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RESEARCH ARTICLE

Distance From Nest and Climate Explain Geographical Trends of Harvester Ant's Food Resource Use: A Multi-Species Approach

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ABSTRACT

Main: Animals not only forage for abundant and nearby resources, but their diets can also be influenced by abiotic and geographic factors. This often results in non-random interactions among species. We investigate how seed density, distance from nest, abiotic (e.g., climate stability, temperature, precipitation) and geographic factors (e.g., latitude, elevation and continental hemisphere) influence the removal of food items (i.e., seeds and dead arthropods) by *Pogonomyrmex* species.

Location: South and North America, from Patagonia to the Rocky Mountains.

Taxon: Genus *Pogonomyrmex* (Formicidae: Hymenoptera).

Methods: Conducting standardised experiments, we performed a seed removal experiment and an assessment of the items retrieved by ant workers of 160 nests from eight *Pogonomyrmex* spp. at 16 sites extending the American continent.

Results: *Pogonomyrmex* ants native to North America removed more seeds than their South American counterpart. In general, results align with optimal foraging theory, indicating a higher probability of seed removal near ant nests. High climate stability correlated with lower seed predation rates, emphasising seed consumption's significance in historically arid environments. Increased precipitation and temperature led to reduced removal of food resources, suggesting reduced water availability and lower mean temperatures increases the consumption of seeds by harvester ants.

Conclusions: Overall, *Pogonomyrmex* ants' food resource use is influenced by a combination of factors such as region, distance from the nest and climate. This study underscores harvester ants' potential impact on plant distribution over large spatial scales consuming seeds from the immediate proximity of their nest and preventing establishment.

1 | Introduction

A main goal of ecology and biogeography is to unravel the variation of ecological interactions over space since they are fundamental in generating biodiversity and maintain the functioning of the ecosystems worldwide (Andresen, Arroyo-Rodríguez, and Escobar 2018). For example, antagonistic interactions such as herbivory, which are distributed all over the world, contribute to maintain a high diversity of tropical plants by reducing the size of their populations by exerting pressures over their abundance/frequency allowing rare species to coexist (Comita et al. 2014; Herrera and Pellmyr 2009; Janzen 1970). Moreover, post-dispersal seed predation (hereafter 'seed predation') can play an important role on the evolution of plants and the structure of their communities by acting as a selective force on seeds with different traits and by influencing the establishment and survival of plant species over space (Harms et al. 2000; Hubbell 1980). Various groups of seed predators, such as rodents, birds and ants, exert contrasting ecological and evolutionary pressures on plants (Peco, Laffan, and Moles 2014), with the relative importance of each group varying across different environments (Brown, Reichman, and Davidson 1979; Lopez de Casenave, Cueto, and Marone 1998). However, most studies assessing the role of granivores (i.e., predators of grass, shrub and forb seeds; Hulme and Benkman 2002) have traditionally considered seed predation by single species on small spatial–temporal scales, neglecting that granivores are highly diverse and widely distributed. Despite the ecological and evolutionary relevance of granivory, we still lack theoretical and robust empirical evidence (based on standardised methods; Marone, Lopez de Casenave, and Cueto 2000) to understand granivory patterns and, consequently, their impact on plant populations at large spatial scales (c.f., Hargreaves et al. 2019).

The seed predation rates can be influenced by seed abundance, with predators choosing to forage on common and spatially abundant resources, rather than rare and spatially distant resources (Harms et al. 2000; Hulme and Benkman 2002; Janzen 1971). In addition, seed predation can be influenced by the seed density in a certain area. Janzen (1970) and Connell (1971) highlighted the importance of density-dependent seed predation in tropical tree dynamics. With greater distances from adult trees, seeds have a more uniform distribution (lower density), which increases survival and thus facilitates species co-existence (due to a reduction in seed predation; Comita et al. 2014). However, this hypothesis also has been shown to be dependent on the environment and influenced by life history stages or life forms (Hyatt et al. 2003). For example, temperate and tropical regions have shown contrasting results (Hyatt et al. 2003). Therefore, to better understand granivory and its consequences, it is essential to evaluate seed removal patterns by similar species and across large distribution areas (Hargreaves et al. 2019; Peco, Laffan, and Moles 2014). From the granivore's point of view, the relationship between removal distance, resource traits and the decisions they must make are determined by the optimal foraging theory (Stephens and Krebs 1986). According to this theory, animals make decisions about where, when and what to eat to maximise their net energy intake per unit time and effort, while minimising costs such as predation risk and handling time (MacArthur and Pianka 1966; Stephens and Krebs 1986).

Several studies have shown that animals forage not only for abundant and nearby resources, but that other factors may also contribute to the non-randomness of the interaction between species (see Marjakangas et al. 2022; Escribano-Avila et al. 2018; Soberón 2007). For instance, resource traits (e.g., size, caloric content, nutritional value) and climate context can determine how species interact and seek resources (Dalsgaard et al. 2013; Dáttilo and Vasconcelos 2019; Escribano-Avila et al. 2018; Soberón 2007). The historical climate stability (hereafter 'climate stability') represents the product of the stability estimates of precipitation and temperature (over the last 21,000 years; Owens and Guralnick 2019). The climate stability can help understand current climate and consequently how species and their ecological functions accumulate in certain regions of the world (Dynesius and Jansson 2000; Fjeldså, Lambin, and Mertens 1999; Sandel et al. 2011). Recently, climate stability has also been identified as a potential factor shaping species interactions (e.g., the specialisation of plant-floral visitor ecological networks increasing with climatic stability; Burin, Guimaraes and Quental 2021; Dalsgaard et al. 2013; Luna et al. 2022). This is because climate, in general, can affect species distribution and resource availability, which influences how species co-occur in space and how they forage (MacArthur and Pianka 1966; Brown et al. 2004). However, it is unknown if climate stability affects granivory. On other hand, current climate can determine how species interact, as precipitation and temperature can shape the importance and role of species within a community and impact how resources are used and partitioned (Corro et al. 2022; Rico-Gray et al. 2012). Current climate plays a crucial role in shaping seed predation by ants, as they directly influence ant behaviour, foraging patterns and the availability of resources, which ultimately impacts ecosystem dynamics (Nascimento, Câmara, and Arnan 2022; Parr and Bishop 2022). Although the effect of climate on a species interaction varies according to the interaction type (i.e., granivory, frugivory, pollination), knowing the general relationship between species interactions with historical and current climate helps us to better understand and predict their variation and correlates over space ultimately allowing us to understand ongoing and future climate changes caused by anthropogenic impacts.

