Tiny habitats of tiny species: the importance of micro-refugia for threatened island-endemic arthropods

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Abstract Island-endemic arthropods are understudied species and likely to be highly threatened with extinction. Analysis of IUCN Red List assessments can be used to highlight important microhabitats requiring conservation for the effective management of island-endemic arthropod biodiversity. We synthesized information on the 296 island-endemic arthropod species assessed as Critically Endangered as of April 2024, the geography of the islands to which they are endemic, and the broad threats they face. These species comprised 33 taxonomic orders, across which an average of 53% of species were limited entirely to tiny, confined areas of habitat: caves, high elevation areas, isolated pools or sea stacks. These micro-refugia are most utilized by crustaceans and least utilized by myriapods. Caves and pools are the most important habitats on temperate islands where habitat degradation threatens crustaceans. On small tropical islands where arachnids and hexapods are threatened by invasive species, refugia are mostly in high elevation areas. Sea stacks appear to be effective refugia from invasive species only for threatened island-endemics with notable long-distance dispersal adaptation. None of the refugia appear effective in sustaining arthropod species immediately threatened by climate change. Using the interaction between arthropod life history, habitat and threats, it is possible to generalize micro-refugia that (1) should be immediately targeted for management, and (2) could yield undescribed or presumed-extinct species. Prioritizing such refugia for management and research can guide efficient expenditure of local capacity. In our case study, on Ascension Island, micro-refugia for seven endemic arthropods covered < 0.1% of the island's total area.

Keywords Arthropods, climate change, endemic species, extinction, habitat degradation, invasive species, IUCN Red List, micro-refugia

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Introduction

Growing evidence indicates that arthropods are in global decline (Hallmann et al., 2017; Seibold et al., 2019; van Klink et al., 2020, 2023; Wagner, 2020). Drivers for these declines are varied and intertwined, but include habitat degradation (Newbold et al., 2018; Seibold et al., 2019; Wagner, 2020), climate change (Wagner, 2020; Outhwaite et al., 2022; Harvey et al., 2023) and non-native species invasion (Bezemer et al., 2014; Wagner, 2020; Fortuna et al., 2022). Such anthropogenic pressures disproportionately affect fragile oceanic island ecosystems (Gray et al., 2019; Fernández-Palacios et al., 2021), home to many endemic species (Kier et al., 2009). Arthropods are globally understudied (Stork, 2018), and previously unknown island-endemic species are frequently discovered (e.g. Sherwood et al., 2024). Given the high rate at which island ecosystems are changing and our often-limited knowledge of island-endemic arthropod biodiversity and ecology (Cardoso et al., 2011; Gray et al., 2019) it is likely that island arthropods are going extinct without our knowledge.

The IUCN Red List of Threatened Species can be utilized for conservation planning and local management of island-endemic arthropods (Rodrigues et al., 2006; IUCN, 2023). Although the Red List criteria have shortcomings when applied to arthropods (Cardoso et al., 2011), combining threat assessments for different species can inform quantitative analyses of shared extinction threats and geographical patterns (Harfoot et al., 2021) and guide global-scale applied conservation (Challender et al., 2023). Approximately 16,700 arthropod species had been assessed for the Red List as of April 2024, of which c. 700 are categorized Critically Endangered (indicating the most immediate risk of global extinction; IUCN, 2023), although this is likely an underestimation of the real number of severely threatened species. Most assessments contain information on the geographical distribution of remnant populations, which may highlight where suitable habitat patches persist despite prevailing threats and thus can inform landscape-scale conservation.

