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Capturing arthropod diversity in complex cave systems

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Abstract

Aim: Identify the optimal combination of sampling techniques to maximize the detection of diversity of cave-dwelling arthropods.

Location: Central-western New Mexico; north-western Arizona; Rapa Nui, Chile.

Methods: From 26 caves across three geographically distinct areas in the Western Hemisphere, arthropods were sampled using opportunistic collecting, timed searches, and baited pitfall trapping in all caves, and direct intuitive searches and bait sampling at select caves. To elucidate the techniques or combination of techniques for maximizing sampling completeness and efficiency, we examined our sampling results using nonmetric multidimensional scaling (NMDS), analysis of similarity (ANOSIM), Wilcoxon signed-rank tests, species richness estimators and species accumulation curves.

Results: To maximize the detection of cave-dwelling arthropod species, one must apply multiple sampling techniques and specifically sample unique microhabitats. For example, by sampling cave deep zones and nutrient resource sites, we identified several undescribed cave-adapted and/or cave-restricted taxa in the south-western United States and eight new species of presumed cave-restricted arthropods on Rapa Nui that would otherwise have been missed. Sampling techniques differed in their detection of both management concern species (e.g., newly discovered cave-adapted/restricted species, range expansions of cave-restricted species and newly confirmed alien species) and specific taxonomic groups. Spiders were detected primarily with visual search techniques (direct intuitive searches, opportunistic collecting and timed searches), while most beetles were detected using pitfall traps. Each sampling technique uniquely identified species of management concern further strengthening the importance of a multi-technique sampling approach.

Main conclusions: Multiple sampling techniques were required to best characterize cave arthropod diversity. For techniques applied uniformly across all caves, each technique uniquely detected between ~40% and 67% of the total species observed. Also, sampling cave deep zones and nutrient resource sites was critical for both increasing the number of species detected and maximizing the likelihood of detecting management concern species.

KEYWORDS

American Southwest, Rapa Nui, cavernicoles, species accumulation curves

1 | INTRODUCTION

Caves are highly sensitive environments often supporting troglomorphic (cave-adapted) invertebrate species with narrow geographic ranges (i.e., occurring within a single cave, watershed or geologic formation). Although some geographic regions are considered hot spots of endemism and subterranean biodiversity (Culver, Master, Christman, & Hobbs, 2000; Culver & Sket, 2000), cave faunas in most areas globally remain largely uncharacterized. Even relatively well-studied regions with monitoring programs frequently yield previously undescribed taxa. For example, in North America, Culver, Christman, Sket, and Trontelj (2004) estimated more than 20 new troglomorphic species are discovered annually.

While numerous studies have sought to identify the most efficacious methods for sampling specific taxonomic groups (Cane, Minckley, & Kervin, 2000; Cardoso, 2009; Cardoso, Crespo, Carvalho, Rufino, & Henriques, 2009; Ellison, Record, Arguello, & Gotelli, 2007) and standardize sampling procedures (Duelli, Obrist, & Schmatz, 1999; Spafford & Lortie, 2013) for surface-dwelling arthropods, no systematic efforts have been undertaken to identify the best practices for surveying terrestrial cavernicolous (cave-dwelling) arthropod communities. However, Dole-Oliver et al. (2009) developed and tested standardized sampling procedures for aquatic cave-dwelling arthropods, and Hunt and Millar (2001) described several cave-dwelling terrestrial invertebrate sampling methods and provided recommendations for their best use. To our knowledge, only one study, Weinstein and Slaney (1995), qualitatively described the efficacy of different arthropod sampling techniques for complete biological surveys in caves.

A review of cavernicolous arthropod studies revealed an array of sampling techniques designed to capture specific taxa. Paquin and Provost (2010) suggested that “hand collecting” (i.e., visual searching for and collecting arthropods using paint brushes and/or aspirators) is preferred for cave-dwelling arthropods due to its selectivity. For well-known or easily distinguishable taxa, researchers can use this approach as it results in fewer animals being removed from the ecosystem. Early on, Barber (1931) and Valentine (1941) favoured baited pitfall traps for capturing omnivorous and carrion beetles due to the quick return rate, while deemphasizing visual searching due to low returns. Because not all arthropods attracted to pitfall traps will be captured, searches around traps prior to removal have been applied by previous workers (Campbell et al., 2011; Martín & Oromí, 1986; Poulson & Culver, 1969; Wynne, 2013; Wynne et al., 2014). For sampling previously unstudied caves in Hawai'i and Australia, Howarth (1980, 1988, respectively) applied a variety of techniques including intensive direct intuitive searches (in promising microhabitats), deploying bait stations (using naturally occurring organic material, tubers, rotting meat, cheese and grains) and to a lesser extent baited pitfall traps—the latter included both live and kill pitfalls.

Researchers have emphasized logistical difficulties in sampling terrestrial cavernicolous arthropods (Howarth, James, McDowell, Preston, & Imada, 2007; Krejca & Weckerly, 2007; Weinstein &

Slaney, 1995; Zgajmajster, Culver, & Sket, 2008), which present challenges for effectively inventorying, managing and conserving sensitive cavernicolous arthropod communities. These include technical access (e.g., caves on cliff faces, deep canyons and rugged mountainous terrain, as well as moving equipment and personnel through constricted cave passageways, deep fissures, pits and vertical passageways often while on rope), considerable equipment requirements (e.g., technical caving, safety and scientific equipment), and awareness and avoidance of sensitive archaeological and geological resources.

Effectively detecting troglomorphic and obligate troglophiles (cave-restricted) species presents further logistical considerations. These animals are typically endemic to a single cave or region (Borges et al., 2012; Christman, Culver, Madden, & White, 2005; Culver et al., 2000; Deharveng et al., 2008; Harvey, Berry, Edward, & Humphreys, 2008; Harvey et al., 2011; Niemiller & Zigler, 2013; Reddell, 1981; Shear, Taylor, Wynne, & Krejca, 2009; Tian, 2011; Wynne & Shear, 2016; Wynne et al., 2014) and often represented by small populations (Mitchell, 1970; Niemiller et al., 2017). Recognizing temporal and spatial heterogeneity of cave habitats (Chapman, 1983; Kane & Poulson, 1976; Pellegrini & Ferreira, 2013; Trontelj et al., 2012) is another important consideration. If biological inventories or monitoring is conducted at an inappropriate time of year, in the wrong locations, or lack the necessary sampling intensity, sensitive species populations may not be detected. For example, Krejca and Weckerly (2007) reported that despite intensive surveys by trained cave biologists, a new cave-adapted species were discovered upon the 40th visit to a Texas cave. Sket (1981) and Culver et al. (2004) reported a new genus of stygobiont after over one hundred site visits to a well-studied Slovenia cave. Because it's impossible for most studies to conduct 40 to 100 site visits per cave, these examples underscore the difficulties with detecting more cryptic species.

