Disturbance Relicts in a Rapidly Changing World: The Rapa Nui (Easter Island) Factor

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Caves are considered buffered environments in terms of their ability to sustain near-constant microclimatic conditions. However, cave entrance environments are expected to respond rapidly to changing conditions on the surface. Our study documents an assemblage of endemic arthropods that have persisted in Rapa Nui caves, despite a catastrophic ecological shift, overgrazing, and surface ecosystems dominated by invasive species. We discovered eight previously unknown endemic species now restricted to caves—a large contribution to the island’s natural history, given its severely depauperate native fauna. Two additional species, identified from a small number of South Pacific islands, probably arrived with early Polynesian colonizers. All of these animals are considered disturbance relicts—species whose distributions are now limited to areas that experienced minimal historical human disturbance. Extinction debts and the interaction of global climate change and invasive species are likely to present an uncertain future for these endemic cavernicoles.

Keywords: caves, disturbance relict hypothesis, ecological shifts, fern–moss gardens, endemic species

Today, virtually no place on Earth exists that has not been affected in some way by human activity. Although caves may be considered somewhat buffered systems (in particular, the deepest reaches of caves), the subterranean realm is no exception. Cave ecosystems are inextricably linked to surface processes. Deforestation (Trajano 2000, Ferreira and Horta 2001, Stone and Howarth 2007), intensive agriculture (van Beynen and Townsend 2005, Stone and Howarth 2007, Harley et al. 2011), livestock grazing (Stone and Howarth 2007), invasive species introductions (Elliott 1992, Reeves 1999, Taylor et al. 2003, Howarth et al. 2007), and global climate change (Chevaldonné and Lejeune 2003) have all been documented to affect cave biology.

Subterranean ecosystems often support unique, species-rich communities, including narrow-range endemic animals restricted to the cave environment. In some regions, caves have been identified as hotspots of endemism and subterranean biodiversity (Culver et al. 2000, Culver and Sket 2002, Eberhard et al. 2005). In addition, cave-restricted animals are often endemic to a single cave, watershed, or region (Reddell 1994, Culver et al. 2000, Christman et al. 2005) and are frequently characterized by low population numbers (Mitchell 1970). Consequently, many cave-restricted animal populations are considered imperiled (Reddell 1994, Culver et al. 2000).

How these animals colonized and ultimately became restricted to caves is generally explained by one of two hypotheses. Occurring primarily within the deepest, most buffered portions of caves, troglomorphic (or cave-adapted) animals are believed to be restricted to this environment because of either climatic or adaptive shifts. The climatic relict hypothesis suggests that, as surface conditions changed (e.g., changes driving advances and retreats of glaciers), some species survived in more-favorable conditions underground (Jeannel 1943, Barr 1968). The surface-dwelling populations ultimately went extinct, whereas the populations successfully colonizing the hypogean environment persisted and evolved into troglomorphic forms. As our knowledge of cave biology improved in tropical regions, numerous troglomorphic species were discovered where climatic shifts associated with glaciations were less pronounced. Because this region was never glaciated and was more climatically stable, tropical cave-adapted animals did not fit the climatic relict paradigm. On discovering epigean congeners living parapatrically with their troglomorphic sister species, Howarth (1982) proposed the adaptive shift hypothesis to explain this phenomenon. He provided additional support for the hypothesis with the observation that, in exposed cavernous rock strata, a significant amount of organic material sinks into cave environments. Because caves are unsuitable habitats for most surface
animals, only those animals preadapted to the subterranean realm are able to exploit this habitat, establish a reproducing population underground, and ultimately make an adaptive shift by evolving into cave-adapted forms.

Some animals may become restricted to caves as a result of anthropogenic activities alone and, as the extent of human impacts on cave ecosystems increases, another explanation is necessary to explain the occurrence of human-induced cave restriction. In addition, as the global human footprint becomes more pronounced and the effects of habitat loss and anthropogenic climate change accelerate, we anticipate that more disturbance relict species are likely to be found within both habitat fragments and relict habitats in caves and on the surface, as well. We propose the disturbance relict hypothesis to explain the occurrence of once-wide-ranging animals now restricted to a particular environment because of human activity.