Harvester ants, such as those belonging to the genus *Pogonomyrmex* Mayr, are a dominant component of invertebrate communities in deserts and grasslands (Johnson 2001). They can remove and consume large amounts of seeds and, to a lesser extent, non-plant resources such as dead arthropods, with outsized impacts on plant diversity and composition (i.e., food webs), soil modification and nutrient transport (i.e., energy flows; MacMahon, Mull, and Crist 2000). The 93 described species of *Pogonomyrmex* inhabit (Johnson 2021), mainly at middle latitudes in North and South America. In arid zones within these regions, rates of seed predation by ants can vary. For instance, granivory (including birds and mammals as seed predators) in North America is exceptionally high, but low levels are the norm for most arid zones (Johnson 2001; Lopez de Casenave, Cueto, and Marone 1998). Empirical evidence has shown that ants are expected to prey less on seeds at higher elevations and in temperate/cold regions, mainly because temperature limits their activity there (MacKay 1985; Hargreaves et al. 2019). Although the effect of granivores is recognised at a local scale, we still lack empirical evidence to better understand the role of granivory, particularly in ecosystems where granivores are a key element that influences plant populations, as is the case in arid environments with an great abundance of *Pogonomyrmex* harvester ants (Johnson 2001; MacMahon, Mull, and Crist 2000). Overall, conducting standardised experiments (across multiple sites and species) and testing hypotheses considering multiple factors can reveal how granivory influences resource allocation, food selection and foraging behaviour across diverse ecological communities (see Thompson 2005).

Here we investigated seed removal (a proxy for seed predation) and food selection trends by harvester ants of the genus *Pogonomyrmex* over a hemispheric scale through a standardised multi-site sampling experiment, with the main goal to disentangling foraging patterns of this genus and their possible drivers. We tested how seed density and distance from nest (as proxies of seed spatial abundance), abiotic (e.g., climate stability, temperature, precipitation) and geographic factors (e.g., latitude, elevation and continental hemisphere) influence the removal of food items (i.e., seeds and dead arthropods) by *Pogonomyrmex* species. Under the framework of the optimal foraging theory, ants maximise their net energy intake while minimising costs, so we expect a higher removal of seeds near than far from the nest and at higher vs. lower seed densities. We also hypothesise that the higher the latitude and lower the elevation, the greater the number of seeds removed, because the centre of *Pogonomyrmex* diversity (higher abundance of individuals and species richness) is found at middle latitudes and low elevations (Johnson 2021), contrary to other seed predator groups (Hargreaves et al. 2019). Moreover, because North American *Pogonomyrmex* species tend to be larger and have bigger nests compared to those in South America, we expect that North American ants would remove more seeds than their South American counterparts (Johnson 2000; Nobua-Behrmann et al. 2013). In general, we postulated that current climate such as higher temperatures should increase ant foraging and consequently seed predation and that precipitation should play an opposite effect, since these ants evolved in environments with low precipitation (e.g., arid zones; Brown, Reichman, and Davidson 1979). Seed predation by ants may be favoured in less predictable environments (i.e., unstable and seasonal ecosystems) because arthropod prey is scarce during dry or cold seasons, but seeds are usually a common and highly profitable resource year round, in addition to being managed and stored over extended periods by ants (Brown, Reichman, and Davidson 1979; MacKay and MacKay 1984). Therefore, we expected that the lower the climatic stability the higher the seed removal rates. In less predictable environments it is expected that ants might also have a diet composed of multiple resources (both seeds and dead arthropods) or that colonies switch between resources depending on their availability (Vullo et al. 2024).

2 | Material and Methods

2.1 | Sampling Sites and Species Description

We conducted our study in 16 sites located from the Argentine Patagonia to the Rocky Mountains of the United States of America (Figure 1A, Table S1). All sampling locations were natural areas. We studied eight abundant *Pogonomyrmex* species from which four species (*P. salinus* Olsen, 1934, *P. badius* (Latreille, 1802), *P. occidentalis* (Cresson, 1865) and *P. barbatus* (Smith, 1858)) belong to the North America faunal group and four species (*P. naegelii* Emery, 1878, *P. mendozanus* Cuezzo & Claver, 2009, *P. pencosensis* Forel, 1914 *and P. sanmartini* Kusnezov, 1953) belong to the South America faunal group (Figure S1, Table S1).

