



# Ecological marginality and recruitment loss in the globally endangered freshwater pearl mussel

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## Abstract

**Aim:** Ecological marginality is the existence of species/populations in the margins of their ecological niche, where conditions are harsher, and the risk of extinction is more pronounced. In threatened long-lived species, the disparity between distribution and population demography may provide understanding of how environmental heterogeneity shapes ecological marginality, potential extinction patterns and range shifts. We set out to evaluate this by combining a species distribution model (SDM) with population-specific demography data.

**Location:** Sweden, 450,000 km<sup>2</sup>.

**Major Taxa Studied:** Freshwater pearl mussel (FPM, *Margaritifera margaritifera*) and two salmonid fish species.

**Methods:** A SDM for the mussel was constructed with MaxEnt using salmonid host fish (*Salmo trutta* plus *S. salar*) density, extreme low and high temperatures, precipitation, altitude, and clay content as explanatory variables. The output was used to test the ecological marginality hypothesis by evaluating whether lowly predicted populations had higher loss of recruitment. Logistic regression was used to explicitly test the factors involved in recruitment loss.

**Results:** Host fish density contributed the most (50.3%) to the mussel distribution, followed by lowest temperature the coldest month (34.3%) and altitude (10.3%), while the remaining explanatory variables contributed minimally (<3.3%). Populations with lower SDM scores lacked recruitment to a significantly higher degree. Populations inhabiting areas at low altitude, with lower densities of host fish, and warmer winter temperatures have lost recruitment to a higher degree.

**Main Conclusions:** We found support for the ecological marginality hypothesis. The patterns indicate that FPM habitat niche may shift northwards over time. Salmonid host fish density seems to be a driving factor for both historical distribution and recent demographic performance. Finally, we emphasize the value of combining SDMs with independent data on population demography as it both lends rigidity to model validation and understanding of how ecological marginality affects species distribution and viability.

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## KEYWORDS

demography, edge, extinction vortex, population, range shifts, species distribution

## 1 | INTRODUCTION

Anthropogenic impacts such as exploitation together with global warming are rapidly changing the environments that organisms experience across the globe and virtually no habitats remain unaffected (Vitousek et al., 1997). The consequences include loss of biodiversity, changes in the distribution of species, and function of ecosystems (Pecl et al., 2017). To predict future consequences of anthropogenic activities, and aid mitigation thereof, it is thus imperative to understand the role of environmental variation for species range dynamics (Vilà-Cabrera et al., 2019). Worryingly though, there remain important gaps in knowledge concerning these matters, for instance relating to the associations among habitat quality variability, distribution range dynamics and extinction vulnerability (Pironon et al., 2017; Vilà-Cabrera et al., 2019).

Ecological niche theory states that a species' distribution range is a geographical reflection of its ecological niche (sensu Hutchinson, 1957) and dispersal capacity (Schwalb et al., 2011). However, environmental conditions typically vary within a species distribution range such that some populations may exist in optimal conditions while others reside in suboptimal conditions, that is, closer to, or in the margins of their ecological niche (Gaston, 1996; Soule, 1973). This may have pronounced impacts on the demographic, genetic and ecological characteristics of species (Kawecki, 2008; Pironon et al., 2017). For instance, ecologically marginal populations are expected to suffer larger risk of population decline and extinction (Stanton-Geddes et al., 2012) but may also evolve adaptive variation that may be crucial to cope with environmental changes (Hampe & Petit, 2005; Kawecki, 2008; Morente-López et al., 2021). It is from both an ecological understanding and conservational point of view crucial to understand how variation in biotic and abiotic factors position populations within the niche (core-marginal) and impact population dynamics and the spatiotemporal distribution of organisms. Yet, this is challenging since it requires comprehensive data on the presence and demographics of populations throughout the species' distribution range, which are often lacking, and which results in hampered understanding of these key processes.

The habitat suitability within the distribution range of an organism have traditionally been viewed within geographical boundaries, for example along latitudinal, longitudinal or altitudinal gradients, and are believed to adhere to the centre-periphery hypothesis (Channell & Lomolino, 2000; Pironon et al., 2017). This hypothesis posits that environmental conditions are optimal near the geographical centre of the range while conditions degrade towards the periphery (Gaston, 1996). However, the suitability of environmental conditions for an organism reflects intricate interactions among multiple biotic and abiotic factors that may be geographically independent (Levins, 1968) such that population demography reflects

the mosaic landscape (environmental niches) rather than predictable geographical boundaries (Pironon et al., 2017; Soule, 1973; Vilà-Cabrera et al., 2019). This is also supported by a growing body of evidence on that abundances and other demographic vital rates (e.g., survival and recruitment success) do not generally decrease towards geographical edges (Channell & Lomolino, 2000; Pironon et al., 2017).

Interestingly, ecological margins are dynamic and may change over time due to changes in environmental conditions such that populations located in "optimal" ecological core habitats may become marginal and vice versa (Soule, 1973). This is of course part of the natural process of succession, but at times when environmental conditions are rapidly changing due to habitat exploitation (Tamario et al., 2021; Tilman et al., 1994) and climate change (Malhi et al., 2020; Perry et al., 2005), the dynamics of ecological core and marginal habitats can be expected to change rapidly (Fréjaville et al., 2020; Vilà-Cabrera et al., 2019). Given this, it is important to identify conditions causing ecological marginality and to improve our understanding on whether and how variation in abiotic and biotic factors within distribution ranges shapes the persistence and demography of species and populations to aid management and conservation and, ultimately, avoid further loss of biodiversity.