There are few studies of arthropod refugia conducted at scales relevant to management (Selwood & Zimmer, 2020). Arthropod conservation at local scales can be hampered when practitioners lack specialist taxonomic knowledge, feel powerless to effect change, or are unmotivated to manage species perceived as non-charismatic or rarely noticed (Lampert et al., 2023). Aiming arthropod management actions at habitats, rather than arthropod populations specifically, could be one method of improving uptake of arthropod conservation by practitioners without prior experience or interest. However, many arthropod species of conservation concern are not present in formally protected and managed habitats (Chowdhury et al., 2023a, b), and arthropods can decline even within managed habitats (Rada et al., 2019). Habitats that are vital to specific threatened arthropods must be identified at spatial scales relevant to the life histories of these species. Such areas are likely to be relatively small, especially on oceanic islands where many arthropod species have reduced dispersal ability in comparison to continental species (Leihy & Chown, 2020). Managing these habitats as a priority may be cost-effective and accessible, removing some of the barriers to arthropod conservation. Beyond the preservation of comparatively well-studied arthropod species with known habitat associations, identification and protection of common, small habitats of importance to arthropods could conserve lesser-studied or even undescribed species. This is especially important as such species can be disproportionately affected by perturbations (Boyle et al., 2024).

We conjectured that Red List assessments of Critically Endangered island-endemic arthropods would highlight common micro-refugia of general relevance to island biodiversity conservation. We defined these micro-refugia as restricted habitat areas of a spatial scale relevant to arthropods that are believed to contain all, or a globally significant proportion, of a species' population and that can readily be delineated by conservation practitioners. Similar to defining regional-scale biodiversity hotspots to support habitat conservation for the largest animals (Myers et al., 2000), identification and protection of fine-scale micro-refugia could facilitate effective local management of some of the smallest animals. We aimed to (1) assess which Critically Endangered island arthropod taxa benefit from specific micro-refugia, (2) identify the broad links between island geography and occurrence of micro-refugia, and (3) quantify the relative importance of specific threats in defining these micro-refugia.

Methods

We accessed all Critically Endangered arthropod assessments on the Red List (IUCN, 2023) in March 2024 (Fig. 1). We filtered assessments by Taxonomy (Arthropoda) and Red List Category (Critically Endangered), downloaded the results and manually filtered species that are endemic to oceanic islands, totalling 296. Across these assessments, we identified four distinct refugia to which species were commonly confined: caves, high elevations, isolated pools (often anchialine) and sea stacks. Each of those categories describe a physically distinct ecological island (e.g. Cartwright, 2019) with documented importance to island-endemic arthropods (e.g. caves, Ashmole & Ashmole, 1997; high elevation, Gray et al., 2019; pools, Marrack et al., 2015; sea stacks, Priddel et al., 2003). Given that it was impossible to perform a literature search without existing keywords to identify such habitats important to arthropods, we consider our categorization of micro-refugia extensive, but inevitably non-exhaustive. Our conclusions on the relative importance of micro-refugia are therefore likely valid but may underestimate the broad importance of the concept.

Most micro-refugia were identified within Red List assessments via the Habitats section and clarified using the text account where the assigned code was unclear: caves are habitat category 7, isolated pools are category 5 but required clarification from the text, and sea stacks are category 6 or 17 but required clarification from the text. High elevation micro-refugia were identified from the Lower Elevation Limit in the Geographic Range section; we identified those micro-refugia where a species' lower elevation limit was higher than the middle elevation for the island to which it was endemic. For each Critically Endangered species we compiled its confinement to one or none of the four habitats and any threats it faces from climate change (category 11 in the Threats section), habitat degradation (all forms of physical modification, including development, agriculture, pollution, resource extraction and others; categories 1–4, 5.3, 6, 7 and 9) and invasive species (category 8). Separately, we compiled information on island area and position, from Sayre et al. (2019).

We analysed the data in *R 4.3.1* (R Core Team, 2023), using the packages *lme4* to fit mixed effect models (Bates et al., 2015) and *ggplot2* to visualize results (Wickham, 2016). Firstly, we fitted a logistic regression to predict the proportion of Critically Endangered species confined to the four micro-refugia amongst the arachnids (class: Arachnida, only represented by taxa of subphylum Chelicerata), crustaceans (subphylum Crustacea), hexapods (insects and springtails; subphylum Hexapoda) and myriapods (centipedes and millipedes; subphylum Myriapoda). We then fitted separate mixed effect logistic regressions to the proportion of cave-, high elevation-, pool-, and sea stack-limited Critically Endangered species on islands of differing area ($\log_{10}$-transformed), maximum elevation ($\log_{10}$-transformed) and tropical position (binary). Taxonomic group (arachnid/crustacean/hexapod/myriapod) was included as a random intercept to control for unexplained difference in effect between arthropods. Next, we fitted further mixed effect logistic regressions to predict the proportion of species confined to each micro-refugium from the broad threats of climate change, habitat degradation and invasive species (all binary). In these, we added island as a random intercept to control for geographical variation in prevailing threats.

