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RESEARCH PAPER

Climate change impact on Amazonian ant gardens

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Abstract

In Amazonia higher Atlantic sea surface temperatures, greenhouse gasses, deforestation and El Niño events result in the greater frequency of severe droughts, although total rainfall has increased due to wetter rainy seasons, something confirmed in French Guiana from available climatic data (1980–2017). Aiming to study the impact of rainfall on ant gardens (i.e., arboreal ant-epiphyte mutualisms that depend on the atmosphere for water; AGs) initiated by the ponerine ant *Neoponera goeldii*, we conducted surveys around the Petit Saut and Régina areas (mean annual rainfall: $\approx 3,000$ mm and $\approx 4,000$ mm, respectively). Each year, near the end of the dry season we recorded the number of these AGs in 10×5 m sections parallel to the roadsides. The Petit Saut survey (1993–2017) revealed that AG density along roadsides varied only slightly in "wet zones" situated along ditches, whereas in "dry zones" where the soil seasonally dries out it dropped sharply during the drastic 1997 dry season. Then, this density, low due to recurrent droughts, dropped again during the drastic successive 2015–2016 dry seasons. In the Régina survey (2006–2017), we had the opportunity to follow the establishment of AGs in a "dry zone". It was represented by a typical sigmoidal curve and then it stabilized with AG densities higher than at its peak in 1996 in dry zones of Petit Saut, showing the importance of rainfall. Here, too, the drastic 2016 dry season adversely affected the AGs. Finally, the epiphytic composition of the AGs was mainly represented by *Aechmea mertensii* (a tank bromeliad), *Anthurium gracile* (Araceae) and *Codonanthe crassifolia* (Gesneriaceae), but AGs with the tank bromeliad are more resistant to droughts. These AGs are at risk in dry zones if drastic successive dry seasons occur in the future as global warming intensifies while those developing in riparian areas might survive.

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Keywords: Adaptation to dryness; Ant gardens; Drought frequency; Epiphytes; Global change; *Neoponera goeldii*; Pioneer formations; Ponerine ants

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Introduction

In intertropical areas, the negative impact of abiotic stresses on all living organisms is exacerbated by climatic changes related to global warming including both rising temperatures (but less than in higher latitudes) and, mostly, more frequent and severe droughts (Erfanian, Wang & Fomenko, 2017; Marengo et al., 2018; Sheldon, 2019).

In addition to adjusting their morphology and physiology by reducing their total biomass while increasing the concentration of anti-stress phytohormones, plants in drought-prone areas depend on mutualisms to survive (e.g., water and nutrient enrichment; biotic protection) (Leal & Peixoto, 2017; Post, 2013). For example, when dryness makes their leaves particularly vulnerable to herbivory, myrmecophytes (i.e., plants providing shelter for ants that, in turn, protect them from defoliators) stimulate their associate ants' activity through the greater production of extrafloral nectar or by hosting more sap-sucking, honeydew-producing ant-attended hemipterans (Dejean, Petitclerc, Azémar & Rossi, 2021; González-Teuber, Bueno, Heil & Boland, 2012; Pringle, Akçay, Raab, Dirzo & Gordon, 2013).

Part of the high angiosperm diversity, epiphytes are particularly species in the Neotropics (Taylor et al., 2021). Depending mostly on the atmosphere for their water and nutrient requirements, they evolved means of coping with irregular water availability. Thus, they augment their chance for survival during the dry seasons thanks to a thick cuticle and crassulacean acid metabolism to reduce water loss, succulent leaves and pseudobulbs to store water, epidermal trichomes for water uptake, and water reservoirs. In the latter case, tank bromeliads impound water *via* a rosette of overlapping leaves, while epidermal trichomes at the bases of the leaves absorb water and nutrients (Chávez-Sahagún, Andrade, Zotz & Reyes-García, 2019; Svensk et al., 2020; Zotz, 2016).