Species distribution models (hereafter SDM) comprise a range of frequently used tools that combine species distribution data with information on environmental or spatial characteristics, both to gain insights into what factors influence the distribution and to create a spatial prediction of the distribution of a focal species (Elith & Leathwick, 2009). Recently it has also been suggested that the conclusions made from SDMs can be improved further by the addition of demographic data, such as population dynamics, abundance or age structure (Elith & Franklin, 2013; Wittmann et al., 2016). Correlating the output from climatic models with species traits or other types of biological data can provide inferences beyond a predicted distribution of a species, and provide an independent validation of the feasibility of the distribution models (Wittmann et al., 2016). However, relatively few studies have so far employed such approaches (Pironon et al., 2017; Wittmann et al., 2016).

Here, we combine SDMs and recruitment data to identify and evaluate the potential role of conditions in structuring the suitability of 442 populations of freshwater pearl mussel (hereafter FPM; *Margaritifera margaritifera*) using Sweden as a study system. FPM is an exceptionally long-lived (>100 years) indicator, keystone and umbrella species (Geist, 2010) whose status is considered to generally reflect that of aquatic ecosystems and their associated biodiversity. The focal populations are distributed throughout the FPMs range in Sweden and comprises 11 latitudinal degrees. Unfortunately, FPM populations are declining, and the species is considered nationally and globally endangered (Lydeard et al., 2004; Moorkens et al., 2017;



Sousa et al., 2020). This decline is believed to reflect deteriorating riverine habitats encompassing both biotic (presence of obligate *Salmo trutta* or *S. salar* host species for FPM parasitic larvae) and abiotic factors (e.g. fragmentation, poor water quality and increased sediment load) (Hoess & Geist, 2020; Young & Williams, 1984), as well as effects of climate change (Baldan et al., 2021; Bolotov et al., 2018). In Sweden for instance, about 30% of all populations are believed to have become extinct since the beginning of the 20th century and out of the remaining populations only 50% are expected to be viable (ongoing recruitment as indicated by the presence of mussels that are less than 50mm and approximately 20-year-old) (Arvidsson et al., 2012). Yet, despite previous attempts to identify environmental conditions that may explain the presence of FPM populations using SDMs (Baldan et al., 2020; da Silva et al., 2022; Lois et al., 2015; Prié et al., 2014; Wilson et al., 2011), none have incorporated mussel recruitment status in their analyses, which have constrained conclusions regarding differential sensitivity to various environmental disturbances that may impact recruitment. Moreover, due to the extreme longevity of FPM this system offers a unique, but overlooked, opportunity to gain novel insights on the consequences on biodiversity of long-term and gradual changes in environmental conditions.

In this study, we set out to (i) identify the major environmental variables that structure the distribution of FPM, (ii) identify core and marginal environmental habitats of FPM respectively, and (iii) evaluate the effect of ecological margins on the viability and extinction risk of populations. To this end, we performed a nation-wide (Sweden) SDM using a presence-only maximum entropy modelling approach (MaxEnt). The model included the local-scale abundance of host species salmonids, maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation the warmest quarter (WorldClim), presence of clay-rich soils or bedrock, and altitude. Finally, we evaluate the role of these environmental variables on the viability of populations by analysing whether and how they affect recruitment.

## 2 | MATERIALS AND METHODS

### 2.1 | FPM—the study organism

The FPM belongs to the highly imperilled group of unionid molluscs (Lydeard et al., 2004). FPM resides in cold, oxygen rich, clear, non-acidified and nutrient poor running waters with suitable bottom substrates (Hoess & Geist, 2020). The life cycle of FPM involves an obligate parasitic stage and is thus entirely dependent on its host species brown trout (*S. trutta*) and Atlantic salmon (*S. salar*) for life history completion. During reproduction, mussel larvae (glochidia) are released into the water, attach to the gills of the host fish and live as a parasite for 9–11 months in northern Europe (Ziuganov et al., 2000). The juvenile mussels then drop from the gills onto the river bed where they bury in the substrate and spend their first 4–8 years (Young & Williams, 1984). The realized distribution of

FPM is likely a combination of climatic gradients (Lois et al., 2015; Wilson et al., 2011), quality of habitat and physicochemical parameters (Degerman et al., 2013; Geist & Auerwald, 2007; Hastie et al., 2000; Hoess & Geist, 2020; Österling et al., 2010), and the presence and abundance of its fish hosts (Chowdhury et al., 2018; Degerman et al., 2013; Inoue et al., 2017).