We performed a standardised seed removal experiment and an assessment of the items retrieved by ant workers at the 16 sites. In each one we selected 10 nests of the *Pogonomyrmex* species (one species was tested in each site) located at a distance of at least 20 m from another colony ($n = 160$ ant nests representing eight species). To perform the samplings in the summer/rainy seasons when the ants are more active, the sites were sampled between May and August for North America (year

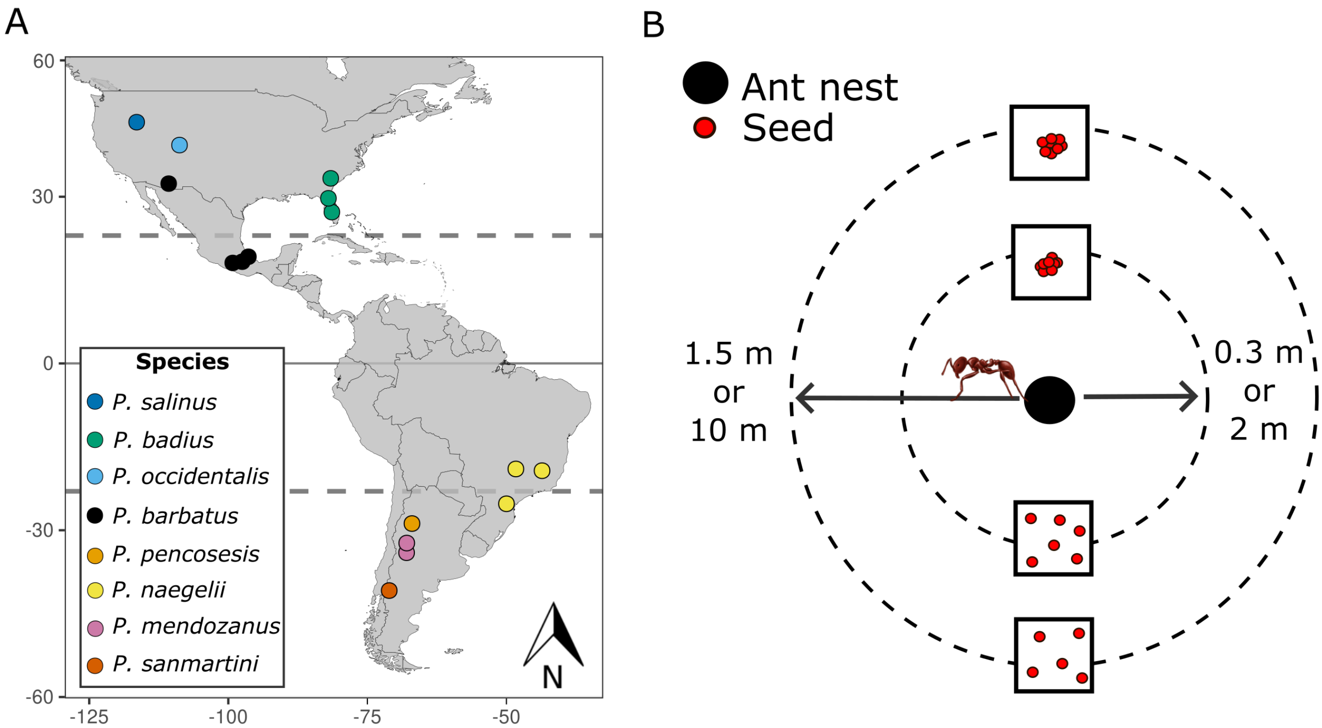

FIGURE 1 | (A) Sampling locations and species of the genus *Pogonomyrmex* studied. (B) Experimental design. The dashed lines indicate the distances from the nest entrance at which the experimental units were placed for species with large or small home ranges for the two distance treatments (near, far). The two seed density treatments (low, high) were located at each distance.

2021) and November and February (year 2021–2022) in South America.

2.2 | Seed Removal Experiment

Because the *Pogonomyrmex* species included in this study vary in home range size, as well as body size (e.g., head length), we divided them in two categories (Table S1) based on previous knowledge: small home range (maximum foraging distance up to 2 m from the nest entrance) and large home range (> 2 m maximum foraging distance; e.g., Belchior, Del-Claro, and Oliveira 2012; Luna, García-Chávez, and Dáttilo 2018). This allowed us to avoid placing the seeds in areas where ants do not forage. Based on the literature, only *P. naegelii* has a small home range. *Pogonomyrmex naegelii* forages for an average distance of less than 2 m (1.55 m; Belchior, Del-Claro, and Oliveira 2012), whereas the other species have longer mean foraging distances (i.e., large home range): *P. badius* (3.4 m; Harrison and Gentry 1981); *P. mendozanus* (3.8 m; Pol, Lopez de Casenave, and Pirk 2011); *P. sanmartini* (maximum foraging distance of at least 10 m, *personal communication*); *P. pencosensis* (8.3 m; Aranda-Rickert and Fracchia 2012); *P. occidentalis* (9.7 m; Crist and MacMahon 1991); *P. salinus* (12 m; Schmasow and Robertson 2016); *P. barbatus* (12.4 m; Luna, García-Chávez, and Dáttilo 2018). In addition, there are different ecologies/foraging strategies for the North vs. the South American species. Regarding the sampled species, those from South American species generally foraging solitarily whereas the selected North American species are mostly column or trunk trail foragers (Crist and MacMahon 1991; Pol, Lopez de Casenave, and Pirk 2011; Belchior, Del-Claro, and Oliveira 2012; Schmasow and Robertson 2016; Luna, García-Chávez, and Dáttilo 2018). For the experiment, we used commercial white millet seeds (*Panicum miliaceum* L., Poaceae) because it has traits similar to most grass seeds preferred by *Pogonomyrmex* species (Pirk and Lopez de Casenave 2011; Miretti, Lopez de Casenave, and Pol 2019) and represents a standardised seed resource in terms of nutrient content and morphological traits such as size (1.73 ± 0.2 mm length, [mean ± SE], $n = 50$), texture and shape. Additionally, the absence of elaiosomes (a lipid-rich seed appendage) imply that removed seeds are predated rather than secondarily dispersed (Anjos et al. 2020; Aranda-Rickert and Fracchia 2011). Pilot experiments were carried out at two sites (in Brazil with *P. naegelii* and in Mexico with *P. barbatus*) to test the attractiveness of these seeds, and the results showed that *Pogonomyrmex* species successfully removed white millet seeds after a short inspection period (a few seconds). In addition, we also tested the distance and area of the experimental unit, the number of seeds in the experimental unit and the viability of the seed after treatment to adjust our standardised protocol (see below). Before the experiment, the seeds were placed in a common freezer for 12 h (seed treatment) to avoid the germination of seeds that were not removed or lost after the experiment.