This hypothesis is applicable beyond caves, because epi-
gean examples of this phenomenon have already been documented. For example, a walking-stick insect, Dryococelus australis, presumed to have been driven to extinction by the unintentional introduction of rats (Rattus rattus), was recently rediscovered on Ball’s Pyramid, an islet near Lord Howe Island, Australia (Priddel et al. 2003). Once occurring throughout Lord Howe Island, the only wild population of these animals is now restricted to cliff-face habitats on Ball’s Pyramid, which are too steep for rats to access. Steep cliff faces on the Hawaiian Islands are also known to support endemic relict plant species, which have been extirpated elsewhere on the islands through competition with nonna-
tive invasive plant species and predation by invasive pigs and goats (Wood 2012). Of these, Wood (2012) reported range rediscoveries of two cliff-face relics and the possible recent extinction of three cliff-face relics. The presumed extinction of these three plant species underscores the precarious per-
sistence of many relict populations as a result of mounting anthropogenic pressures.

A case study from Rapa Nui caves
Famous for its megalithic statuary (moai), Rapa Nui (Easter Island) has served as a cautionary parable for contemporary societies of the perils of unsustainable resource use (Diamond 2005). Several environmental and geographic variables, including geographic isolation, a small size, a shallow topographic relief, a low latitude relative to the equa-
tor, and aridity (when compared with other South Pacific islands) predisposed Rapa Nui to dramatic human-induced environmental change (Rolett and Diamond 2004). The severity of human impacts was probably also exacerbated by the sensitivity of the native ecosystem to fire (Mann et al. 2008) and an extended drought during this time megalithic civilization emerged (e.g., Orliac and Orliac 1998, Mann et al. 2008, Sáez et al. 2009).

Because of the fragile environment and intensive human demands placed on it, Rapa Nui appears to have experienced a catastrophic ecological shift (sensu Scheffer et al. 2001) as a result of large-scale deforestation soon after Polynesian colonization, which occurred sometime between 800 and 1200 CE (Martinsson-Wallin and Crockford 2001, Hunt and Lipo 2006, Wilmshurst et al. 2011). Evidence suggests that during this time, the predominantly native ecosystem shifted from a palm-dominated forest to a largely grassland community (Flenley et al. 1991, Mann et al. 2008, Sáez et al. 2009).

Hundreds of years later, during the midnineteenth century, Rapa Nui was converted into pastureland for a century-long sheep-grazing operation (Fischer 2005). On the basis of a fossil pollen analysis, Mann and colleagues (2008) found evidence that a remnant population of the endemic palm (Paschalococos dispera) may have persisted in rugged terrain (perhaps the first documented disturbance relict), but the tree was probably driven to extinction by livestock. Another once island-wide endemic tree, the toromiro (Sophora toromiro), lingered until the mid-1950s (Heyerdahl and Fordon 1961) but later became extinct in the wild (Flenley et al. 1991)—another possible casualty of livestock grazing.

Today, the island environment is dramatically different from what the first Polynesian colonists encountered. All native terrestrial vertebrates and many native plants have gone extinct. On the basis of fieldwork and the available literature, JJW and FGH determined that nearly 400 arthro-
pod species are known to occur on Rapa Nui. Prior to this current study, roughly 5% (21 species) were believed to be endemic (i.e., species believed to have evolved only on the island) or indigenous (i.e., species that arrived and estab-
lished a population on the island without human assistance). Of these 21 recognized endemic arthropods, only one recently described species (Collembola: Coecobrya kentethi) was detected within a cave (Jordana and Baquero 2008). This discovery raised the question of whether additional endemic arthropods use the subterranean environment. We began a series of studies in 2008 to address this question. We systematically surveyed arthropod communities in 10 Rapa Nui caves and their adjacent surface habitats to find any additional endemics and to determine the degree to which they were restricted to cave habitats (refer to the supplemental material for our methods).

The Rapa Nui caves within our study area appear to exhibit little environmental variation. We found that the average temperatures range from 16.5 degrees Celsius (°C; standard deviation [SD] = 0.5°C) in entrances and skylights (n = 3 caves, hourly data collected over 4 days in July and August 2008 and July and August 2009) to 19.4°C (SD = 1.5°C) in the deepest reaches of the caves (n = 4 caves, hourly data collected over 4 days in July and August 2011). We also found that the cave atmospheric relative humidity maintained a nearly water-saturated level in the deepest portions of the caves studied during the sampling period, and we suspect that these conditions persist during much of the year.