### 2.2 | FPM data

Data containing known localities of FPM populations was obtained from a national database, “Musselportalen” (<https://miljodata.slu.se/MVM/>) at the Swedish University of Agricultural Sciences, with sampling dates ranging from 1980 to 2016. The standardized monitoring method used by trained field personal is based on visual search in wadeable streams, using an aquascope (SEPA, 2010). The method does not include digging into the substrate, a precautionary measure to avoid damaging young mussels, which means that young mussels that are buried might be overlooked. Otherwise, the sampling procedure is similar to the new European standard (Boon et al., 2019) (European Standard EN 16859:2017), with sampling of both mussels (size, density) and a habitat description. Each geographic presence of a “population” has been put where the highest density of mussels within a confined reach was found. The extracted data comprises 657 localities, corresponding to 630 rivers, with the presence of FPM.

Based on the standardized field inventories, these populations have been classified into recruiting ( $N = 306$ ; presence of mussels that are <50mm) or not recruiting ( $N = 281$ ; absence of mussels that are <50mm), while the recruitment status of 72 populations were unclassified due to lack of standardized screening for young mussels. The presence of mussels smaller than 50mm suggests that reproduction probably has occurred during the last 20 years (Arvidsson et al., 2012), and at this stage mussels are generally found on the surface of the bottom (Bergengren, 2001), that is, visible with the sampling procedure used.

### 2.3 | Explanatory layers

Explanatory variables for the SDM were chosen based on biological relevance for the species (Geist, 2010; Söderberg & Henrikson, 2020) and needed to have a geographical range of the study area (Sweden) and be readily downloadable and curable. We constructed the model on altitude, three climatic variables (see below), host fish density (Degerman et al., 2013), and the presence of clay soils (von Proschwitz & Wengström, 2021) (Figure S1). Data on macro-habitat characteristics such as substrate composition, average flow and water quality did not meet the above requirements.

The bioclimatic variables (averages for the years 1970–2000; WorldClim) were downloaded in 2.5-min resolution, and all other layers were projected and sampled in the same resolution (Figure S1). The layers chosen from Wordclim were elevation, BIO5: “maximum

temperature the warmest month”, BIO6: “minimum temperature the coldest month”, BIO18: “precipitation the warmest quarter”. We chose to include only these three climatic variables for statistical reasons (decrease multicollinearity and variance inflation) and for biological reasons: extreme temperatures are detrimental to FPM with a suggested thermal tolerance interval of 0–25°C (Hastie et al., 2003); lacking data on actual flow, and reasoning that precipitation regulates flows in streams, especially during drought-prone parts of the season, we used precipitation during the warmest quarter as a proxy for restricted flow conditions. FPM prefer a water velocity within the interval 0.25–0.75 m/s (Björk, 1962; Hastie et al., 2000).

Areas predominant with clay are unsuitable for FPM (von Proschwitz & Wengström, 2021; Wilson et al., 2011). A soil and bed-rock raster was generated using data from the Geological Survey of Sweden (SGU) (See Supplementary Information for details) (Figure S1).

Finally, a salmonid density raster was constructed containing pixel-average density of host species brown trout and Atlantic salmon, FPM's only hosts in the European range (Chowdhury et al., 2018; Degerman et al., 2013; Marwaha et al., 2021; Salonen et al., 2017) (Figure S1). The raster was created by averaging the log-density from electrofishing data retrieved from Swedish Electrofishing RegiSter (SERS) at the Swedish University of Agricultural Sciences and included information from over 18,000 electrofishing sites all over Sweden.

## 2.4 | On the SDM

Since the mussel database in large only contains *presences* we deployed a presence-only species distribution modelling (SDM) method, MaxEnt, which produces predictions on the relative suitability compared to background (Elith et al., 2011; Phillips et al., 2006). We used robust options and limited response gradients to contain only linear or quadratic features, leaning towards under-fitting rather than over-fitting (Merow et al., 2013). Having overly complex and perhaps not completely biologically feasible response gradients in MaxEnt models may result in overfitting at the cost of generalizability (Lois et al., 2015; Merow et al., 2013; Wilson et al., 2011). Ten thousand background points were sampled. Three replicates were done using cross-validation as run type. Regularization multipliers of 3 were performed to reduce model complexity and further decrease the risk of overfitting (Merow et al., 2013). We interpret the SDM output/scores as “relative probability of occurrence” for FPM (Elith et al., 2011).

Sampling density heavily impact the outcome of presence-only models (Phillips et al., 2009). To compensate for this and improve the performance of the model, we generated a sampling density layer (Figure S2) such that background data was drawn from the same spatial distribution as the occurrence data. This bias compensation raster was created by calculating kernel density from all sampling events contained in the mussel sampling database (Figure S2) with function `kde2d` in R package ‘MASS’ with bandwidth  $h = 0.8$ .

Of the 657 populations, 169 did not overlap with the salmonid density layer due to lack of electrofishing inventories, meaning that 488 populations were eligible for the SDM. Of the 488 populations, 47 did not have information on mussel recruitment status, meaning that the models testing ecological marginality or linking environment to recruitment status directly were performed on 442 eligible populations.

