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ORIGINAL ARTICLE

One ant's trash is another ant's treasure: Army ant middens provide resources for diverse ant assemblages

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Abstract

The army ant *Eciton burchellii* boasts more animal associates than any other animal species yet described, but the relationship between army ants and other ant species has only been studied in the context of predation. The waste deposits (middens) of army ant colonies are nitrogen-rich, a potentially high-value nutrient source for leaflitter arthropods. We explored this bottom-up role of army ant middens in the context of tropical ant communities. Our three main questions were the followings: (1) Which ant species forage on army-ant middens? (2) How does the bi-phasic life cycle of army ant colonies (affecting midden size, persistence, and abundance) affect which and how many ant species a midden boasts? (3) How do the ants that forage on army ant middens differ across elevations? Across 39 bivouacs, we found 36 species of ants foraging on army ant middens. These included highly predatory ants, nitrogen-limited arboreal ants, and fungus-farming ants. Per-midden richness was significantly lower for the usually smaller middens deposited during the nomadic phase and was higher for the typically larger middens deposited during the statary phase. Per-midden richness was not significantly different across elevations, but there was far greater species turnover across elevations than across phases within the same elevational site. Our results suggest that army ant middens are an important resource for a wide variety of tropical ants, informing a better understanding of the complex network of associations revolving around this keystone species.
Abstract in Spanish is available with online material

KEYWORDS
bottom-up, coprophagy, Costa Rica, detritivore, diversity, Dorylinae, Formicidae, pupal case

1 | INTRODUCTION

Colonies of the Neotropical army ant *Eciton burchellii* (Westwood) are hosts to the most diverse assemblage of animal associates known to science (Rettenmeyer et al., 2011). Charismatic examples include kleptoparasitic birds in the family Thamnophilidae that feed on insects fleeing swarm raids (Brumfield et al., 2007) and butterflies that follow nomadic army ant colonies to feed on the feces of these antbirds (Ray & Andrews, 1980). Army ant colonies also play host to numerous parasitic inquiline arthropods with varying degrees of host specificity and cryptic speciation (Rettenmeyer, 1962b; von Beeren et al., 2016a, 2016b; von

Beeren & Tishechkin, 2017). Meanwhile, hundreds of obligate associates and opportunistic scavengers alike subsist on waste material deposited in the conspicuous above-ground refuse piles of highly epigeic army ants (Rettenmeyer, 1962a; Rettenmeyer et al., 2011). These nitrogen-rich mounds of discarded army ant corpses, prey remains, and feces draw a multitude of flies, beetles, true bugs, mites, and even other species of ants (Rettenmeyer, 1962a; Rettenmeyer et al., 2011). Due to their importance as top predators in tropical forests, the relationship between army ants in subfamily Dorylinae and sympatric non-doryline ants has been explored almost exclusively from a top-down perspective (Hoenle et al., 2019; Kaspari et al., 2011; LaPolla et al., 2002; Otis et al., 1986; Peters et al., 2013; Vieira & Höfer, 1994). However, the nitrogen-rich middens of *E. burchellii* have the potential to be an important food source for a variety of tropical leaflitter ants. To our knowledge there has been only one previous account of ants foraging on army ant middens in the unpublished dissertation material of Rettenmeyer (1962a). Here we present the results of the first systematic survey of the community of ants that reap nutritional benefits from proximity to these nomadic top predators.

The bivouacs, or temporary nests, of *E. burchellii* are coordinated living structures composed of interlocking worker ants that encase, protect, and incubate the brood and queen (Kronauer, 2020; Schneirla et al., 1954). Middens of the above-ground bivouacking *E. burchellii* are typically located immediately beside or below the bivouac (Rettenmeyer, 1963). However, because *E. burchellii* colonies are highly nomadic, they produce a new midden every time a bivouac is formed in a new location (Figure 1). Colonies of *E. burchellii* are phasic, going through periods of nomadism corresponding to the period of about 16 days when the synchronous brood cohort is in the larval stage (Gotwald Jr., 1995; Rettenmeyer, 1963; Schneirla et al., 1954b). Following this period, mass pupation coincides with the beginning of a more sessile (statary) period of approximately 20 days during which time the next cohort of eggs is laid (Gotwald Jr., 1995). Although foraging is less frequent and foraging parties are smaller during the statary phase (Schneirla, 1971; Teles da Silva, 1982), great time spent in a single location causes the accumulation of far larger midden piles among statary bivouacs (henceforth, "statary middens") than is typically observed for refuse deposits of nomadic bivouacs (henceforth, "nomadic middens") (Rettenmeyer, 1963). Based on these numbers, we estimate 13.51 (typically smaller) nomadic midden piles are produced per colony per month, with typically larger statary middens produced at a rate of 0.84 per colony per month. Assuming *E. burchellii* colonies range from densities of 0.10–0.79 colonies per km^2 across their biogeographic range, as found in surveys by O'Donnell et al. (2007), we can estimate that this species produces 1.35–10.67 new nomadic middens and 0.08–0.66 new statary middens per km^2 per month. Therefore, although transient and spatiotemporally unpredictable, army ant middens are a common potential high-value protein source in many Neotropical forests. Given this discrepancy in refuse volume, midden number, and persistence between statary and nomadic middens, we asked whether and to what degree statary versus nomadic middens boast different foraging ant assemblages. We hypothesized that larger statary middens boast a greater diversity of ant foragers.

