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ECOSYSTEMS

Drosophila nasuta (Diptera, Drosophilidae) in Brazil: a decade of invasion and occupation of more than half of the country

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Abstract: As a result of human activities and natural dispersal, exotic species can be brought to new areas, where they become established and spread, becoming invaders. These species are responsible for the loss of biodiversity and cause ecosystemic harm throughout the world. In this paper, we report the rapid, broad geographic expansion of the invasive fly *Drosophila nasuta* in Brazil. An 84% increase was found in its area of occupation in the country compared to previous studies. The present data reveal its arrival to the Pantanal wetlands in a location more than one thousand kilometers from the closest previous record in the *Cerrado* biome. We present the first record of *D. nasuta* in the Atlantic Forest in the states of Paraíba and Bahia. We report its introduction in the Amazon Forest in the state of Amazonas approximately 700 kilometers from previous records. The relative abundance of *D. nasuta* in this biome increased fivefold in comparison to a previous study. In the first decade of invasion in Brazil, *D. nasuta* has already colonized more than half of the country. The present data reveal its invasive potential and underscore the importance of following up the possible negative effects of this biological invasion.

Key words: Abundance distribution, Amazon Forest, Atlantic Forest, exotic species, Pantanal wetlands.

INTRODUCTION

The increase in transportation routes, trade and tourism has favored the geographic expansion and establishment of species with adaptive potential (Seebens et al. 2018). When arriving to new territories, some of these species cause economic and/or ecological harm and are recognized as invasive species (Heringer et al. 2021, Cordero et al. 2023). From the ecological standpoint, invasive species can alter the composition and abundance of native species due to competition or predation, contributing to local extinction and ecosystemic imbalance (Pyšek et al. 2020), making such species one of the main causes of the loss of biodiversity (Mollot et al. 2017).

Insects stand out with regards to biological invasion both in terms of the number of reports and the impacts of these invasions (Kenis et al. 2009, Brockerhoff & Liebhold 2017, Fenn-Moltu et al. 2023). This is the most diversified group of organisms on the planet, accounting for approximately 75% of the biodiversity of all animal species described (Nayak et al. 2021). Insects are responsible for various ecological processes and interactions, such as pollination,

seed dispersal, predation, nutrient cycling and the regulation of plant and animal populations (Scudder 2017).

Considering only insects from the family Drosophilidae, three invasions were recorded in Brazil in the last 10 years: *Drosophila suzukii* (Deprá et al. 2014), *D. nasuta* (Vilela & Goñi 2015) and *Zaprionus tuberculatus* (Cavalcanti et al. 2022). Among these insects, the Asian species. *D. suzukii* and the African species *Z. tuberculatus* are a threat to fruit farming. *Drosophila suzukii* has caused harm to diverse crops, such as strawberry, black berry, guava and Surinam cherry, causing economic losses for fruit farming in the country (Santos 2014, Andreazza et al. 2016, Zanuncio-Junior et al. 2018, Wollmann et al. 2020). *Zaprionus tuberculatus* is considered a secondary pest in invasion areas, preferably depositing its eggs on fruits damaged by primary pests, such as *D. suzukii* (Amiresmaeili et al. 2019).

Drosophila nasuta is native to Asia (Kitagawa et al. 1982). Since its first detection in Brazil in 2013, it has been reported in the Atlantic Forest (Batista et al. 2016, Silva et al. 2020), *Cerrado* (savanna) (Leão et al. 2017), *Caatinga* (xeric shrubland) (Montes et al. 2021), Amazonia (Medeiros et al. 2022) and Fernando de Noronha Island (Rafael et al. 2020). Unlike the pattern displayed by other invasive species of drosophilids, such as *Z. indianus* and *D. malerkotliana*, which are more abundant in anthropized areas (Gottschalk et al. 2007, Garcia et al. 2012), *D. nasuta* has demonstrated a preference for conserved environments in areas of invasion (David et al. 2014, Silva et al. 2020).

In the Atlantic Forest of the state of Pernambuco, the seasonal pattern of drosophilids was studied prior to the arrival of *D. nasuta*, with records of a greater abundance of Neotropical species in comparison to exotic species in the rainy season and the opposite pattern in the dry season (Coutinho-Silva et al. 2017). Since the arrival of *D. nasuta*, the abundance of Neotropical drosophilids has been decreasing in the region, especially in the rainy season, when *D. nasuta* has become more abundant (Garcia et al. unpublished data). The rapid geographic expansion, the possible preference for conserved areas of vegetation and the probable negative effects of *D. nasuta* on Neotropical species underscore the urgent need for monitoring of this biological invasion.