## 2.5 | Measurements of geographical peripherality

Two different measurements of centrality-peripherality were calculated to see whether and how recruitment status was associated with a centre-periphery hypothesis (Figure S3). First, a concave hull was constructed (with R package ‘concaveman’, concavity = 1.4). This method is based on the assumption that the habitat quality decreases with proximity to the range edge (Pironon et al., 2017) and populations that have a longer distance to the polygonal edge are more “central”. Concave hull is a simple yet accepted and standard method for estimating range edge from a set of occurrences (Burgman & Fox, 2003). For a second and a density-dependent way to measure centrality, a kernel density layer was constructed (Xu et al., 2021) using the mussel data points; where populations are densely distributed, they get a high value, and vice versa where populations are scarcely distributed. This measurement is based on the assumption that population density is correlated with habitat quality. Kernel density was calculated with function `kde2d` in R package ‘MASS’ with bandwidth  $h = 0.8$ . The two measurements were lowly correlated ( $r = 0.07$ ) indicating that they quantify somewhat different aspects of geographical periphery.

## 2.6 | Mussel recruitment status, climate and salmonids

A logistic regression with binomial link was used to analyse whether and how the climatic and salmonid density layers (Table 1) were associated with recruitment status, that is, the presence of mussels <50 mm.

Confidence intervals for proportion of recruiting populations for each predicted quartile were calculated using the following formula, where  $p$  is proportion,  $z$  is 1.92 (corresponding to a confidence level of 0.95) and  $n$  is the sample size:

$$CI = p \pm z \times \sqrt{\frac{p(1-p)}{n}}$$

## 3 | RESULTS

### 3.1 | SDM results

Host fish salmonid young-of-the-year density contributed the highest to the model fit (50.3%) (Figure 1), followed by the lowest temperature of the coldest month, which contributed 34.3% to the model, and



TABLE 1 Explanatory layers used to explain species distribution and demography patterns of freshwater pearl mussel in Sweden

Predictors	Details (unit)	Min	Mean	Max	Transformation
Salmonid density	Salmonid density (individuals per 100 m <sup>2</sup> )	0	0.42	2.95	log(x + 1)
BIO6	Minimum temperature coldest month (°C)	-21.8	-12	-0.5	-
Elevation	Elevation above mean sea level (m)	-2	331	1667	-
Clay content	Clay content in soil or bedrock (0%-100%)	0	7.9	100	-
BIO18	Precipitation of warmest quarter (mm)	95	216	341	-
BIO5	Maximum temperature warmest month (°C)	0.5	19.1	23.4	-

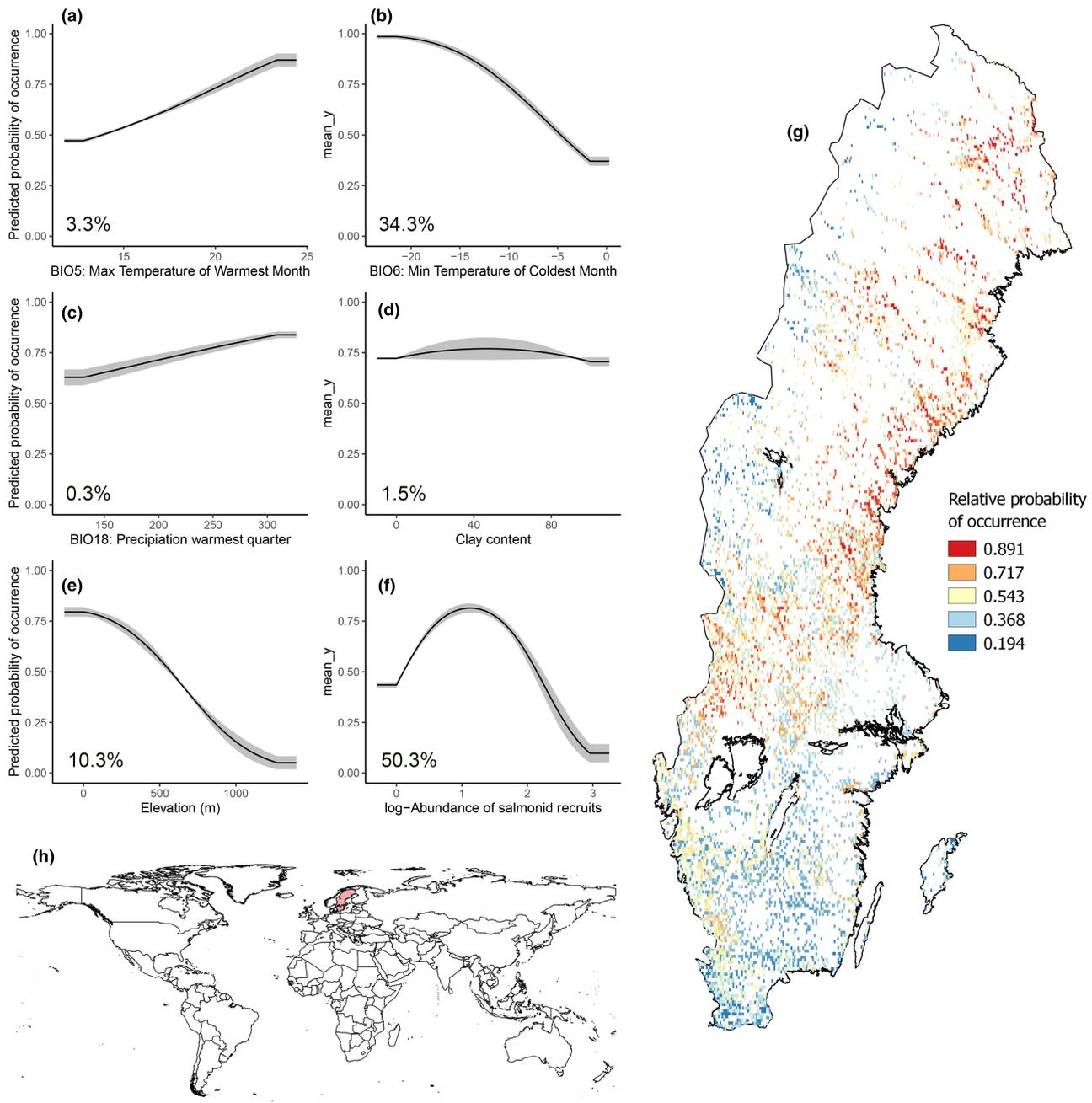
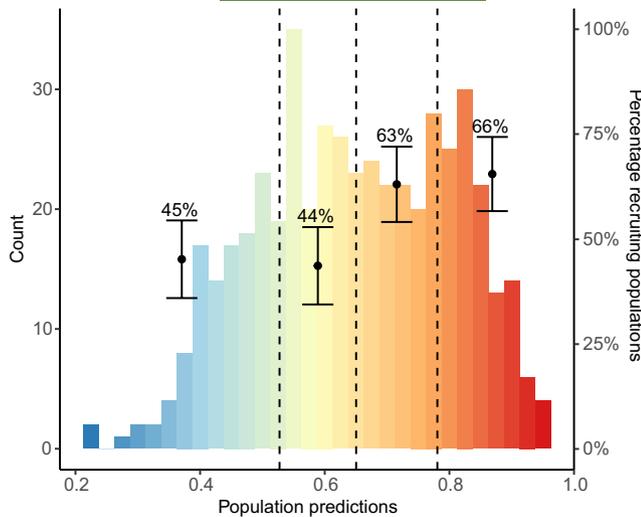