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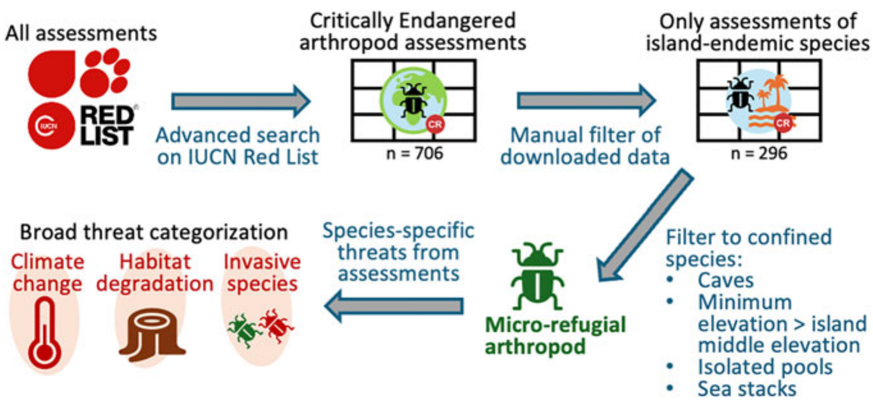

Fig. 1 The process of filtering IUCN Red List assessments, identifying Critically Endangered arthropods confined to micro-refugia, and finally extracting species-specific threat information coded into categories within assessments.

Finally, we examined the spatial scale of micro-refugia via a case study: the isolated Ascension Island in the South Atlantic. It is the only oceanic island we are aware of that has endemic arthropods reportedly confined to all four types of micro-refugia that we describe, belonging to the Arachnida, Crustacea and Hexapoda. The island is heavily degraded by invasive species (Ratcliffe et al., 2009; Sharp & Tawatao, 2023). The Ascension-endemic blind spider *Catonetria caeca* has only ever been observed in a single cave (Millidge & Ashmole, 1994; Ashmole & Ashmole, 1997), and the endemic flightless fungus moth *Erechthias grayi* was discovered in a tiny patch of remnant native grasses and mosses on a high-elevation ridgeline surrounded by thick non-native vegetation (Davis & Mendel, 2013). Ascension also has two endemic shrimp species, *Procaris ascensionis* and *Typhlatya rogersi*, which are found only in neighbouring anchialine pools (Chace & Manning, 1972; Biernbaum, 1996), and three endemic pseudoscorpions, *Garypus titanius*, *Neocheiridium ashmoleorum* and *Stenowithius duffeyi*, confined to a sea stack (Sherwood et al., 2024). We calculated and summed the areas of these four irreplaceable micro-refugia. The cave and high-elevation ridgeline were measured across their widest point in the field by tape measure, and we conservatively over-estimated their area by using these length measurements as diameters to derive separate circular areas. The areas of the anchialine pools and sea stack were estimated from drone and satellite imagery, respectively.

Results

Of the 296 Red List assessments, 281 were based on Criterion B, which uses geographical range and is the recommended criterion for minimizing taxon bias in arthropod assessments (Cardoso et al., 2011). A few species were assessed using Criteria A (population size reduction; 20 assessments), C (small population size and decline; 2) or D (very small or restricted population; 3), and none using Criterion E (quantitative analysis of extinction risk). Afrotropical island arthropods were most frequently represented (111 assessments), followed by Palearctic (74), Indomalayan (52), Australasian (27), Neotropical (22) and Oceanian (10) taxa. The greatest number of assessments were of Hexapods (154), followed by crustaceans (72), arachnids (40) and myriapods (30). The most common threats were habitat degradation (228 assessments), invasive species (136) and climate change (110).