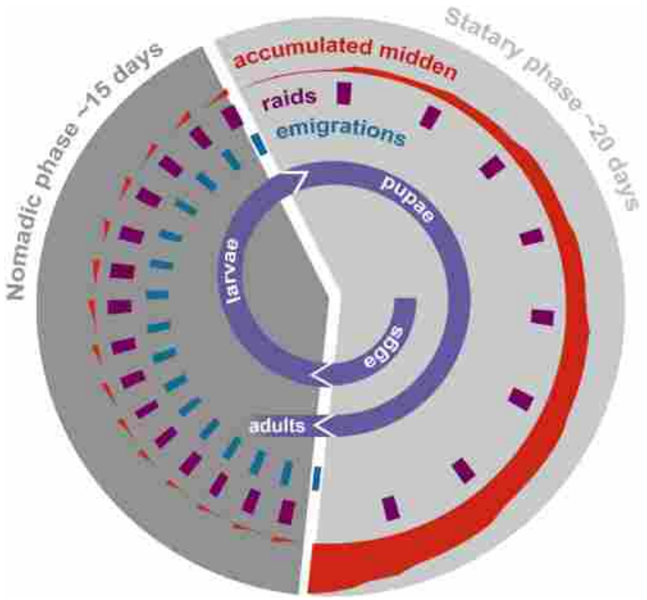

FIGURE 1 Cyclical lifecycle of the army ant *Eciton burchellii* showing the overlapping developmental stages of the synchronous brood, phasic contrasts in colony movement (emigrations), group foraging excursions (raids), and a visual representation of midden accumulation. Illustration by Kaitlin Baudier.

Within its range in Central America, *Eciton burchellii parvispinum* Forel occurs across multiple elevations and life zones (Kumar & O'Donnell, 2009). We asked to what extent midden-foraging ant assemblages differ across this elevational expanse. Lack of seasonal variation in temperature in the tropics causes a greater array of unique microclimates that drive increased rates of climatic specialization and speciation (Ghalambor et al., 2006; Janzen, 1967). As a result, substantial species turnover occurs in tropical ant communities across 0–1750 m elevation (Longino & Colwell, 2011), the range across which *E. burchellii parvispinum* is commonly found in northwestern Costa Rica (Baudier & O'Donnell, 2018; Watkins, 1976). We therefore expected high species turnover in army ant midden-foraging ants across elevations. To test this, we compared midden ant assemblages across elevations in northwestern Costa Rica.

2 | METHODS

2.1 | Field sites and observations

Three sites on the Pacific slope of the continental divide in Northern Costa Rica were surveyed for army ant midden attendance (Figure 2a): lowland tropical dry forest and tropical moist forest in Santa Rosa National Park (10°53′N, 85°46′W, 100–300 meters above sea level, henceforth "masl"), transitional premontane moist

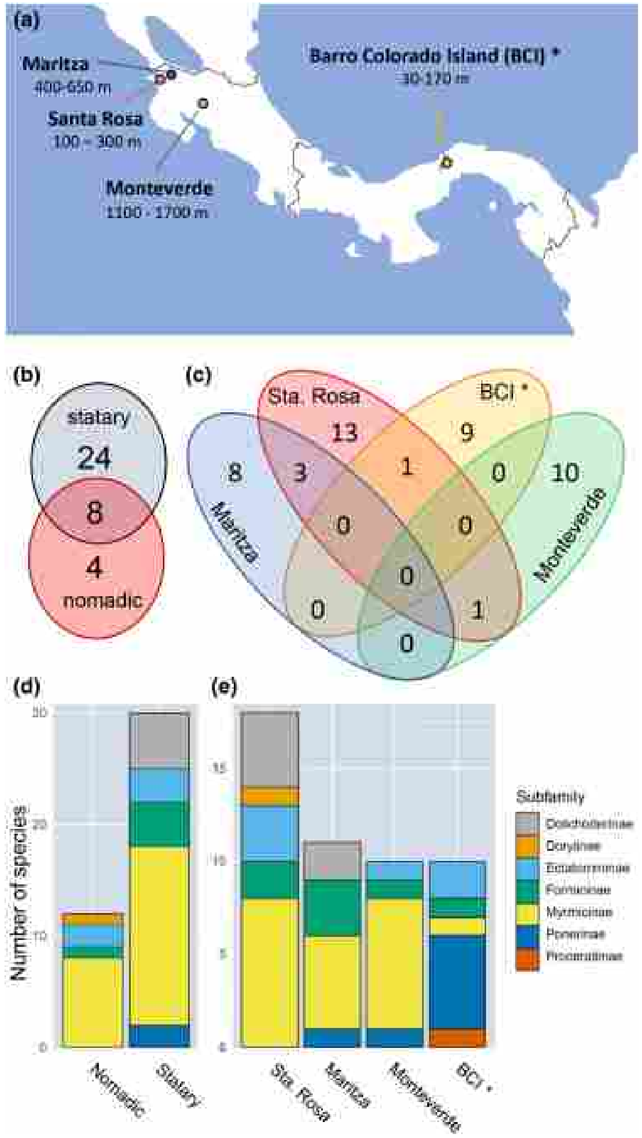

FIGURE 2 (a) Map showing the three Costa Rican sites in which midden-foraging ants of *Eciton burchellii parvispinum* were studied and BCI in Panama, where middens of *E. burchellii foreli* were surveyed by Rettenmeyer (1962a)*. (b) Venn diagram showing species overlap according to colony phase. (c) Venn diagram showing species overlap across sites. (d) Taxonomic composition according to colony phase. (e) Taxonomic composition according to site.