Although caves have been described as buffered environ-
ments (Tuttle and Stevenson 1978), environments within the shallow reaches of caves are expected to be less resistant to changing atmospheric conditions at the surface, whereas
the deeper reaches of caves may be more insulated from the surface environment. On Rapa Nui, the fern–moss garden environment occurring within both cave entrances and the areas beneath skylights (figure 1) appears to have been at least somewhat insulated from intensive environmental changes that occurred on the surface. This habitat occurs on the cave floors and low walls and extends from the light zones (entrance area) into the twilight zones. The presence of a cave-restricted endemic fern (Blechnum paschale; DuBois et al. 2013) and an endemic moss species (Fissidens pascuanus; Ireland and Bellolio 2002) already suggests that these partially protected environments represent an important refugium on Rapa Nui.

**Discovery of new endemic species in a severely degraded landscape**

We report the persistence of at least eight island-endemic and two Polynesia-endemic arthropod species on Rapa Nui that appear restricted to cave environments (table 1, figure 2). This discovery amounts to nearly one-third of the known endemic species on the island. None of these animals were detected in previous entomological studies (e.g., Fuentes 1914, Olalquiaga 1946, Kuschel 1963, Mockford 1972, Campos and Peña 1973), nor did we detect them during our surface sampling effort. All 10 endemic species were found in the fern–moss gardens near cave entrances or beneath skylights, and most of these species ranged further into the caves. Seven of these species ranged into what we identified as the transition zone (totally dark passages between the twilight zone and the more stable deep zone), and six were detected within the presumed deep zone (cave passages characterized as completely dark with relatively stable temperatures, nearly water-saturated atmosphere, and little to no airflow; see Howarth 1982).

Two of the species have also been reported from a limited number of other Polynesian islands and may have arrived with early Polynesians. The ancient Polynesian navigators are well known for traveling from island to island with canoe plants (Whistler 2009). They introduced these plants across the South Pacific Islands for food, medicine, materials for canoe building, and other purposes. A new species of isopod (Styloniscus sp.) was recently discovered on both Rapa Nui and Rapa Iti (3400 kilometers [km] to the southwest of Rapa Nui). On Rapa Iti, this animal was collected from the dead leaves of the bird's nest fern (Asplenium nidus). In addition, a springtail (Lepidocyrtus olena) previously known only on the Hawaiian Islands (Christiansen and Bellinger 1992; 7224 km to the north by northwest of Rapa Nui) was also among the species found within Rapa Nui caves. On Rapa Nui, we found both animals in cave entrances within a forested pit entrance and in the fern–moss gardens, as well as in the deeper reaches of several caves. We suggest that these animals may represent canoe bugs—arthropods transported across the South Pacific Ocean aboard canoes within the soils of cultivars. We further predict that these animals will be detected on intervening islands in Polynesia.

Alternatively, these animals may have arrived by rafting on vegetation debris. De Queiroz (2005) convincingly argued that the extent of global oceanic dispersal of plants and animals has been underestimated. Therefore, we wanted to examine this possibility for these two species. An examination of a map of oceanic currents (USASF 1943) suggests that dispersal between Hawaii and Rapa Nui is unlikely, given three bands of dominating equatorial currents running in an oscillatory pattern easterly and westerly. Therefore, it is unlikely that rafting debris carrying dispersing animals could travel orthogonal to these prevailing cross currents and ultimately reach the shores of Rapa Nui. However, oceanic dispersal from Rapa Iti to Rapa Nui is plausible, because the South Pacific Gyre spirals from Rapa Iti toward Rapa Nui. Dispersal by rafting in the opposite direction is unlikely.

None of the animals found during our study have morphological characters suggestive of cave adaptation, nor do we suggest that these animals retreated into caves in

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**Figure 1. Relict fern–moss garden habitats from two different entrances of cave Q15-038, in Rapa Nui National Park, on Easter Island, Chile. The endemic fern (Blechnum paschale) occurs along cave floors and walls amid several moss species. Most of the disturbance relict species discovered were detected within this habitat. Photographs: Dan Ruby, University of Nevada, Reno.**
### Table 1. Endemic disturbance relict species identified from Rapa Nui National Park, Easter Island, Chile.

