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Human Pressure meets Climate Change: The Extinction Vortex of the Freshwater Pearl Mussel *Margaritifera margaritifera*
How does the Evolutionary History Relate to the Current Status as Endangered Species?

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Abstract

The Freshwater Pearl Mussels *M. margaritifera* is an endangered Holartic species in the family of *Margaritiferadae* in the order of *Unionoidea* and Class of *Bivalvia*. *M. margaritifera* is found in North America, Europe and through into Siberia. It has been declining throughout the European part with a negative forecast on survivability of the species [1] IUCN[1]. The longevity of *M. margaritifera* and the fragility of the reproduction conditions as well as habitat selectivity regarding environmental requirements pose difficult niche conditions for the species. Population decline is not only related to species-specific intrinsic characteristics and extrinsic factor like water pollution (IUCN[2]), but also caused by the introduction of invasive species such as the less specialised, non-threatened Freshwater Zebra Mussel *Dreissena polymorpha* (Araujo, 2006). We discuss the vulnerability of the species in the light of the conceptual framework of *Modern Synthesis, MS* and the *Extended Evolutionary Synthesis, EES* [2]. In the outlook we review the conservation status and briefly evaluate the opportunities of EES driven approaches for further research on re-establishment of the species [3].

Keywords: *M. margaritifera;* Holartic species; Environmental; Reproduction; Freshwater pearl mussels; Invasive species; Agrarian sector, Water pollution

Introduction: Habitat Requirements of *M. margaritifera* for Survival and Reproduction

Early evolutionary theory (discussed in: Kutschera & Niklas [4]) provides a preliminary framework to explain the evolutionary history and the current endangered status of *M. margaritifera* as 'one of the most sensitive macroinvertebrate species targeted by the Water Framework and Habitat Directives' [5][3]. In 2010, the endangered species consisted out of 200 million, mostly mature individuals 'with little replacement as mature animals die' [1]. The current population is characterized by high fragmentation and large numbers of isolated, under-critical subpopulations without genetic interchange[4] [6]. With a complex reproduction lifecycle that requires different habitats at different stages of the metamorphosis cycle the Freshwater Pearl Mussel is adapted to niche conditions that are currently no longer intact due to water pollution, siltation of riverbeds, climate and temperature changes, and loss of fauna.

[1]https://www.iucnredlist.org/species/12799/128686456
[2]*Ibit.*
[3]*Generation length for M. margaritifera is approximately 30 years, so a three-generation prediction of 90 years has been used to evaluate the population losses. Overall, in the last 90 years for Europe there has been a decline of 81.5%; a loss of 87% for EU countries. The overall global reduction in population size over the same period is 61.5%. Source: IUCN [16].*
[4]*IUCN, 2017. The IUCN Red List of Threatened Species International Union for Conservation of Nature, Gland, Switzerland (2017)* http://www.iucnredlist.org

Freshwater Pearl Mussels have separate male and female animals. Reproduction occurs when sperms are released into the open water via the male's siphon and are carried to the eggs via the female inhalant siphon and fertilisation occurs in the female brood chambers. The eggs develop into the larval stage, called *glochidia*, which are temporarily brooded in the female gills from June each year, and are then released into the open water in high numbers in an event lasting one to two days [7,8]. In a *larva stage* the mussel relies on the presence of suitable fish like Brown Trout (*Salmon Trutta*) or Atlantic Salmon (*Salmon Salar*) for hosting the *glochidia larvae* as cysts in their gillies over the winter season. Both, juvenile, and mature mussels have specific niche requirements for further development. They require a clean and calcium free water quality, oligotroph conditions and oxygen rich rivers [6]. In the juvenile and adult stage *M. margaritifera* is susceptible to silt in riverbeds as it obstructs the intertestinal system and the intake of oxygen [9]. In addition, silt does not provide enough foothold for the mussel. It prefers gravel or sand to bury over two thirds of its shell-depth body in the riverbed and is sessile in nature in the mature stage [5,6,10][5].

M. margaritifera is a filter feeder. Because of its filtering effect on water the relationship between Salmonids and Freshwater Pearl Mussels is symbiotic which makes it susceptible to loss of specific fauna as it took place in Europe and North America with the introduction of the non-native Rainbow Trout (*Oncorhynchus mykiss*) and over-fishing. All these characteristics underline the uniqueness of the highly specialist Freshwater Pearl Mussel and the threat that it is facing in its ecological niche[6] (Figure 1 & 2).

Figure 1: Distribution Map of M. margaritifera. Source: Nature Serve and Department of Fisheries and Oceans Canada & IUCN 2018. *Margaritifera margaritifera*. The IUCN Red List of Threatened Species. Version 2020-2/.

Photo in the natural habitat. Source: IUCN 2017 (photo copyright by Ian J.Killen).

Kingdom	Phylum	Class	Order	Family
Animalia	Mollusca	Bivalvia	Unionoida	Margaritiferidae

Figure 2: Taxonomy of *M. margaritifera*. Source: IUCN red list.

M. margaritifera is on the Brink of Extinction: The Impact of Environmental Conditions, Human Pressure and Species-Specific Characteristics.

Much of the threat to this species can be explained by high human pressure and changing environmental conditions in the last centuries: Araujo reports that 'one out 5000 Freshwater Pearl Mussels generates a mother of pearl and those pearls have made the species a first target of systematic and vast exploitation in Europe, which can be dated back to Austrian sources in the 12th century' (Araujo, 2006). Environmental factors are freshwater pollution and siltation of riverbeds, which can be linked to industrialisation, and the use of fertilizers in the agrarian sector. Dry weather conditions and floodings that affect riverbeds are another cause of mortality of *M. margaritifera* in all metamorphic stages [8,11,12].