FIGURE 1 Output from species distribution model of freshwater pearl mussel in Sweden. Response gradients showing how each explanatory variable influenced the marginal probability of occurrence of the freshwater pearl mussel with all other variables set at their mean (a–f). Line and shadowed area show the mean response from the three replicated model runs  $\pm 1$  SD. The percentages show “percentage contribution” of each variable to the model outcome. The spatial predicted probability of occurrence as estimated from the MaxEnt model is shown on the map to the right (g), which is projected in SWEREF99TM to reduce spatial distortion. The location of this regional study is shown in red in the world map (h) projected in WGS84.

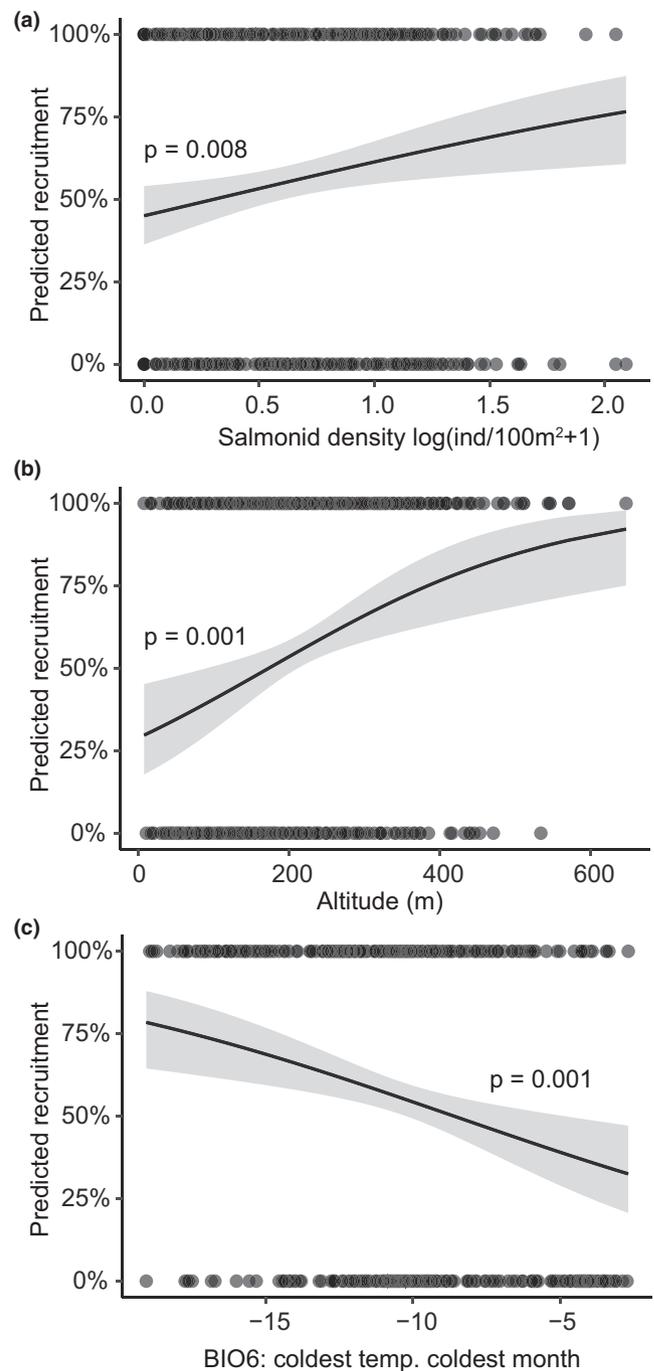


**FIGURE 2** Plot illustrating how relative habitat suitability is associated with recruitment status in freshwater pearl mussel in Sweden. Each freshwater pearl mussel population's location has a predicted habitat suitability score from the MaxEnt model. When split into quartiles, the better predicted half of populations has significantly higher proportion of recruitment than the lower predicted half, lending support to the marginal population hypothesis. The colour gradient corresponds to that of the map in Figure 1. The points show proportion ( $\pm 95\%$  confidence intervals at  $n = 111$ ) of recruiting populations in each quartile.

altitude, which contributed 10.3% (Figure 1). The relative probability of FPM presence increased with young-of-the-year salmonid densities up to 15 individuals/m<sup>2</sup> whereafter it dropped. The probability of FPM presence decreased with higher minimum temperature of the coldest month and with altitude. Variables "maximum temperature the warmest month", "precipitation during the warmest quarter", and "soil clay content" did not contribute to model fit ( $<3.3\%$  each). The area under the receiver operating curve for this model was 0.682 (Figure S4).

### 3.2 | Population marginality and recruitment loss

We extracted the relative habitat suitability (or SDM) score to each of the included FPM populations. Scores varied from low (0.21) to high (0.96) with a mean of 0.65 (Figure 2). These scores indicate the marginality of each population as they are based on a combination of the response gradients of all six included explanatory variables. We performed an analysis where we investigated whether and how marginality (SDM scores) was associated with recruitment loss. A logistic regression showed that SDM scores were positively associated with the presence of small ( $<50$  mm) mussels ( $Z = 3.97$ ,  $p < 0.0001$ ), illustrating that lowly predicted populations have suffered higher rate of recruitment loss and therefore experience potential on-going extinction. The populations in the highest predicted quartile in the relative suitability model had recruitment in 66% of the cases ( $n = 112$ ), compared to 45% of the cases ( $n = 112$ ) in the lowest predicted quartile (Chi-square test,  $\chi^2 = 8.38$ ,  $df = 1$ ,  $p = 0.004$ ) (Figure 2).