forest near Maritza Biological Station (10°58′N, 85°30′W, 400–650 masl), and premontane to lower montane wet forests in Monteverde (10°18′N, 84°49′W, 1100–1700 masl). At each site, we used standard walking-encounter methods on small forest trails to locate army ant raids (Kumar & O'Donnell, 2009), following the direction of army-ant-carried food items back to the bivouac. We determined the phase of each bivouac based on the developmental stage of the developing synchronous brood within, with bivouacs housing larvae deemed nomadic and bivouacs housing pupae deemed statary. Once at the bivouac, middens were located by searching for a small column of worker ants (refuse workers) extending from the bivouac to a pile of debris being actively deposited. Using this method, we surveyed a total of 39 bivouacs in the rainy seasons of 2015 and 2016, finding 30 unique middens among them. Subject colonies in this study represent a subset of those used in a previous collective thermoregulation study (Baudier et al., 2019). For further details on field methods, including how colonies were located, tracked, and delineated, see Baudier et al. (2019) and Baudier and Pavlic (2022).

We observed all middens twice a day for as long as the bivouacs were present. Middens were checked for ant foragers in the morning between 07:00 and 10:00 and in the afternoon and evening between 14:00 and 20:00. When the bivouac was in one location for multiple days (indicative of statary bivouacs that left substantial midden piles), surveys continued until one observation (under 24 h) after the colony had left the bivouac site due to colony emigration. An ant on the midden was considered a midden forager if it was observed mandibulating or carrying material of any kind from the midden. Notes were taken on interspecies interactions and on foraged materials when carried items were visually identifiable (e.g., disarticulated insect tergites). Morphospecies at each midden were identified using a hand lens. Voucher specimens of each morphospecies were collected into 95% ethanol before being pointed and identified using morphological characters. Voucher specimens of all midden-foraging ant species identified in this study have been deposited in the Cornell University Insect Collection, Ithaca, NY, USA (CUIC#000061841-000061987).

2.2 | Data analysis

All analyses were conducted using R version 4.2.1 (R Core Team, 2022). Fisher's exact tests were used to compare presence vs. absence of midden-foraging ants at statary versus nomadic middens. Because the mid-elevation site was less well-sampled (Maritza, $N=6$ bivouacs), we excluded this site from frequency analysis and used a Fisher's exact test to compare frequency of middens with or without foragers between the high- and low-elevation sites (Monteverde & Santa Rosa, respectively). We used the 'specaccum' function in the package 'vegan,' with default settings, to generate species accumulation curves across phases and sites using surveyed midden number as a measure of effort. We compared the total number of observed species on each midden across phases (nomadic vs. statary) using a Mann–Whitney *U* test. We compared the total number of species observed on each midden across the three surveyed sites using a Kruskal–Wallis test. To investigate whether phase and site predicted the number of species simultaneously foraging on a single midden, we used a generalized linear mixed model (GLMM) analysis (assuming a Poisson distribution), with species number per observation as the response variable, colony ID and midden ID as nested random factors, and phase, site, and the interaction between phase and site as fixed factors. We used pairwise contrasts to compare phases within each site while also accounting for other random and fixed factors; reported p values were adjusted for multiple comparisons by Bonferroni correction.

3 | RESULTS

3.1 | The majority of army ant middens are foraged by ants

We observed midden piles for 30 of the 39 surveyed bivouacs (10 in low-elevation Santa Rosa, 6 in mid-elevation Maritza, and 14 in high-elevation Monteverde). All bivouacs for which middens were not located (4 in Santa Rosa, 0 in Maritza, and 5 in Monteverde) were nomadic. These nomadic bivouacs were either not present long enough to produce a substantial refuse pile (e.g., a colony emigrating twice in one night) or were located in very enclosed subterranean sites. Although most subterranean bivouacs in this study did produce aboveground refuse piles, underground middens in these few cases may or may not have formed in unobservable locations. We observed 21 of 30 middens being foraged by at least one species of ant during at least one observation period. Of the 166 midden observations, 42.8% yielded at least one midden-foraging ant species.

A maximum of nine ant species were observed foraging on the same statary midden over multiple days. Likelihood for middens to be foraged did not differ when an army ant colony was present compared to the first observation after the colony had emigrated to a new bivouac location (Fisher's exact $p = .251$), and so observations before and immediately after emigrations have been pooled in all analyses.

