

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, *trogomorphic* (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 epigeal 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 epigeal 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 nonnative invasive plant species and predation by invasive pigs and goats (Wood 2012). Of these, Wood (2012) reported range rediscoveries of two cliff-face relicts and the possible recent extinction of three cliff-face relicts. The presumed extinction of these three plant species underscores the precarious persistence 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 equator, 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 the time this megalithic civilization emerged (e.g., Orliac and Orliac 1998, Mann et al. 2008, Sáez et al. 2009, Stenseth and Voje 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 disperta*) 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 Ferdon 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 arthropod 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 established a population on the island without human assistance). Of these 21 recognized endemic arthropods, only one recently described species (Collembola: *Coecobrya kennethi*) 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 environments (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



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.

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 olenae*) 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

Table 1. Endemic disturbance relict species identified from Rapa Nui National Park, Easter Island, Chile.

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

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. ^a*Styloniscus* sp. was also detected within the leaf litter of ferns on Rapa Iti. ^bThis is the first record of this springtail occurring off Hawaii.

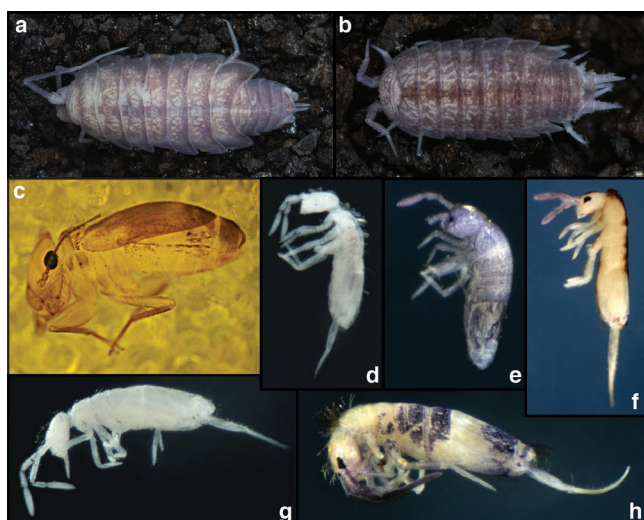


Figure 2. Disturbance relict species in Rapa Nui caves. (a) *Hawaiioscia* sp. (9.8 millimeters [mm] long). Micrograph: Caitlin Chapman and Neil Cobb, Colorado Plateau Museum of Arthropod Biodiversity (CPMAB), Northern Arizona University. (b) *Styloniscus* sp. (3.2 mm). Micrograph: Caitlin Chapman and Neil Cobb, CPMAB. (c) *Cyptophania pakaratii* (2.8 mm). Source: Reprinted with permission from Mockford and Wynne (2013), courtesy of Zootaxa. (d) *Coecobrya* sp. (1.4 mm). (e) *Pseudosinella* sp. (0.8 mm). (f) *Lepidocyrtus olenae* (1.2 mm). (g) *Coecobrya kennethi* (1.1 mm). (h) *Seira* sp. (1.8 mm). Micrographs (d–h): Ernest C. Bernard.

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 relicts 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 relicts than climatic relicts. 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 relicts appear to be restricted only to caves supporting these habitats.

Persistence uncertain for disturbance relicts 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 relicts 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 relicts, 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 pit-fall 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

The supplemental material is available online at <http://bioscience.oxfordjournals.org/lookup/suppl/doi:10.1093/biosci/biu090/-/DC1>.

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