Epiphytes provide resources and habitat for small animals, mostly ants with which they have developed different forms of mutualisms, including myrmecophytism (Zotz, 2016). Also, "ant gardens" (AGs), abundant in the Neotropics, are mutualistic interactions between limited numbers of ant and epiphyte species wherein arboreal AG-ants build a nutrient-rich carton nest into which they incorporate the epiphyte seeds they have gathered from the surroundings (Corbara, 2020). The seeds germinate and the seedlings grow so that their roots stabilize the carton walls of the nest and anchor the entire structure (Fig. 1). AGs represent one of the most evolved ant-plant associations because the epiphytes are dispersed, protected and provided with nutrients by associate ants that, in turn, receive food rewards (e.g., fruit pulp and extrafloral nectar). They can be seen as "flagship entities" to be preserved as they contribute to canopy diversity through their mutualistic ants and epiphytes, commensals and parasites of these associations, and, for tank bromeliads, aquatic microorganisms and invertebrates (Orivel & Leroy, 2011). Yet, ecological niche

modeling and network approaches that integrate biological interactions suggest that Neotropical AGs resist perturbations related to current and future climatic changes, and their geographical distribution is predicted to increase (Morales-Linares, Corona-López, Toledo-Hernández & Flores-Palacios, 2021a,b).

This study, conducted in French Guiana, was based on an empirical approach where we looked for the impact of variations in climatic parameters on AGs initiated by the ponerine ant *Neoponera goeldii*. We asked the following questions. (1) Are droughts detrimental to *N. goeldii*-associated AGs? (2) Did the epiphytic composition of the AGs play a role in their surviving the droughts?

Materials and methods

Study sites and collection of climatic data

This study was conducted in French Guiana along roadsides around Petit Saut and Régina in two areas with different pluviometry (mean annual rainfall: ≈ 3000 mm and ≈ 4000 mm, respectively; Groussin, 2001). The rainy season extends from December to June and the dry season from August to November; July, intermediary, was not taken into account. In both areas, each year near the end of the dry season, we recorded the number of *N. goeldii*-associated AGs, including incipient ones, in 10×5 m sections parallel to the roadsides.

Around Petit Saut, a first survey (1993–2017) was conducted along the sides of Route 1 ($5^{\circ}9'0''\text{N}$; $52^{\circ}42'0''\text{W}$ – $5^{\circ}7'48''\text{N}$; $52^{\circ}43'27''\text{W}$), along the road leading to Petit Saut ($5^{\circ}6'10''\text{N}$; $52^{\circ}57'52''\text{W}$ – $5^{\circ}4'10''\text{N}$; $53^{\circ}3'1''\text{W}$), and along the dirt road to the Montagne Plomb (around $5^{\circ}4'10''\text{N}$; $52^{\circ}58'47''\text{W}$ and $5^{\circ}2'43''\text{N}$; $52^{\circ}57'19''\text{W}$). These roadsides were cleared 9 years before the beginning of this survey. We obtained data from this entire 25-yearlong period for eight "dry zones" where the soil dries out during droughts that intermingle with four "wet zones" situated along ditches that remain wet during the dry season (i.e., 89 and 59 sections measuring 10×5 m, respectively).

Around the city of Régina, a second survey (2005–2017) was conducted in a "dry zone" situated between Route 2 near kilometric point 118 ($04^{\circ}13'8''\text{N}$; $52^{\circ}7'17''\text{W}$) and a dirt road where we had the opportunity to follow the establishment of the AGs (i.e., 18 sections measuring 10×5 m surveyed each year).

We obtained the values for climatic parameters from weather stations (*Cimel Electronique*, Paris, France) managed by the *Hydreco* field station and the *INRAE* for the Petit Saut area and by *Météo-France* for the Régina area (for details, see Appendix A, available online; number of consecutive dry days: less than 5 mm of rain per day). Furthermore, because droughts in Amazonia have become more frequent and severe although total rainfall has increased due to wetter rainy seasons (Espinoza, Ronchail, Marengo &



Fig. 1. (A). During the foundation stage of their colonies, *Neoponera goeldii* queens first build a small nest of rough carton into which they plant the seeds of certain epiphytes; the first seedlings are shown. (B). A typical *N. goeldii*-associated ant garden with an *Ae. mertensii* in bloom (photos Bruno Corbara). (C). An incipient colony with some well-developed *Aechmea mertensii* individuals and numerous seedlings.