**FIGURE 3** Predicted effect plots from a logistic regression of the recruitment of freshwater pearl mussel in Sweden on the significant variables salmonid density, altitude and coldest temperature coldest month (see Table 2 for full model). Populations with (a) higher average abundance of young salmonids, at (b) higher altitude, and at (c) locations with colder winter temperatures had recruitment to a significantly higher degree.

### 3.3 | Associations of recruitment status to climate variables and salmonid density

To evaluate whether and how environmental factors influenced the recruitment loss, a logistic regression with recruitment status (1/0) as response variable and all six explanatory variables (Table 1) was



**TABLE 2** Results from logistic regression relating salmonid density, maximum temperature warmest month (BIO5), minimum temperature of coldest month (BIO6), precipitation during warmest quarter (BIO18), elevation and clay content to recruitment status for each freshwater pearl mussel population ( $n = 442$ ) in Sweden

Predictors	Estimate	SE	CI	Z statistic	<i>p</i>
(Intercept)	-4.76	3.95	-12.56–2.96	-1.20	0.228
BIO5	0.21	0.16	-0.11–0.53	1.28	0.200
BIO6	-0.12	0.04	-0.20 to -0.05	-3.18	<b>0.001</b>
BIO18	-0.01	0.01	-0.02–0.00	-1.46	0.144
Altitude	0.01	0.00	0.00–0.01	3.28	<b>0.001</b>
Clay content	0.00	0.01	-0.01–0.02	0.73	0.463
Salmonid density	0.66	0.25	0.18–1.16	2.65	<b>0.008</b>

Abbreviations: CI, 95% confidence interval; SE, standard error.

performed. The model results showed that populations at higher altitude (GLM;  $Z = 3.28$ ,  $p = 0.001$ ), in areas with lower temperature during the coldest month (GLM;  $Z = -3.18$ ,  $p = 0.001$ ) and in areas with higher abundance of young-of-the-year salmonids (GLM;  $Z = 2.65$ ,  $p = 0.008$ ) were generally more viable, as indicated by ongoing recruitment (Figure 3; Table 2).

### 3.4 | Associations of recruitment status to measurements of geographical periphery

To analyse whether and how recruitment status was associated with geographical periphery, logistic regressions linking recruitment (1/0) to population specific periphery score was performed. Neither concave hull (logistic regression;  $Z = 1.15$ ,  $p = 0.25$ ) or kernel density (logistic regression;  $Z = -1.54$ ,  $p = 0.12$ ) calculations of centre-periphery were significantly associated with recruitment status.