The experiment was designed to assess how the distance from the nest (i.e., proximity) and resource density affect seed removal by *Pogonomyrmex* ants. To evaluate the effect of distance, the area around each of the studied nests was first divided into two zones: (i) near (2 m from the nest entrance for species with large home ranges and 30 cm for species with small home ranges) and (ii) far (10 m from the nest entrance for species with large home ranges and 1.5 m for species with small home ranges; Figure 1B). Once the distance areas were set, we placed one experimental unit at each of the distances (near and far), that was further divided into sub-plots to assess how seed density affects seed removal (low or high density; Figure 1B). For species with large home range we placed (i) 20 seeds in an area of 1 × 1 m (0.002 seeds per cm^2; low density) and (ii) 20 seeds in an area of 25 × 25 cm inside the 1 × 1 m quadrant (0.032 seeds per cm^2; high density), whereas for species with small home range we placed (i) 20 seeds in an area of 20 × 20 cm (0.05 seeds per cm^2; low density) and (ii) 20 seeds in an area of 5 × 5 cm inside the 20 × 20 cm quadrant (0.8 seeds per cm^2; high density). In summary, our experimental design included 40 experimental units per site since each of the 10 ant nests had 4 experimental units (2 distances × 2 densities × 10 nests = 40 experimental units; Figure 1B). Our experimental design is a block (i.e., the nest) design, each block receiving four treatments: *low density/near the nest*, *low density/far from the nest*, *high density/near the nest*, *high density/far from the nest*.

Twenty-four hours before the start of the experiment, we established the experimental units in a quadrant of bare soil, eliminating all branches, rocks and leaves from the soil surface. During this time, based on the direction of movement of the most workers, we have decided on the orientation of the experimental units to optimise seed removal. The experimental units were monitored over the period when harvester ants were more active in each location (e.g., late morning and early afternoon). Two hours after the experiment started (i.e., during the peak activity of some species such as *P. naegelii*), we recorded the number of seeds that were removed in all experimental units.

2.3 | Assessment of Items Retrieved

To assess the items retrieved (‘native’ seeds and dead arthropods) of each *Pogonomyrmex* species ($n = 144$ ant nests, 7 species), we collected food items retrieved by ant workers from each nest for 45 min (during the period of highest colony activity). The number of ant nests in this part of the study was lower since it was not possible to assess the items retrieved by ant workers of all the species in the sampling sites (e.g., *P. occidentalis*). The assessment of items retrieved was done by using a sheet of A4 paper as a tool to isolate and capture the worker in their course back to the nest, and a fine brush to remove the food item from their mandible. The collected material was later categorised in the laboratory as seeds (fruits of a single seed, such as caryopses and achenes) or dead arthropods (whole or fragmented organisms).

2.4 | Environmental Data

To test how abiotic and geographic factors contribute to explain harvester ant's food resource use, we obtained climate and geographic variables (absolute latitude and elevation) for each location (Table S1). We considered three climate variables describing the current and historical conditions of the sampling sites: mean annual temperature (MAT), mean annual precipitation (MAP) and climate stability. For each variable, a global raster was obtained, the location of each site was added, and climate conditions were extracted. Temperature and precipitation layers were obtained from WorldClim 1.4 (resolution of 2.5′; Hijmans et al. 2005). The climate stability raster (2.5° of resolution) was obtained by multiplying two different rasters: (i) temperature stability and (ii) precipitation stability. The values of the resultant raster were scaled to range from 0 (low climatic stability) to 1 (high climatic stability). These data cover the entire climatic stability of our planet during the last 21,000 years, covering a large spatial and temporal scale. Temperature and precipitation stability were calculated by estimating the inverse of the mean standard deviation of the temperature and precipitation regimes between time slices of 1000 years over the last 21,000 years (since the last glacial maximum) with the *climateStability* (Owens and Guralnick 2019) and *terra* (Hijmans 2023) packages in R version 4.3.1 (R Core Team).

2.5 | Data Analysis

2.5.1 | Seed Removal Experiment

We used a generalised linear mixed model (GLMM) to test the effects of the fixed factors, distance from the nest entrance (i.e., near and far), seed density (i.e., low and high density) and continental hemisphere (North or South America), on the probability of white millet seed removal by the different *Pogonomyrmex* species. The distance from the nest to the experimental unit was proportional to the species' home range size (Figure 1B), controlling for this effect. For this model, we declared a series of random effects: sampling site, nest (block) and species. It is worth mentioning that the approach used had the main objective to understand geographical trends of *Pogonomyrmex* species interactions with resources, rather than focusing on single species interactions. This is why sampling site (i.e., research group), nest, and species are considered as random factors, since we needed to control for the variation of each of the categories introduced to our statistical model. The model was fitted with a binomial error distribution and *logit* link function. Moreover, the variation explained by the model was quantified using R^2 (m) (i.e., marginal R^2), which describes the variation explained by the fixed factors, and R^2 (c) (i.e., conditional R^2), which describes the variation explained by the fixed and random factors (Nakagawa and Schielzeth 2013). In this case, we used the Delta method for the estimation of both marginal and conditional R^2. After assessing the role of distance and density in seed removal, we assessed the role of geographic and climatic variables on seed removal by each nest. For this, we made a sum of how many seeds were removed by each nest in the experiment; this was possible since all the nests studied were subjected to the same experimental design. In this way, we evaluated at a hemispheric level how climate and geography affect seed removal. The model was fitted using the number of seeds removed in each colony regardless of the distance from the nest entrance and the density of seeds. However, although here we evaluate the effects of climatic and geographical variables, this does not mean that the effect of other factors (distance and density) is left aside. We used a general additive model (GAM) with sampling site (i.e., research group) and species as random factors. For the climatic (mean annual temperature, mean annual precipitation and climate stability) and geographic variables (latitude and elevation) we used the thin plate regression splines with a base dimension of $k = 4$ in all cases, which is sufficient to predict nonlinear responses including those with marked asymptotic behaviour. Because seed removal events are expected to be clustered by the collective foraging activity of ants, the GAM model was fitted with the negative binomial distribution and the *logarithmic* link function with a theta value of 0.3 (theta defines the shape of the negative binomial distribution). All environmental variables were standardised by subtracting the mean of each climate factor from the dataset and dividing this by its standard deviation. This step was carried out to ensure that the variables have a mean of 0 and a standard deviation of 1, which facilitates meaningful analysis.