Segura, 2018; Marengo et al., 2018), we verified how climatic parameters varied between seasons and over time from available climatic data obtained between 1980 and 2017 (Appendix A).

Neoponera goeldii and their main associated epiphytes

Likely because founding queens select sun-exposed sites, *N. goeldii*-initiated AGs are frequent in dry, pioneer vegetal formations. Their main associated epiphytes in French Guiana are *Aechmea mertensii* (a tank bromeliad), *Anthurium gracile* (Araceae) and *Codonanthe crassifolia* (Gesneriaceae). Exposed to sunlight, *Ae. mertensii* individuals are amphora-shaped for better water retention, but, they are smaller and produce fewer fruits and seeds than individuals initiated by other AG-ants (Leroy et al., 2017; Orivel & Leroy, 2011).

Although their associate epiphytes provide them with the elaiosomes from their seeds (i.e., a food reward for ants, which act as dispersal agents), fruit pulp and, sometimes, extrafloral nectar, AG-ants need to forage on the host tree

and surrounding vegetation to feed their colonies (Orivel & Leroy, 2011).

Impact of climatic parameters on *Neoponera goeldii*-associated AGs

In the survey conducted in the Petit Saut area, to quantify the potential effects of climatic parameters on the number of AGs in both the dry and wet zones, we used generalized linear mixed-effects models (GLMM; Poisson distribution, log link function). The response variable (count data) corresponds to the numbers of AGs per 10×5 m section in the eight dry and the four wet zones sampled repeatedly during the 1993–2017 period. Treatment (i.e., dry and wet zones), rainfall during both dry and rainy seasons, mean maximal temperature and consecutive dry days were included as fixed factors in the model, while the zone name and year of sampling were included as crossed random effects. Continuous predictor variables were centered and scaled to avoid instability during model fitting (package lme4 in Bates, Mächler, Bolker & Walker, 2015; R Core Team, 2020; see Appendix A: Table S4).

Tracking the establishment of the AGs in the Régina area

This survey was conducted between 2005 and 2017 in a dry zone in the comparatively wet and hot Régina area (see Appendix A). This zone was cleared by bulldozers in 2001; we began to follow the establishment of new AGs by incipient *N. goeldii* colonies after host pioneer treelets (mostly *Vismia* spp.; Hypericaceae) reached ≈ 1 m height in 2003–2004.

In addition, when their density became stable we obtained further information on the impact of climatic parameters through a comparison with the dry zones in the first survey (i.e., Mann-Whitney U test) as well as the impact of the most drastic drought ever recorded in Amazonia that occurred in 2016 (see Appendix A).

Role of tank bromeliads in AGs surviving the droughts

During field surveys conducted between 1992 and 1995 we noted that after the dry season some AGs devoid of the tank bromeliad *Ae. mertensii* were withering and their associate *N. goeldii* colonies were dead. Thus, between 1996 and 2004, we conducted a census in dry zones situated along the road leading to Petit Saut (76 AGs recorded mostly composed of the epiphytes *Ae. mertensii*, *An. gracile* and *Co. crassifolia*, see above). We then compared the survival curves of *N. goeldii* colonies from AGs with versus those without *Ae. mertensii* in their epiphytic composition using the Log-rank (Mantel-Cox) test (R Core Team, 2020).

Further observations were made between 1992 and 2017 on AGs situated in different areas to record what opportunistic ant species sheltered in abandoned AGs.