<table>
<thead>
<tr>
<th>Class or subclass</th>
<th>Order</th>
<th>Family</th>
<th>Genus and species</th>
<th>Location</th>
<th>Endemism</th>
<th>Endemism justification</th>
</tr>
</thead>
<tbody>
<tr>
<td>Malacostraca</td>
<td>Isopoda</td>
<td>Philosciidae</td>
<td>Hawaiioscia sp.</td>
<td>Fern–moss gardens, transition zone</td>
<td>Rapa Nui endemic</td>
<td>Endemic genus previously known only from four species in lava tube caves in Hawaii (Taitt and Howarth 1997); differs in presence of pigment and well-developed eyes.</td>
</tr>
<tr>
<td>Malacostraca</td>
<td>Isopoda</td>
<td>Styloniscidae</td>
<td>S*Styloniscus sp.</td>
<td>Fern–moss gardens, transition zone, forested pit</td>
<td>Polynesia endemic</td>
<td>Known only on Rapa Iti and Rapa Nui; group of species characterized by a large lobe on the ischium (second leg segment proximal to the body) on the seventh or last pereopod (leg) of the male.</td>
</tr>
<tr>
<td>Collembola</td>
<td>Entomobryomorpha</td>
<td>Entomobryidae</td>
<td>Coecobrya sp.</td>
<td>Fern–moss gardens, transition zone, deep zone</td>
<td>Rapa Nui endemic</td>
<td>Distinct from Coecobrya kennethi.</td>
</tr>
<tr>
<td>Collembola</td>
<td>Entomobryomorpha</td>
<td>Entomobryidae</td>
<td>C. kennethi</td>
<td>Fern–moss gardens, deep zone</td>
<td>Rapa Nui endemic</td>
<td>Jordana and Baquero 2008; Rafael Jordana, University of Navarra, Pamplona, Spain, personal communication, 29 August 2013.</td>
</tr>
<tr>
<td>Collembola</td>
<td>Entomobryomorpha</td>
<td>Entomobryidae</td>
<td>Entomobrya sp.</td>
<td>Fern–moss gardens, forested pit</td>
<td>Rapa Nui endemic</td>
<td>Resembles Entomobrya pseudodecora from Bahia Blanca province, Brazil, but differs in pattern on fourth abdominal segment and foot claw characters.</td>
</tr>
<tr>
<td>Collembola</td>
<td>Entomobryomorpha</td>
<td>Entomobryidae</td>
<td>Lepidocyrtus olena</td>
<td>Fern–moss gardens, transition zone, deep zone, forested pit</td>
<td>Polynesia endemic</td>
<td>Known previously only on Hawaii (Christiansen and Bellinger 1992); slight difference in distal pleural seta of the head may suggest divergence from the Hawaiian group.</td>
</tr>
<tr>
<td>Collembola</td>
<td>Entomobryomorpha</td>
<td>Entomobryidae</td>
<td>Pseudosinella sp.</td>
<td>Fern–moss gardens</td>
<td>Rapa Nui endemic</td>
<td>Specimen does not match any known Pseudosinella species.</td>
</tr>
<tr>
<td>Collembola</td>
<td>Entomobryomorpha</td>
<td>Entomobryidae</td>
<td>Seira sp.</td>
<td>Fern–moss gardens</td>
<td>Rapa Nui endemic</td>
<td>Has similar pattern to Seira gobalezai, from Hawaii, but the chaetotaxy differs; also resembles Seira reichenspergeri, from Santa Catarina province, Brazil, but foot claw characters are different.</td>
</tr>
<tr>
<td>Collembola</td>
<td>Entomobryomorpha</td>
<td>Paronellidae</td>
<td>Cyphoderus sp.</td>
<td>Fern–moss gardens, transition zone</td>
<td>Rapa Nui endemic</td>
<td>A single specimen but distinct from all other Cyphoderus spp. in combinations of many characters.</td>
</tr>
<tr>
<td>Insecta</td>
<td>Pscoptera</td>
<td>Lepidopsocidae</td>
<td>Cytophania pakarati</td>
<td>Fern–moss gardens, deep zone</td>
<td>Rapa Nui endemic</td>
<td>Sexually reproduces (all other known Cytophania are parthenogenetic); spermathecal sac much larger and less wrinkled than those of other congeneres (Mockford and Wynne 2013).</td>
</tr>
</tbody>
</table>

Note: The transition zone is the aphotic zone between the twilight and cave deep zones (refer to Howarth 1982). The transition and deep zone environments were estimated. *Styloniscus sp. was also detected within the leaf litter of ferns on Rapa Iti. **This is the first record of this springtail occurring off Hawaii.
response to environmental change on the surface. Rather, as the island-wide ecological shift to a grassland community occurred, we suggest that these arthropods were already using caves, as well as terrestrial surface habitats, just as many of their close relatives do today. As suitable leaf-litter and soil habitats became progressively unavailable because of grassland expansion and intensive livestock grazing, these animals were ultimately isolated and restricted to the cave environment. Therefore, we believe that they represent a previously common component of the predisturbance leaf-litter and edaphic fauna. These species represent disturbance relics of animal populations that were historically more broadly ranging.