In the present study, we report the geographic expansion of *D. nasuta* in Brazil in the Atlantic Forest and Amazonia and we detected the arrival of this species in the Pantanal biome.

MATERIALS AND METHODS

Study area

Brazil is the fifth largest country in the world, one of the most megadiverse countries on the planet (Mair et al. 2023) and home to six biomes: the Amazon Forest, Atlantic Forest, *Caatinga* (xeric shrubland), *Cerrado* (savanna), Pantanal wetlands and Pampas (low grasslands) (IBGE 2019). In this study, the presence of *D. nasuta* was investigated in areas of the Amazon Forest, Atlantic Forest and Pantanal wetlands.

The Amazon is the largest tropical forest on Earth (Agudelo et al. 2020), occupying approximately half of the area of Brazil (IBGE 2019) and housing approximately one-third of the species richness on the planet (Meirelles-Filho 2004). This is one of the biomes with the most deforestation in Brazil, which has favored the introduction of exotic species (Vieira et al. 2008, Rutt et al. 2019). In the Amazon Forest, the drosophilids sampled here were collected from the campus of the Universidade Federal do Amazonas in the city of Manaus (MAN, 3°6'S; 59°58'W) in an area of 260 hectares of dense rainforest. The climate in the region is wet

equatorial, with average annual precipitation of 2930 mm and average temperature of 27.2°C (Calixto et al. 2019, Climatempo 2023a). The period of greatest rainfall extends from November to April (Climatempo 2023a).

The Atlantic Forest is one of the biomes with the greatest species richness and rates of endemism on the planet (Carvalho et al. 2021). The forest covers approximately 15% of the area of Brazil (IBGE 2019). Since the colonization of the country beginning in the 1500s, this biome has been intensely deforested, with only 12% of its original area remaining (Ribeiro et al. 2009). The Atlantic Forest is also one of the Brazilian biomes with the most records of invasive species (Dechoum et al. 2021). The high level of biological richness and the high number of species in danger of extinction make this biome one of the priority hotspots for conservation (Rezende et al. 2018).

Sampling of drosophilids was performed in two areas of the Atlantic Forest in Northeast Brazil: Guaribas Biological Reserve (GUA, 6°42'S; 35°10'W) and the campus of the Universidade Federal da Bahia in the city of Salvador (SAL, 13°0'S; 38°30'W). GUA is a conservation unit of dense rainforest with an area of 4051 hectares in the municipalities of Mamanguape and Rio Tinto in the state of Paraíba (IBAMA 2003). Sampling of drosophilids in SAL occurred in a forest fragment measuring 57 hectares. Both regions have a warm, wet climate with an average temperature of 25°C and rainfall concentrated mainly between February and September (CONDER 1994). Average annual rainfall is approximately 850 mm in GUA and approximately 1300 mm in SAL (Climatempo 2023b,c).

Pantanal occupies 1.8% of the area of the country and is the largest continuous floodplain on the planet. It is recognized by the United Nations Educational, Scientific and Cultural Organization (UNESCO) as a Biosphere Reserve and Natural Heritage of Humanity (IBGE 2019). Agricultural and livestock farming are the main factors responsible for the anthropic impacts on this biome, along with the presence of invasive species (Alho et al. 2011, IBGE 2019). Drosophilid sampling in the Pantanal occurred in the municipality of Cáceres (CAC, 16°4'S; 57°41'W) in the state of Mato Grosso in an area of gallery forest vegetation. The climate is warm and wet tropical, with a dry winter, average annual precipitation of 1200 mm and average annual temperature of 27°C (Climatempo 2023d). The rainy season spans from October to March and the dry season is from April to September (Rizzini et al. 1988).

Sampling and identification of drosophilids

In each study area, drosophilids were captured with 10 traps made of plastic bottles containing banana as bait (Tidon & Sene 1988). The traps were suspended 1.5 m from the ground and distributed along trails at a minimum distance of 30 meters from each other and 50 meters from the edges of the forest fragments, remaining deployed for three consecutive days.

All sampling took place in the dry season. Sampling was performed in January 2020 in SAL, November 2021 in GUA, April 2022 in CAC and June 2022 in MAN.