Results

Impact of climatic parameters on *Neoponera goeldii*-associated AGs

In the Petit Saut area we noted a significant difference in the number of AGs in 10×5 m sections situated in wet zones compared to those situated in dry zones (GLMM: Estimate \pm SE = 1.11 ± 0.27 , $Z = 4.14$; $P < 0.001$). Indeed, the number of AGs was not significantly impacted by climatic parameters in wet zones, whereas in dry zones it decreased during drastic dry seasons (Estimate \pm SE = 0.54 ± 0.10 , $Z = 5.19$ $P < 0.001$; see also Fig. 2). The 1997 dry season was the driest and hottest with the highest number of consecutive dry days ever recorded (these parameters are correlated; see Appendix A and the gray vertical band in Fig. 2 for 1997); it caused a strong decrease in the mean number of AGs in the dry zones (Fig. 2). This decrease

was amplified in subsequent years because incipient *N. goeldii* colonies with epiphyte seedlings, present between 1993 and 1996, were unable to survive from 1997 to 2008 likely due to recurrent low rainfall during the dry seasons (i.e., below 300 mm; Fig. 2). Moreover, most of the AGs in the Petit Saut area did not survive the drastic successive 2015–2016 dry seasons (i.e., 200 mm of rainfall or less; Fig. 2).

In Régina this effect was felt to a lesser degree likely due to a less severe 2015 dry season (i.e., 300 mm of rainfall), but the very low value for 2016, similar to that of Petit Saut with less than 200 mm of rainfall (see Appendix A: Fig. S1), was associated with a strong decrease in the mean number of AGs (Fig. 3).

Tracking the establishment of the AGs in the Régina area

The colonization by *N. goeldii* in the Régina area was characterized by a typical sigmoidal curve with an increasing mean number of AGs between 2005 and 2013 followed by stabilization (Fig. 3). Correspondingly, we recorded each year four to twelve incipient *N. goeldii* colonies with epiphyte seedlings (see Figs. 1A, C); they thus had survived the dry seasons.

When between 2013 and 2015 the density of the AGs stabilized, their mean number, ≈ 3.5 per 10×5 m section (Fig. 3), was higher than in the dry zones in the Petit Saut area at its peak in 1996 with values below 2.5 per 10×5 m section (Fig. 2; comparisons from core data: 3.63 ± 0.25 ; $N = 54$ versus 2.46 ± 0.14 ; $N = 89$; normality test failed; Mann-Whitney test: $U = 1542.5$; $Z = 3.4856$; $P = 0.0002$).

Role of tank bromeliads in AGs surviving the droughts

In the dry zones in the Petit Saut area, out of 76 AGs recorded at the beginning of this survey in 1996, the tank bromeliad *Ae. mertensii* was present in the epiphytic composition of 49 of them and absent from the 27 others. None of the latter sheltered a live *N. goeldii* colony after 1998 (Fig. 4), likely due to the drastic 1997 dry season (Fig. 2C), and the epiphytes withered and died shortly thereafter. In contrast, of the 49 AGs with *Ae. mertensii*, eight (16.3%) sheltered a live *N. goeldii* colony in 2000 (Fig. 4). A comparison of the survival curves (AGs with versus without *Ae. mertensii*) resulted in a significant difference (Log-rank test: $\chi^2 = 19.24$; $df = 1$; $P < 0.0001$) showing a higher survival of AGs when *Ae. mertensii* is present.

Overall, we noted that AGs with *Ae. mertensii* that had lost their associate *N. goeldii* colony were occupied