In other regions of the globe, caves have been identified as supporting relict species believed to have formerly ranged widely in surface environments but that are now restricted to the cave environment as a result of climatic shifts. In the Western United States, moss gardens within some cave entrances have been identified as relict habitats of the last glacial maximum and now support species restricted to these habitats (e.g., Benedict 1979, Northup and Welbourn 1997). Former leaf-litter-dwelling animals are also believed to have retreated into caves and appear to be cave restricted (rather than cave adapted) within all or a portion of their former range because of the climatic shifts associated with retreating and advancing glaciers (e.g., Peck and Lewis 1978, Peck 1980, Shear et al. 2009).

Given the lack of glacial activity and the island’s long history of intensive human use and disturbance, animals now restricted to the cave environment on Rapa Nui are more likely to represent human-induced disturbance relics than climatic relics. As anthropogenic activities on Rapa Nui continued (and perhaps accelerated), the wider ranges (potentially island wide) that these animals once used dwindled, and subpopulations ultimately became restricted to pockets of suitable habitat (e.g., fern–moss gardens of caves). Today, these disturbance relics appear to be restricted only to caves supporting these habitats.

**Persistence uncertain for disturbance relics on Rapa Nui**

Because most of the new species reported here are endemic to Rapa Nui, we know that they have successfully endured dramatic environmental changes and biological invasions over the past several hundred years. However, half of these endemics were detected in low numbers (i.e., \( n \leq 5 \) individuals), and some of these animals may represent at-risk populations. Extinction is often characterized by time lags, and at-risk populations may persist for long periods of time near extinction thresholds prior to becoming extinct (Brooks et al. 1999, Hanski and Ovaskainen 2002, Vellend et al. 2006). These extinction debts (see Tilman et al. 1994) are often associated with populations that have been isolated following a significant environmental perturbation, such as habitat loss or fragmentation, as is the case with the disturbance relics presented here. In addition, none of these species were found in surface habitats, and many of their populations may be small. Therefore, recolonization of the cave environment is probably very limited or nonexistent, and the rescue effect (see Brown and Kodric-Brown 1977) is unlikely to play a role in the long-term persistence for any of these relict populations.

These animals have survived anthropogenic impacts associated with a several-hundred-year history of intensive human use, including deforestation, agriculture, and livestock grazing, as well as at least 100 years of interactions (i.e., competition and predation) with invasive species. However, even if extinction debt is not in play for these disturbance relics, these animals face an uncertain future because of the associated impacts of global climate change, potential competition with well-established invasive species, and further competition with and predation by newly introduced invasive species. Other researchers suggest that the interaction of global climate change and invasive species presents significant challenges for the persistence of surface-dwelling endemic arthropods within other island ecosystems (Vitousek et al. 1997, Chown et al. 2007, Fordham and Brook 2010), and we have found that these pressures are mounting in Rapa Nui caves, as well.

We suggest that the combined effects of anthropogenic climate change and competition, predation, and niche
displacement by invasive species will be among the greatest threats to the persistence of these cave-restricted animals. In particular, we expect different zonal environments to respond differently to anthropogenic climate change. The temperatures within cave deep zones approximate the average annual surface temperature (Pflitsch and Piasecki 2003, Wynne et al. 2008), whereas the environment within the cave entrance represents a combination of both surface and cave climatic regimes (Howarth 1982, 1987). On the basis of this relationship, we suggest that cave climates (temperature and relative humidity) within the entrance and midcave zonal environments will respond more quickly to rising surface temperatures and that cave deep zone climates will have a lag response. We expect cave-obligate species’ populations to respond similarly. Animal populations occurring within cave entrances and midcave areas may respond more quickly than will populations occurring within cave deep zones.

Using information from other regions and South Pacific islands, we expect that current climate change patterns will present additional challenges for these endemic species through changes in precipitation patterns. In general, precipitation is expected to decrease in warmer subtropical regions (IPCC 2007). Chu and colleagues (2010) reported that long-term trends in increased drought conditions were projected for the Hawaiian Islands, and it seems reasonable to suggest that increased drought conditions may also occur on Rapa Nui. This may result in the loss of some fern–moss gardens from some caves, a reduction in area of this environment in other caves, or seasonal persistence of fern–moss gardens in still other caves. By extension, this will present challenges for the persistence of the endemic arthropod populations that inhabit this environment.