2.5.2 | Assessment of Items Retrieved

We used GLMM to assess the number of items retrieved by *Pogonomyrmex* ants. The fixed factors were the type of item removed (i.e., native seeds and dead arthropods), mean annual temperature, mean annual precipitation and climate stability. The random factor in the model was the identity of the nest nested within each sampling site. The model was fitted with the negative binomial distribution and the *logarithmic* link function. For this model, we additionally measured its corresponding marginal and conditional R^2 values using the Delta method (Nakagawa and Schielzeth 2013). For our analyses we used R version 4.4.0 (R Core Team 2024) with the packages lme4 (Bates et al. 2015), boot (Davison and Hinkley 1997), car (Fox and Weisberg 2019), multcomp (Hothorn, Bretz, and Westfall 2008), mgcv (Wood 2003) and DHARMa (Hartig 2022) for model diagnosis.

3 | Results

3.1 | Seed Removal Experiment

Our seed removal experiment showed that more seeds were removed by *Pogonomyrmex* ants when they were located near their nest (9.97 ± 0.45 removed seeds [mean ± SE]) compared to when they were located far from the nest (6.41 ± 0.39). Seed density only affected the number of seeds removed when they were closer and at low density (10.43 ± 0.62) than when seeds were closer and at high density (9.52 ± 0.64; Table 1a; Figure 2A). Conversely, we observed that *Pogonomyrmex* ants native to North America remove significantly more seeds (11.17 ± 0.39) compared to those from South America (4.37 ± 0.37; Figure 2B). Note that this result shows the trends of all the species considered in the study without focusing on a single species, since our approach aimed to find general patterns.

Seed removal was negatively associated with climate stability, which explained 68% of the total model deviance (pseudo-$R^2 = 0.68$; Figure 2C). There was no significant relationship between mean annual precipitation and seed removal. Mean annual temperature was removed from the final model as it was collinear with climate stability; however, in a model where all variables were included (latitude, elevation, temperature, precipitation and climate stability), its effect on seed removal was not statistically significant (temperature: $F = 0.98$, $p = 0.08$; precipitation: $F = 1.32$, $p = 0.25$; latitude: $F = 0.82$, $p = 0.36$; elevation: $F = 0.04$, $p = 0.84$) but the effect of climate stability was significant ($F = 7.72$, $p = 0.006$). In general, we found no significant effect of geographical variables (i.e., latitude, elevation) on seed removal (Table 2).

3.2 | Assessment of Items Retrieved

When we assessed which type of food item was retrieved by *Pogonomyrmex* ants (seed or dead arthropods) we found that seeds (43.74 ± 7.01 retrieved seeds by colony [mean ± SE]) were collected more than dead arthropods (2.39 ± 0.23 retrieved arthropods by colony; Table 1b). The collection of food items by *Pogonomyrmex* ants decreased with increasing mean annual precipitation (Figure 3A) and temperature (Figure 3B). We

TABLE 1 | Results from the fitted GLMM listed by model: (a) Seed removal experiment and (b) assessment of items retrieved by ants.

Model	Factor	χ^2	df	*p*
(a) Seed removal experiment	Distance (Di)	284.98	1	**0.0001**
Marginal $R^2 = 0.37$; Conditional $R^2 = 0.97$	Density (De)	2.04	1	0.15
	Continent hemisphere	9.32	1	**0.002**
	Di × De	5.87	1	**0.01**
(b) Assessment of items retrieved by ants	Item type	147.59	1	**0.0001**
Marginal $R^2 = 0.56$; Conditional $R^2 = 0.83$	Mean annual precipitation	12.31	2	**0.001**
	Mean annual temperature	14.57	2	**0.002**
	Climate stability	2.14	2	0.34

Note: Values in bold denote statistical significance. Deviance values were obtained by using Wald Type III χ^2 tests.

FIGURE 2 | (A) Mean (±SE) removal probability for seeds offered experimentally near or far from the nest entrance and at high or low densities. Raw data for each treatment is also shown. Different letters denote statistical differences between the treatments. (B) Mean (±SE) removal probability for seeds offered experimentally by *Pogonomyrmex* faunal groups of north or South America. Raw data for each treatment is also shown. (C) Relationship between the total number of removed seeds per colony and the climate stability (i.e., the product of the stability estimates of precipitation and temperature) of sampling locations. The line denotes the adjusted slope for the data, and the ticked lines denote its standard error. Data for each species are shown with a different colour (colours are the same as in Figure 1A).