3.2 | Taxa of midden-foraging ants

We observed 36 ant species foraging on army ant middens (Figure 2b,c; Table 1; two additional morphospecies were identified to genus only), only one of which, *Ectatomma ruidum* (Roger), was previously observed foraging on army ant middens (Rettenmeyer, 1962a), bringing the total number of army ant midden-associated ants that have been identified to species to 43 to date. Midden-foraging ant species in this survey were taxonomically diverse, spanning six ant subfamilies, with the highest number of species in subfamily Myrmicinae (Figure 2d,e). Among the myrmicine midden foragers were a notable number of fungus-farming species (6 species in 4 genera were observed foraging on 6 different middens) and species in the genera *Pheidole* and *Cephalotes*. We observed no species belonging to subfamily Proceratiinae and fewer ponerine midden foragers than reported by Rettenmeyer (1962a) in Panama. Our observation of a colony of the predominantly subterranean army ant *Labidus coecus* (Latreille) raiding a midden in lowland Santa Rosa adds the subfamily Dorylinae to the list of those observed foraging on the middens of *E. burchellii*.

3.3 | Effects of army ant colony phase

We found no difference in the presence versus absence of midden-foraging ants between the nomadic and the statary phases (Table 2; Fisher's exact: $p = .109$). However, species accumulation curves indicated higher cumulative species richness on statary middens compared to nomadic middens (Figure 3a). Consistent with this, per-midden richness was also higher for statary middens than for nomadic middens (Figure 3b; Mann–Whitney *U* test with continuity correction: $U = 47$, $p = .006$). The average number ± SE of ant species that foraged each midden was 1.00 ± 0.31 during the nomadic phase and 3.20 ± 0.67 during the statary phase (2.10 ± 0.42 across all middens).

There was high species overlap between phases, with nomadic middens having fewer phase-unique species (33.3% of nomadic midden-foraging species) than statary middens (75% of statary midden-foraging species) (Figure 2b; Table 1). Our ability to discern how common it was for a colony of midden-foraging ants to attend sequential middens of the same army ant colony was limited by our observations of sequential bivouacs of the same colony being relatively low (30 bivouacs were observed across 21 colonies). Midden-foraging ant species *Holcoponera strigata* (Norton), *Pheidole biconstricta* Mayr, *Pheidole psilogaster* Wilson, *Pheidole pugnax* Dalla Torre, *Pheidole tenuicephala* Longino, and *Procryptocerus batesi* Forel were observed at least at two consecutive middens produced by the same army ant colony. However, only in one instance did we directly observe recruitment of foragers from an abandoned midden to that of the colony's next bivouacking site. In this case, *P. biconstricta* foragers were observed trailing from the old statary midden to the midden of a newly formed early nomadic bivouac approximately 4 meters away. In this instance, they followed the same apparent route used by the army ants during emigration the night before. This was the shortest emigration distance in our study. The distance of *E. burchellii* emigrations is commonly being more than ten times this length (Rettenmeyer, 1963; Teles da Silva, 1977).

Due to the short period of time army ant colonies stay in one location during the nomadic phase, we were able to collect fewer observations per nomadic midden than per statary midden. If this had caused nomadic middens to be relatively under-observed compared to statary middens, we would expect a higher incidence of single-observation species among nomadic middens. However, we found the opposite. Of the 17 species recorded from only a single observation in this study, only 3 of them were observed on nomadic middens, the other 14 being on statary middens (adjusted for observation number: 8.3% of nomadic observations vs. 13.1% of statary observations). Despite nomadic bivouacs having fewer per-bivouac observations, single-observation species were recorded on only 20% of nomadic middens, as compared to 73% of statary middens. This suggests that nomadic middens were sufficiently sampled.

3.4 | Site differences

High-elevation Monteverde and low-elevation Santa Rosa did not differ in the frequency of middens being attended by at least one midden-foraging ant (Table 2, Fisher's exact: $p = .679$). Although species accumulation curves suggested that army ant middens in low

TABLE 1 Ant foragers of *Eciton burchellii* middens, including accounts from Barro Colorado Island (BCI) in Panama as reported by Rettenmeyer (1962a).

	Site				Phase	
	Santa Rosa (100–300 masl)	Maritza (400–650 masl)	Monteverde (1100–1700 masl)	BCI (30–170 masl)	Nomadic	Statary
Number of middens with ant foragers	$N=10$	$N=6$	$N=14$		$N=15$	$N=15$
Dolichoderinae						
Azteca cf. *velox* Forel	3	1				4
Azteca instabilis (Smith)		3				3
Azteca sp.	1			X		1
Dolichoderus bispinosus (Olivier)	1					1
Tapinoma melanocephalum (Fabricius)	1					1
Dorylinae						
Labidus coecus (Latreille)	1				1	
Ectatomminae						
Ectatomma ruidum (Roger)	2			X	1	1
Ectatomma tuberculatum (Olivier)	1					1
Holcoponera strigata (Norton)	2		2		1	3
Gnamptogenys sulcate[a] (Roger)				X		
Formicinae						
Brachymyrmex obscurior Forel	1					1
Camponotus abscisus Roger			1		1	
Camponotus contractus buttesi Forel[a,b]				X		
Camponotus mucronatus Emery		1				1
Camponotus novogranadensis Mayr	2	1				3
Camponotus JTL-011		1				1
Myrmicinae						
Acromyrmex coronatus (Fabricius)			2		1	1
Carebara[a] sp.				X		
Cephalotes minutus (Fabricius)	2				1	1
Cephalotes multispinosus (Norton)	1					1
Cephalotes scutulatus (Smith)		2				2
Cyphomyrmex minutus Mayr	1					1
Cyphomyrmex salvini Forel			1			1
Cyphomyrmex sp.		1				1

(Continues)

TABLE 1 (Continued)