Numerous human activities negatively impact cave ecosystems and their rare and endemic inhabitants—heightening the need to conduct thorough biological inventories. These impacts may include, but are not limited to, forest conversion (Culver, 1986; Trajano, 2000), mining (Elliott, 2000), groundwater pollution (Aley, 1976; Graening & Brown, 2003; Notenboom, Plénet, & Turquin, 1994), water extraction and water impoundments (Lisowski, 1983; Olson, 2005; Ubick & Briggs, 2002), alien species introductions (Elliott, 1992; Howarth, 1981; Howarth et al., 2007; Reeves, 1999; Taylor, Krejca, Smith, Block, & Hutto, 2003), global climate change (Badino, 2004; Chevalloné & Lejeune, 2003), livestock grazing (Borges et al., 2012) and recreational use (Culver, 1986; Howarth & Stone, 1993; Pulido-Bosch, Martín-Rosales, López-Chicano, Rodríguez-Navarro, & Vallejos, 1997). This underscores the urgency for developing a methodological approach to efficiently and systematically sample cavernicolous arthropod communities.

Such an approach is important for interpreting landscape-scale patterns, as well as further developing the field of cave ecology and making evidence-based management decisions. The lack of a

standardized sampling protocol (specifically targeting the highest efficiency and completeness possible) for sampling cave-dwelling terrestrial arthropods challenges our ability to make meaningful regional and potentially global comparisons between caves and across geographic regions. Additionally, comparable data sets across landscapes will further assist ecologists in better quantifying cave communities, as well as furthering our understanding of the relationship between cave habitats and cave-dwelling arthropod diversity.

Sampling techniques should be highly efficient in return per unit effort and should yield as complete a record of the cave-dwelling arthropod community as possible. Schneider and Culver (2004) employed a systematic sampling protocol (baited pitfall traps and direct intuitive searches in cave deep zones) to evaluate completeness of these techniques using rarefaction curves. None of their curves for their study caves reached an asymptote. They suggested, due to issues of rarity, roughly half the species likely to exist were detected (Schneider & Culver, 2004). Similarly, in a landscape scale study of subterranean beetle diversity in the Dinaric karst region of Western Europe, Zgajmajster et al. (2008) concluded more intensive sampling was required to detect most of the hypogean beetles in the region.

In this study, we examined differences across a standardized set of terrestrial cavernicolous arthropods sampling techniques in terms of efficiency (return per unit effort) and completeness (in detecting as many species as possible). We also investigated differences in detectability of select taxonomic groups and species of management concern across all sampling techniques. Our aim was to provide a recommended set of standardized procedures for surveying cave-dwelling arthropods.

2 | METHODS

2.1 | Study areas

We studied caves in El Malpais National Monument, New Mexico and Grand Canyon-Parashant National Monument, Arizona, United States and Rapa Nui (Easter Island) National Park, Rapa Nui, Chile (Figure 1). El Malpais National Monument (ELMA; 34.9006°N, 107.9943°W) encompasses ~1,522 km² in west-central New Mexico, United States. The region consists of at least eight major lava flows ranging from 3,000 to 100,000 years in age (Cascadden, Kudo, & Geisman, 1997). Vegetation types include mixed conifer and ponderosa pine (*Pinus ponderosa*) forest at higher elevations gradating to piñon-juniper woodlands and grasslands at lower elevations (Bleakly, 1997). All sites were lava tube caves ($n = 10$) of various geological ages and ranged in elevation from 1,991 to 2,334 m above sea level (ASL).

Grand Canyon-Parashant National Monument (PARA; 36.4015°N, 113.6997°W) in north-western Arizona, United States, encompasses approximately 4,451 km². The monument is characterized by deeply incised canyons, mesas and mountains. Study sites occurred in both juniper (*Juniperus* spp.) shrublands ($n = 4$ caves) and lowland Mojave Desert scrub ($n = 6$). Except for one basaltic fissure cave, all caves were located within the Supai, Kaibab or Redwall limestone formations. Elevation of caves ranged from 736 to 1,590 m ASL.

Rapa Nui National Park, located on Rapa Nui, Chile (RAPA; 27.1130°S, 109.3496°W), encompasses approximately 42 km² in area. All sites were lava tube caves ($n = 6$) and located within the Roiho lava flow, which is the island's youngest lava flow (estimated between 0.02 and 0.13 Ma years old; O'Connor, Stoffers, &

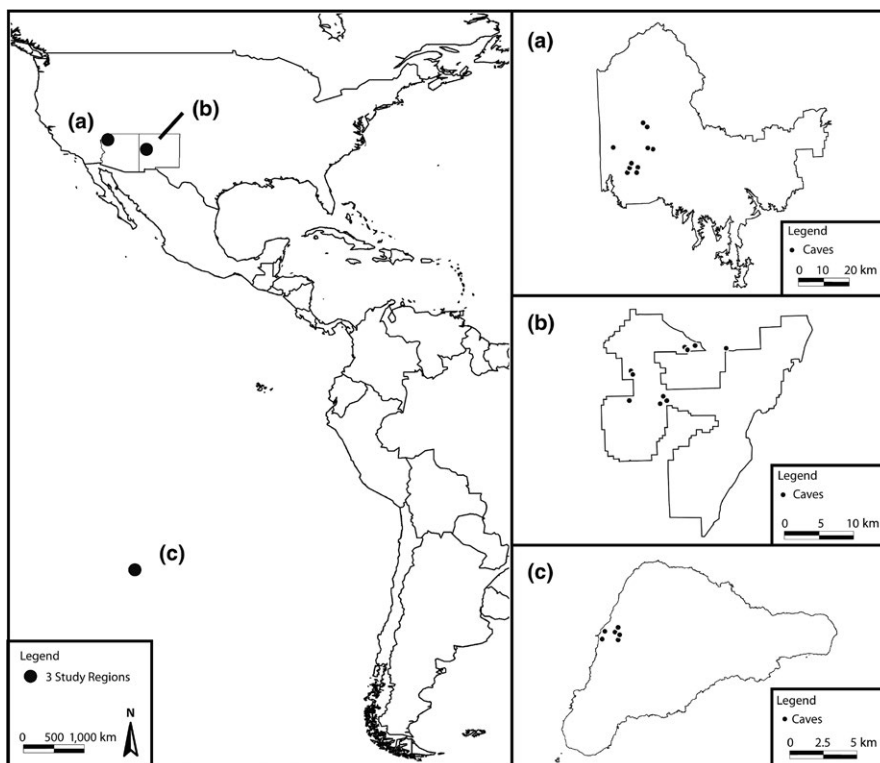


FIGURE 1 Left panel, Western Hemisphere from the United States south through South America. Study areas designated a, b, c with black dot denoting general study area locations. Right panels from top to bottom: (a) Grand Canyon-Parashant National Monument, north-western Arizona, United States; (b) El Malpais National Monument, west-central New Mexico, United States; and (c) the island of Rapa Nui, Chile; For study sites, black dots represent general cave locations

McWilliams, 1995). The surrounding landscape is characterized by gently rolling hills (i.e., extinct scoria cones) with a coastal cliff escarpment flanking the western boundary. Vegetation consisted of grassland and guava (*Psidium guajava*) shrub with fig (*Ficus* spp.), avocado (*Persea americana*), eucalyptus (*Eucalyptus* spp.) and banana (*Musa × paradisiaca*) trees occurring within many of the cave entrances. Elevation ranged from 32 to 126 m ASL.

