicus	100
	Pheidole sp.3	28
24%	*Ectatomma muticum*	20
	Pheidole radoszkowiskii	22
26%	*Pheidole sp.4*	29

	Wasmannia auropunctata	29
	Pheidole radoszkowiskii	54
32%	*Pheidole sp.3*	380
	Camponotus crassus	60
49%	*Solenopsis sp.4*	90
54%	*Solenopsis sp.3*	73
	Pheidole radoszkowiskii	100
	Pheidole sp.4	48
59%	*Camponotus crassus*	31
	Camponotus bicolor	30
61%	*Pheidole radoszkowiskii*	69
75%	*Camponotus sp.3*	101
82%	*Pheidole radoszkowiskii*	329
98%	*Camponotus bicolor*	28

Table S3. Ant species that interacted with seeds during the seed removal rate in the most and least urbanized areas of the urbanization gradient. Also presents the functional group classification of each species, along with their categorization as specialists or generalists, according to the author's Leal et al. (2012) and Filgueiras et al. (2019).

Urban land cover category	Ant genus	Functional group	Generalist/Specialist
Interacting with seeds in:			
Less urbanized areas (<30%)	*Camponotus*	Arboreal subordinate	Specialist
	Cephalotes	Arboreal subordinate	Specialist
	Crematogaster	Arboreal subordinate	Specialist
	Dorymyrmex	Opportunist	Generalist
	Ectatomma	Opportunist	Generalist
	Gnaptogenys	Epigaeic omnivore	Generalist
	Neoponera	Epigaeic predator	Specialist
	Odontomachus	Epigaeic predator	Specialist
	Pheidole	Epigaeic omnivore	Generalist
	Pseudomyrmex	Arboreal subordinate	Specialist
	Solenopsis	Cryptic omnivore	Specialist
More urbanized areas (>50%)	*Atta*	Leaf-cutting Attini	Generalist
	Camponotus	Arboreal subordinate	Specialist
	Crematogaster	Arboreal subordinate	Specialist
	Pheidole	Epigaeic omnivore	Generalist

Urban land cover category	Ant genus	Functional group	Generalist/Specialist
	Solenopsis	Cryptic omnivore	Specialist
	Wasmannia	Epigaeic omnivore	Generalist

3 CONSIDERAÇÕES FINAIS

Nossos resultados representam uma contribuição significativa para a compreensão dos efeitos da urbanização nas comunidades de formigas e nos serviços ecossistêmicos prestados por esses organismos, com foco na dispersão de sementes (Capítulo 3). Observamos que, embora a riqueza e abundância das formigas se mantenham constantes ao longo do gradiente de urbanização (Capítulo 1), a composição das comunidades de formigas se altera consideravelmente com o aumento da urbanização, favorecendo espécies generalistas em detrimento de espécies especialistas. Isso sugere que a urbanização pode impactar as interações ecológicas essenciais e modificar o papel das formigas nos ecossistemas urbanos. Além disso, os resultados do Capítulo 2 indicaram que a urbanização não influenciou diretamente a tolerância térmica máxima das formigas, mas que algumas alterações morfológicas, como a redução do tamanho das mandíbulas e pernas de Atta sexdens, ocorreram em áreas mais urbanizadas. Esses resultados apontam para a plasticidade das formigas frente às modificações no ambiente urbano.

Quanto à dispersão de sementes, os achados do Capítulo 3 demonstraram uma redução na taxa de remoção de sementes com o aumento da urbanização, sugerindo que a qualidade desse serviço ecossistêmico diminui à medida que o nível de urbanização se intensifica. As formigas de áreas urbanizadas, como Pheidole, Camponotus e Solenopsis, foram classificadas como dispersores de baixa qualidade, removendo as sementes a distâncias menores e realizando uma limpeza das sementes sem efetivamente removê-las. Em contrapartida, espécies de áreas menos urbanizadas, como Odontomachus bauri, mostraram ser dispersores mais eficientes, removendo sementes a distâncias maiores e contribuindo de forma mais eficaz para a regeneração vegetal. Esses resultados indicam que a urbanização pode afetar diretamente os processos ecológicos essenciais, como a regeneração da vegetação, ao alterar as comunidades de formigas e a eficiência da dispersão de sementes.

Essas descobertas são de relevância significativa, pois evidenciam como a urbanização pode impactar não apenas a composição das comunidades de formigas, mas também a qualidade dos serviços ecológicos que elas prestam, como a dispersão de sementes. A substituição de formigas especialistas por generalistas e a diminuição da eficiência na remoção de sementes sugerem que a regeneração da vegetação nas

áreas mais urbanizadas pode ser comprometida. Esse cenário é especialmente importante considerando o crescente ritmo de urbanização e a necessidade de estratégias de conservação que integrem a preservação da biodiversidade e dos serviços ecossistêmicos nas cidades.