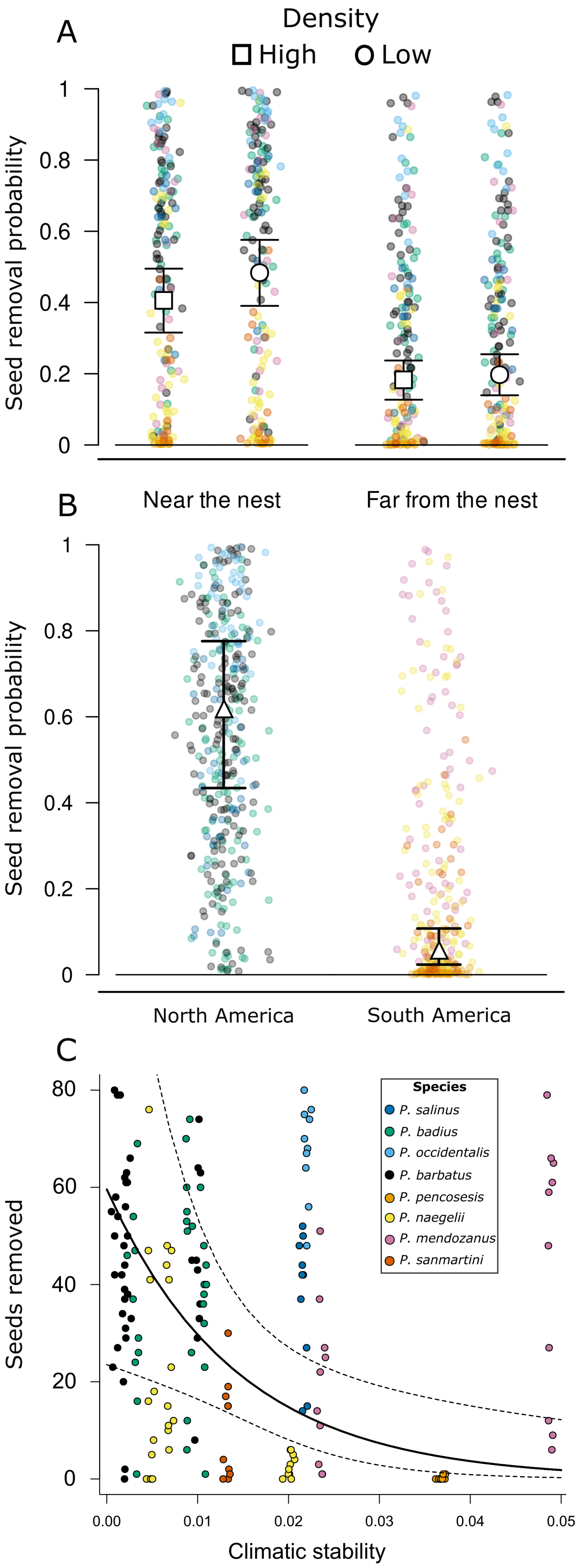

FIGURE 2 | Legend on next page.

found no relationship between the collection of food items with climate stability (Table 1b).

4 | Discussion

Our standardised multi-site experiment across the American continent showed that the closer to the nest a resource is, the higher the probability of it being removed by *Pogonomyrmex* species, although seed density only influenced the number of seeds removed when they were closer to the nest. This result partially supports our hypothesis, which posited that these factors (i.e., seed density and distance from nest) could indeed impact seed removal (but see Rissing 1988). This is consistent with optimal foraging theory which predicts that most species prefer to travel shorter distances to find food resources (see Stephens and Krebs 1986), resulting in shorter foraging time and optimised energy investment in collecting resources (Fewell 1988). On the hand, we observed that *Pogonomyrmex* ants native to North America removed more seeds than their South American counterpart. Moreover, we observed that with increasing precipitation and temperature (mean annual), ants remove fewer items (both seeds and dead arthropods), indicating that food removal levels of *Pogonomyrmex* ants are strongly shaped by reduced water availability and lower mean temperatures, partially supporting one of our climate hypotheses. We also observed that the more stable the climate (over the last 21,000 years), the lower the rates of seed removal, consistent with seeds having been a major component of ant diets in historically highly seasonal arid environments, for example, which is consistent with a commonly advocated hypothesis postulated more than 50 years ago by Brown, Reichman, and Davidson (1979). Finally, latitude and elevation did not impact resource removal rates, rejecting our hypothesis regarding the geographical variables. In summary, our findings suggest that different factors play a crucial role in predicting the interactions between granivores and resources on extensive spatial scales. The fact that distance (a factor already known to affect foraging in *Pogonomyrmex* ants at the species level and at local scales) can be detected by studying several species at a hemispheric scale indicates the consistency of some general patterns within this group of harvester ants that could provide valuable information on the dynamics of seed predator effects, which are discussed below.

TABLE 2 | Results of the GAM model fitted to assess the relationship between seed removal with climatic (mean annual temperature, mean annual precipitation and climate stability) and geographic variables (latitude and elevation).

Factor	*F*	df	*p*
Latitude	0.007	1	0.93
Elevation	2.98	1	0.08
Mean annual precipitation	2.83	1	0.09
Climate stability	7.32	1	**0.007**

Note: Values in bold denote statistical significance.

Collecting resources in the immediate vicinity of the nest can be more effective for harvester ants in terms of energy intake (Anjos et al. 2019; Schmasow and Robertson 2016). Higher rates of seed removal near the nest by *Pogonomyrmex* ants have already been reported (Luna et al. 2021; Pol, Lopez de Casenave, and Pirk 2011), but in this case our result comes from an experiment on a large spatial scale involving eight species. It is worth mentioning that despite each species living in very different environments that are influenced by many different factors (e.g., temperature, precipitation, etc); we were able to identify distance as a factor that affects all the studied species. This