Drosophilids were identified using taxonomic keys and species descriptions (Breuer & Pavan 1950, Malogolowkin 1952, Magalhães & Björnberg 1957, Vilela 1983, Vilela & Bächli 1990, Vilela et al. 2002, Rohde et al. 2010, Vilela & Goñi 2015, Poppe et al. 2016, Yuzuki & Tidon 2020). Cryptic species were recognized by an inspection of the male terminalia. For such, the final portion of the abdomen of each individual was removed and treated with 10% potassium hydroxide, followed by staining with fuchsin acid and dissection in glycerol (Bächli et al. 2004). The terminalia were mounted on slides with Canada

balsam and examined under a microscope (magnification: 400 X). The number of females of cryptic species was estimated calculating each species' sex ratio. Voucher specimens were deposited in the drosophilid collection of the Laboratório do Genoma, Universidade Federal Rural de Pernambuco, Brazil.

Drosophila nasuta was identified according to Vilela & Goñi (2015) by the light body color, brown longitudinal band on half of the dorsal area of the pleura, a silvery whitish frons in the head region when seen from the front, a row of cuneiform setae on the anteroventral side of the femur of the front legs, wings with a costal index of ca. 3.1 and characteristics of the male terminalia.

The distribution areas of *D. nasuta* and distances between sampling points were estimated using Google Earth (2023).

RESULTS

A total of 6338 drosophilids were collected from the four study locations. Neotropical species were represented by 19 species and 971 individuals. Exotic species were represented by six species and 5367 individuals. *Drosophila nasuta* was the third most abundant exotic species (N=215) and was recorded in all areas investigated (Table I).

In all locations, the abundance of exotic species surpassed that of Neotropical species. The relative abundance of exotic species was highest in SAL (95.81%) and lowest in MAN (68.76%). The highest relative abundance of *D. nasuta* was found in MAN (6.21%), followed by the areas of the Atlantic Forest (5.35% in GUA and 2.11% in SAL) and Pantanal (0.77% in CAC) (Table I).

Drosophila nasuta was the fifth most abundant species in MAN, surpassed only by the Neotropical species *D. paulistorum* and *D. willistoni* and the exotic species *D. malerkotiliana* and *Z. indianus*. The abundance of *D. nasuta* in SAL was only exceeded by *D. malerkotliana* and *Z. indianus*. *Drosophila nasuta* was the fourth most representative species in GUA, following the exotic species *D. malerkotiliana* and *D. simulans* and the Neotropical species *D. willistoni* (Table I).

The present study reports the occurrence of *D. nasuta* in the Pantanal biome for the first time and expands the area of occurrence of the species in the Amazon and Atlantic Forests (Figure 1). Based on records of *D. nasuta* in different locations in Brazil, the species has spread throughout an area of 4.6 million km^2, corresponding to 55% of the country.

The new record of *D. nasuta* in the city of Manaus is the first for the state of Amazonas and is 710 km from the closest previous record in the municipality of Uruará in the state of Pará (Figure 1). The species has spread throughout an area of at least 83,000 km^2 in this biome, corresponding to 18% of the Amazon Forest.

The new record of *D. nasuta* in the municipality of Guaribas is the first for the state of Paraíba and constitutes the northernmost point in the Atlantic Forest, 140 km from the closest previous record in the municipality of Moreno in the state of Pernambuco. This is also the first record of *D. nasuta* in the Atlantic Forest in the state of Bahia (Figure 1). Considering previous records and the new locations of occurrence, we estimate the presence of the species in approximately 42,000 km^2 of the Atlantic Forest, corresponding to 32% of the area of this biome.

With regards to Pantanal, the closest geographic point of the area with a report of *D. nasuta* was the city of Brasília in the *Cerrado* biome at a distance of approximately 1100 km.

Table I. List of neotropical and exotic drosophilids collected in Amazon Forest (Universidade Federal do Amazonas=MAN), Atlantic Forest (Guaribas Biological Reserve=GUA and Universidade Federal da Bahia=SAL) and Pantanal (Cáceres=CAC).