	Site				Phase	
	Santa Rosa (100–300 masl)	Maritza (400–650 masl)	Monteverde (1100–1700 masl)	BCI (30–170 masl)	Nomadic	Statary
Mycetomoellerius squamulifer (Emery)	1					1
Pheidole biconstricta Mayr			2		2	
Pheidole insipida Forel			1			1
Pheidole psilogaster (Wilson)			3		2	1
Pheidole pugnax Dalla Torre	1	3			2	2
Pheidole susannae Forel	2	1				3
Pheidole tenuicephala Longino			4		2	2
Pheidole sp.				X		
Procryptocerus batesi Forel			2		1	1
Sericomyrmex amabilis Wheeler	1					1
Solenopsis geminata (Fabricius)	1					1
Solenopsis sp.				X		
Stenamma felixi Mann			1			1
Strumigenys gundlachi (Roger)				X		
Temnothorax subditivus Wheeler	2					2
Wasmannia auropunctata Roger		1			1	
Ponerinae						
Anochetus mayri Emery				X		
Leptogenys imperatrix Mann			1			1
Mayaponera arhuaca (Forel)[a]				X		
Mayaponera constricta (Mayr)[a]				X		
Neoponera apicalis (Latreille)		1				1
Neoponera villosa (Fabricius)				X		
Pachycondyla harpax (Fabricius)				X		
Ponera sp.				X		
Proceratiinae						
Proceratium micrommatum (Roger)				X		

Note: Current species names are listed, except for *Camponotus* JTL-011, a description of which can be found on AntWeb (California Academy of Science, 2022).

[a] A synonym was reported by Rettenmeyer (1962a).

[b] Dubious identification.

TABLE 2 Counts of middens with or without midden-foraging ants.

	Midden ants absent	Midden ants present
Colony phase		
Nomadic	7	8
Statary	2	13
Elevations		
Low-elevation (Santa Rosa)	3	7
Mid-elevation (Maritza)	0	6
High-elevation (Monteverde)	6	8

Note: Fisher's exact tests showed no difference in the proportion of middens foraged by ants across colony phases ($p=.109$) or across sites that were sufficiently sampled to test (excluding mid-elevation Maritza; $p=.679$).

elevation Santa Rosa support higher ant richness than those in high-elevation Monteverde (Figure 3c), per-midden richness did not differ across the three sites (Figure 3d; Kruskal–Wallis: $X^2=2.69$, $df=2$, $p=.260$).

Species composition varied drastically across inter-elevational sites surveyed as part of this study and also compared to reports from Rettenmeyer (1962a) on Barro Colorado Island (BCI) in Panama (Figure 2c, Table 1). We observed no midden-foraging species in common across all three sites, but some widely distributed species were observed in more than one site. For instance, we observed *E. ruidum* attending middens in low-elevation Santa Rosa, as did Rettenmeyer (1962a) in low-elevation BCI. However, *E. ruidum* represents a species complex (Aguilar-Velasco et al., 2016; Meza-Lázaro et al., 2018), and so whether this is truly a conspecific observation is unclear. *Holcoponera strigata* was also observed midden-foraging both in low-elevation Santa Rosa and high-elevation Monteverde. *Azteca velox* Forel, despite being an arboreal species, was perhaps the most common and most intense midden-foraging ant at lowland and mid-elevation sites. *Camponotus novogranadensis* Mayr and *Pheidole susannae* Forel were also found foraging on middens in both high and mid-elevation sites. All other midden-foraging ant species were observed within only one site (Table 1).

3.5 | Effect of site and phase on the number of simultaneously midden-foraging species

A maximum of six ant species were observed foraging simultaneously on the same statary midden. However, in 84.5% of instances where midden-foraging ants were observed, two or fewer species were simultaneously present. There was a significant interaction between site and phase as predictors of the number of species simultaneously observed foraging on the same midden ($X^2=6.27$, $df=2$, $p=0.043$; Table S1). While nomadic middens had greater simultaneous foraging species than statary middens in high-elevation Monteverde ($p=0.040$), phase was not a significant predictor of per-observation richness in low- and mid-elevation sites (Figure 3e & Table S2).

3.6 | Behavioral observations: Foraged items

The most foraged midden items across all sites and ants were pieces of dismembered prey arthropods (individual tergites, legs, and other body parts), small granules of what appeared to be frass, or other unidentifiable material (Figure 4). Nearly all the species we report here were observed primarily collecting these materials, with two notable exceptions. First, at mid- and low-elevation statary bivouacs, *Azteca* spp. (in addition to collecting insect remains) intensely collected discarded army ant pupal cases (Figure 4). Second, on multiple sequential days, we observed *Cephalotes multispinosus* (Norton) workers collecting bird feces from atop and near to the midden (Figure S1). However, all other *Cephalotes* in this study were observed only collecting discarded arthropod pieces.

3.7 | Behavioral observations: Aggressive interactions at middens

In most observations, midden-foraging ants and army ant dump workers showed no sign of interspecific aggression, passing one another without any interactions other than occasional antennation. The one exception was *Azteca instabilis* (Smith) in mid-elevation Maritza. On three occasions, *A. instabilis* workers were observed capturing roaming soldiers, large workers, and small workers of *E. burchellii parvispinum* (as defined by Franks, 1985). The *A. instabilis* collectively transported the captured army ants less than a meter up the trunk of a nearby tree before pinning and dismembering them (Figure 5). At their nests, *A. instabilis* workers use similar behavioral aggression to defend their nests against *E. burchellii* (Dejean et al., 2014); however, to our knowledge, this is the first report of such aggression at the site of an army ant bivouac.