The per cent of Critically Endangered species confined to micro-refugia varied between taxonomic groups (logistic regression: $\chi^2_4 = 47.36$, $P < 0.001$; Fig. 2). On average, 92% of crustacean species were confined to micro-refugia, 48% of arachnids, 39% of hexapods and 20% of myriapods. The per cent of the four micro-refugia varied significantly between taxonomic groups ($\chi^2_9 = 76.90$, $P < 0.001$). Crustaceans mostly utilized pools (75% of species), whereas arachnids, hexapods and myriapods primarily occurred in high elevation areas (65, 84 and 100% of species, respectively; for myriapods, n = 1 only).

Cave micro-refugia were most common on islands with high maximum elevation ($Z = 2.12$, $P < 0.05$) and outside the tropics ($Z = -3.22$, $P < 0.01$; Fig. 3a), but their frequency was not influenced by island area ($Z = -1.70$, $P > 0.05$). Critically Endangered arthropod species threatened by habitat degradation were positively assocated with cave micro-refugia ($Z = 2.09$, $P < 0.05$; Fig. 3b) and those threatened by invasive species were negatively associated with cave micro-refugia ($Z = -3.01$, $P < 0.01$). There was no significant association between species threatened by climate change and cave micro-refugia ($Z = 0.40$, $P > 0.05$). High elevation micro-refugia were most common on small ($Z = -3.96$, $P < 0.001$), elevated ($Z = 2.73$, $P < 0.01$) and tropical ($Z = 2.90$, $P < 0.01$) islands. Association with high elevation refugia was positive for arthropods threatened by invasive species ($Z = 3.89$, $P < 0.001$) and negative for those threatened by habitat degradation ($Z = -2.45$, $P < 0.05$). Again, there was no significant effect of climate change threats ($Z = 0.75$, $P > 0.05$). Isolated pool refugia were associated with low elevation islands ($Z = -5.17$, $P < 0.001$) and islands outside the tropics ($Z = -2.88$, $P < 0.01$) but there was no significant association with island area ($Z = 1.47$,

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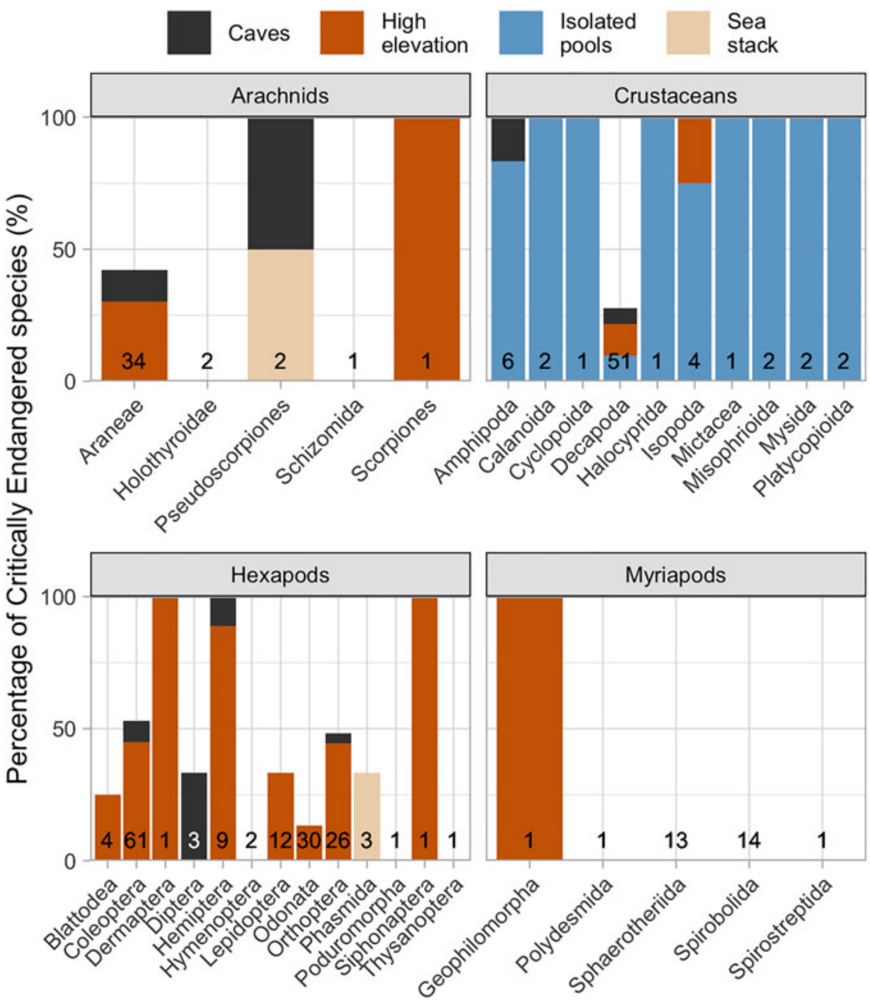