	MAN	GUA	SAL	CAC
Neotropical species				
Drosophila annulimana Duda	0	0	0	8
Drosophila cardini Sturtevant	14	0	0	0
Drosophila cardinoides Dobzhansky and Pavan	0	0	1	0
Drosophila ellisoni Vilela	7	0	0	0
Drosophila equinoxialis Dobzhansky	16	0	0	0
Drosophila fumipennis Duda	0	3	0	0
Drosophila nebulosa Sturtevant	3	4	44	9
Drosophila neocardini Streisinger	6	0	2	0
Drosophila neoelliptica Pavan and Magalhães	19	0	0	0
Drosophila mercatorum Patterson and Wheeler	0	11	1	5
Drosophila paulistorum Dobzhansky and Pavan	184	36	0	6
Drosophila pictilis Wasserman	0	4	5	0
Drosophila prosaltans Duda	35	0	44	12
Drosophila repleta Wollaston	15	0	0	0
Drosophila saltans Sturtevant	2	0	0	0
Drosophila sturtevanti Duda	22	20	12	25
Drosophila tropicalis Burla and Cunha	7	0	0	0
Drosophila willistoni Sturtevant	123	201	14	34
Rhinoleucophenga lopesi Malogolowkin	0	10	0	7
Exotic species				
Drosophila ananassae Doleschall	0	0	1	6
Drosophila malerkotliana Parshad and Paika	748	591	2557	497
Drosophila nasuta Lamb	90	56	62	7
Drosophila simulans Sturtevant	34	68	1	4
Scaptodrosophila latifasciaeformis Duda	27	11	14	152
Zaprionus indianus Gupta	98	31	179	133
Total	1450	1046	2937	905

DISCUSSION

Prior to the present records, *D. nasuta* occupied 2.5 million km^2 in Brazil (Medeiros et al. 2022). With the new locations of occurrence reported here, the area of occupation of the species has increased by 84%, corresponding to more than half of the country in approximately ten years of invasion. Compared to other drosophilid invasions in Brazil in this decade (Deprá et al. 2014, Cavalcanti et al. 2022) *D. nasuta* is the species with the greatest potential for geographic expansion.

The expansion potential of *D. nasuta* in Brazil is similar to that reported for the African drosophilid *Z. indianus*, which first reported in the country in 1999 (Vilela 1999) and was found in several Brazilian biomes in less than ten years (De Toni et al. 2001, Santos et al. 2003, Tidon et al. 2003, David et al. 2006). In some invaded areas, *Z.*