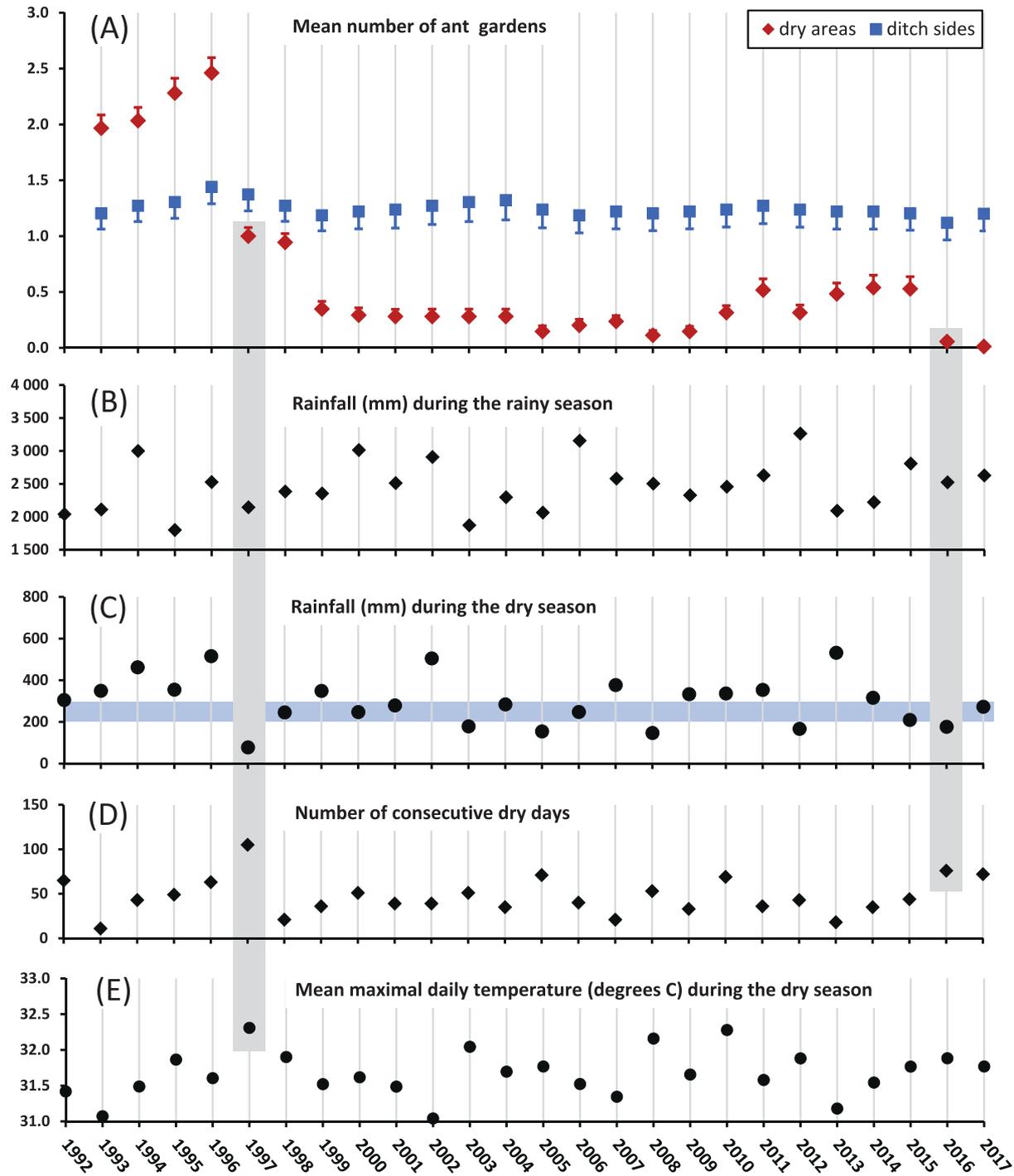


Fig. 2. Petit Saut area: comparisons of the mean numbers of ant gardens (AGs) per 10×5 m sections surveyed between zones affected by the dry season ($N = 89$) and zones situated along a ditch ($N = 59$) with information on the main climatic parameters (rainy season: December–June; dry season: August–November). The gray vertical bands highlight the relationships between severe dry seasons and the corresponding mean numbers of AGs (details in Appendix). The blue horizontal band delimits the threshold for the failure of colony foundations during severe dry seasons (i.e., 300 mm of rainfall), whereas many AGs did not survive the drastic dry seasons (i.e., 200 mm of rainfall or less).

secondarily by *Odontomachus haematodus* (Ponerinae) or *Camponotus cingulatus* (Formicinae); exceptionally we recorded *Neoponera villosa* (Ponerinae), *Azteca* sp., *Dolichoderus bidens* (both Dolichoderinae), *Ca. atriceps*, and *Ca. renggeri*.