Currently, three well-established invasive species may pose considerable risk to the persistence of several endemic populations of cavernicoles on Rapa Nui. For example, Porcellio scaber, a globally distributed invasive isopod, was the most commonly detected arthropod in both surface pitfall traps (n = 4100) and within caves (n = 402). Although we did not specifically investigate competition between native and invasive arthropod species, the low number of individuals detected for the two endemic isopod species compared with the large number of P. scaber could be a result of interspecific competition. In addition, Howarth and colleagues (2001) considered P. scaber to be one of the most damaging alien arthropods in the native ecosystems in Hawaii. Oxidus gracilis, a cosmopolitan millipede (n = 146), and Periplaneta americana, the American cockroach (n = 79), were the second and third most abundant invasive arthropods detected in our study. On the Hawaiian Islands, Stone and Howarth (2007) identified both of these species as threats to endemic cavernicolous arthropod populations. Given the substantial number of opportunities for additional invasive species introductions (due to regular and frequent tourist travel to the island and the island’s reliance on mainland Chile for perishable goods), these endemic species may face additional pressures because of competition and predation from newly colonizing invasive species.

Conversely, provided these endemic species are able to persist despite the growing threats of global climate change and invasive species, Rapa Nui fern–moss gardens and the endemic species that they support may serve as important source habitats for endemics colonizing deep zone habitats. In New Mexico lava tube caves, moss garden habitats have been identified as supporting arthropod populations capable of colonizing cave deep zones and, perhaps, evolving into cave-adapted forms (Northup and Welbourn 1997). Of the Rapa Nui endemics, six of eight were detected beyond the fern–moss garden habitats in the cave deep zone environment. Given that troglomorphic relatives are widely documented for both Isopoda and Collembola, it is not unreasonable to suggest that some of these animals may establish populations within cave deep zones and may ultimately evolve into cave-adapted forms. In fact, all four known congeners of Hawaiioscia sp., the Rapa Nui endemic isopod, are troglomorphic species known only from the Hawaiian Islands (Taiti and Howarth 1997).

Conclusions
As the human footprint becomes more pronounced on our planet, we can expect to find once-widespread plant and animal species becoming isolated disturbance relicts restricted to fragments of suitable habitat. Unfortunately, although some large plant species (i.e., trees) may persist in small areas, we do not anticipate large-body terrestrial vertebrates to become disturbance relicts in small habitat fragments, at least not without heavy extinction debts (see Newmark 1987, 1995). Animal disturbance relicts will probably include smaller-body animals, such as arthropods, and perhaps small vertebrate species. Present and future disturbance relicts may have high extinction debts, and global climate change and invasive species will likely further challenge the persistence of these relict populations.

For Rapa Nui, despite these severe and persistent anthropogenic impacts, the disturbance relicts presented here persist today. However, we know nothing about the life histories and population dynamics of these animals, nor do we know to what extent human-induced climate change and biological invasions may ultimately affect these populations. Given that most of these disturbance relicts were detected in low numbers, we suggest that the presumed cave-restricted species presented here are imperiled. In addition, we have demonstrated the importance of caves as repositories for endemic species; nearly one-third of the island’s presently known endemic arthropod species occur within caves. Accordingly, the conservation and management of caves and the fern–moss garden habitat should be considered the highest priority for protecting the island’s endemic fauna. Appropriate management of the caves supporting these animals should include obtaining information on their life history, population structure, and habitat requirements, as well as identifying potential competitors and predators of
these disturbance relict species. This information is urgently needed to help safeguard their persistence in a rapidly changing world.

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Supplemental material


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Supplemental Material for Online Publication

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and; Consejo de Monumentos – Rapa Nui, Hanga Roa, Easter Island, Chile.

Figure 1. Study area (black rectangle) indicating the general location of the 10 study caves and locations of surface sampling grids (black dots), Rapa Nui National Park, Easter Island, Chile.

**Study Area**

We sampled 10 caves on the Roiho lava flow, ~5 km north of Hanga Roa, Easter Island, Chile (Figure 1). The landscape surrounding the study area was characterized by gently rolling hills (i.e., extinct scoria cones) with coastal cliff faces flanking the western boundary. Vegetation was grassland and invasive guava (*Psidium guajava*) shrub. Within many of the cave entrances and skylights (i.e., holes in the ground formed by the partial collapse of the cave roof), several invasive tree species occurred including fig (*Ficus* sp.), avocado (*Persea*)
americana), apple banana (*Musa x paradisiaca*), rose apple (*Syzygium jambos*), guava (*Psidium guajava*) and *Eucalyptus* species.