Para uma compreensão mais aprofundada dos impactos da urbanização na biodiversidade e nos serviços ecossistêmicos, seria importante realizar estudos adicionais que investiguem os efeitos da urbanização sobre diferentes aspectos do comportamento das formigas, como a sua atividade de forrageamento e as interações com outras espécies. Além disso, estudos mais detalhados sobre as comunidades de formigas em áreas verdes urbanas e a quantificação dos impactos da redução da dispersão de sementes podem fornecer informações cruciais para o desenvolvimento de estratégias de manejo e conservação em ambientes urbanos, visando a promoção da sustentabilidade e o equilíbrio ecológico nas cidades.

REFERÊNCIAS

Ahrné, K., Bengtsson, J., & Elmqvist, T. (2009). Bumble bees (Bombus spp) along a gradient of increasing urbanization. PloS one, 4(5), e5574.

Alberti, M., Correa, C., Marzluff, J. M., Hendry, A. P., Palkovacs, E. P., Gotanda, K. M., ... & Zhou, Y. (2017). Global urban signatures of phenotypic change in animal and plant populations. Proceedings of the National Academy of Sciences, 114(34), 8951-8956.

Almeida, W. R., Vieira, A. S., Arruda, R. O., & Izzo, T. J. (2013). Seed dispersal by ants in Neotropical savannas: Are seed traits more important than ant traits? Journal of Tropical Ecology, 29(6), 537-543.

Alonso, L. E., & Agosti, D. (2000). Biodiversity studies, monitoring, and ants: An overview.

Andersen, A. N. (1988). Dispersal distance as a benefit of myrmecochory. Oecologia, 75, 507-511.

Andersen, A. N. (1997). Using ants as bioindicators: multiscale issues in ant community ecology. Conservation ecology, 1(1).

Andersen, A. N. (2019). Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. Journal of Animal Ecology, 88(3), 350-362.

Andersen, A. N., & Morrison, S. C. (1998). Myrmecochory in Australia's seasonal tropics: effects of disturbance on distance dispersal. Australian Journal of Ecology, 23(5), 483-491.

Andersen, A. N., Fisher, A., Hoffmann, B. D., Read, J. L., & Richards, R. (2004). Use of terrestrial invertebrates for biodiversity monitoring in Australian rangelands, with particular reference to ants. Austral ecology, 29(1), 87-92.

Andersen, A. N., Parr, C. L., Lowe, L. M., & Müller, W. J. (2007). Contrasting fire-related resilience of ecologically dominant ants in tropical savannas of northern Australia. Diversity and distributions, 13(4), 438-446.

Andrew, N. R., Hart, R. A., Jung, M.-P., Hemmings, Z., & Terblanche, J. S. (2019). Behavioural plasticity and thermal tolerance in a changing climate: Warming affects thermal limits but not the thermal dependence of locomotion in ants. Frontiers in Physiology, 10, 1500.

Arnan, X., & Blüthgen, N. (2015). Using ecophysiological traits to predict climatic and activity niches: lethal temperature and water loss in M editerranean ants. Global Ecology and Biogeography, 24(12), 1454-1464.

Arnan, X., Blüthgen, N., Molowny-Horas, R., & Retana, J. (2015). Thermal characterization of European ant communities along thermal gradients and its implications for community resilience to temperature variability. Frontiers in Ecology and Evolution, 3, 138.

Aronson, M. F., Nilon, C. H., Lepczyk, C. A., Parker, T. S., Warren, P. S., Cilliers, S. S., ... & Zipperer, W. (2016). Hierarchical filters determine community assembly of urban species pools. Ecology, 97(11), 2952-2963.

Assessment, M. E. (2005). Ecosystems and human well-being (Vol. 5, p. 563). Island Press, Washington, DC.

Bailey, Evann L., "Os efeitos da urbanização na morfologia dos insetos: uma meta-análise" (2021). Teses de honra.

Battin, J. (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. Conservation Biology, 18(6), 1482-1491.

Baudier, K. M., Mudd, A. E., Erickson, S. C., & O'Donnell, S. (2015). Microhabitat and body size effects on heat tolerance: Implications for responses to climate change. Journal of Experimental Biology, 218(4), 373-380.

Beattie, A. J. (1985). The evolutionary ecology of ant-plant mutualisms. Cambridge University Press.

Beaumont, K. P., Mackay, D. A., & Whalen, M. A. (2012). The effects of prescribed burning on epigaeic ant communities in eucalypt forest of South Australia. Forest ecology and management, 271, 147-157.