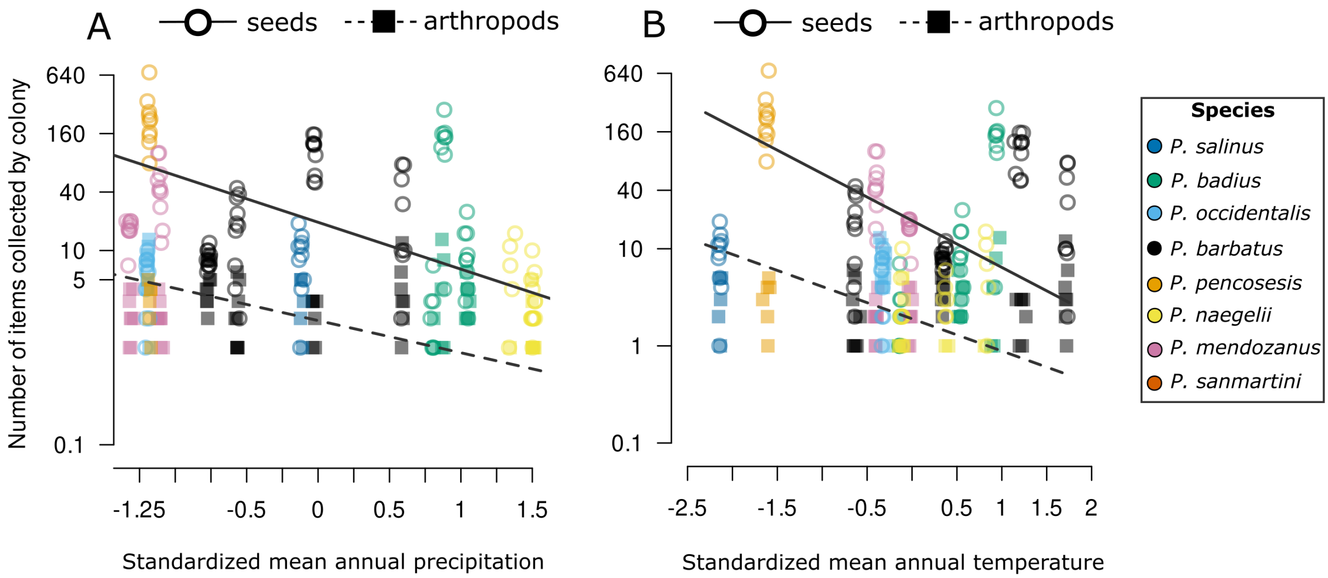

FIGURE 3 | Relationship between the number of items (seeds or arthropods) retrieved by colony and the standardised mean annual precipitation (A) and the standardised mean annual temperature (B) of sampling locations. The lines denote the adjusted slopes for the data. Negative values of the standardised mean annual precipitation and temperature correspond to individual values below the average considering all the sampled sites, while positive values correspond to individual values above the total average. Data for each species are shown with a different colour (colours are the same as in Figure 1A).

result is expected according to optimal foraging theory, but here we also give empirical evidence that is consistent despite the context of each of the studied species. Optimal foraging theory is widely recognised as the theoretical framework that distinguishes the main factors determining the feeding strategies of most species. For example, along the entire Norwegian coast, the establishment of seabird colonies in certain locations is based on minimising the distances between breeding and foraging sites (driven by availability and predictability of fish larvae), which facilitates foraging for central-place foragers (Sandvik et al. 2016).

Harvester ants are central-place foragers, a strategy that drives the evolution of a generalist diet that takes advantage of all available resources around the nest (Orians and Pearson 1979; Rico-Gray and Oliveira 2008). The fact that the studied species remove more seeds from the immediate proximity of their nests may have implications for plant distribution because this behaviour may not allow the establishment of seedlings from species that are collected immediately surrounding the nest (Pirk and Lopez de Casenave 2014). This impact on plant distribution has been discussed and recognised for at least two decades (MacMahon, Mull, and Crist 2000); however, here, we provide empirical evidence that supports previous hypotheses of the possible effects of *Pogonomyrmex* ants on plants which were in some cases just anecdotal (MacMahon, Mull, and Crist 2000; Taber 1999).

Our results revealed no relationship between seed removal rates and latitude, aligning with findings from a global literature review that investigated the impact of seed predation on over 200 plant species (Moles and Westoby 2003). Despite current empirical studies that have reinforced the well-established pattern of lower rates of granivory by vertebrates and invertebrates at higher latitudes (see Hargreaves et al. 2019), we expected an opposite pattern. However, we observed that *Pogonomyrmex* ants native to North America removed more seeds than those that live in South America. This might be because *Pogonomyrmex* ants in North America are larger and build bigger nest (up to 10,000 workers by colony) compared to those species in South America (Johnson 2000; Nobua-Behrmann et al. 2013). The larger colony size and nest structure in North American species are adaptations to the harsher, more resource-scarce environments they inhabit (Brown, Reichman, and Davidson 1979). In these arid regions, storing a significant amount of food is crucial for colony survival during periods of scarcity, which drives their more intensive seed harvesting behaviour (Taber 1999). In contrast, South American *Pogonomyrmex* ants typically face more stable and abundant resource availability (e.g., Cerrado savanna vs. Sonoran desert), reducing the need for large-scale seed removal and extensive food storage (Brown, Reichman, and Davidson 1979; Taber 1999). Regarding elevation, in the small range sampled (38–1610 m a. s. l.), *Pogonomyrmex* ants seem to have overcome the high elevation conditions imposed by the temperature and shorter growing season. For instance, MacKay (1985) showed that *P. montanus* (located at 2100 m) invested a higher percentage of the accumulated energy in colony growth compared to other *Pogonomyrmex* species located at 300 and 1500 m. However, it is important to note that high elevation can limit the occurrence of the harvester ants, just as it does for most species (MacArthur 1972; Rahbek et al. 2019). For instance, there are only a few *Pogonomyrmex* species that inhabit regions above 3000 m, which were only recently described in the high elevation altiplano habitats of northern Argentina and Chile (Johnson 2021). An evaluation of the removal rates in the *Pogonomyrmex* species of these high-altitude localities would allow this hypothesis to be tested more decisively.