Fig. 2 Per cent of Critically Endangered arthropods from 33 orders that were reported as being confined to one of four micro-refugia. Numbers above the x-axes represent the number of individual species assessments from each taxonomic order.

$P > 0.05$; model had no random intercept, as all pool-limited species were crustaceans). We were unable to fit converging models predicting the proportion of pool refugia or sea stack refugia from threats because of small sample sizes and incomplete assessments. All species in pool refugia were threatened by habitat degradation ($n = 3$ only, because of missing data on Red List assessments), and all species on sea stack refugia were threatened by invasive species ($n = 2$).

We estimated Ascension micro-refugia to total 60,410 m^2 (Fig. 4). The interior floor area of the cave site was estimated to be c. 980 m^2 and the area of the high-elevation ridgeline c. 480 m^2. The surface areas of the anchialine pools (at highest tide) and the sea stack were estimated to be 1,200 m^2 and 57,750 m^2, respectively. Although land, water surface and subterranean areas are not usually combined in this way, for the purpose of providing a scale reference, these values sum to just 0.06% of Ascension's total 97.22 km^2 area.

Discussion

Micro-refugia could be useful targets for intensive management, especially on degraded islands where capacity for arthropod conservation is limited. They comprise extremely small portions of island habitat that are easily identifiable by conservation practitioners even if they have only limited prior specialist knowledge of arthropods. Such sites are disproportionately important for arthropod biodiversity on islands, which are themselves disproportionately important to global biodiversity (Kier et al., 2009).

The reasons why arthropod species are confined to micro-refugia vary. Crustaceans are confined to pools by their life history; they evolved in these often tiny habitats. This is also true for cave specialist arachnids and hexapods. These habitats are naturally resilient to perturbation; for example, environmental filtering in caves reduces their susceptibility to non-native species invasion (Nicolosi et al., 2023). Pools and caves should not be considered remnant habitat, but nonetheless may harbour small and vulnerable populations of endemic arthropods. These species are more threatened by habitat degradation on temperate islands and thus management should focus on conservation of their specific habitat structure and microclimate.

Conversely, micro-refugia in high elevation areas and on sea stacks may occur when species invasion reduces native arthropod occupancy area on small tropical islands. Invasions of non-native species have been less studied on

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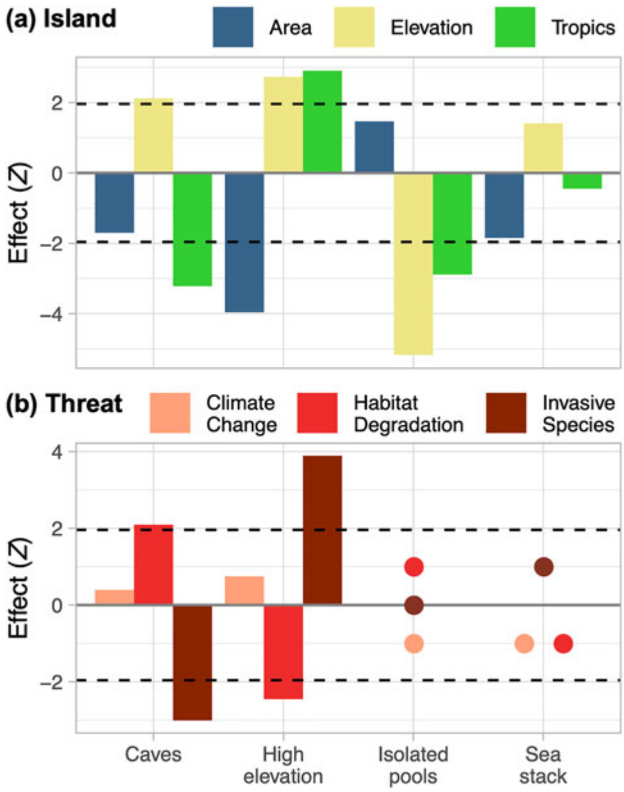