Berg, R. Y. (1975). Myrmecochorous plants in Australia and their dispersal by ants. Australian Journal of Botany, 23(3), 475-508.

Bestelmeyer, B. T. (2000). The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. Journal of Animal Ecology, 69(6), 998-1009.

Bishop, C. A., Woundneh, M. B., Maisonneuve, F., Common, J., Elliott, J. E., & Moran, A. J. (2020). Determination of neonicotinoids and butenolide residues in avian and insect pollinators and their ambient environment in Western Canada (2017, 2018). Science of the Total Environment, 737, 139386.

Blair, R. B. (2001). Birds and butterflies along urban gradients in two ecoregions of the United States: is urbanization creating a homogeneous fauna?. In Biotic homogenization (pp. 33-56). Boston, MA: Springer US.

Blight, O., Orgeas, J., Renucci, M., Tirard, A., & Provost, E. (2009). Where and how Argentine ant (Linepithema humile) spreads in Corsica?. Comptes rendus. Biologies, 332(8), 747-751.

Bolund, P., & Hunhammar, S. (1999). Ecosystem services in urban areas. Ecological economics, 29(2), 293-301.

Bond, WJ* &Slingsby, P. (1983). Seed dispersal by ants in shrublands of the Cape Province and its evolutionary implications. South African Journal of Science, 79(6), 231-233.

Brightwell, R. J., Bambara, S. B., & Silverman, J. (2010). Combined effect of hemipteran control and liquid bait on Argentine ant populations. Journal of economic entomology, 103(5), 1790-1796.

Buchholz, S., Gathof, A. K., Grossmann, A. J., Kowarik, I., & Fischer, L. K. (2020). Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. Landscape and Urban Planning, 196, 103731.

Buczkowski, G., & Bennett, G. W. (2006). Dispersed central-place foraging in the polydomous odorous house ant, Tapinoma sessile as revealed by a protein marker. Insectes Sociaux, 53, 282-290.

Buczkowski, G., & Richmond, D. S. (2012). The effect of urbanization on ant abundance and diversity: a temporal examination of factors affecting biodiversity.

Burkman, C. E., & Gardiner, M. M. (2014). Urban greenspace composition and landscape context influence natural enemy community composition and function. Biological Control, 75, 58-67.

Cadotte, M. W. (2017). Functional traits explain ecosystem function through opposing mechanisms. Ecology Letters, 20(8), 989-996.

Camara, T., N. Andersen, A., Nascimento, G., & Arnan, X. (2024). Thermal Tolerance and Species Distributions: Interactions Between Latitude, Elevation and Arboreality in Ants. Diversity and Distributions, 30(11), e13936.

Canner, J. E., Dunn, R. R., Giladi, I., & Gross, K. (2012). Redispersal of seeds by a keystone ant augments the spread of common wildflowers. Acta oecologica, 40, 31-39.

Carpanezzi, A. A., Oliveira, E. B., & Santos, H. R. (1990). Definição de áreas degradadas e princípios básicos para recuperação de ecossistemas florestais. Embrapa Florestas, Documentos 18.

Cavalcante-Pinto, K. (2020). INFLUÊNCIA DA URBANIZAÇÃO NA MORFOLOGIA E CANTO DE Dendropsophus cruzi: UMA AVALIAÇÃO EM PARQUES URBANOS NO CERRADO GOIANO.

Cerda, X., Retana, J., & Cros, S. (1997). Thermal disruption of transitive hierarchies in Mediterranean ant communities. Journal of animal ecology, 363-374.

Cerdá, X., Retana, J., & Cros, S. (1998). Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. Functional Ecology, 12(1), 45-55.

Chen, Y. H., & Neoh, K. B. (2023). Urbanization causes shifts in the functional traits and foraging activity, and alters food particle size preference and biomass removal of urban-dwelling ants. Frontiers in Ecology and Evolution, 11, 1044485.

Del Toro, I., Ribbons, R. R., & Pelini, S. L. (2012). The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). Myrmecological News, 17(0), 133-146.

Diamond, S. E., Sorger, D. M., Hulcr, J., Pelini, S. L., Toro, I. D., Hirsch, C., ... & Dunn, R. R. (2012). Who likes it hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. Global Change Biology, 18(2), 448-456.

Dunning, J. B., Danielson, B. J., & Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. Oikos, 169-175.

Elizalde, L., Arbetman, M., Arnan, X., Eggleton, P., Leal, I. R., Lescano, M. N., ... & Pirk, G. I. (2020). The ecosystem services provided by social insects: traits, management tools and knowledge gaps. Biological Reviews, 95(5), 1418-1441.

