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CONGERIA IN THE DINARIC KARST: CONSERVATION AND SCIENTIFIC STUDY OF A UNIQUE CAVE-DWELLING BIVALVE GENUS

ABSTRACT

Congeria, one of the few extant genera of cave-dwelling bivalve mollusks, is endemic to the Dinaric Karst and currently comprises three distinct species with highly fragmented distributions, facing serious threats of extinction. Here we highlight the unique life history traits exhibited by *Congeria* and discuss the potential of ongoing and future scientific research in addressing the critical challenges associated with its conservation. The subterranean waters of the Karst represent a highly stable yet vulnerable ecosystem that has been significantly impacted by human activities over the past few decades. Hydrotechnical projects have notably reduced water flow to underground habitats that are essential for the reproduction and survival of *Congeria*, leading to habitat loss and severe population declines in several areas. These challenges, together with water pollution, intensive agriculture and tourism, are projected to cause further population decreases in the coming decades, exacerbated by inadequate regulatory measures and our limited understanding of the biology of these bivalves. Scientific advancements, which include the recently completed sequencing of the genome of *C. kuscerei*, have the potential to provide critical insights into previously unexplored aspects of *Congeria* biology, unveiling the molecular mechanisms underlying its adaptive success in this challenging environment. Such research may offer a platform for an improved understanding of the factors underpinning the adaptation of *Congeria* to the subterranean environments and a comprehensive assessment of the genetic health, demographic history and resilience of the three extant species in the face of habitat alterations.

RIASSUNTO

Congeria, uno dei pochi generi esistenti di molluschi bivalvi cavernicoli, è endemica del Carso Dinarico e attualmente comprende tre specie distinte con una distribuzione altamente frammentata, che devono affrontare gravi minacce di estinzione. In questo lavoro si evidenziano le peculiari caratteristiche biologiche di *Congeria*, discutendo il potenziale della ricerca scientifica in corso e futura nell'affrontare le sfide critiche associate alla sua conservazione. Le acque sotterranee del Carso rappresentano un ecosistema altamente stabile ma vulnerabile, che è stato significativamente impattato dalle attività umane

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negli ultimi decenni. I progetti idrotecnici hanno ridotto notevolmente il flusso d'acqua verso gli habitat sotterranei che sono essenziali per la riproduzione e la sopravvivenza di *Congeria*, causando la riduzione dell'habitat adatto alla sua sopravvivenza e un grave declino della popolazione in diverse aree. Si ritiene che questo fattore, insieme all'inquinamento idrico, all'agricoltura intensiva e al turismo, possa causare ulteriori diminuzioni della popolazione nei prossimi decenni, aggravate dalle misure normative inadeguate e dalla nostra limitata comprensione della biologia di questi bivalvi. I progressi scientifici, tra cui il sequenziamento del genoma di *C. kusceri* recentemente completato, hanno il potenziale per fornire approfondimenti critici su aspetti finora inesplorati della biologia di questo organismo, svelando i meccanismi molecolari alla base del suo successo adattativo in questo ambiente particolare. Queste ricerche possono offrire una piattaforma per una migliore comprensione dei fattori alla base dell'adattamento di *Congeria* agli ambienti sotterranei e una valutazione completa sul suo stato di salute genetica, della storia demografica e della resilienza delle tre specie esistenti di fronte alle alterazioni dell'habitat.