## 4 | DISCUSSION

By applying a SDM across over 400 populations throughout the Swedish distribution range, we show that the abundance of juvenile salmonids (obligate host for parasitic FPM larvae), winter temperature and altitude were key variables in predicting habitat suitability of FPM. Variables maximum temperature of the warmest month, precipitation during the warmest quarter and soil clay content did not contribute much to the fit of the distribution model. By combining the predictions of the SDM with recruitment data, we demonstrate that populations predicted to inhabit suboptimal environmental locations more seldom had recruitment, suggesting that these ecologically marginal populations suffer from potentially increased extinction risk. More specifically, we uncover that populations inhabiting areas at low altitude, with lower densities of obligate host fish species, and warmer winter temperatures have lost recruitment to a higher degree. We did not find any support for the geographical centre-periphery hypothesis, as none of the measurements were associated with recruitment status. This can be due to Sweden not being at the large-scale geographical edge to the entire species as FPM exists down to Portugal and Austria-Bavaria (Geist, 2010). In southern locations in Europe, the

average temperature is higher which in conjunction with fine sediments (clay) and poor interstitial water flow may decrease the oxygen levels in the bottom substrates, negatively affecting juvenile mussels. Also, the lower density of human population in Sweden may have less impacted streams and rivers compared to regions further south (Dobler et al., 2019), which may contribute to the observed patterns being slightly different from those. However, the results still show that there is no evidence of small-scale (i.e., for a subpart of the whole species distribution) geographical periphery on population performance. Together, these findings improve our understanding of ecological marginal habitats and their role in population viability and aid predictive models on the consequences of environmental change on biodiversity.

### 4.1 | SDMs identify ecological marginal populations

The relative probability of FPM occurrence increased with young-of-the-year salmonid densities up to circa 15 individuals/100m<sup>2</sup>, after which, however, it dropped (Figure 1). This likely reflects a disparity in habitat niches between FPM and the salmonids. The mussels inhabit mainly (ultra-)oligotrophic waters whereas salmonids can exist and thrive at increasing levels of nutrients. This hump-shaped association should thus not be interpreted as high salmonid density having a negative effect on the occurrence of mussels per se, but rather that high salmonid density is indicative of a river with more adverse habitat conditions for the mussel. The highest abundance of salmonids is found in shallow waters (Donadi et al., 2019), a habitat that may change rapidly with flow conditions and are more prone to sediment deposition that may be harmful for mussel juveniles (Baldan et al., 2021). Being a less vagile species, FPM may have to choose an intermediate habitat, optimizing the trade-off between high abundance of salmonids and the risk of hazardous conditions. The SDM adds to the existing body of knowledge that sufficient abundance of salmonid host species is crucial in structuring the distribution of FPM (Arvidsson et al., 2012; Degerman et al., 2013).

That the relative habitat suitability increased with decreasing minimum temperature the coldest month is indicative of a northern-southern gradient in habitat suitability. The prevalence of cold, uncoloured and nutrient-poor rivers is higher in northern Sweden (Brandt

et al., 2009), which should benefit FPM as increased sediment load (Österling & Högberg, 2014) and eutrophication (Degerman et al., 2013) have shown to be problematic for FPM. This response gradient may also suggest that FPM is prone to a northern-ward climate change-mediated distribution shift (which is also suggested by the geographical variation in recruitment loss; see section below). Colder regions have lower risk of reaching high water temperatures (>25°C), which could cause stress and limit the range of FPM (Hastie et al., 2003). The key role of temperature is also supported by that altitude, which impacts thermal regimes of aquatic habitats (Råman Vinnå et al., 2021), was negatively related to the habitat suitability (contributed with 12.8% to the model fit). The negative effect of altitude acts antagonistically with the cold temperature variable, creating an optimum inhabitable range of temperature and altitude, again stressing the fact that the habitat of a species is formed by a combination of abiotic and biotic factors (as host fish abundance) creating a mosaic of suitable habitats in the landscape (Figure 1).

That we did not see any strong evidence for geographical periphery based on the measurements analysed in this study might be because the Swedish population of mussels only consist of a part of the whole distribution. Contrastingly, the SDM scores of habitat suitability were able to predict to a significant degree the populations that had recruitment loss. Consistent with the theory of ecological marginality (Soule, 1973), we found that the marginal of the modelled multidimensional niche was associated with populations that lacked ongoing recruitment. This represents a rare demonstration on how a mosaic of abiotic and biotic interactions may shape the demography of populations. Admittedly, the discriminatory accuracy of the SDM was moderate, likely in part due to limited model features (to linear and quadratic) and through applying a regularization multiplier to decrease overfitting. Moreover, the discriminatory accuracy of our SDM may also be influenced by not accounting for variation in microhabitat suitability (Hastie et al., 2000), sediment load (Baldan et al., 2021), and eutrophication (Degerman et al., 2013), due to lack of data. Nonetheless, the association between SDM scores and FPM recruitment supports the biological relevance of the model and emphasizes that the SDM output prediction layer can be an important tool for conservation of FPM. For instance, the output prediction layer (available to download as Supplementary Information) can be utilized for identifying known and unknown core populations of high conservation value and marginal areas of high restoration value and needs, and for targeting areas for potential inventories.