Elizalde, L., Arbetman, M., Arnan, X., Eggleton, P., Leal, I. R., Lescano, M. N., ... & Pirk, G. I. (2020). The ecosystem services provided by social insects: traits, management tools and knowledge gaps. Biological Reviews, 95(5), 1418-1441.

Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P. J., McDonald, R. I., ... & Tidball, K. (2013). Stewardship of the biosphere in the urban era. Urbanization, biodiversity and ecosystem services: challenges and opportunities: a global assessment, 719-746.

Espadaler, X., & López-Soria, L. (1991). Rareness of certain Mediterranean ant species: fact or artifact?. Insectes Sociaux, 38, 365-377.

Folgarait, P. J. (1998). Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity & Conservation, 7, 1221-1244.

Fuller, R. A., Irvine, K. N., Devine-Wright, P., Warren, P. H., & Gaston, K. J. (2007). Psychological benefits of greenspace increase with biodiversity. Biology letters, 3(4), 390-394.

Gallegos, S. C., Bartomeus, I., & González-Varo, J. P. (2014). Seed dispersal by frugivorous ants in a Mediterranean agroecosystem: Modulating roles of ant and plant species. Acta Oecologica, 58, 26–34.

García-Nieto, A. P., Geijzendorffer, I. R., Baró, F., Roche, P. K., Bondeau, A., & Cramer, W. (2018). Impacts of urbanization around Mediterranean cities: Changes in ecosystem service supply. Ecological Indicators, 91, 589-606.

Gaston, K. J. (2000). Global patterns in biodiversity. Nature, 405(6783), 220-227.

Gaston, K. J., Ávila-Jiménez, M. L., & Edmondson, J. L. (2013). Managing urban ecosystems for goods and services. Journal of Applied Ecology, 50(4), 830-840.

Gibb, H., & Hochuli, D. F. (2002). Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biological conservation, 106(1), 91-100.

Gibb, H., Parr, C. L., & Dunn, R. R. (2018). Global trends in the effects of climate and urbanization on ant assemblages. Global Ecology and Biogeography, 27(5), 580-591.

Goodness, J., Andersson, E., Anderson, P. M. L., & Elmqvist, T. (2016). Exploring the links between functional traits and cultural ecosystem services to enhance urban ecosystem management. Ecological Indicators, 70, 597-605.

Gorb, E., & Gorb, S. (2003). Seed dispersal by ants in a deciduous forest ecosystem: mechanisms, strategies, adaptations. Springer Science & Business Media.

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.

Grimm, N. B., Faeth, S. H., Golubiewski, N. E., Redman, C. L., Wu, J., Bai, X., & Briggs, J. M. (2008). Global change and the ecology of cities. Science, 319(5864), 756-760.

Gunther, R. W., & Lanza, J. (1989). Variation in attractiveness of Trillium diaspores to a seed-dispersing ant. American Midland Naturalist, 321-328.

Gusmão, F. A., Sibinel, N., & de Carvalho Campos, A. E. (2011). Control of tramp ants (Hymenoptera: Formicidae) with methoprene baits. Sociobiology, 57(2), 329-339.

Heterick, B. E., Lythe, M., & Smithyman, C. (2013). Urbanisation factors impacting on ant (Hymenoptera: Formicidae) biodiversity in the Perth metropolitan area, Western Australia: Two case studies. Urban Ecosystems, 16, 145-173.

Hoffmann, B. D., & Andersen, A. N. (2003). Responses of ants to disturbance in Australia, with particular reference to functional groups. Austral Ecology, 28(4), 444-464.

Hohlenwerger, C. C. (2022). Efeito da estrutura da paisagem sobre a provisão dos serviços de polinização e controle de pragas (Doctoral dissertation, Universidade de São Paulo).

Hölldobler, B., & Wilson, E. O. (1990). The ants. Harvard University Press.

Holway, D. A., & Suarez, A. V. (2006). Homogenization of ant communities in mediterranean California: the effects of urbanization and invasion. Biological conservation, 127(3), 319-326.

Horvitz, C. C. (1981). Analysis of how ant behaviors affect germination in a tropical myrmecochore Calathea microcephala (P. & E.) Koernicke (Marantaceae): microsite selection and aril removal by neotropical ants, Odontomachus, Pachycondyla, and Solenopsis (Formicidae). Oecologia, 51, 47-52.

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. Annual review of ecology and systematics, 13, 201-228.

Hughes, L., & Westoby, M. (1992). Effect of diaspore characteristics on removal of seeds adapted for dispersal by ants. Ecology, 73(4), 1300-1312.

Ivanov, K., & Keiper, J. (2009). Effectiveness and biases of winkler litter extraction and pitfall trapping for collecting ground-dwelling ants in northern temperate forests. Environmental Entomology, 38(6), 1724-1736.