2.2 | Field sampling

Study sites were sampled from 2007 through 2011. ELMA work was conducted during 06–14 October 2007 and 07–15 October 2008. PARA caves were investigated during 01–06 May 2007, 16–25 August 2007, 12–21 May 2008, 05–12 March 2009, 17–19 November 2009, 05–07 May 2010 and 01–03 September 2011. We studied caves on RAPA during 16–21 August 2008, 04–08 December 2008, 28 June–17 July 2009 and 01–07 August 2011.

To avoid the risk of over-collecting possible endemic and/or cave-adapted/restricted species, all specimens were collected judiciously. When observers were able to readily identify an individual to species, those observations were tallied on field forms, and the individuals were released. To further reduce the likelihood of unnecessary mortalities, we used “live capture” baited pitfall traps, and deep zone baits were placed directly on the cave floor, walls and ceiling.

2.3 | Techniques applied to all caves

We compared the relative efficacy of opportunistic collecting (OC), timed searches (TS) and baited pitfall trapping (PT), as well as a combination of systematic techniques (TS and PT, hereafter referred to as interval search or IS) in terms of sampling efficiency and completeness.

For all caves, maps were used to determine our sampling interval. Because we strived toward obtaining the most comprehensive representation of arthropod communities within our study caves, each site was sampled from entrance (i.e., drip line) to the back of the cave. Our sampling interval was 10% of the total cave length (e.g., for a 100-m-long cave, the sampling interval was 10 m). At each sampling interval, three sampling stations (one at each wall and one at cave centreline) were established and represented an individual sampling array. Fewer than three sampling stations for a given array occurred in two cases: (a) when the cave passageway width was ≤ 5 m, one station was designated in the best available location; or, (b) when exposed bedrock was encountered and no materials were available to aid in creating ramp-ways into the trap, the sample station was excluded.

At each sampling station, we deployed live capture baited PT. Each trap consisted of two ~900-ml nested plastic containers (13.5 cm high, 10.8-cm-diameter rim and 8.9-cm-diameter base). A teaspoon (~5 g) of peanut butter (Santa Cruz Organic® Creamy at ELMA and PARA; Jif® Creamy for RAPA) was placed in the bottom of the exterior container. At the bottom of each inner container, we made several dozen ~1-mm-diameter holes so the bait could

“breathe” to attract arthropods. Attempts were made to counter sink each pitfall trap within the cave sediment. When this was not possible, we built ramps using local materials (e.g., rocks and wooden debris) so arthropods could access the trap and fall in (Ashmole, Oromí, Ashmole, & Martín, 1992). To maximize trap effectiveness and discourage small mammals, we placed small rocks around the edges of the trap and then covered the mouth of the trap with a cap rock. Pitfall traps were deployed for 3 to 4 days (3-day deployment durations were driven by logistical constraints). Before removal of traps, we inspected the external cup in the event that arthropods were able to move through the holes of the inner cup.

For TS, we searched for arthropods within a 1-m radius around each sampling station. A 1- to 3-min timed search (1 min if no arthropods were observed, three if arthropods were detected) was conducted before PT deployment and prior to trap removal. The total number of sample stations dictated time expenditure per cave. For example, when a total of 30 sampling stations were deployed, TS ranged from 30 to 90 min per cave.

OS is an approach for sampling cave-dwelling arthropods as encountered (e.g., Peck, 1989; Ferreira, Martins, & Yanega, 2000; Reeves, Jensen & Ozier, 2000; Wynne & Pleytez, 2005); by design, the method was often applied in an unsystematic fashion. In this study, OC occurred as the survey team traversed the length of each cave, between sampling arrays, and while deploying and removing PT, and conducting TS. This technique was applied at least twice per cave (during PT deployment and retrieval trips) with at least two trained observers collecting and/or recording arthropods as encountered. For example, a cave with three observers would result in three individual OC per site visit. Because we conducted two site visits per cave, this resulted in six OC samples for each cave.

2.4 | Additional sampling techniques

Because caves are highly heterogeneous in their distribution and occurrence of microhabitats, it is not possible to apply an interval sampling approach without either missing or ineffectively sampling areas that may support unique arthropod communities. We encountered moss gardens within entrances and beneath skylights of two (ELMA-0008 and ELMA-0012; Wynne, 2013; Wynne & Shear, 2016) and root curtains from two (ELMA-0303 and ELMA-0315; Wynne, 2013) ELMA caves. Fern-moss gardens occurred within entrances and beneath cave skylights of five of six lava tube caves on Rapa Nui (Wynne et al., 2014). For most caves containing moss or fern-moss gardens, we conducted direct intuitive searches (DIS) with an unlimited search radius in which we intensively searched for arthropods by examining moss and ferns, looking on and beneath cobbles and boulders and inspecting cave sediment. For root curtains, we gently searched root masses protruding from cracks within cave ceilings of cave deep zones (Wynne, 2013). DIS were conducted for 1 hr (20 min \times 3 observers searching) within each of these habitats.

Cave deep zones were differentially sampled. This environmental zone is characterized by complete darkness, stable temperature, a near-water saturated atmosphere and low to no airflow (as in

Howarth, 1980). For select PARA and RAPA caves, we used combined bait sampling (B) and DIS to examine deep zones of three RAPA caves (Q15-074, Q15-076/078 and Q15-113) and two PARA caves (PARA-1001 and PARA-2204). Because B and DIS sites were often collocated within deep zones, we referred to these sampling techniques collectively as B/DIS. Deploying multiple bait types in cave deep zones is a common method for inventorying troglomorphic arthropods (Howarth et al., 2007; Peck & Kukulova-Peck, 1981; Reeves, 2001; Reeves, Jensen, & Ozier, 2000). Baits were placed directly on the cave floor and within cracks and crevices on the floors, ceilings and walls and deployed for 4 to 5 days. We used different bait types to maximize attracting different taxonomic groups including: (a) sweet potato (*Ipomoea batatas*), (b) fresh chicken livers for PARA and longfin bigeye fish (*Cookeolus japonicus*) entrails for RAPA and (c) small diameter branches from locally occurring plants—juniper trees (*Juniperus* spp.) for PARA and hibiscus (*Hibiscus rosa-sinensis*) and ngaoho (*Caesalpinia major*) for RAPA. Two to three stations of each bait type were deployed within the deep zone of each Rapa Nui cave, and four bait stations of each type were deployed in the two Parashant caves. Also, we conducted one DIS within each deep zone by inspecting the cave floor (each at 10 min per 1 m²). Finally, we conducted one DIS (1 hr × 1 observer searching) within the deep zone of PARA-3504.