SAŽETAK

Congeria, jedan od rijetkih rodova školjkaša koji žive u špiljama, endem je dinarskog krša. Ovaj rod obuhvaća tri vrste, svaka vrlo fragmentirane rasprostranjenosti, koje se trenutno suočavaju s ozbiljnim prijetnjama izumiranja. U ovom radu ističemo jedinstvene biološke značajke roda *Congeria* i raspravljamo o potencijalu trenutnih i budućih znanstvenih istraživanja u rješavanju kritičnih izazova koji su povezani s očuvanjem ovih školjkaša. Podzemne vode Dinarskog krša predstavljaju vrlo stabilan, ali ranjiv ekosustav koji je u posljednjih nekoliko desetljeća pod značajnim utjecajem ljudskih aktivnosti. Hidrotehnički zahvati značajno su smanjili protok vode u podzemna staništa koja su neophodna za reprodukciju i opstanak vrsta roda *Congeria*, što je dovelo do gubitka staništa i značajnog smanjenja veličina populacija u nekoliko područja. Predviđa se da će ovi izazovi, uz onečišćenje vode, intenzivnu poljoprivredu i turizam, u narednim desetljećima uzrokovati daljnja smanjenja populacija. Neadekvatne regulatorne mjere i naše ograničeno razumijevanje biologije ovih školjkaša dodatno pogoršavaju situaciju. Znanstveni napredak, koji uključuje nedavno dovršeno sekvenciranje genoma vrste *C. kusceri*, ima potencijal pružiti značajan uvid u prethodno neistražene aspekte biologije roda *Congeria*, otkrivajući molekularne mehanizme koji stoje u osnovi njezine uspješne adaptacije na izazovni okoliš špilja. Genomska istraživanja mogu omogućiti bolje razumijevanje čimbenika koji omogućuju pojavu prilagodbi vrsta roda *Congeria* na podzemni okoliš te pružiti platformu za sveobuhvatnu procjenu genetskog zdravlja, demografske povijesti i otpornosti triju postojećih vrsta trenutno suočenih sa značajnim promjenama staništa.

THE UNIQUE ADAPTIVE TRAITS OF CONGERIA

The Dinaric Karst region, which extends across Croatia, Slovenia, and Bosnia and Herzegovina, is recognized as one of the most important hotspots of subterranean biodiversity in the world. This rich diversity is attributed to ancient geological events that have shaped the unique Karst ecological niches (CULVER & SKET, 2000), creating isolated underground environments that differ significantly from the surface due to the relative stability of abiotic conditions, such as temperature, humidity, and water chemistry, across seasons. However, this stability presents challenges for the survival of life forms, primarily due to energy limitations, as these ecosystems lack sunlight-driven photosynthesis (HUPPOP, 2012). Far from being devoid of life, Karst underground environments harbor unique life forms that display peculiar adaptations that have been acquired over millions of years of evolution. Among these, the genus *Congeria* stands out as a remarkable example of evolutionary adaptation. Indeed, while gastropods are among the most abundant components of invertebrate troglofauna (CULVER, 2012), the bivalve *Congeria* is one of the very few cave-dwelling non-gastropod mollusks known to science. Moreover, the presence of this animal in the Dinaric Karst is of particular interest due to its status as a tertiary relict. Indeed, the family Dreissenidae, to which *Congeria* belongs, was widespread during the Tertiary Period in the Paratethys Sea. The survival of

Congeria to the mass extinctions at the end of the Miocene was accompanied with a transition to a subterranean lifestyle, unlike its relatives *Mytilopsis* and *Dreissena*, from which *Congeria* diverged ~22.8 and ~37.4 MYA, respectively (MORTON, VELKOVRH & SKET, 1998; STEPIEN et al., 2001; BILANDŽIJA et al., 2013; MORTON & PULJAS, 2013).

Recent phylogenetic analyses have revealed that what was once considered a single species is actually comprising of three distinct species endemic to the Dinaric Karst: *Congeria kusceri* BOLE, 1962 (Figure 1), the first one to be discovered and formally described, *Congeria mulaomerovici* MORTON & BILANDŽIJA, 2013, and *Congeria jalzici* MORTON & BILANDŽIJA, 2013 (MORTON & BILANDŽIJA, 2023). Despite their similarity, these species display distinctive morphological and genetic features, being the result of speciation processes believed to have occurred during the Pliocene (BILANDŽIJA et al., 2013).