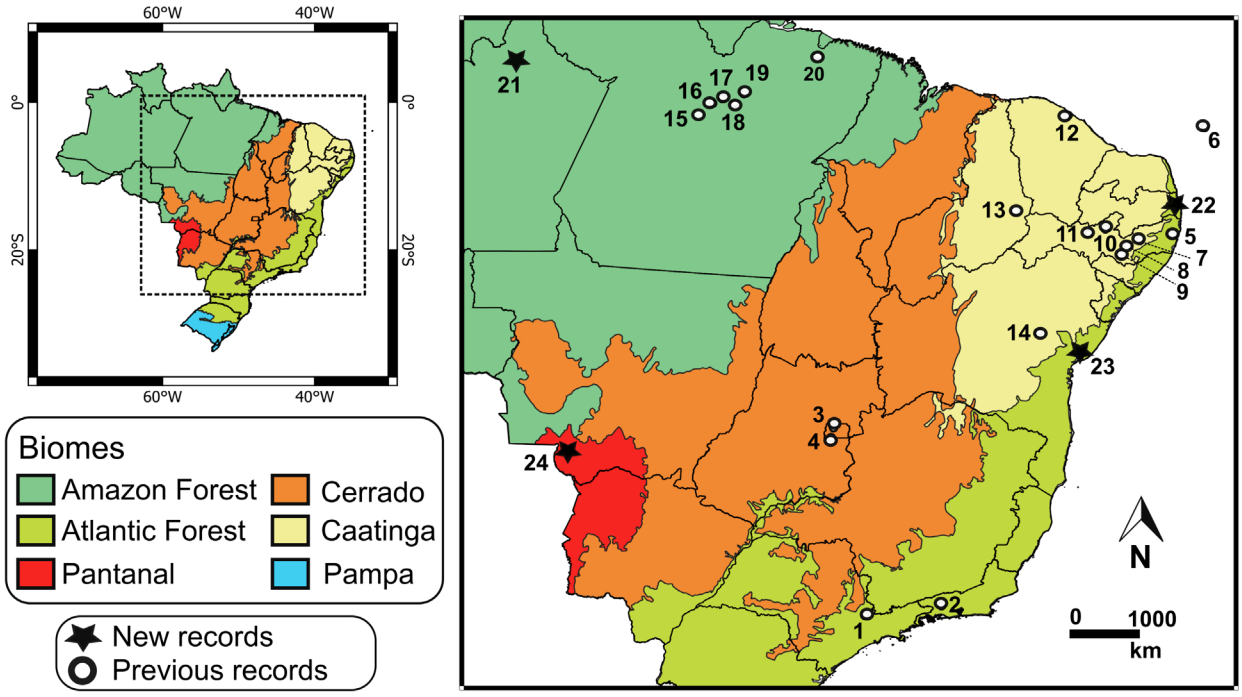

Figure 1. Map of Brazil (left side) with indication of biomes. Map of locations with records of invasive species *Drosophila nasuta* (right side). Circles indicate previous records of species: 1- Vilela & Goñi (2015), 2- Batista et al. (2016); 3- Deus & Roque (2016), 4- Leão et al. (2017), 5- Silva et al. (2020), 6- Rafael et al. (2020); 7 to 14 Montes et al. (2021); 15 to 20 Medeiros et al. (2022). Stars indicate new records reported in present study: 21- Manaus, Amazonas, 22- Guaribas Biological Reserve, Paraíba, 23- Salvador, Bahia and 24- Cáceres, Mato Grosso.

indianus has become a fruit farming pest (Nava et al. 2007, Vieira et al. 2019) and its possible competition with Neotropical drosophilids has been reported (Garcia et al. 2008). These data underscore the importance of monitoring the negative impacts that may be caused by the rapid invasion of *D. nasuta* in different Brazilian biomes.

Garcia et al. (2022) projected global areas of risk of invasion by *D. nasuta*. The authors detected the high probability of occurrence of the species in the Atlantic Forest in the states of Paraíba and Bahia, which was also reported in the present investigation. In this biome, the species has been recorded from latitude 6° (present study) to 23° (Vilela & Goñi 2015), revealing its adaptive capacity to inhabit areas with various climatic conditions and distinct habitats. *Drosophila nasuta* is one of the dominant drosophilids in different areas of the Atlantic Forest (Vilela 2015, Silva et al. 2020), which, together with the present findings, demonstrates its invasive success in this biome.

A niche modeling study projected the expansion of the geographic distribution of *D. nasuta* in the Amazon Forest and Pantanal wetlands (Garcia et al. 2022), which was also reported in the present study. Among the locations monitored here, *D. nasuta* had the highest relative abundance in the Amazon Forest (6.2%), representing a nearly fivefold increase since it was first recorded in this biome in 2017 (1.3%) (Medeiros et al. 2022). These results demonstrate the adaptive success of the species in the Amazon Forest and the importance of the continuation of its monitoring in the area. In the Pantanal the abundance of *D. nasuta* was low in the present study (less than 1%).

Exotic drosophilids surpassed Neotropical species in abundance in all areas investigated.

As a single sampling campaign was conducted in the dry season in each location and considering seasonal variations in the abundance of drosophilids (Bizzo et al. 2010, Coutinho-Silva et al. 2017), further sampling should be performed in these areas to determine whether this pattern is maintained. The greater abundance of exotic species, many of which are recognized as invasive, could contribute to the extinction of native species and lead to the homogenization of the biota, which is an important component of the current biodiversity crisis (Morri et al. 2019). The process has been accelerated by the destruction of natural environments that Brazil has undergone intensely in recent years (Oliveira et al. 2023).

The rapid geographic expansion of *D. nasuta* in Brazil and its adaptive success in different biomes indicate the enormous invasive potential of this species. Silva et al. (2020) observed the preference of *D. nasuta* for conserved areas and its seasonal pattern coinciding with some species of native drosophilids. These results alert to the possible negative effects of this species on the diversity of Neotropical drosophilids.

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Author contributions

The following authors contributed to this study: TCSLM - Identification of drosophilids from Amazon Forest and Pantanal Wetland. MFSS - Sampling and identification of drosophilids from Bahia (Atlantic Forest). MMSS - Sampling of drosophilids from Pantanal. JSA - Sampling of drosophilids from Amazon Forest. CHCBN - Sampling and identification of drosophilids from Paraíba (Atlantic Forest). ACLG and MAM - Conception and design of the study. Review of identifications of drosophilids, organization and analysis of results. Writing, reviewing and editing of the manuscript. ACLG - Funding acquisition.