2.5 | Taxonomy

All specimens were identified to the lowest taxonomic level possible. Across all study areas, specimens representing both accidentals and cave-dwelling arthropods were included in this analysis. We attempted to separate larval Lepidoptera specimens into operational taxonomic units for inclusion in the analyses, while specimens of larval stage Diptera were excluded from analysis.

Species-level identifications for many of the specimens and new species designations were provided by Drs. Rolf Aalbu (Tenebrionidae), Max Barclay (Coleoptera), Thomas Barr (Carabidae), Glené Mynhardt (Coleoptera: Ptinidae), Stewart Peck (Coleoptera: Leiodidae), Ernest Bernard (Collembola), Theodore Cohn (Orthoptera: Rhaphidophoridae), Jostein Kjaerandsen and Sarah Oliveira (Diptera: Mycetophilidae), Jon Gelhaus and Chen Young (Diptera: Tipulidae), Mark Harvey (Pseudoscorpiones: Chernetidae), Robert Johnson (Hymenoptera: Formicidae), Lynn Kimsey (Hymenoptera: Tiphidae), Edward Mockford (Psocoptera), Barry O'Connor (Acari), Pierre Paquin (Araneae), William Shear (Myriapoda, Opiliones) and Stefano Taiti (Isopoda).

2.6 | Analysis

We examined differences between how both morphospecies and coarse level taxonomic groups (i.e., typically at the order level) were detected across sampling techniques for all study areas (ELMA, PARA and RAPA) using nonmetric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) with the Bray–Curtis distance index. Both tests were conducted using R's "vegan" package.

Because caves are highly heterogeneous environments (Chapman, 1983; Kane & Poulson, 1976; Pellegrini & Ferreira, 2013; Trontelj et al., 2013) and arthropod sampling was conducted randomly and systematically, we sampled areas where arthropods did not occur and/or were not detected. This resulted in a large number of samples where no arthropods were encountered. As only 19% to 38% of our samples detected arthropods, we pooled samples per method per cave. This resulted in collapsing the total number of samples from between 323 and 666 to between 24 and 30 samples across the three study areas. Our last step was to then remove any remaining "no data" samples prior to running the analysis. We then conducted our analysis by grouping (or "blocking") each study area data set at the cave level.

For NMDS, each data set was square root transformed and standardized using Wisconsin double standardizations. Both transformations improve performance (Oksanen et al., 2017). We ran NMDS at both the morphospecies and coarse taxonomic groups for each study area data set using 500 random starts. The higher the R^2 value, the better the goodness of fit of the data. ANOSIM is a nonparametric permutation procedure used to examine dissimilarities in diversity between groups of treatments (Clarke, 1993), which enabled us to examine diversity levels across sampling methods; the number of permutations was set at 999. For both of these analyses, we examined differences between OC, TS and PT.

We then used Wilcoxon signed-rank tests (test statistic = W ; $\alpha = 0.05$ for all tests) to examine finer-scale differences between sampling techniques across all paired comparisons for (a) observed richness (S_{obs}), (b) sampling efficiency by effort, (c) sampling efficiency by time expended and (d) completeness. Paired comparisons were made for each study area and for study areas combined. Because we did not apply DIS or B/DIS uniformly in all caves, we examined differences between OC, TS, PT and combined PT and TS (or IS) only. For S_{obs} , we used the S_{obs} value for each technique (OC, TS, PT and IS) from each cave to examine all paired comparisons. This approach was repeated for efficiency by sampling effort (rate of return by dividing S_{obs} by the total number of samples per technique) and time expended (rate of return by dividing S_{obs} by the estimated number of minutes required to apply each technique). For pitfall trapping, we did not use the total amount of time traps were deployed; rather we summed the total time required to deploy and retrieve pitfall traps and process each traps' contents upon retrieval. Unless otherwise noted, all analyses were conducted using RStudio 1.1.383 (R Studio Core Team, 2017).

For completeness, we used two approaches to examine how effectively each technique captured richness. First, we used ESTIMATES 9.1 (Colwell, 2013) to calculate a suite of species richness estimators using the data from all sampling techniques combined for each cave. Estimators examined include Chao 2, ICE, Jackknife 1, Jackknife 2 and Bootstrap (refer to Magurran, 2004 for estimator details). Because their performance may vary across datasets (Walther & Moore, 2005), examining the results of multiple estimators is recommended (Hortal, Borges,

& Gaspar, 2006). All data sets were randomized 1,000 times. Next, we selected the most parsimonious estimators based upon typical species accumulation curve shape expressing most asymptotic behaviour (i.e., curve increases as most common species are detected, then begins to asymptote as more rare species are detected) and standard deviations of ≤ 2.0 . Completeness values per technique per cave were calculated by dividing S_{obs} by the most parsimonious estimator value (*sensu* King & Porter, 2005). Because sample sizes were small for many of the caves surveyed, we generated Mao Tau species accumulation curves at the study area level to examine relative completeness for each sampling technique and combination of all sampling techniques. We examined regional completeness by visually examining curve shape.

Finally, to identify any taxonomic group-specific patterns across techniques, we summarized detections for both individual study area and study areas combined using both absolute values and descriptive statistics. We also wanted to ascertain whether species of management concern were detected differentially across techniques, so we identified the extent to which each technique resulted in the detection of undescribed species (i.e., species new to science), range expansions for known species (for ELMA and PARA) and newly catalogued alien species (for RAPA).

3 | RESULTS

We tallied the total number of individuals, morphospecies and coarse taxonomic groups for each study area. At ELMA, we detected 400 individuals representing 62 morphospecies within 16 orders. We detected 1,873 individuals (1,180 individuals of one cricket morphospecies within one cave) representing 63 morphospecies in 17 orders within PARA caves. For RAPA caves, we detected 1,940 individuals representing 53 morphospecies within 16 orders (plus three cases where specimens were identified to “Class” level). Refer to Additional Supporting Information, Appendix S1, Tables S1.1–S1.3, for species lists of each study area.