Similar to most other troglobites (CULVER, 1982), these species lack pigmentation. Interestingly, while being fully dependent on water for feeding and reproduction, *Congeria* is able to survive for up to two months exposed to air, thereby displaying a remarkable adaptation to the variability of water levels that typically occur in the cave systems of the Dinaric Karst. During these events and the subsequent rise of water levels, *Congeria* displays a high tolerance towards temperature changes (MORTON & PULJAS, 2013; PULJAS et al., 2014; JOVANOVIĆ GLAVAŠ, JALŽIĆ & BILANDŽIJA, 2016). *Congeria* also exhibits a range of other adaptations that are characteristic of K-selected organisms, such as delayed reproduction, low fecundity, larger egg size, and increased longevity compared with its epigeal relatives. For instance, *Congeria kusceri* can live for over 50 years (PULJAS et al., 2014), a significant lifespan compared to most other bivalves, which seldom surpass 15 years in the wild (MOSS et al., 2016). Sexual maturity is reached around 10 years of age, and both shell growth and reproduction follow annual cycles strictly influenced by seasonal variations of water temperature and chemistry (MORTON & PULJAS, 2013). During reproduction, only a few offspring are produced, with larvae initially brooded in maternal ctenidia before developing further in mantle pouches. This reproductive strategy contrasts sharply with the R-selected life history of their epigeal close relatives (e.g. *Dreissena* spp. and *Mytilopsis* spp.), which are known for rapid reproduction and opportunistic growth, being considered highly successful invasive species in several regions (FERNANDES, SALGUEIRO & MIYAHIRA, 2022; KARATAYEV & BURLAKOVA, 2022).



Fig. 1 - A photograph of three *Congeria kusceri* adult individuals attached to the substrate in a period of low water levels, highlighting the lack of shell pigmentation. Note that based on morphometric data obtained from Jama u Predolcu, adult individuals display a shell length of about 11.5 ± 3.0 mm. This corresponds to 27.8 ± 12.7 years of age, which can be accurately estimated thanks to the microscopic analysis of shell growth lines in the umbonal region.

CURRENT THREATS TO THE SURVIVAL OF *CONGERIA* IN THE DINARIC KARST

Congeria faces numerous threats associated with human activities and is primarily challenged by habitat alterations due to water management practices. The Karst ecosystems depend on specific hydrological conditions, and even minor disruptions can have profound impacts on their fragile components. For example, changes in water levels, especially when accompanied by pollution, can adversely affect the reproductive success of *Congeria*, by disrupting its gametogenic cycle, spawning season timing, and larval dispersal. Such disturbances can lead to long-term population declines, exacerbated by the inherently low reproductive rates and limited dispersal potential of this bivalve. Therefore, traits that contribute to a heightened extinction risk, such as narrow habitat specialization, poor dispersal capabilities, and sensitivity to human disturbances (CHICHORRO et al., 2020), make *Congeria* particularly susceptible to extinction.

Although all the three formally described *Congeria* species are likely exposed to similar threats, we will here discuss in detail the situation of *C. kusceri*, which has been subjected to more intense scrutiny in the past few decades. This species inhabits the lower Neretva River basin in southern Herzegovina and Dalmatia, with documented populations currently found at eight sites divided between the river's northwest and southeast sides (BILANDŽIJA et al., 2013) (Figure 2). Hydrotechnical constructions have dramatically altered the upper Neretva River and its tributaries, notably affecting subsurface water levels. A prominent example is represented by the Trebišnjica River, where natural flooding patterns in the Popovo polje were disrupted by the construction of dams and canalization initiated in the 1960s. This prevented the biological minimum flow needed to sustain the underground connections between Trebišnjica and Neretva, leading to the desiccation of nearly 500 sinkholes and caves and the drying up of numerous springs along the Neretva and Adriatic coast (VRANJEŠ, PRSKALO & DŽEBA, 2013). The precise impact of this phenomenon on *C. kusceri* is difficult to quantify, as no pre-construction population surveys had ever been conducted. In his first historical description of the species in 1962, Bole identified three Popovo polje caves (Žira, Meginja, and Baba) as sites with abundant populations, particularly in Meginja. Today, out of these three locations, *C. kusceri* survives only in Žira ponor, the type locality of the species. This cave, which is currently flooded more sparsely than in the past, once had walls densely covered with mussels, which created layers up to 10 cm thick. Presently, the presence of bivalves is limited to a small area of 6 m², with the floor littered with shell debris. This would lead to a conservative estimate suggesting a >99% population reduction in Žira ponor over the past 60 years. This alarming decline mirrors similar losses in other Popovo polje caves. Another notable population loss for example occurred at Izvor-špilja kod kapelice Sv. Mihovila after the completion of hydrotechnological works. Even though live mussels were observed post-construction (JALŽIĆ, 1998), the subsequent population decline was likely influenced by factors such as the widening of the cave entrance, allowing increased light exposure that could alter microbial community structures critical to *C. kusceri* survival (RIGONI, BILANDŽIJA & ENGEL, 2023). Further threats to *C. kusceri* arise from the degradation of water quality in the Neretva basin due to pollutants from agriculture and inadequate wastewater management. Moreover, salinity increases due to seawater intrusion during summer, and this phenomenon is exacerbated by upstream dams, posing additional risks (VRANJEŠ, PRSKALO & DŽEBA, 2013). Tourism may be also considered a non-negligible risk for *C. kusceri* in some locations. For example, recent construction in the Jama u Predolcu cave have improved tourist access with unpredictable impacts on the unique fauna of this cave, which also includes other highly vulnerable filter feeders, such as polychaete tubeworms and sponges.