[5]https://www.duhallowlife.com/ird-duhallow-life/freshwater-pearl-mussel-margaritifera-margaritifera

[6]*Ibit.*

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Despite these *extrinsic factors*, species-specific characteristics or *intrinsic factors* have a considerable impact on the survivability of *M. margaritifera*. For the latter, the role of inheritance in *Modern Synthesis, MS* holds valid explanatory power to explicate the slow, linear physical and behavioural adaptations of the species to its ecological niche [13]. If the longevity of *M. margaritifera* of or more (Mutvei & Westermark 2001) and the complex and fragile reproduction cycle are taken into consideration, the species population must have become suited to its environmental conditions in a gradual and slow process of adjustment. This follows MS framework and underlines the statement that 'phenotypic transitions typically occur through multiple small steps, leading to gradual evolutionary change' (comparison of the core assumptions of the classical MS and the EES. In: Laland et al. [2]). It must be assumed that *M. margaritifera's* evolutionary developmental capacity, or its *phenotypic plasticity*, i.e. the capacity of an organism to change its phenotype in response to the environment [2] is low.

The high fragmentation into unconnected and isolated subpopulations in rivers leaves *M. margaritifera* without genetic interchange [6,14]). In accordance with evolutionary development theory, the separation, or isolation of small subpopulation must be understood as a lack of opportunity for genetic mutation of the species. This hinders fast niche construction and 'scaling up across individuals in a population, and over time, to generate directional changes' (Discussion of *evolutionary development* or the so-called *evo-devo* approach. In: Laland et al. [2]). Although over generations remaining sub-populations became more and more suited to its specific environmental conditions, the niche environment in which it found itself, changed in a pace the species could not cope with [4]. What makes *M. margaratifera* vulnerable to extinction is the *low heritable variation* in each population.

Physical and behavioural adaptation of competitors: Freshwater Zebra Mussel Dreissena polymorpha

M. margaritifera also suffers from the spreading of the invasive *unioida* Zebra Mussel *Dreissena polymorpha* which attaches itself to the shell of native *unionoid* mussels with the result of reduction of populations and, in extreme cases, their localised extirpations [15]. The small bivalve *Dreissena polymorpha* is an invasive species that originates from the […] geographic zone covering the Caspian and Black Seas […] and spreads all across Europe via the waterways network, dug in the 18th-20th centuries to link Eastern and Western Europe (Araujo 2006). In stark contracts to *M. margaritifera* it can be found at silted and polluted sites such as in *euryocious* water conditions. As a characteristic feature it can attach itself to different surfaces (including boats and infrastructures) due to the anatomy of its *mollusc*, and travels to new locations. Araujo discusses the success of this less specialised Freshwater Mussel in comparison to *M. margaritifera*. Because *Dreissena polymorpha* can withstand significant environmental variations and is resistant to lack of water for approximately seven days (Araujo, 2006) it is better adapted to changing *extrinsic conditions*. Belonging to the order of unioida, Zebra mussel also rely on a *glochae mechanism*, but the larvae can drift in the water for several weeks and then settle onto any hard surface they can find. The lifespan of a zebra mussel is four to five years and female zebra mussels begin to reproduce within 6–7 weeks of settling [16]. Following this, the scenario for survival of this species is positive due to a higher probability of random genetic change, which can lead to functional and facilitated phenotypic variation and biodiversity within the species [2].

Summary and Outlook: The current Status and future Challenges for the Conservation of Freshwater pearl mussel

Literature on *M. margaritifera* and conservation reports demonstrate that freshwater mussels are declining globally and 'despite simultaneous efforts to restore mussel habitat over the last 25 years, natural reproduction still does not occur in some countries, such as in the Czech Republic or in Luxemburg' [17]. While conservation priorities over European countries and North America vary widely, ranging from preventing imminent extinction to maintaining living population and habitat reconstruction as well as provision of host fish, human pressure and destruction of habitats continue to constitute the highest risk for extinction of the species.

Conservation includes the collection and storage of viable *glochidia*, the installation of different rearing systems in the larvae and juvenile stages of the Freshwater Pearl Mussel, as well as captive breeding programmes, restoration of oligotrophic streams and silted riverbed reconstruction [11,18,19]. As a result of these integrated actions, self-sustainability of Austrian populations of *M. margaritifera* has slightly improved [5]. This can be explained by an elaborate intervention scheme which is closely linked to the metamorphosis of Freshwater Pearl Mussel. Thomas, et al. [20] state that 'as with other conservation projects, isolated captive breeding of the freshwater pearl mussel cannot compensate for loss of critical habitats unless it is combined with in-situ conservation. Thomas et al. [20] In the Austrian case, integrated actions are directed to the *intrinsic sensitivity* and *extrinsic factors* which modify the implementation of conservation and/or recovery plans [5,21]. Apparently, the balance between the species' *intrinsic factors* and *extrinsic factor* modifications determine the success of implementation of conservation and/ or recovery plans [21].

For future research it might be interesting to pay more attention to the observation of *genetic drifts* in the inbreeding and breeding programs and to the complex symbiotic relationships in the local ecosystems for a renewed assessment of the conservation status of the Freshwater Pearl mussel. Historical events and *biotic factors* like genetic alterations in host fish, disease occurrence and competition with invasive species such as

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the *Dreissena polymorpha* as well as *abiotic factors* (light intensity, rainfall, water temperature or soil nutrients in the respective rivers) might have caused mutations in the subpopulations that can affect the survivability of *M. margaritifera* - not as a species but a form of life [22]. Novel characteristics may occur in the employment of various intervention schemes - either through mutation or through facilitated variation, which might hold the key to survivability.

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