Janzen, D. H. (1967). Why mountain passes are higher in the tropics. The American Naturalist, 101(919), 233-249.

Koch, F., & Vohland, K. (2004). Ants along a southern African transect-a basis for biodiversity change monitoring (Insecta, Hymenoptera, Formicidae). Zoosystematics and Evolution, 80(2), 261-273.

Kotze, D. J., Lowe, E. C., MacIvor, J. S., Ossola, A., Norton, B. A., Hochuli, D. F., ... & Hahs, A. K. (2022). Urban forest invertebrates: how they shape and respond to the urban environment. Urban Ecosystems, 25(6), 1589-1609.

Kühsel, S., Brückner, A., Schmelzle, S., Heethoff, M., & Blüthgen, N. (2017). Surface area–volume ratios in insects. Insect science, 24(5), 829-841.

Leal, I. R. (2003). Dispersão de sementes por formigas na caatinga. Ecologia e conservação da caatinga, 593-624.

Leal, I. R., & Oliveira, P. S. (1998). Interactions between Fungus-Growing Ants (Attini), Fruits and Seeds in Cerrado Vegetation in Southeast Brazil 1. Biotropica, 30(2), 170-178.

Leal, I. R., Filgueiras, B. K., Gomes, J. P., Iannuzzi, L., & Andersen, A. N. (2012). Effects of habitat fragmentation on ant richness and functional composition in Brazilian Atlantic forest. Biodiversity and Conservation, 21, 1687-1701.

Leal, I. R., Wirth, R., & Tabarelli, M. (2007). Seed dispersal by ants in the semi-arid Caatinga of north-east Brazil. Annals of botany, 99(5), 885-894.

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(1), 173-181

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(5), e5480.

Lengyel, S., Gove, A. D., Latimer, A. M., Majer, J. D., & Dunn, R. R. (2010). Convergent evolution of seed dispersal by ants, and phylogeny and biogeography in flowering plants: a global survey. Perspectives in Plant Ecology, Evolution and Systematics, 12(1), 43-55.

Lessard, J. P., & Buddle, C. M. (2005). The effects of urbanization on ant assemblages (Hymenoptera: Formicidae) associated with the Molson Nature Reserve, Quebec. The Canadian Entomologist, 137(2), 215-225.

Lessard, J. P., Dunn, R. R., & Sanders, N. J. (2009). Temperature-mediated coexistence in temperate forest ant communities. Insectes Sociaux, 56, 149-156.

Li, B., Chen, D., Wu, S., Zhou, S., Wang, T., & Chen, H. (2016). Spatio-temporal assessment of urbanization impacts on ecosystem services: Case study of Nanjing City, China. Ecological Indicators, 71, 416-427.

Lopez Moreno, I. R., & Diaz Betancourt, M. E. (1995). Study of biodiversity in urban ecosistems. Arbor (Espana), 151(596).

Lopez-Moreno, I. R., Diaz-Betancourt, M. E., & Suarez-Landa, T. (2003). Social insects in human-impacted environments: The ants of Ciudad de Coatepec, Veracruz, Mexico]. Sociobiology, 42(3), 605-622.

Lubertazzi, D., Aliberti Lubertazzi, M. A., McCoy, N., Gove, A. D., Majer, J. D., & Dunn, R. R. (2010). The ecology of a keystone seed disperser, the ant Rhytidoponera violacea. Journal of Insect Science, 10(1), 158.

Luke, S. H., Fayle, T. M., Eggleton, P., Turner, E. C., & Davies, R. G. (2007). Functional structure of ant and termite assemblages in old growth forest, logged forest and oil palm plantation in Malaysian Borneo. Biodiversity and Conservation, 23(11), 2817–2832.

MA (Millennium Ecosystem Assessment). Ecosystems and human well-being: the as sessment series (four volumes and summary). Washington, DC: Island Press; 2005.

Mace, G. M., Norris, K., & Fitter, A. H. (2012). Biodiversidade e serviços ecossistêmicos: uma relação multifacetada. Tendências em Ecologia e Evolução, 27, 19–26.

Majer, J. D. (1983). Ants: bio-indicators of minesite rehabilitation, land-use, and land conservation. Environmental management, 7, 375-383.

Majer, J., & Brown, K. (1986). The effects of urbanization on the ant fauna of the Swan Coastal Plain near Perth, Western Australia. Journal of the Royal Society of Western Australia, 69(1), 13-17.

Maklakov, A. A., Immler, S., Gonzalez-Voyer, A., Rönn, J., & Kolm, N. (2011). Cérebros e a cidade: pássaros passeriformes de cérebro grande têm sucesso em ambientes urbanos. Cartas de biologia, 7(5), 730-732.