The negative relationship we found between climate stability and seed predation rates can be explained by the hypothesis that granivory evolved in unstable (e.g., arid) environments (Brown, Reichman, and Davidson 1979). Under these conditions, invertebrates (a high protein resource) are scarce throughout the year and seeds are a more constant and predictable food resource (Brown, Reichman, and Davidson 1979). *Pogonomyrmex* species most likely evolved from a carnivorous ancestor that prevailed in arid environments (Wheeler 1910), which is further supported by the phylogenetic relationship between *Pogonomyrmex* and its sister genus *Hylomyrma* Forel. Both genera constitute a well-supported clade sister to *Patagonomyrmex* Johnson & Moreau, and collectively form the tribe Pogonomyrmecini, restricted to the American continent. Species in *Patagonomyrmex* and *Hylomyrma* are found in mesic habitats and are not specialist seed harvesters (Ward et al. 2015), and granivory and the preference for arid environments are evidently derived traits for *Pogonomyrmex* (Ward et al. 2015). The divergence between *Pogonomyrmex* and *Hylomyrma* and, thus, the putative adaptation to arid environments may be older (48–50 Ma; Ward et al. 2015) compared to the measured climate stability (since the last glaciation). Beyond that, these adaptations mostly likely resulted in many radiation processes of harvester ant species at places where *Pogonomyrmex* and *Hylomyrma* diverge. In our study, the influence of historical and current climate seems to be determined more by precipitation than by temperature, and this may be because the latter varies an order of magnitude less than precipitation on the data collected. Other studies have highlighted that climate stability may play a role in determining how species interact. For instance, plant-floral visitor interactions may have developed lower specialisation in more stable environments because generalist lineages have prevailed in such environments (Burin, Guimaraes and Quental 2021; Luna et al. 2022; Schleuning et al. 2012).

Temperature has shown idiosyncratic effects on how species interact. Here, we found that temperature can explain how harvester ants interact with seeds and arthropods. On local and regional scales, temperature increases seed predation (Davis and Raghu 2010; Orrock et al. 2015), mainly in desert regions (Luna et al. 2021). However, in these regions night-time temperatures drop dramatically, especially during the winter at high latitudes (e.g., Parque Nacional Nahuel Huapi in Patagonia). In other words, with this temperature range, these desert regions experience lower mean annual temperatures than tropical areas such as the Brazilian savanna. Therefore, considering a hemispheric scale and *Pogonomyrmex* species as a dominant group of granivores ants, we found that ants collect more resources in sites with lower mean annual temperatures. Likewise, higher precipitation reduced the total intake of resources (both seed and dead arthropods). Precipitation directly promotes plant productivity (i.e., seed availability; Schemske 2002). So, why do ants remove more seeds with decreased precipitation? (see Orrock et al. 2015).

Arid environments (e.g., deserts, desert grasslands) support a greater abundance of seed predators (e.g., rodents) and their parasites and pathogens. This could lead to a 'top-down' regulation in which the activity of top predators affects lower trophic levels (Brown and Ernest 2002), and harvester ants occupy the same trophic level as rodents in these ecosystems (Brown and Ernest 2002; MacMahon, Mull, and Crist 2000). Overall, the precipitation impacts on the search for resources, disrupting trophic relationships in aquatic and terrestrial ecosystems (Pires et al. 2016; Romero et al. 2022). In addition, we expected that in more arid areas ants show a higher level of seed caching, since more arid and desert region more variable its inter-annual precipitation level. Caching behaviour seems to be selected more intensely in more arid environments, as a hedge against years of low productivity (MacMahon, Mull, and Crist 2000). Finally, seed caching would likely have been coincident with or following soon after the evolution of granivory.

Our study encompasses multiple study sites and species to elucidate the global patterns of granivory by *Pogonomyrmex* species. For the first time, a standardised multi-site experiment was conducted in the two diversity hotspots of this genus (i.e., deserts/arid areas of South and North America). We found that seed distance from nest, seed density (partially) and abiotic factors (e.g., precipitation, temperature and climate stability) simultaneously explain seed predation by harvester ants. We confirmed the effect of distance on seed predation expected from the optimal foraging theory. However, the effect of seed density on predation only affected the number of seeds removed when they were closer to the nest. Geographical features, such as latitude and elevation, also do not influence predation rates. Under the current scenario of desertification of many environments (Burrell, Evans, and De Kauwe 2020) and climate changes (Donat et al. 2016), substantial changes can occur in the distribution and abundance of *Pogonomyrmex* ants and the plant species on which they prey. Plant species distributed near *Pogonomyrmex* ant's nests are likely to be more threatened by high rates of seed predation, which may exacerbate the negative effects of shifting climate conditions and habitat disturbance on them (Marone and Pol 2021). Away from the nests higher rates of seed survival and a greater diversity of plant species are expected. Therefore, the presence of these harvester ants add evidence that support the Janzen–Connell hypothesis (Connell 1971; Janzen 1970), although density-dependent effects should be tested in future studies. Overall, our study provides new insights and helps to understand some ecological and evolutionary aspects of one of the most important and ubiquitous groups of seed predators on American continent.

Author Contributions

D.A., P.L., K.D.-C. and W.D. conceptualised the experimental design. All authors performed the research and collected data. D.A., P.L. and R.G. analysed and interpreted data. All authors contributed to writing the manuscript, led by D.A. and P.L.

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Anonymised version. Field samplings were carried out without the need for permission.

Ethics Statement

This study did not require any approval from ethics committees.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code supporting the results have been archived in appropriate public repositories (Figshare) and with the following DOI https://doi.org/10.6084/m9.figshare.24625287.v4.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.