FIG. 3 Effects of island geography (a) and broad threat (b) on the number of island-endemic arthropod species confined to four micro-refugia. Bars that extend beyond the horizontal dashed lines represent significant effects at $P < 0.05$. Models could not be fitted to predict threat effect on isolated pools or sea stacks because of small samples sizes. In lieu of Z-values, dots at $y = 1$ indicate all arthropod species were threatened, at $y = 0$ some were threatened, and at $y = -1$ no arthropod species were threatened.

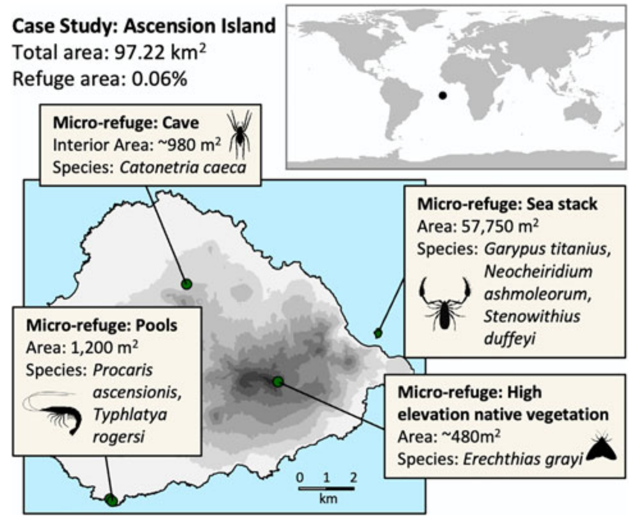

FIG. 4 Ascension, the heavily degraded oceanic island of our case study, showing the locations of the four arthropod micro-refugia fitting our definitions.

tropical than on temperate islands (Chong et al., 2021), but tropical lowlands appear disproportionately susceptible to invasive species, which has been linked to historical human colonization and habitat modification (Fernández-Palacios et al., 2021). Given the seemingly disproportionate importance of high elevations to endemic arthropods on some islands (Gray et al., 2019) and the high prevalence of high elevation micro-refugia on small islands that could perceivably become substantially colonized by invasive species, it is plausible that the high-elevation micro-refuges of at least some arthropods are remnants of equivalent lowland habitats degraded through invasion. Sea stacks are even less well studied, but they may become vestigial strongholds for highly threatened arthropods under specific circumstances. Only two arthropod species in our Red List dataset, the Lord Howe stick insect *Dryococelus australis* (presumed locally extinct on Lord Howe Island but rediscovered on Ball's Pyramid; Priddel et al., 2003) and the world's largest pseudoscorpion *Garypus titanius* (presumed locally extinct on Ascension mainland; Sherwood et al., 2024), are confined to sea stacks. Both were likely predated to extinction by invasive rats (Rudolf & Brock, 2017; Wilkins et al., 2019). Both pseudoscorpions (Lee, 1979; Xing et al., 2018) and stick insects (Suetsugu et al., 2018; Suetsugu et al., 2023) are adapted for long-distance dispersal aided by birds. We propose that sea stacks are vital micro-refugia from invasive predators but perhaps only for such uncommonly dispersal-adapted arthropods.