Martinson, H. M., & Raupp, M. J. (2013). A meta-analysis of the effects of urbanization on ground beetle communities. Ecosphere, 4(5), 1-24.

McCain, C. M., & King, S. R. B. (2014). Body size and activity times mediate mammalian responses to climate change. Global Change Biology, 20(6), 1760-1769.

McDonnell, M. J., & Hahs, A. K. (2015). Adaptation and persistence of species in urban environments. Ecology Letters, 18(8), 873-886.

McGranahan, G., Balk, D., & Anderson, B. (2007). The rising tide: assessing the risks of climate change and human settlements in low elevation coastal zones. Environment and urbanization, 19(1), 17-37.

McIntyre, N. E. (2000). Ecology of urban arthropods: A review and a call to action. Annals of the Entomological Society of America, 93(4), 825-835.

McPhearson, T., Haase, D., Kabisch, N., & Gren, Å. (2016). Avançando na compreensão da natureza complexa dos sistemas urbanos. Ecological Indicators , 70 , 566-573

Meléndez-Jaramillo E, Sánchez-Castillo L, Segura Martínez MaTJ, Sánchez-Reyes UJ (2023) Vegetation changes along an urbanisation and atmospheric pollution gradient in Mexico. Nature Conservation 54: 179-202.

Melillo, J., & Sala, O. (2008). Ecosystem services. Sustaining life: how human health depends on biodiversity, 75-115.

Merckx, T., Kaiser, A., & Van Dyck, H. (2018). Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. Global Change Biology, 24(8), 3837-3848.

Mitchell, M. G., & Devisscher, T. (2022). Strong relationships between urbanization, landscape structure, and ecosystem service multifunctionality in urban forest fragments. Landscape and Urban Planning, 228, 104548.

Morante-Filho, J. C., Faria, D., Mariano-Neto, E., & Rhodes, J. (2015). Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the Brazilian Atlantic Forest. PLoS One, 10(6), e0128923.

Munhae, C. D. B., Bueno, Z. A. F. N., Morini, M. S. C., & Silva, R. R. (2009). Composition of the ant fauna (Hymenoptera: Formicidae) in public squares in Southern Brazil. Sociobiology, 53(2), 455.

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(5), 1244-1250

Niemelä, J. (1999). Ecology and urban planning. Biodiversity & Conservation, 8(1), 119-131.

Nkem, J. N., De Bruyn, L. L., Grant, C. D., & Hulugalle, N. R. (2000). The impact of ant bioturbation and foraging activities on surrounding soil properties. Pedobiologia, 44(5), 609-621.

Oi, D. H., Pereira, R. M., Stimac, J. L., & Wood, L. A. (1994). Field applications of Beauveria bassiana for control of the red imported fire ant (Hymenoptera: Formicidae). Journal of Economic Entomology, 87(3), 623-630.

Oi, D. H., Vail, K. M., & Williams, D. F. (2000). Bait distribution among multiple colonies of Pharaoh ants (Hymenoptera: Formicidae). Journal of Economic Entomology, 93(4), 1247-1255.

Oliveira P.S. & Freitas A.V.L. (2004). Ant-plant-herbivore interactions in the neotropical Cerrado savanna. Naturwissenschaften, 91, 557-570.

Oliveira, F. M., Andersen, A. N., Arnan, X., Ribeiro-Neto, J. D., Arcoverde, G. B., & Leal, I. R. (2019). Effects of increasing aridity and chronic anthropogenic disturbance on seed dispersal by ants in Brazilian Caatinga. Journal of Animal Ecology, 88(6), 870-880.

Oliveira, P. S., Galetti, M., Pedroni, F., & Morellato, L. P. C. (1995). Seed cleaning by Mycocepurus goeldii ants (Attini) facilitates germination in Hymenaea courbaril (Caesalpiniaceae). Biotropica, 518-522.

Pacheco, R., & Vasconcelos, H. L. (2007). Invertebrate conservation in urban areas: ants in the Brazilian Cerrado. Landscape and Urban Planning, 81(3), 193-199.

Pacini, E. (1990). Mercurialis annua L.(Euphorbiaceae) seed interactions with the ant Messor structor (Latr.), Hymenoptera: Formicidae. Acta Botanica Neerlandica, 39(3), 253-262.

Pal, A. K., & Sengupta, A. (2019). Urbanization and ownership of polluting vehicles: a study from urban India. In Handbook of Research on Economic and Political Implications of Green Trading and Energy Use (pp. 340-354). IGI Global.

Parr, C. L., Andersen, A. N., Chastagnol, C., & Duffaud, C. (2007). Savanna fires increase rates and distances of seed dispersal by ants. Oecologia, 151, 33-41.