4 | DISCUSSION

4.1 | Interpretation of quantitative data

The most striking predictor of midden-foraging ant richness in our survey was army ant colony phase. Larger and longer-lasting statary middens supported significantly higher ant species richness over the durations of time they were observed (Figure 3a,b). As for species compositional differences according to phase, most ant species observed foraging on statary middens were never seen foraging on the typically smaller and more ephemeral nomadic middens. By contrast, more than half of the nomadic midden-foraging ant species were also found at statary middens (Figure 2b). Together with many species accounts arising from occurrence at a single statary midden (Table 1), this suggests that a larger number of incidental midden-foraging ants may occur at

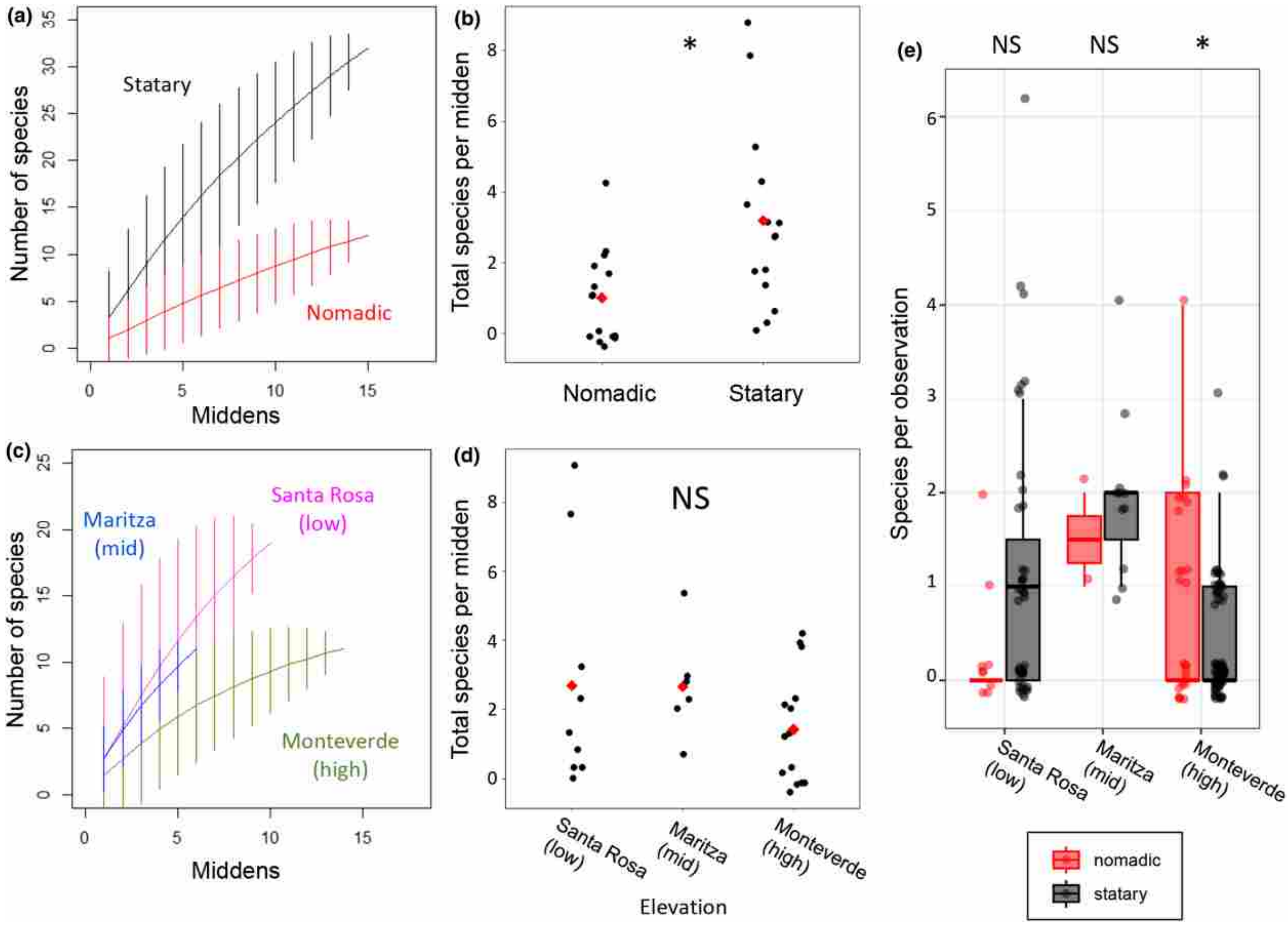

FIGURE 3 Differences in midden-foraging species number according to army ant colony phase and site. In (a) and (c) species accumulation curves were calculated using number of sampled middens as a metric of effort. Confidence intervals in all accumulation curves are ± standard deviation. Total species number observed for each midden within each phase (B) or across elevations (D) is shown with jitter to improve visualization of overlapping points. Red diamonds are group means. "*" indicates $p < .05$. "NS" indicates $p > .05$. (e) Results of mixed-effect models exploring the interactive effects of phase and site on the number of simultaneously foraging ant species in each observation. Results of pairwise post-hoc contrasts are shown above.

larger and more enduring statary middens. Meanwhile, lower ant richness at nomadic middens and some evidence of nomadic midden-to-midden foraging (especially in some *Peidole* spp.) suggest that nomadic middens, which are more abundant but usually smaller and more temporary, are foraged by a small subset of species with foraging strategies adapted to utilization of patchy food sources.