Discussion

Using two different approaches conducted during long-term surveys, we show that *N. goeldii*-associated AGs can resist high temperatures and wide seasonal rainfall variations

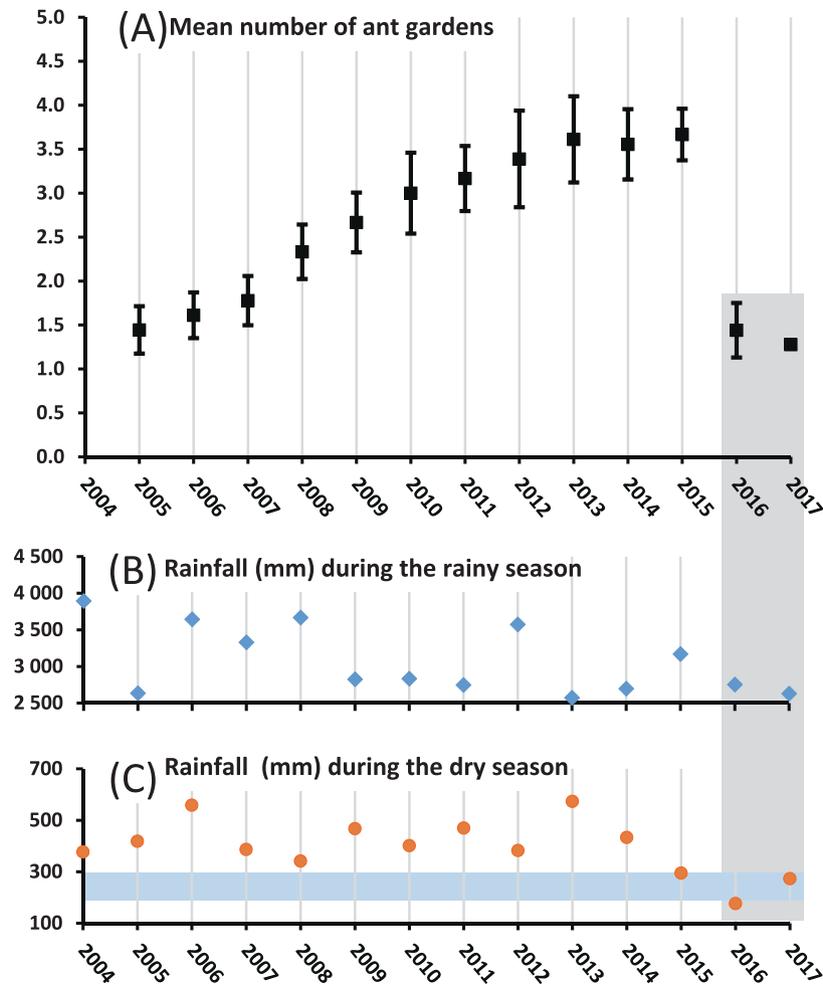


Fig. 3. Régina area: mean numbers of ant gardens per 10×5 m sections in the zone surveyed with information on pluviometry. The numbers of consecutive dry days and the mean maximal daily temperature are not shown due to low inter-annual variations (details in Appendix). The meaning of the gray vertical and blue horizontal bands are explained in the legend to Fig. 2.

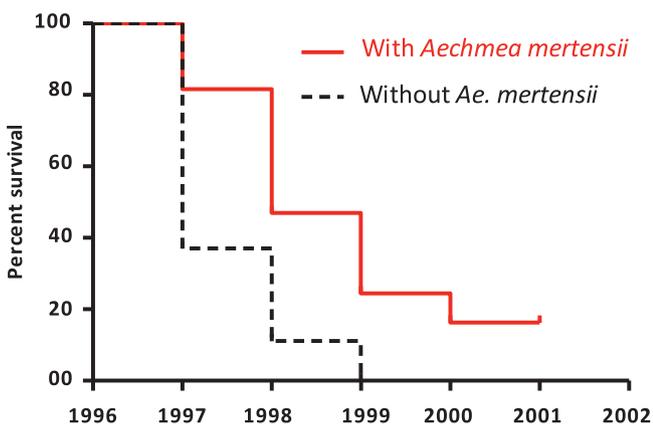


Fig. 4. Comparison of the survival of the *Neoponera goeldii* colonies in AGs with versus without the tank bromeliad *Aechmea mertensii* in their epiphytic composition (1996: *Ae. mertensii* belonged to the epiphytic composition of 49 of the AGs and was absent from the 27 others).