## 4.2 | Factors associated with population recruitment loss

The results from the logistic regression evaluating associations between environmental variables and recruitment mirrored those of the SDM in that low altitude, warmer temperatures during winter and low densities of young salmonids were associated with recruitment loss. Regarding the first (altitude), it is reasonable that the associations with recruitment are explained by the inherent impact of

altitude on thermal regimes, such that habitats in these locations to a lesser degree reach temperatures that may stress FPM. That this is not reflected by the data on highest temperature of the warmest month may be due to that these data are means of a longer period, that is without extreme values. It could also be related to that low altitude and southern areas are more exposed to higher levels of eutrophication and sediment load due to higher proportion of agricultural areas (Donadi et al., 2021; Österling & Högberg, 2014). Concerning the salmonid density, a positive association to the viability of FPM populations was expected due to their role as obligate hosts for the FPM larvae, which also corroborates with earlier studies (Arvidsson et al., 2012; Degerman et al., 2013; Lois et al., 2015; Österling et al., 2008), but see Geist et al. (2006) and the results of the SDM in the present study. However, this study is the first to show that distribution and recruitment loss is linked, and both are impacted by salmonid abundance.

## 4.3 | Conservation of FPM at times of rapidly changing environments

Freshwater pearl mussel belongs to the critically endangered group of pearly mussels (Unionoidea) that are rapidly declining due to limited dispersal by fragmentation, loss of host fish species and habitat degradation (Lydeard et al., 2004; Strayer, 2008). The harsh truth is that, unless something changes, many unionid species are facing extinction (Böhm et al., 2021). Research that identifies measures that increase resilience and viability of unionid populations and facilitate selection among populations and habitats for conservation and rehabilitation is thus imperative (Geist, 2010).

A key contribution of this study is that it emphasizes the importance of management and conservation measures to be designed and implemented to target FPM and salmonid populations simultaneously. The obligate salmonid host species of FPM larvae are also under intense anthropogenic pressure (Donadi et al., 2021) and many populations are rapidly declining and under threat of extinction, in large parts due to the same causes as to the decline of FPM (Österling & Högberg, 2014). As such, efforts aiming at restoring habitat, physicochemical and hydrological features to rehabilitate salmonid populations will, in the end, be promotional for reversing the large-scale extinction vortex of FPM. One important aspect is that the dispersal of FPM largely rely on their parasitic stage on the more vagile salmonids since adult mussels are mainly sessile. This allows mussel populations to maintain or find new suitable habitats within the river over time as well as colonize other rivers (e.g., tributaries or other main channels) which creates an important buffer against both local and larger scale environmental changes (Modesto et al., 2018). Dams and other obstructive features can restrict movements, destruct or convert habitats, change the amplitude and timing of hydrology, and impact sediment transport (Tamario et al., 2019), which all impact salmonid and FPM populations negatively (Rytwinski et al., 2020; Vaughn & Taylor, 1999; Warren et al., 2015). Also, increased isolation may prevent gene



flow between marginal and core FPM populations and can increase risks of detrimental effects of genetic stochasticity and inbreeding in small populations (Geist, 2010; Kawecki, 2008). In fact, loss of genetic diversity in peripheral FPM populations has already been recorded (Stoeckle et al., 2017). Management and conservation efforts targeting dams with impoundments, hydrological regulation, and definitive migration barriers for removal can thus create a cascade of positive effects that can improve conditions for both salmonids and mussel and, ultimately, transform marginal habitats for the latter to core ones.

Finally, our findings also propose that increasing temperatures from global warming may influence the distribution of organisms by changing the core-marginal population dynamics. This is indicated by the predicted role of winter temperatures in shaping the distribution of FPM and also by recruitment loss in populations in areas of low altitude habitats and with warmer winters (Hastie et al., 2003). This suggests that the optimal habitat suitability of FPM may shift to higher altitude and/or more northern areas over time and ultimately result in local extinctions and a reduced southern distribution range of FPM (Bolotov et al., 2018). A warming climate may also lead to changes in catchment processes that can have effects on hydrology, fine sediment dynamics and on the host fishes, which may all directly, indirectly and interactively affect FPM (Baldan et al., 2021; da Silva et al., 2022). The increased sediment and nutrient input predicted from global warming will lead to a decrease in the availability of interstitial oxygen, which will be particularly hazardous for juvenile mussels (Baldan et al., 2021). Together, this illustrates how anthropogenic activities can impact both small-scale and large-scale core-marginal population dynamics.

## 5 | CONCLUSIONS

The widespread loss of FPM recruitment is a clear warning signal on the deteriorating states of our freshwater ecosystems. We show that SDMs in combination with demographic data can advance the understanding of how different factors contribute to marginality with consequences on population and species persistence. The results indicate that the recruitment loss is likely due to a cumulative sum of different types of exploitations, and even global warming, pushing populations towards the margins of their present niches. Reducing current and future anthropogenic pressures and rehabilitating habitats is key to reversing the margin-ward trajectory, and just as different exploitations act in concord, so do restorative efforts.

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## CONFLICTS OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Data Dryad at <https://doi.org/10.5061/dryad.dncjsxm2c>.

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## BIOSKETCHES

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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