For comparisons by technique, NMDS analysis reported low stress for both morphospecies (MS) and coarse taxonomic groups (CTG; Figure 2) across all study areas: ELMA MS ($R^2 = 1$, stress = 0.0001) and CTG ($R^2 = 0.997$, stress = 0.004), PARA MS ($R^2 = 0.994$, stress = 0.074) and CTG ($R^2 = 0.981$, stress = 0.139) and RAPA MS ($R^2 = 0.957$, stress = 0.078) and CTG ($R^2 = 0.991$, stress = 0.093). Initially, NMDS for ELMA MS and RAPA MS analysis showed stress nearing zero and point clustering vertically along the left side of the y-axis. This result may be indicative of the large number of zeroes (i.e., resulting from a large number of individual records where a technique was applied but few species were detected) potentially increasing the

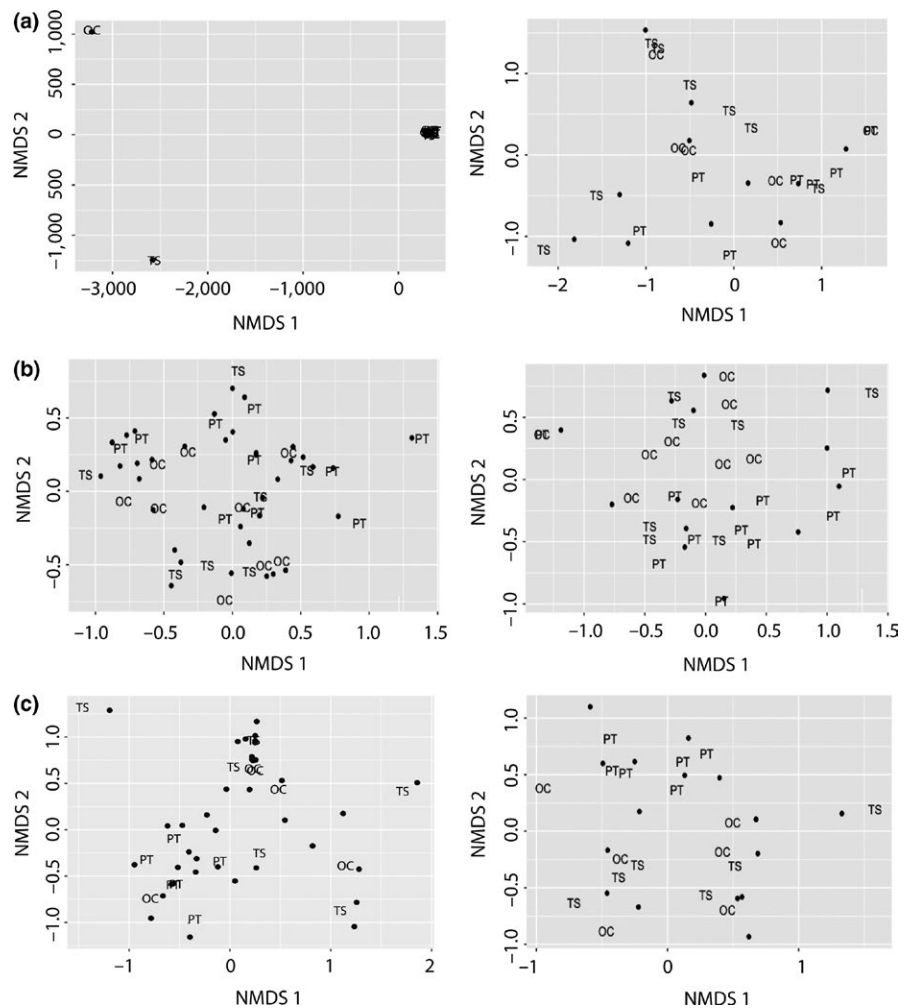


FIGURE 2 NMDS results of cave-dwelling arthropod sampling data by morphospecies (left) and coarse taxonomic groups (i.e., Order level or higher; right) for (a) El Malpais National Monument, (b) Grand Canyon-Parashant National Monument and (c) Rapa Nui National Park. Graphs represent Bray-Curtis dissimilarity ordinations for the three sampling techniques—opportunistic collecting (OC), baited pitfall trapping (PT), and timed searches (TS). All data sets were square root transformed and standardized using Wisconsin double standardizations. To obtain the lowest stress result, we applied the recommended 500 random starts to each data set

likelihood of outliers. We successfully removed the outlier for RAPA MS to obtain an ordination. ELMA MS ordination was not possible, given the paucity of data. However, when we collapsed the MS data sets to create the CTG data sets, this greatly reduced the number of zero-values. The resultant ELMA CTG output exhibited less questionable behaviour as both had low stress and moderate clustering of data points by technique. ANOSIM results (Table 1) were significant across all study areas: ELMA ($R = 0.019$, $p = 0.041$); PARA ($R = 0.111$, $p = 0.001$); and, RAPA ($R = 0.284$, $p = 0.001$).

To further examine the differences across sampling techniques, we examined paired comparisons using Wilcoxon signed-rank tests (W) for S_{obs} , sampling effort by number of samples, sampling effort by time expended and completeness (Table 2). For S_{obs} , OC and IS were significantly different for ELMA ($W = 50$, $p = 0.024$) and all regions combined ($W = 280$, $p = 0.008$). For efficiency by effort for both number of samples collected and time expended, over half (or >59%; 19 of 32) of these paired comparisons were significantly different (refer to Table 2). For completeness, we observed significant differences for OC and IS for all regions combined ($W = 170$, $p = 0.0136$).

When identifying the most parsimonious richness estimators for each cave for completeness, we found second order jack-knife (Burnham & Overton, 1978, 1979) and bootstrap (Burnham & Overton, 1978; Smith & van Belle, 1984) estimators performed best for all but one cave (Additional Supporting Information, Appendix S2, Table S2.1). For six caves (four at ELMA and two in PARA), we detected between one to four morphospecies. These resultant estimators were either close to the actual number, or equalled the number, of species detected and curve shape exhibited exponential behaviour. Because this is likely a small sample size effect, we did not calculate completeness values, and these caves were excluded from further analysis.

None of the species accumulation curves for any of the study areas for single techniques or all sampling techniques combined approached an asymptote (Figure 3). In all cases, more sampling is required to detect all species theoretically expected (or to attain asymptotic behaviour). Curves for OC across all study areas and DIS for ELMA exhibited the least asymptotic behaviour.

For all study areas, many morphospecies were detected by only one sampling technique. The highest rate of single technique

detections was for PARA at 66.7%. ELMA was second at 59.7%, while RAPA had the lowest level of single technique detections at 39.6%.

For the most speciose groups, we examined the relationship between detectability and sampling technique. Across study areas, spiders were most often detected using visual search techniques and rarely detected using PT. Of the 37 spider morphospecies, five (~14%) were detected with PT (among other techniques) and none were detected only with PT. Regarding spider abundance, of the 333 individuals detected, only six individuals (<2%) were detected using PT. For the 24 beetle morphospecies, six (24%) were detected with PT only, 11 (~46%) were detected with PT and at least one visual sampling technique, and seven (~29%) were detected by one or more of the visual sampling techniques (and not detected by PT). For Collembola (13 springtail morphospecies across all study areas), four (~31%) were detected by PT only, four (~31%) with PT and at least one visual sampling technique and five (~38%) using one or more visual sampling techniques. Of note, two RAPA collembolans, representing undescribed endemic species, were detected with only DIS within fern-moss gardens (Bernard et al., 2015). For Diptera ($n = 22$, across all study areas), most morphospecies (68.2%; 15 of 22 morphospecies) were detected through a combination of visual search techniques. Four morphospecies (~18%) were detected using B/DIS including a new species of keroplatid fly at PARA, which is troglomorphic in its larval stage. Only three morphospecies (~14%) were detected with both PT and visual search techniques.