Pećarević, M., Danoff-Burg, J., & Dunn, R. R. (2010). Biodiversity on Broadway-enigmatic diversity of the societies of ants (Formicidae) on the streets of New York City. PloS one, 5(10), e13222.

Penn, H. J., & Crist, T. O. (2018). From dispersal to predation: A global synthesis of ant–seed interactions. Ecology and evolution, 8(18), 9122-9138.

Perfecto, I., & Philpott, S. M. (2023). Ants (Hymenoptera: Formicidae) and ecosystem functions and services in urban areas: a reflection on a diverse literature. Myrmecological News, 33.

Pesquero, M. A., Elias Filho, J., Carneiro, L. C., Feitosa, S. B., Oliveira, M. A., & Quintana, R. C. (2008). Formigas em ambiente hospitalar e seu potencial como transmissoras de bactérias. Neotropical Entomology, 37, 472-477.

Pik, A. J., Oliver, I., & Beattie, A. J. (2002). Taxonomic sufficiency in ecological studies of terrestrial invertebrates. Austral Ecology, 27(5), 555–564.

Pimm, S. L., Russell, G. J., Gittleman, J. L., & Brooks, T. M. (1995). The future of biodiversity. Science, 269(5222), 347-350.

Portnoy, S., & Willson, M. F. (1993). Seed dispersal curves: behavior of the tail of the distribution. Evolutionary Ecology, 7, 25-44.

Pyšek, P., & Jarošík, V. (2005). Residence time determines the distribution of alien plants. In Invasive plants: ecological and agricultural aspects (pp. 77-96). Basel: Birkhäuser Basel.

Pyšek, P., Richardson, D. M., Rejmánek, M., Webster, G. L., Williamson, M., & Kirschner, J. (2004). Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon, 53(1), 131-143.

Queiroz, A. C. M., Ribas, C. R., & Schoereder, J. H. (2017). Effects of habitat loss and fragmentation on the ecological processes of leaf-litter ants: A global review. Biological Conservation, 206, 5–19.

Rey, S., & Espadaler, X. (2004). Area-wide management of the invasive garden ant Lasius neglectus (Hymenoptera: Formicidae) in Northeast Spain. Journal of Agricultural and Urban Entomology, 21(2), 99-112.

Rissing, S. W. (1986). Indirect effects of granivory by harvester ants: plant species composition and reproductive increase near ant nests. Oecologia, 68, 231-234.

Rota, T. (2018). Effects of intraspecific variability of invertebrates' phenotype on litter decomposition (Doctoral dissertation, Université Paul Sabatier-Toulouse III).

Sanford, M. P., Manley, P. N., & Murphy, D. D. (2009). Effects of urban development on ant communities: implications for ecosystem services and management. Conservation Biology, 23(1), 131-141.

Santiago, G. S. M., Vasconcelos, H. L., & Camacho, G. P. (2018). The effects of urbanization on biodiversity and ecosystem services: A synthesis for ants. Urban Ecosystems, 21(1), 145–156

Santini, L., González-Suárez, M., Russo, D., Gonzalez-Voyer, A., von Hardenberg, A., & Ancillotto, L. (2019). One strategy does not fit all: determinants of urban adaptation in mammals. Ecology Letters, 22(2), 365-376.

Santos, M.N. Pesquisa sobre formigas urbanas: abordagens e lacunas. Inseto. Soc. 63, 359–371 (2016).

Savage, V. M., Gillooly, J. F., Brown, J. H., West, G. B., & Charnov, E. L. (2004). Effects of body size and temperature on population growth. The American Naturalist, 163(3), 429-441.

Schneiberg, I., Boscolo, D., Devoto, M., Marcilio-Silva, V., Dalmaso, C. A., Ribeiro, J. W., ... & Varassin, I. G. (2020). Urbanization homogenizes the interactions of plant-frugivore bird networks. Urban Ecosystems, 23, 457-470.

Schneider, A., Friedl, M. A., & Potere, D. (2009). A new map of global urban extent from MODIS satellite data. Environmental research letters, 4(4), 044003.

Schultz, R., & Busch, T. (2009). The northernmost record of the invasive garden ant, Lasius neglectus (Hymenoptera: Formicidae). Myrmecological News, 12, 183-186.

Seto, K. C., & Pandey, B. (2019). Urbanization and global environmental change. Cambridge University Press.

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences, 109(40), 16083-16088.

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences, 109(40), 16083-16088.

Silva, J. L. S., Cruz-Neto, O., Rito, K. F., Arnan, X., Leal, I. R., Peres, C. A., ... & Lopes, A. V. (2020). Divergent responses of plant reproductive strategies to chronic anthropogenic disturbance and aridity in the Caatinga dry forest. Science of the total environment, 704, 135240.