in dry pioneer formations, but not the drastic dry seasons illustrating their limits *vis-à-vis* drought. Also, the presence of the tank bromeliad *Ae. mertensii* in the epiphytic composition of the AGs favors their surviving the droughts.

Impact of climatic parameters on *Neoponera goeldii*-associated AGs

In Amazonia, the greater frequency of drastic dry seasons from 1997 to 2017 was mostly related to anomalous sea surface temperatures in the Atlantic Ocean amplified by the effects of deforestation and greenhouse gasses, although El Niño also played a role (Erfanian et al., 2017; Marengo et al., 2018; Sheldon, 2019; see also Appendix A).

The strong decrease in "active" AGs in the dry zones in the Petit Saut area, which started in 1997 (Fig. 2A), is not likely due to high temperatures because the maximum value noted there during the dry season (32.3 °C in 1997; Fig. 2) was lower than all those recorded in Régina (above 33 °C

except in 2013; see Appendix A: Table S3) where the number of AGs was increasing (Fig. 3). This is in line with their overall distribution which is positively related to temperature (Morales-Linares et al., 2021a). Indeed, resistance to high temperatures applies to both the epiphytes (see Müller, Albach & Zotz, 2018; Rodríguez-Quiel & Zotz, 2021) and the *N. goeldii* colonies that select sites exposed to the Sun; their workers forage nocturnally, thus avoiding high diurnal temperatures (Orivel & Leroy, 2011; see also Spicer et al., 2017 for arboreal ants being high temperature-tolerant).

The importance of humidity during the dry season was brought to the fore by the survey conducted along permanently wet ditches in Petit Saut while in Régina high seasonal rainfall permitted AGs to colonize a pioneer dry zone (Figs. 2, 3). Conversely, drastic droughts (e.g., 1997 and 2015–2016 in Petit Saut; 2016 in Régina) resulted in a strong decrease in AG densities in dry zones, showing the limits of their tolerance to dryness (Figs. 2, 3). Indeed, AG-epiphytes are well adapted to drought (Chávez-Sahagún et al., 2019; Zotz, 2016), even though, except for tank bromeliads, they depend on their associate ants to maintain moisture in the substrate where their roots are anchored; otherwise, they wither and die (Orivel & Leroy, 2011; Schmit-Neuerburg & Blüthgen, 2007). Although arboreal ant species are desiccation-resistant (Bujan, Yanoviak & Kaspari, 2016), colony foundation, a very exposed phase of their life cycle, is vulnerable to drought (Aron & Deneubourg, 2020).

After a strong decrease in AGs following a drastic drought, their likelihood of regeneration from the few remaining is obligatorily slow during subsequent years due to a lower production of new queens that, furthermore, need to successfully found new colonies. The failure of colony foundations and so the development of new AGs is likely due to the presence of a threshold situated around 300 mm of rainfall. Indeed, in the Petit Saut area, lower values were recorded only three times in 17 years (1980–1996) compared to nine times in 12 years (1997–2008) (see Appendix A: Fig. S1B). In the latter case, mild dry seasons in 2002 and 2007 had no visibly favorable effect (see Fig. 2). Because our censuses were conducted near the end of the dry seasons, this type of "delayed effect" reflects the balance between newly-formed AGs that survived and old ones that died. The return to mild conditions since 2009 was followed by an increase in new AGs only in 2010, whereas in 2015 enough AGs survived the drastic dry season to maintain a value similar to previous years (Fig. 2A, C).

Role of tank bromeliads in AGs surviving the droughts

We showed that the presence of the tank bromeliad *Ae. mertensii* buffers the impact of severe dry seasons (Fig. 4)

probably due to its ability to impound water at night when condensation permits dew to form on its cold leaves, compensating the lack of rainfall (Chávez-Sahagún et al., 2019; Zotz, 2016).