Besides the threats posed by human activities in the Neretva river basin, *C. kusceri*, like many other subterranean organisms, may significantly suffer from the effects of climate change,

due to its adaptation to a highly stable environment (MAMMOLA et al., 2019a, 2019b), since its ability to withstand long-term temperature alterations remains uncertain. In general, climate change may disrupt precipitation patterns, potentially lowering cave humidity and extending the period these bivalves are exposed to air. Importantly, the interspecific relationships between *Congeria* and the other components of the food web are poorly understood, complicating predictions about how climate change might impact them (RIGONI, BILANDŽIJA & ENGEL, 2023).

In light of its fragmented distribution and evident rapid population decline, *C. kusceri* is classified as a vulnerable species within the European Red List of non-marine mollusks (CUTTELOD, SEDDON & NEUBERT, 2011) and as critically endangered on the Croatian Red List of subterranean fauna (BILANDŽIJA & JALŽIĆ, 2009), being also listed in the EU Habitats Directive. Nevertheless, our poor knowledge of many aspects of the biology of this species currently hinders the identification of effective measures aimed at the conservation of this species.

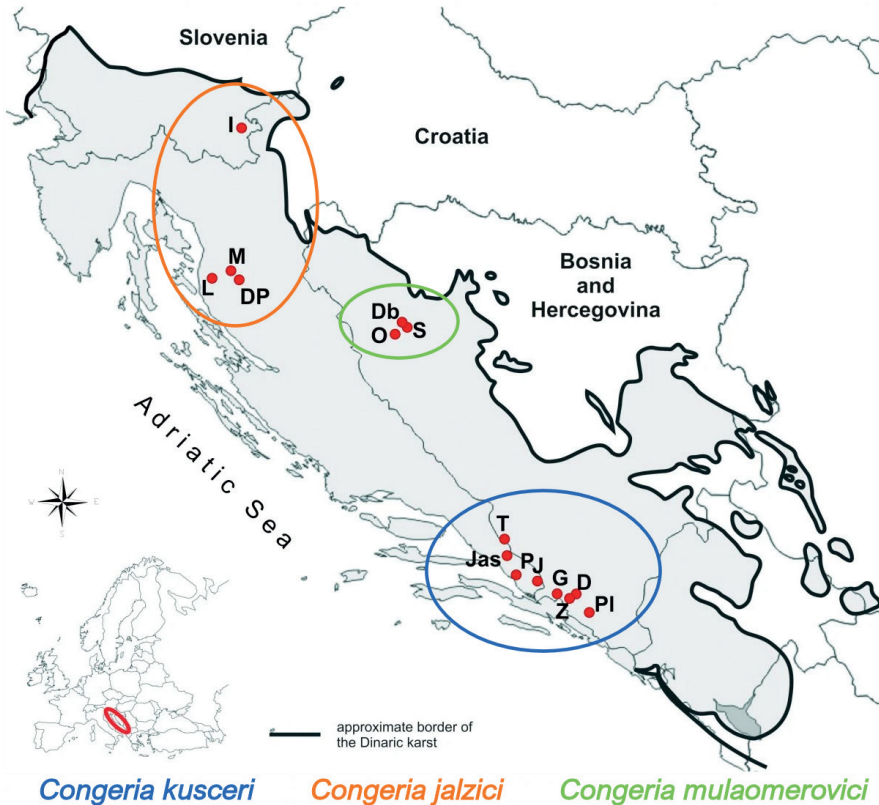


Fig. 1 - A map of the Dinaric Karst showing all known localities where living populations of the three *Congeria* species (indicated with different colors) occur. Species assignment was confirmed by the analysis of molecular markers. (i). Bela Krajina Region (*C. jalzici*), (SI): I, Izvir Jamske Školjke. (ii). Lika Region (*C. jalzici*), (HR): M, Markov Ponor; L, Lukina jama–Trojama Cave System; Dp, Dankov Ponor. (iii), north-western Bosnia (*C. mulaomerovici*), (BA): O, Oko; S, Suvaja; Db, Dabarska Pećina. (iv), Neretva Basin, southern Dalmatia (HR) and Herzegovina (BA) (*C. kusceri*): T, Tihaljina; Jas, Jasena Ponor; P, Pukotina u Tunelu Polje Jezero–Peračko Blato; J, Jama u Predolcu; G, Gradnica; Z, Žira; D, Doljašnica; Pl, Plitica. Modified from Bilandžija et al. 2013.

NEW OPPORTUNITIES COMING FROM ADVANCED SCIENTIFIC RESEARCH

The urgent need for genetic research to conserve endangered freshwater bivalves is widely recognized. Such studies are critical for understanding the factors underlying the adaptation of a species to its habitat, preserving existing genetic diversity and minimizing genetic risks during restoration initiatives (JONES, HALLERMAN & NEVES, 2006; LOPES-LIMA et al., 2014). With this respect, recent advancements in genomic technologies have paved the way for comprehensive investigations into bivalve genomes, shifting away from the traditional approaches based on the analysis of a few evolutionarily conserved molecular markers. These advances have recently allowed obtaining a complete, chromosome-scale reference genome assembly for *C. kusceri* (GenBank ID: GCA_027627225.1), which displays similar size (1.6 Gb), repeat content and gene density to its epigeal relatives. This important resource is presently undergoing in-depth analyses thanks to the joint collaborative efforts of the University of Trieste and the Ruder Boskovic Institute of Zagreb, which are expected to greatly enhance our knowledge of this species thanks to the application of different approaches aimed at answering pressing questions concerning the biology of this species (Figure 3).