Regarding per-observation richness (the number of species observed simultaneously foraging the same midden), the effect of phase was site-dependent, with significantly more species simultaneously foraging nomadic middens in high-elevation Monteverde (Figure 3e). Together, this suggests that higher cumulative forager richness on statary middens is mainly explained by greater turnover of foraging species over time, not by statary middens supporting greater numbers of simultaneously foraging species. Although statary middens are typically larger, they do not boast higher numbers of simultaneously foraging species. Whether and to what degree this pattern can be explained by competitive exclusion at middens is an interesting question worth future exploration.

Consistent with our predictions, we also report greater species turnover across high-, mid-, and low-elevation sites in our survey than we saw across phases within sites (Figure 2c). This is likely primarily driven by high ant species turnover across these life zones (Longino & Colwell, 2011). However, despite this high turnover in midden-foraging ant species across sites, the relationship between richness and site is more nuanced. Species accumulation curves suggested that army ant middens in high-elevation Monteverde supported a smaller number of ant species than middens in low-elevation Santa Rosa (Figure 3c), but total midden richness was not significantly different among the sites (Figure 3d). These superficially contrasting results are caused by greater species turnover across sampled middens in the lowlands than across middens at high elevation. That midden-foraging ant richness on a site-wide scale was lower in high-elevation Monteverde than in low-elevation Santa Rosa is consistent with, and likely explained by, the tendency of ant species richness in general to decrease as elevation increases across sites in northwestern Costa Rica (Smith et al., 2014). Studies

FIGURE 4 Close-up view of a late statary midden of *E. burchellii parvispinum* observed in low-elevation Santa Rosa, consisting of dismembered arthropod corpses and army ant pupal cocoons that were frequently collected by *Azteca*. Photo by Kaitlin Baudier.

measuring ant richness across elevations in the Neotropics commonly report mid-elevation peaks from about 400–800 m above sea level (Longino & Branstetter, 2019; Smith et al., 2014). Due to sample size limitations at our mid-elevation site (Maritza), we could not test with confidence whether midden-foraging ant richness follows a similar trend. However, Maritza was notably the only site in our survey for which all midden observations yielded at least one midden foraging species (Figure 3e). Surveys with increased mid-elevation sampling are needed for more rigorous investigation.

4.2 | Notable guilds of midden-foraging ants

We observed fungus-farming ants foraging on army ant middens across all sites surveyed in this study. The only previously described relationships between army ants and fungus-farming ants are predatory. There are multiple accounts of army ants in the genera *Nomamyrmex* and *Neivamyrmex* raiding fungus-farming ant colonies in search of brood (LaPolla et al., 2002; Powell, 2011; Powell & Clark, 2004; Souza & Moura, 2008; Swartz, 1998; Watkins, 1968). Genetic analysis of prey items has also shown evidence of army ants in the genera *Neivamyrmex* and *Eciton* (though not *E. burchellii*) feeding on fungus-farming ant brood (Hoenle et al., 2019). However, most fungus-farming ant species collect dead insects, insect frass, and other detritus as substrate to grow the fungal crops they rely upon for food (De Fine Licht & Boomsma, 2010; Seal & Tschinkel, 2008; Sosa-Calvo et al., 2015; Waller, 1989). Multiple species of *Cyphomyrmex*, including two in this survey, are known to forage for carcasses of arthropods, including other species of ants, for use as platforms and/or nourishment of their fungal gardens (Adams & Longino, 2007; Mehdiabadi & Schultz, 2010; Weber, 1941, 1957; pers obs. Zoppas de Albuquerque). It is intuitive, then, that army ant middens, dense sources of both frass and dead insects, would be foraged by these ants. This suggests that the occurrence of *E. burchellii* in a tropical forest may benefit sympatric fungus-farming ants.

FIGURE 5 *Azteca instabilis* midden-foragers attacking, removing, and dismembering a small worker (a) and soldier (b) of *E. burchellii parvispinum* in the mid-elevation site Maritza. Photos by Kaitlin Baudier.

Another distinct group of ants observed repeatedly foraging on army ant middens were arboreal ants. This included ants in the genera *Azteca* and *Cephalotes*. Among tropical ants, arboreal species tend to be especially nitrogen-limited (Davidson, 1997; Yanoviak & Kaspari, 2000). Consistent with previous accounts of army ant midden-foraging *Azteca* in Panama (Rettenmeyer, 1962a), we observed several species of *Azteca* foraging on dead insects and cocoons at mid- and low-elevation middens in Costa Rica. A large portion of the materials collected by these *Azteca* colonies appeared to be empty pupal cases, which the army ants had discarded on the midden pile in the last week of the statary phase as synchronous adult emergence occurred. Indeed, all observations of *Azteca* in this study were on statary army ant middens (Table 1). In many cases, the rate at which *Azteca* removed pupal cases was equivalent to the discard rate by the army ant colonies themselves, leaving little to no accumulation of them on the midden. This is no small feat given that late-statary *E. burchellii* colonies can discard more than 10,000 pupal cases over the course of just a few days (Gotwald Jr., 1995). Why *Azteca* collects these pupal cases so intensely remains unclear. Whether their value is nutritional, constructional, or otherwise remains to be tested.