**Safeguarding Cave Resources**

To protect cave resources, codes were used instead of cave names and cave coordinates were not disclosed. Also, we provided the general location of our study area rather than actual cave locations plotted on the study area map. Rapa Nui National Park, Corporación Nacional Forestal (CONAF), Hanga Roa, Easter Island, Chile has a database relating cave codes to cave names, as well as coordinates for all of the study caves. Additionally, a copy of this paper, which includes a table of cave names with associated cave codes, is on file with Rapa Nui National Park, CONAF, Hanga Roa, Easter Island, Chile and CONAF, Jefe Departamento, Diversidad Biológica, Gerencia de Areas Protegidas y Medio Ambiente, Santiago, Chile.

**Arthropod Sampling of the Cave Environment**

We systematically sampled 10 caves during three research trips (16 - 21 August 2008; 28 June - 17 July 2009; and, 01 - 07 August 2011). For all caves, care was taken to avoid disturbing or damaging archaeological and geological resources. For six caves (all greater than 50 m in length), we used systematic sampling (i.e., interval sampling using live capture baited pitfall traps and timed searches, timed direct intuitive searches within fern-moss gardens, and timed direct intuitive searches and bait sampling in approximated cave deep zones), as well as opportunistic collecting of arthropods. An additional four caves, less than 50 m in length, contained fern-moss garden (FMG) habitats within cave entrances or beneath
cave skylights. We sampled habitats within these caves using timed direct intuitive searches. **Table 1** provides a summary describing how the caves were sampled. Wynne (2014) provides additional information on cave-dwelling arthropod sampling, as well as a morphospecies list of all cave-dwelling arthropods detected during the study.

For caves greater than 50 m in length, cartographic maps were required to establish the interval sampling grid (**Figure 2A**). We used 10% of the total cave length as our sampling interval (e.g., for a 1,000-m long cave, the sampling interval was every 100 m). We established up to 10 sampling arrays (one sampling station at either wall and one at cave centerline totaling ≤ 3 sampling stations = 1 sampling array). Fewer than three sampling stations per array occurred once when we were unable to establish the sampling station because it occurred within the middle of a pool of water.

At each sampling station, we deployed live capture baited pitfall traps. We used two 907-g stacked plastic containers (13.5 cm high, 10.8 cm diameter rim and 8.9 cm base). A teaspoon of peanut butter was used as bait and placed in the bottom of the exterior container. At the bottom of the interior container, we made several dozen holes so the bait could “breathe” to attract arthropods (e.g., Barber 1931). Attempts were made to counter-sink each pitfall trap within the cave sediment or roof-fall rocks. When this was not possible, we built ramps around each trap using local materials (e.g., rocks, wooden debris, etc.) so arthropods could access the trap and fall in (e.g., Ashmole et al. 1992). To discourage invasive rats from disturbing the traps, we placed rocks around the edges of each trap and then covered the opening of the trap with a cap rock. Pitfall traps were deployed for four days.
Figure 2. Schematic of different cave sampling techniques applied to Rapa Nui caves. [A] A interval sampling grid example for live capture baited pitfall traps, timed searches, and opportunistic collecting (each walk between traps, from array 1 to 2, represents one sample). Sample array numbers (1 through 10) are provided on the left outside the cave boundary. [B] An example of bait sampling (three bait types labeled 1 through 3 for sweet potato, chicken liver, and locally occurring branches, respectively) and timed direct intuitive searches within estimated cave deep zones.

For timed searches, we established a 1-m radius around each sampling station (where the pitfall trap would be deployed) and searched for arthropods within that ~3-m circle. A one to three minute timed search (one minute if no arthropods were observed, three if arthropods were detected) was conducted before pitfall trap deployment and prior to trap removal.
Opportunistic collecting was conducted by three observers as they traversed the length of each cave. This technique was applied as the observers were in transit between sampling arrays while deploying and removing pitfall traps and conducting timed searches. This technique was not applied while at sampling stations and was resumed after the observers were in transit once again. This method of opportunistic collecting occurred twice per cave (both during pitfall trap deployment and retrieval trips) with three observers searching for arthropods. For example, a cave containing 10 sample station arrays, there were 27 individual “random walks” per site visit (i.e., nine random walk samples times three observers who were collecting between stations). Because we conducted two site visits per cave, there would be a total of 54 samples (Figure 2A). Additionally, for some caves, arthropods were collected as encountered opportunistically during other, unrelated site visits.