Thus, the water accumulated in the bromeliad tanks, gathered and transported by the associate ants to maintain moisture in the AG substrate, permitted the other epiphyte species to survive (see Orivel & Leroy, 2011; Schmit-Neuerburg & Blüthgen, 2007). At night, we frequently saw *N. goeldii* workers gathering drops of dew or water from the *Ae. mertensii* tanks and then transporting them to the nest. This is easily observable as they use surface tension to carry droplets of liquid between their mandibles (see illustration in Collet, 2004), a behavioral adaptation in most ponerine ants because they cannot store liquids in the crop due to the morphology of their proventriculus.

Furthermore, *Ae. mertensii* can survive for years after the death of the AG colony because it absorbs water and nutrients through specialized trichomes in its tanks. Also, after the death of their mutualist ants, AGs with *Ae. mertensii* are inhabited by opportunistic ant species, mostly *O. haematodus* and *Ca. cingulatus* (see Results), due to the scarcity of available arboreal nesting sites (Orivel & Leroy, 2011).

Spatial distribution of *N. goeldii*-initiated AGs

The selection of sun-exposed branches by *N. goeldii* founding queens (Orivel & Leroy, 2011) explains why their associate AGs are abundant in pioneer formations, particularly along paved and dirt roadsides. This was noted in this study, in Columbia (Martínez & Buitrago, 2017) and in central Amazonia where their density increases from rainforests to dry formations (Marini-Filho, 1999); relatively frequent in the xeric Brazilian caatinga (Madison, 1979), they are scarce in rainforest canopies (Dejean et al., 2018).

These AGs also occur in riparian rainforests as do other AG-ant species (Madison, 1979; Morales-Linares et al., 2016; see also Appendix A: Table S5). Riparian areas will be a refuge if droughts in Amazonia become more frequent and severe because streams and rivers will likely persist through greater total rainfall due to wetter rainy seasons (Espinoza et al., 2018; Marengo et al., 2018; see also Appendix A: Figs. S2B, C). Furthermore, AG survival is bolstered by the attractiveness of the seeds of the epiphytes associated with different AG-ant species, so that the latter grow the same epiphyte species (Orivel & Leroy, 2011). Thus, each AG-ant species benefits from the presence of the others as all participate in the formation of a seedbank of adequate epiphyte species. Finally, the ability of *N. goeldii*-initiated AGs to survive severe climatic conditions is also made possible by their dispersal along riverbanks and roadsides, or natural and artificial corridors interconnecting different vegetal formations (Naiman, Décamps & Pollock, 1993; Rodríguez-Iturbe, Muneeppeerakul, Bertuzzo, Levin &

Rinaldo, 2009) where they might find favorable growing conditions.

Conclusions

In Amazonia, extreme climatic events related to climate change translate into a greater frequency of severe droughts that might be detrimental to *N. goeldii*-associated AGs in dry zones, something particularly true if drastic successive dry seasons occur in the future. Yet, the ability of these AGs to also develop in riparian areas will permit many individuals to survive these droughts (see present results on wet zones situated along ditches) as, in parallel, wetter rainy seasons are predicted, ensuring the presence of streams and rivers. By benefitting from natural and artificial corridors, these AGs might later conquer new vegetal formations if mild conditions occur. These empirical results are in line with those conducted at the Neotropical scale on most AG-ant and AG-epiphyte species showing that this small network structure (i.e., 11 AG-ant and 20 AG-epiphyte species) where different ant species are associated with the same epiphyte species likely confers resistance to future climatic changes (Morales-Linares et al., 2021a,b). Indeed, mutualisms can promote species survival as well as ecological diversity and resistance to invaders (Qian & Akçay, 2020).

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2022.02.004](https://doi.org/10.1016/j.baae.2022.02.004).

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.baae.2022XXXX](https://doi.org/10.1016/j.baae.2022XXXX).

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