Most isopod morphospecies ($n = 6$) were detected on Rapa Nui, while two cave-restricted morphospecies were detected in two Parashant caves. For the six RAPA morphospecies, half were detected by both PT and visual search techniques and half using only visual search techniques. Of these, the new Polynesian endemic species, *Styloniscus manuvaka*, Taiti & Wynne, 2015; was detected using TS only, while the new island endemic, *Hawaiioscia rapui* Taiti & Wynne, 2015; was detected using both PT and OC (Taiti & Wynne, 2015). Both cave-restricted PARA isopod morphospecies were detected using DIS within each cave's deep zone.

Regarding management concern species, nine new undescribed morphospecies were discovered, and two range expansions were documented on ELMA (Wynne, 2013). We detected three morphospecies using DIS only—a troglomorphic dipluran, *Haplocampa* n. sp.? (which was first observed by Northup & Welbourn, 1997), a potentially undescribed cave-adapted species of planthopper, *Fulgoroidea* n. sp.? (probably family Cixiidae) from the root curtains of two caves (Wynne, 2013) and a relict/cave-restricted millipede, *Austrotyla awishoshola*, Wynne & Shear, 2016; within the moss gardens of one cave (Wynne & Shear, 2016). For the remaining six undescribed species, two were detected by all techniques, one with both OC and DIS, two with TS only and one solely with PT. Range expansions for two tiphiid wasp species (*Tiphia andersoni* Allen, 1971 and *Tiphia nona* Allen, 1965) were confirmed with DIS in moss gardens (Wynne, 2013).

For Parashant, 13 new undescribed species and one range expansion of one cave-restricted species were documented. Four

TABLE 1 ANOSIM results for morphospecies and coarse taxonomic groups (order level or higher) for El Malpais (ELMA) and Grand Canyon-Parashant (PARA) National Monuments, United States and Rapa Nui (RAPA) National Park, Chile

	Morphospecies	Coarse taxonomic group
ELMA	0.121 (0.045)	0.156 (0.029)
PARA	0.256 (0.001)	0.353 (0.001)
RAPA	0.258 (0.006)	0.235 (0.004)

All analyses were conducted by blocking by cave. We sampled 10 caves at both ELMA and PARA, and six RAPA caves. R statistic is provided as first value with p -values appearing in parentheses. All tests were significant at $p < 0.05$.

TABLE 2 Summary of Wilcoxon signed-ranks tests (W) with p values for all paired comparisons for opportunistic collecting (OC), interval sampling (timed searches and baited pitfall trapping; IS), pitfall trapping (PT) and timed searches (TS)

	TS-PT	PT-OC	TS-OC	OC-IS
Observed richness (S_{obs})				
El Malpais	19 (0.43)	37.5 (0.084)	32 (0.28)	50 (0.024)
Parashant	25 (0.36)	21 (0.723)	15.5 (0.778)	41 (0.184)
Rapa Nui	11.5 (0.916)	6.5 (0.462)	4.5 (0.248)	13 (0.688)
All regions	154 (182)	154.5 (0.625)	116 (0.512)	280 (0.008)
Efficiency by effort (number of samples/method)				
El Malpais	43 (0.018)	9.5 (0.138)	6 (0.058)	10 (0.084)
Parashant	55 (0.002)	4 (0.014)	0 (0.009)	1 (0.004)
Rapa Nui	21 (0.031)	2 (0.094)	0 (0.031)	1 (0.063)
All regions	274 (3.765e-05)	41.5 (0.001)	7 (4.673e-05)	21 (1.332e-05)
Efficiency by effort (time expended/method)				
El Malpais	1 (0.013)	31 (0.343)	44 (0.013)	45 (0.084)
Parashant	6 (0.027)	6 (0.027)	41 (0.033)	23 (0.695)
Rapa Nui	1 (0.063)	8 (0.688)	20 (0.063)	12 (0.844)
All regions	15 (7.643e-05)	121 (0.27)	287.5 (9.06e-05)	211 (0.38)
Completeness				
El Malpais	8 (0.361)	18 (0.156)	12 (0.844)	20 (0.063)
Parashant	21 (0.272)	10 (1)	8 (0.353)	26 (0.313)
Rapa Nui	13 (0.688)	7 (0.566)	4 (0.219)	14 (0.563)
All regions	114 (0.08)	84 (0.965)	61 (0.178)	170 (0.0136)

Results for S_{obs} , efficiency by sampling effort (S_{obs} divided by number of samples per technique), efficiency by time expended (S_{obs} divided by number of minutes required to apply technique) and sampling completeness (S_{obs} divided by estimated richness) are presented. We set $\alpha = 0.05$ and considered all tests significant at $p \leq 0.05$ level. Within each cell, W is provided with p -values included within parentheses. Significance is presented as values in bold font.

undescribed troglomorphic morphospecies were detected using B/DIS within cave deep zones. Six undescribed species were identified with both PT and visual search techniques, one morphospecies was detected using PT only, one using a combination of visual search techniques, and one with B/DIS and visual search techniques. The range expansion of the cave-restricted millipede, *Pratherodesmus voylesi* Shear 2009, was determined using B/DIS within cave deep zones.

Nine new/undescribed morphospecies and 12 newly catalogued alien species were identified on Rapa Nui. Detections of undescribed species included two morphospecies detected with DIS within fern-moss gardens, two with PT only, two with OC only and the remaining three morphospecies using two or more visual search techniques. For the 12 newly catalogued alien species, four were identified only by TS. The remaining eight were detected by more than one sampling technique.

4 | DISCUSSION

Developing a standardized sampling protocol for terrestrial cave-dwelling arthropods is important for interpreting landscape-scale patterns, furthering our understanding of cave ecology and making evidence-based conservation and management decisions.

Without the development of a standardized sampling protocol (specifically targeting the highest efficiency and completeness possible) for terrestrial cave-dwelling arthropods, it also becomes more challenging to make meaningful regional and global comparisons between caves.

This study represents the first attempt to quantitatively examine the efficacy of various techniques for sampling terrestrial cave-dwelling arthropods and examine the utility of various sampling techniques within a conservation and management context. While we do not claim these techniques represent “the” protocol for sampling cave-dwelling arthropod diversity, we are hopeful our findings will be useful in establishing a foundational framework for addressing both terrestrial cave-dwelling arthropod community research questions, as well as improving biological inventory sampling designs.