We applied additional sampling techniques in two cases: (1) caves contained fern-moss gardens (FMG), and (2) caves were tentatively identified as containing deep zone environments. FMG occurred within cave entrances and beneath skylights. For three of four caves containing FMG, two observers spent 40 minutes (2 observers at ~20 minutes each) searching for arthropods. For the fourth cave, which contained three FMG within cave entrances and beneath skylights, we spent two hours (2 observers at ~20 minutes each within each FMG) searching for arthropods. Observers carefully searched for arthropods beneath rocks (replacing them to their exact location once done), on mud flats, and directly within the ferns and moss.
In 2011, we sampled the potential cave deep zones of four caves using timed direct intuitive searches and bait sampling (Figure 2B). In most cases, caves had at least two deep zone habitats. We conducted one timed direct intuitive search by inspecting the cave floor for 10 minutes within a 1-m radius within each potential deep zone. Bait sampling occurred for four to five days and consisted of placing baits directly on the ground or within cracks and fissures on cave walls, ceilings and floors. We used three bait types: (1) camote (or sweet potato tubers; *Ipomoea batatas*), (2) chicken and fish entrails, and (3) small diameter branches from locally occurring shrubs: hibiscus (*Hibiscus rosa-sinensis*) and ngaoho (*Caesalpinia major*). We deployed three bait stations per bait type within each potential deep zone of each cave sampled.

For the four caves less than 50 m in length that contained FMG habitats, we conducted two site visits and sampled using timed direct intuitive searches. Three observers spent 20 minutes each within each FMG searching for arthropods (totaling two hours of search time within each of these habitats).

**Arthropod Sampling of the Surface Environment**

In 2009, we established two 15 × 20 meter surface sampling grids – one along the western extent (near the coast) and the other further inland at the approximate center of our study area. Traps were deployed from 28 June through 08 July 2009. Trap spacing was at 5-m with a total of 20 pitfall traps per grid (total = 40 surface traps). Pitfall traps were constructed with a 22-cm segment of SDR 35 PVC pipe (3.2-cm inner diameter), which served as the outer sleeve. A 32 mm (ID) × 200 mm-long borosilicate glass test tube was
inserted within the PVC sleeve. A 7.6-cm segment of SDR 35 PVC pipe (5.1 cm inner diameter) was cut in half. One half was used to construct the pitfall trap cover, which was secured to the PVC sleeve with 16 gauge steel wire and duct tape. A space of approximately 2 cm was permitted between the cover and rim of the test tube. The test tube was three-quarters filled with propylene glycol. All pitfall traps were countersunk to ground surface and deployed for 10 days.

**Microclimate Data Collection of the Cave Environment**

For each cave, we collected hourly temperature data for three to four days using HoboPro© remote data loggers. For six caves where we applied interval sampling and opportunistic collecting (during 2008 and 2009), efforts were made to deploy a data logger at either each sampling array (i.e., an array consists of three sampling stations – one station at either wall and one station at the cave center line) or every other sampling array. For four caves where timed direct intuitive searches were applied within FMG habitats only, one data logger was placed within the sampling area. During the deep zone sampling effort, one data logger was deployed at close proximity to bait sampling stations. Data loggers were deployed for the same duration of time as each sampling technique (see the “Arthropod Sampling of the Cave Environment” section above for durations of time for each technique).

*Table 1. Number of samples per sampling technique for caves studied in Rapa Nui National Park, Easter Island, Chile. Sampling techniques applied were live capture baited pitfall trapping (BPT), time-constrained searches (TS), opportunistic collecting (OC), timed direct*
intuitive searches of fern-moss gardens (DIS-FMG), timed direct intuitive searches of potential deep zones (DIS-DZ), and bait sampling (Bait) of potential deep zones.

<table>
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<th>*Cave Codes</th>
<th>BPF</th>
<th>TS</th>
<th>OC</th>
<th>DIS-FMG</th>
<th>DIS-DZ</th>
<th>Bait</th>
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</tbody>
</table>

*We used cave codes rather than cave names to protect cave resources. Rapa Nui National Park, Hanga Roa, Easter Island, Chile has a database with cave names and codes.

**Curation of Arthropod Specimens**

Holotypes of all new species will be deposited at Museo Nacional de Historia Natural in Santiago, Chile. Voucher specimens will be deposited at either the Bishop Museum in Honolulu, Hawai‘i or as temporary loans to taxonomic specialists. Curation of voucher specimens will require cooperative agreements between Museo Nacional de Historia Natural and interested parties.
References cited