Our analysis confirms the existence of micro-refugia for threatened island-endemic arthropods, and that they vary according to taxonomic group, island geography and threats. We found no evidence that any of the micro-refugia were associated with climate change, despite 37% of Critically Endangered arthropods being reportedly threatened by it. This supports prior work that found climate refugia to be important at much larger spatial scales (Keppel et al., 2015; Balantic et al., 2021). Our findings suggest that island-endemic arthropods are unable to find effective local-scale refuge from climate change.

We recommend prioritizing caves, high-elevation areas of native habitat, isolated pools and sea stacks of oceanic islands for arthropod conservation. An equivalent approach for plant conservation in continental Europe (plant micro-reserves) successfully complemented large protected areas and increased taxonomic knowledge. In some cases, such micro-reserves were found to contain additional threatened species, detected only after establishment (Fos et al., 2017). We expect that similar management of arthropod micro-refugia on islands would yield equivalent benefits alongside existing larger protected areas. Close examination may indicate significant overlap with micro-refugia for island-endemic plant species, especially at high elevations. Where threatened island arthropods are not currently known from our broad micro-refugium habitats, we suggest that local stakeholders rapidly examine those places for potentially undetected species that may be at immediate risk of global extinction. Such unique and important ecological sites may also yield yet-undescribed arthropod species that have remained undiscovered because of their tiny areas of occupancy. Where threatened arthropods are known, we recommend those micro-refugia should be legally protected and local management plans formulated for their long-term preservation. On Ascension, for example, the cavernous sole locality of *C. caeca* received local council approval in 2024 as a novel protected area of < 0.02 km². Formal designation of the protected area on Ascension requires the formulation of a government-led management plan for the habitat and associated species, which should ensure long-term maintenance of the site. In the case of this specific micro-refugium, proposed management actions occur infrequently and thus do not require employment of an additional conservation practitioner by the local government.

Especially on degraded islands where local capacity for arthropod conservation may be limited, focused management of arthropod micro-refugia may be a starting point from which to prevent species extinctions in the short term. Even occasional maintenance of such tiny habitat areas, for example by clearing encroaching invasive vegetation or suppressing non-native rodents (Chin et al., 2024), may require only a few person-hours but provide great benefit to threatened arthropod populations constrained there. In comparison, actions that could yield equivalent benefit to larger, vertebrate species at spatial scales appropriate to their preservation would require far greater capacity. In this way, the small spatial scales of potential arthropod management are beneficial. Although, maintenance of tiny habitats is unlikely to be sufficient for permanent arthropod species conservation, it may facilitate site-specific ecological research and subsequent evidence-based species management in the long term.

Red List assessment of arthropod species can be confounded by criteria that were not designed with small-bodied animals or highly localized endemics in mind (Cardoso et al., 2011), so associated data should be interpreted with caution. We recognize that island-endemic arthropods may be disproportionately assessed via Criterion B as Critically Endangered because of their naturally limited ranges. Assessments are likely to also be biased with respect to reported threats, taxonomic groups and geography, depending on the researchers submitting them. Extremely limited species ranges reported in assessments are probably biased, as arthropod species detection inevitably increases with search effort and specialist expertise. In addition, and perhaps most importantly, our analysis is based on Red List assessments for a limited number of island-endemic arthropods. As such, we encourage local conservation practitioners to contribute to island arthropod Red Listing efforts, which may reveal additional micro-refugia and cryptic habitats that are globally important in future analytical syntheses. These caveats, however, do not reduce the validity of our main conclusion: tiny habitat patches, which comprise small areas of the islands on or near which they occur, are irreplaceable for threatened arthropods. Their targeted management represents a cost- and capacity-effective solution for preventing the global extinction of island-endemic arthropod species.

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Author contributions Study design, data collation and analysis: AS; writing: both authors.

Conflicts of interest None.

Ethical standards No specific approval was required for this analysis, as all Red List assessments were freely available online and area measurements on Ascension were conducted by AS in his capacity as a local government officer. This research abided by the *Oryx* guidelines on ethical standards.

Data availability Data are freely accessible from the IUCN Red List of Threatened Species (IUCN, 2023) and the USGS Global Islands dataset (Sayre et al., 2019).

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