We observed that different sampling techniques were better suited for targeting different taxonomic groups and species of management concern, which underscored the importance of applying multiple sampling techniques to best capture cave-dwelling arthropod diversity. ANOSIM analysis of morphospecies and coarse taxonomic groups indicated dissimilarities across sampling techniques, and we observed differences when examining Wilcoxon signed-rank tests for S_{obs} , sampling efficiency by effort, sampling efficiency by time expended and sampling completeness. Because the sampled

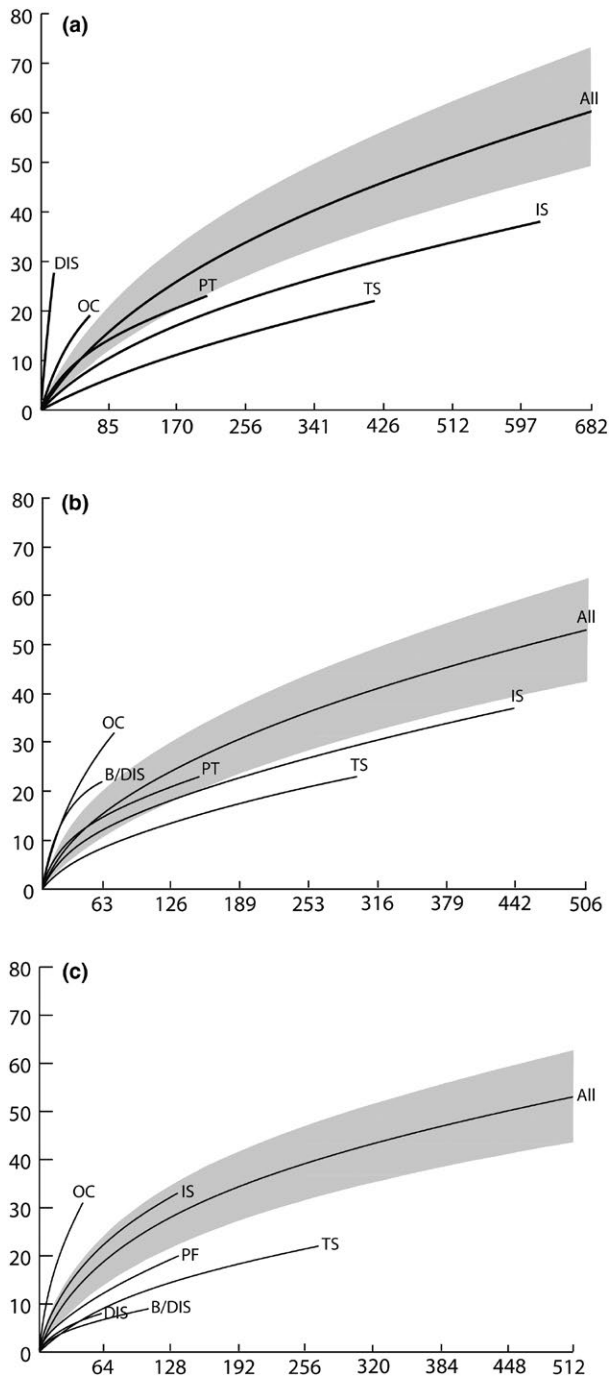


FIGURE 3 Mao Tau species accumulation curves per technique for (a) El Malpais National Monument, (b) Grand Canyon-Parashant National Monument and (c) Rapa Nui National Park. Curves are provided for all techniques (All), opportunistic collecting (OC), timed-search (TS), pitfall trapping (PT) and interval sampling (IS; timed-search and pitfall trapping combined), bait sampling and direct intuitive searches combined (B/DIS) of cave deep zones, and direct intuitive searches (DIS) of moss and fern-moss gardens. 95% confidence intervals are provided for all techniques only. Confidence intervals for other curves were similar. Each point along each curve line represents an average of 1,000 randomizations

cave deep zones and nutrient resource sites did not occur uniformly within all 26 caves, the resultant data were not included in the quantitative analysis.

However, we still found compelling differences across all techniques using descriptive statistics. For coarse taxonomic groups, had we relied on pitfall trapping for spiders or visual searches for beetles, we would have detected only ~14% and ~30% of their diversity, respectively. The use of B/DIS in deep zones and DIS in nutrient resource sites was shown to be of considerable importance. Without these techniques nearly one third of the cave-adapted/restricted species would not have been detected. On Parashant, we detected four troglomorphic species by applying two additional sampling techniques (B/DIS) within select cave deep zones. In one cave (PARA-1001), we detected two new troglomorphic species—a pseudoscorpion (*Hesperochernes bradybaughi* Harvey & Wynne, 2014) and a fungus beetle (*Ptomaphagus parashant*, Peck & Wynne, 2013)—both are posited to be single cave endemics (Harvey & Wynne, 2014; Peck & Wynne, 2013). We also identified potentially two new species of a cave-restricted isopods (*Brackenridgia* n. sp. 1 & 2; Stefano Taiti, *in litt.*; Wynne, 2010) from PARA-2204 to PARA-3507 caves. For the recently described cave-restricted millipede, *Pratherodesmus voylesi*, we expanded its range by ~64 km to the south by southwest (Wynne, 2010; refer to Shear et al., 2009) using B/DIS sampling at PARA-2204 and PARA-3507 caves. Finally, we discovered a new species of fly (likely of the family Keroplatidae), which is troglomorphic in its larval state (Wynne, 2010) from the deep zone of PARA-3507. All of these animals should be considered species of management concern.

By sampling nutrient resource sites, we identified several species that were not revealed using IS and OC. Moss gardens at both ELMA (Northup & Welbourn, 1997) and select Oregon caves (Benedict, 1979) were identified as relict habitats of the Last Glacial Maximum and may support once widespread species now restricted to this environment. On Rapa Nui, sampling fern-moss gardens resulted in the discovery of at least eight new species (Bernard, Soto-Adames, & Wynne, 2015; Mockford & Wynne, 2013; Taiti & Wynne, 2015). These animals represent endemic relict species of a severely environmentally degraded island ecosystem and thus should be considered critically important to conservation and management (Wynne et al., 2014). Fern-moss garden habitat supported the highest concentration of endemic species on the island (Wynne et al., 2014) and is therefore considered one of the most important terrestrial habitats on Rapa Nui (Wynne et al., 2016).

Stone, Howarth, Hoch, and Asche (2005) underscored the importance of tree roots as significant habitats for cave-adapted animals. Using DIS in root curtains of two ELMA caves, we discovered a potentially undescribed species of troglomorphic planthopper (Wynne, 2013). Had DIS not been applied in these areas, the potential importance of RAPA fern-moss gardens would not have been recognized, nor would the ELMA planthopper have been detected.

4.1 | Visual searches at trapping stations

Including a visual search technique with any trapping effort greatly improves sampling completeness. Other workers (Humphreys, 1991; Martín & Oromí, 1986; Peck, 1976; Poulson & Culver, 1969;

Schneider & Culver, 2004) have used various visual search techniques around traps as part of their sampling design. Whereas our analysis qualitatively found some differences in paired comparisons between TS and PT, the most compelling result was the detection of four undescribed species (including one troglomorphic spider from ELMA and one cave-restricted isopod from RAPA) and two newly catalogued alien species (on RAPA) by TS only. Because the additional time required per cave is relatively low and the results can be rather important from a management perspective, TS with a defined search radius should be coupled with all trapping efforts.