Although no genome assembly is currently available for *Mytilopsis* spp., the closest extant relative of *Congerina*, genomic resources are available for both *Dreissena* (CALCINO et al., 2019; MCCARTNEY et al., 2019) and *Mya arenaria* (PLACHETZKI et al., 2020) which might serve as an outgroup for comparative studies. This approach might uncover the molecular factors underpinning the acquisition of the unique life history traits associated with the adaptation to the subterranean environment by *C. kusceri*. In detail, similar to other documented cases in cave-dwelling animals, we might expect to identify the loss or pseudogenization of genes critically involved in biological processes fundamental for epigeal life, but not essential for cave survival, such as tissue pigmentation or circadian rhythm regulation (FRIEDRICH, 2013; POLICARPO et al., 2020). On the other hand, other gene families might have undergone significant expansion, offering a great potential for gene neofunctionalization and improved fitness in the unique Karst environment.

Large-scale molecular analyses also have the potential to unlock the means by which *Congerina* modulates gene expression in different tissues in response to seasonal variations, during key processes such as gametogenesis and shell growth, or even to assess whether and to which extent it is capable of responding to biotic and abiotic stress. For example, RNA-sequencing has already proved to be an efficient method to elucidate the seasonal gene expression dynamics crucially associated with shell growth and reproduction cycles in *C. kusceri*, providing a highly detailed overview on the biological processes and molecular pathways differentially regulated in response to changes in water temperature and chemistry (SCAPOLATIELLO et al., 2023).

The genome assembly may also improve our understanding of the genetic structure of *Congerina*, which would be vital for providing crucial information to assess the chances of survival of the species in the long term. Such knowledge would be of the utmost importance, given the fragmented distribution of the species across subterranean habitats, which may lead to persistent inbreeding and genetic bottlenecks, threatening the viability of isolated populations. The ability to identify areas of high genetic diversity or unique haplotypes can prioritize conservation efforts, as demonstrated in other endangered freshwater bivalves (ELDERKIN et al., 2007).

Advanced population genetics studies relying on modern techniques, such as RADseq, ddRAD and 2b-RAD, would certainly greatly benefit from the use of an annotated genome assembly as a reference.