Ślipiński, P., Żmihorski, M., & Czechowski, W. (2012). Species diversity and nestedness of ant assemblages in an urban environment. European Journal of Entomology, 109(2).

Stanley, A. M., & Arceo-Gómez, G. (2020). Urbanization increases seed dispersal interaction diversity but decreases dispersal success in Toxicodendron radicans. Global Ecology and Conservation, 22, e01019.

Stevens, G. C. (1992). The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. The American Naturalist, 140(6), 893-911.

Streitberger, M., & Fartmann, T. (2015). Vegetation and climate determine ant-mound occupancy by a declining herbivorous insect in grasslands. Acta Oecologica, 68, 43-49.

Tamashiro, R. A., Milligan, P. D., & Palmer, T. M. (2019). Left out in the cold: temperature-dependence of defense in an African ant–plant mutualism.

TEEB (The Economics of Ecosystems and Biodiversity), 2011. Rewarding benefits through payments and markets; chapter 5, in: ten Brink, P. (Ed.), TEEB in National and International Policy Making. Earthscan, London, pp. 177 257.

Teixido, A. L., Fuzessy, L. F., Souza, C. S., Gomes, I. N., Kaminski, L. A., Oliveira, P. C., & Maruyama, P. K. (2022). Anthropogenic impacts on plant-animal mutualisms: A global synthesis for pollination and seed dispersal. Biological Conservation, 266, 109461.

Theodorou, P., Baltz, L. M., Paxton, R. J., & Soro, A. (2021). Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. Evolutionary Applications, 14(1), 53-68.

Theodorou, P., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T. E., & Paxton, R. J. (2016). Pollination services enhanced with urbanization despite increasing pollinator parasitism. Proceedings of the Royal Society B: Biological Sciences, 283(1833), 20160561.

Underwood, E. C., & Fisher, B. L. (2006). The role of ants in conservation monitoring: if, when, and how. Biological conservation, 132(2), 166-182.

Urban, M. C. (2024). Climate change extinctions. Science, 386(6726), 1123-1128.

Van Hamburg, H., Andersen, A. N., & Meyer, W. J. (2004). Ant community development on rehabilitated ash dumps in South Africa. Restoration Ecology, 12(3), 312–319.

van Heezik, Y. M., Dickinson, K. J., & Freeman, C. (2012). Closing the gap: communicating to change gardening practices in support of native biodiversity in urban private gardens. Ecology and society, 17(1).

Vasconcelos, H. L., Maravalhas, J. B., & Feitosa, R. M. (2017). Effects of fire disturbance on ant communities in the Brazilian Cerrado. Biotropica, 49(5), 586–594.

Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! Oikos, 116(5), 882-892.

Warren, R. J., & Giladi, I. (2014). Mutualism fails when climate response differs between interacting species. Global Change Biology, 20 (12), 3642-3650.

Weber, M. G., & Keeler, K. H. (2013). The phylogenetic distribution of extrafloral nectaries in plants. Annals of botany, 111(6), 1251-1261.

Westoby, M., French, K., Hughes, L., Rice, B., & Rodgerson, L. (1991). Why do more plant species use ants for dispersal on infertile compared with fertile soils?. Australian Journal of Ecology, 16(4), 445-455.

Westoby, M., Rice, B., Shelley, J. M., Haig, D., & Kohen, J. L. (1982). Plants' use of ants for dispersal at West Head, New South Wales. In Ant-plant interactions in Australia (pp. 75-87). Dordrecht: Springer Netherlands.

Wilson, E. O., & Books, V. Conservation ethics based on evolution?.

Wu, J. (2014). Urban ecology and sustainability: The state-of-the-science and future directions. Landscape and urban planning, 125, 209-221.

Yamaguchi, T. (2004). Influence of urbanization on ant distribution in parks of Tokyo and Chiba City, Japan I. Analysis of ant species richness. Ecological Research, 19, 209-216.

Yamaguchi, T. (2005). Influence of urbanization on ant distribution in parks of Tokyo and Chiba City, Japan II. Analysis of species. Entomological Science, 8(1), 17-25.

Zara, L., Tordoni, E., Castro-Delgado, S., Colla, A., Maccherini, S., Marignani, M., ... & Bacaro, G. (2021). Relações entre táxons no ecossistema urbano mediterrâneo: um estudo de caso da cidade de Trieste. Indicadores Ecológicos, 125, 107538.

Zhou, D., Tian, Y., & Jiang, G. (2018). Spatio-temporal investigation of the interactive relationship between urbanization and ecosystem services: Case study of the Jingjinji urban agglomeration, China. Ecological indicators, 95, 152-164.