Unlike *Azteca*, arboreal ants in the genus *Cephalotes* were never observed collecting pupal cases. The species of *Cephalotes* we observed foraging on army ant middens either have poorly described life histories or are considered arboreal herbivores predominantly feeding on nectar, extrafloral nectaries, or inflorescences (Antoniazzi et al., 2020; Gillette et al., 2015; Schmid et al., 2014). The tendency towards herbivory in this genus causes nitrogen limitation, a selective force driving the coevolution of nitrogen-recycling gut flora that enables some species of *Cephalotes* to obtain nitrogen from vertebrate wastes including bird feces (Hu et al., 2018). Consistent with this, we observed in one case *C. multispinosus* descending to the forest floor to feed on bird feces left atop and near an army ant midden. However, both *Cephalotes minutus* (Fabricius) and *Cephalotes scutulatus* (Smith) were not observed collecting any bird feces but instead appeared to obtain nitrogen via direct foraging of discarded arthropod pieces from among midden contents.

A guild we expected to be prominent foragers of protein-rich wastes of army ants were other highly predatory ants. According to both natural history and stable isotope analysis, army ants (Subfamily Dorylinae) and certain members of subfamily Ponerinae (Hanisch et al., 2020) are among the most predatory ants. Consistent with this notion, reports of ant species present on Panamanian army ant middens by Rettenmeyer (1962a) included eight ponerine species. By contrast, we observed only two ponerines in our survey in northern Costa Rica (Figure 2e). However, we also observed the subterranean army ant *L. coecus* midden-foraging. Most Neotropical army ant species consume live arthropod prey (Kronauer, 2020). However, accumulating contrary reports suggest that *L. coecus* may have more diverse raiding habits, having been observed collectively feeding on turtle eggs (da Costa Reis et al., 2021) and even seeds (Ruzi et al., 2021). Other highly predatory ants observed foraging on army ant middens both in this study and on BCI (Rettenmeyer, 1962a) were members of the subfamily Ectatomminae. Ants in this subfamily often deploy solitary foragers that engage in sit-and-wait predation to capture live insect prey (Lima & Antonialli-Junior, 2013; Ostwald et al., 2018; Schatz & Wcislo, 1999; Wheeler, 1986). However, intra-specific stealing of food items is also well described (McGlynn et al., 2015). We observed members of this subfamily solitarily foraging on army ant midden material in both high and low elevation sites.

Overall, we observed notable differences in the ant fauna observed in our study as compared to that of Rettenmeyer (1962a). In addition to climatic and geographic differences, it is worth considering that differences in our results may at least in part be explained by important contrasts in the natural history of *E. burchellii parvispinum* versus *Eciton burchellii foreli* Mayr (the sub-species found on BCI). These sub-species differ in their geographic range (Watkins, 1976), and there has been substantial genetic divergence between them (Winston et al., 2017). Importantly, these subspecies also differ in bivouacking site choice. Colonies of most subspecies of *E. burchellii* (including *E. burchellii foreli*) typically bivouac in elevated sites in trees or on the ground (Soare et al., 2011). However, elevated bivouacs are scarcely observed in *E. burchellii parvispinum*, and more than half the time colonies bivouac in very underground or enclosed cavities (Baudier et al., 2019; Baudier & Pavlic, 2022). Middens are therefore likely available in different microhabitats across the two studies as well.

4.3 | Conclusions

Results of this survey raise new questions about how reliant each observed midden-foraging ant species is on army ant waste as a resource. Do some midden-foraging ants seek army ant middens directly, or are all midden-foraging events the result of random incidental encounters, as suggested by Rettenmeyer (1962a)? Although all middens we documented in this study were on the forest floor, we observed several arboreal species of ant consistently foraging them (i.e., *Cephalotes* spp. and *Azteca* spp.). These observations seem inconsistent with the notion of exclusively incidental midden encounter. If certain ant species do actively seek army ant middens, the detection and utilization of these resources present their own sets of challenges about which we also know little.

Regardless of the closeness of association between army ants and their midden-foraging ant species, describing this ecological association and directional flow of nutrition in tropical ecosystems is important. The army ant *E. burchellii* is a top predator and keystone species in Neotropical forests (Kaspari et al., 2011; Pérez-Espona, 2021; Rettenmeyer et al., 2011), but due to its aboveground foraging, bivouacking, and emigration strategies, it is also especially vulnerable to extirpation due to human disturbances such as canopy removal (Kumar & O'Donnell, 2009), habitat fragmentation (Partridge et al., 1996; Schöning et al., 2006), and anthropogenic climate change (Baudier et al., 2015, 2019). Such ecological disturbances can have direct effects on local communities and can also destabilize interspecies associations (Diamond et al., 2016). Continued exploration of the many associations of tropical army ants is therefore of high basic and applied value.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: https://doi.org/10.5061/dryad.xpnvx0kj5 (Robles López et al., 2023).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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