Accurate population estimates are crucial for conservation planning, yet conducting such studies using traditional methods in subterranean habitats poses significant challenges. For

example, diver surveys are resource-intensive and impractical for large-scale monitoring. Developing alternative methods for reliable population estimates is a pressing task, necessitating innovation and validation to ensure their efficacy in diverse environments. In this context, environmental DNA (eDNA) offers a promising tool for delineating with more precision the current range of distribution of *Conger*, assessing sites where historical populations were documented, and exploring new subterranean habitats inaccessible to traditional surveys. This method could shed light on unresolved genetic relationships, such as the connection between *C. jalzici* populations in Slovenia and Croatia, which are geographically isolated (Figure 3) yet genetically similar.

Among the countless opportunities offered by modern molecular approaches, the characterization of the microbiota associated with *Conger* is certainly not of secondary importance, as these components may be associated with the health status of the organism, undergoing significant variations in case of environmental alterations. Two recent examples of these applications are represented by the characterization, obtained through a combination of 16S rDNA sequencing and proteomics approaches, of the bacterial communities associated with *C. jalzici* in Markov ponor (BIELEN et al., 2024) and by the identification of five novel Picorna-like viruses associated with *C. kusceri* in the pit Jama u Predolcu (SCAPOLATIELLO et al., 2022).

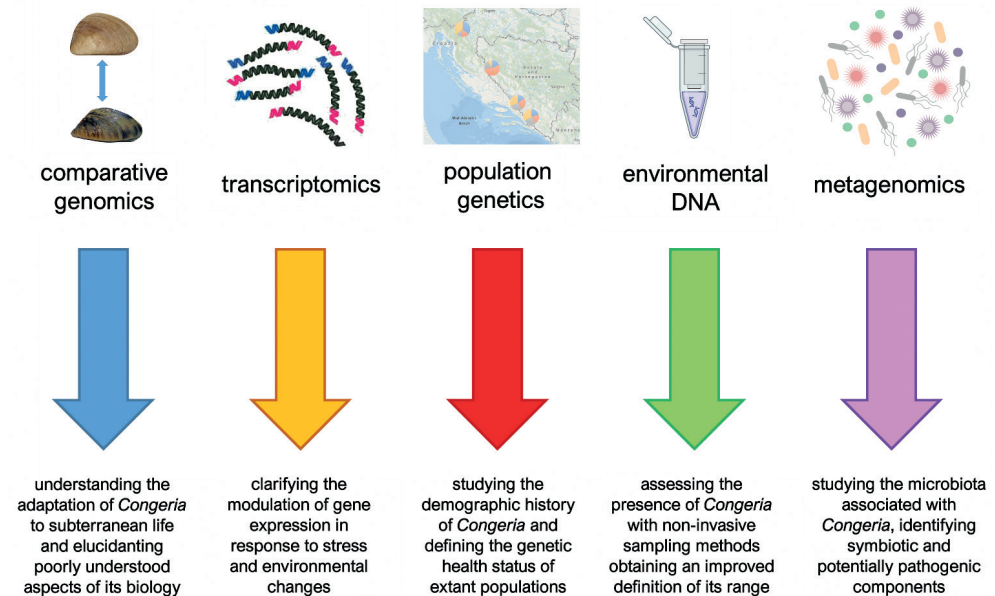


Fig. 3 - A schematic representation of the major areas of interest where scientific studies could provide a benefit for the survival of *Conger*.

CONCLUSIONS

We are currently facing the sixth mass extinction event that, unlike the previous ones caused by natural phenomena, is primarily driven by human activities, leading to an unsustainable use of land, water and energy, and to climate change. According to several studies, the species loss rate may be up to 100 times higher than the background extinction rate (CEBALLOS et al.,

2015). Sixty years after its formal description, *Congeria* is already facing severe extinction threats, linked with its fragmented geographic distribution and the escalating human impact on subterranean water ecosystems. The degradation of these fragile habitats, compounded by a lack of sufficient protective regulations, further imperils the survival of the three congeneric species found in the Dinaric Karst. The situation demands immediate attention, with research urgently needed to address fundamental questions about the ecological and physiological traits that determine the adaptation of *Congeria* to its unique environment, and the genetic health of extant populations. However, an improved understanding of the biology of this species must be paired with prompt intervention from local authorities and the allocation of appropriate financial resources for conservation initiatives. Together, these actions are critical to safeguarding *Congeria* from extinction. The stakes are high, and without concerted efforts to address these challenges, the extinction of these unique organisms may become an irreversible reality.

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