For this study, TS (conducted within a 1 m radius of each PT) were limited from 1 to 3 min. While a slight refinement from Peck (1976), a further improvement would be to extend TS time per sampling station. Campbell et al. (2011) searched for arthropods for 5 min using a much larger radius (5 m) around each pitfall trap. Because of the significance of TS in the detection of management concern species, we propose at least a 3–5 min search (using the same decision rule discussed above) prior to trap deployment and removal.

4.2 | Multiple technique, multiyear approach

We observed no clear patterns to suggest IS was a better sampling technique than OC for observed richness, efficiency by number of samples, efficiency by amount of time expended or completeness. However, IS techniques typically detected more individuals and morphospecies than OC, but neither approach identified as many species as all techniques combined—especially when we incorporated the additional morphospecies detected by sampling cave deep zones and nutrient resource sites within cave entrances. These patterns were observed for both individual caves and study areas. For most of our study caves, the number of observed morphospecies more than doubled for all techniques combined compared with the number of morphospecies detected by any single technique.

The accumulation curves for all techniques combined were most asymptotic (i.e., flatter) for all techniques combined than for curves generated using data from single techniques. These findings indicate that using multiple techniques is essential, but also that more sampling (i.e., additional site visits) is required before “all species” are detected and the theoretical asymptote is achieved. In other cave-dwelling arthropod studies, nonasymptotic curve shape was partially attributed to the cryptic behaviour and/or small population sizes of cave-adapted organisms. Schneider and Culver (2004) reported none of their species accumulation curves neared asymptotic behaviour in their analysis of West Virginia troglomorphic arthropods. Reporting similar asymptotic behaviour of their species accumulation curves, Gallão and Bichuette (2015) emphasized that sensitive cave-adapted species may be overlooked due to limited sampling; this could result in incorrect management decisions being made based upon incomplete information.

Additionally, we recommend using a multiyear study design with multiple site visits per year during the most biologically productive, warmest and wettest time of year (e.g., postmonsoons in the south-western United States, early austral summer for RAPA)

as a necessary study design component. Although caves are somewhat buffered environments, subterranean animal communities do respond to seasonal changes (e.g., Biswas, 2010; Dole-Oliver et al., 2009; Ducarme, Andre, Waulty, & Lebrun, 2004; Hancock & Boulton, 2009; Howarth, 1982). For example, the desiccating effect of cold dry air on caves (i.e., the winter effect; Barr, 1968; Howarth, 1980) frequently drives cave-adapted organisms into small cracks and fissures where they are more difficult to detect. Thus, sampling for troglomorphic taxa during a less optimal time of year may result in detecting fewer troglomorphic species.

Several additional techniques, not evaluated in this study, may be considered to further improve the ability to better characterize diversity and detect troglomorphic species of management concern. These techniques include the direct sampling of mesocaverns (Howarth, 1983; Ueno, 1977), DNA analysis to further refine species designations (Paquin & Hedin, 2004; Wessel et al., 2013), introducing irritants (e.g., smoke and diluted alcohol) into crevices to flush out animals, and building artificial mesocaverns in otherwise barren passages to draw troglomorphic arthropods out of cave pore spaces so they may be detected (Howarth, 1983; Ueno, 1977).

4.3 | An appeal to biologists

Through the application of standardized procedures even when sampling for specific taxonomic groups, those workers (e.g., biologists and taxonomists) may contribute to both addressing ecological questions and providing information to better guide management decisions. Presently, no standardized sampling protocols exist for any terrestrial cave-dwelling taxonomic group. While coleopterists (Aalbu, 1989; Barber, 1931; Valentine, 1941) have favoured pitfall traps for the inventory of beetles, no efforts have been made to standardize this approach. For sampling millipedes, Mesibov, Taylor, and Brereton (1995) reported that 4 weeks of hand collecting during the fall was more efficient than an intensive pitfall trapping effort involving trapping 7 days per month for over 1 year. Cardoso (2009) tested and proposed a standardized spider sampling protocol for surface species. The findings of Mesibov et al. (1995) and Cardoso (2009) hold promise for further shaping standardized sampling in cave systems.

As taxon-specific systematic sampling procedures are developed and tested, these techniques may facilitate more meaningful statistical comparisons at local and landscape scales and offer additional insights towards the development of an all cavernicole sampling protocol. Importantly, we encourage cave biologists to record and describe, in as much detail as possible, the specific collection methods applied during their surveys.

5 | CONCLUDING REMARKS

Presently, a universal set of standardized methods to survey terrestrial biodiversity of caves does not exist. We reported that methods useful for the inventory of one taxonomic group might not be as effective in detecting other taxonomic groups. Our fieldwork results

provide a measure of the relative effectiveness of a variety of survey techniques and show that no single technique is as effective as a combination of techniques in achieving maximum efficiency or completeness in surveying terrestrial cave arthropod communities. We hope that our work provides part of the foundation towards a more standardized survey protocol that will both optimize survey outcomes and facilitate more robust statistical comparisons across cave communities.

Until additional studies comparing techniques are conducted and new sampling techniques are developed and tested, we recommend using the entire sampling design applied here—factoring in the recommended improvements. Each technique contributed significantly to the detection of arthropod species, and thus, all techniques should be considered important. Furthermore, always targeting cave deep zones and nutrient resource sites, as well as additional time for timed searches and multiyear sampling (during the most biologically productive/wettest and warmest times of year), are necessary refinements that will result in more complete survey outcomes.

We further suggest each sampling technique interacted in a unique way with distinct arthropod behaviours, likely due to habitat requirements, movement patterns and ecology of different species. Thus, applying multiple sampling techniques resulted in maximizing the number of cave-dwelling species detected. Additionally, a multiple technique/multiyear approach will be required to adequately detect species of potential management concern (e.g., cave-adapted/restricted species and newly arriving alien species) and develop a long-term framework to monitor changes related to human impacts (e.g., global climate change and alien species' introductions).

We have demonstrated there is no easy recipe to address the detection of cryptic taxa, and sampling cave systems is challenging on many levels. Our hope is that the techniques provided here, and the proposed improvements, will be further tested, scrutinized and improved for broader use in other geographic regions. While imperfect, we view this as a critical first step towards developing a comprehensive strategy for systematically sampling arthropods in terrestrial cave ecosystems.

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BIOSKETCH

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Author contributions: J.J.W. collected and analysed data, wrote the manuscript and coordinated manuscript submission; J.J.W. and K.V. conceived the study and developed and refined cave arthropod sampling methods; K.V. assisted with data collection in Arizona and New Mexico; B.G. provided guidance in data analysis and contributed to the study design; J.J.W., S.S., F.G.H., B.G. and K.V. guided manuscript development and edited manuscript drafts.

SUPPORTING INFORMATION

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

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