Current and projected UK distribution of bryozoan host of the Proliferative Kidney Disease in salmonid fish

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Abstract

Proliferative kidney disease (PKD) has been identified as a main driver of decline in brown trout (*Salmo trutta*) populations across Europe. *Tetracapsuloides bryosalmonae* is the causative agent of PKD, leading to yearly aquaculture losses of >20%, costing the UK around £2.5 million per year. This study collates primary presence records of *T. bryosalmonae's* primary host, the freshwater bryozoan *Fredericella sultana*. This data is utilised in species distribution modelling to identify areas predicted to be of high habitat suitability for *F. sultana* to infer species presence. Warming temperatures are known to exacerbate symptoms of PKD, making this an important system to study in the context of climate change. Therefore, data from the 6th phase of the Coupled Model Intercomparison Project (CMIP6) of the latest climate models are employed in this study to predict species range shifts, and inform on the potential of PKD spread across the UK in the coming decades. Maximum entropy modelling predicts optimal winter temperatures for *F. sultana* between 2-4°C, with a summer tolerance threshold of 16°C. The models also revealed that the future climates may increase habitats suitable for bryozoans in the north of the UK, with fewer areas of optimal winter climates in the south between the years 2041-2060. This information is essential in understanding the possible future threats of PKD, to tackle the issue of food insecurity and economic loss that will inevitably grow with global climate warming.

Introduction

The Earth's surface temperature in the last three decades has been warmer than any year since 1850 (Rodriguez *et al*, 2015). In an age where the human race is becoming increasingly connected online, the climate crisis is at the forefront of many conversations concerning economic growth, human health, food security, and water availability. One of the most cited climate papers of 2020, 'World Scientists' Warning of a Climate Emergency' gathers over 11,000 scientists' signatures from around the world to declare a climate emergency (Ripple *et al*, 2019). The most recent IPCC report has declared a 'code red' for humanity (IPCC, 2021), stating that global temperatures have already risen by 1.1°C since pre-industrial times. Such growing media attention to the climate crisis continues to call for further scientific research surrounding potential future climate scenarios, and the risks the warming planet faces.

In a business-as-usual climate scenario, the temperature experienced by an average human is projected to change more in the coming decades than it has over the past six millennia (Xu *et al*, 2020). Currently, economic and population growth are among the greatest drivers of CO2 increase (Ripple *et al*, 2019). Therefore, the possible detrimental effects of increasing global temperatures are beginning to motivate a change in economic and population policies in favour of measures designed to tackle or adapt to climate change. Most recently, international efforts have attempted to limit the increase of global mean temperature by 1.5°C, as decided in the Paris Agreement (Tong *et al*, 2019). These constant changes in climate policy (alongside other anthropogenic influences) all impact the way climate will evolve over the coming years.

Mapping future climate change scenarios is challenging due to considerable uncertainty of predictions regarding the evolution of climate within the next century. As we enter a new geological epoch dubbed the Anthropocene (Crutzen & Stoermer, 2000), humans continue to transform the abiotic and biotic conditions on Earth (Turner & Clark, 1990; Steffen *et al*, 2004; Millenium Ecosystem Assessment, 2005). The future global climate is dependent on anthropogenic and natural drivers, for example, the direction of technological advancement, land use change, policy choices, and international cooperation and competition (Collins *et al*, 2013). As global mean temperatures continue to rise in the coming decades, ecosystems will find adapting to these rapidly changing climate conditions difficult (Fischlin *et al*, 2007). Therefore, future ecological systems will differ greatly from present, a notion described as ‘ecological novelty’ (Kueffer, 2015).

Novel ecological systems, and the rate of adaptation in agriculture and farming will strongly influence global food security, which remains at the head of climate conversations. Research has shown that human populations have resided in a narrow part of the global climatic envelope for millennia, in mean annual temperatures averaging around 11°C to 15°C (Xu *et al*, 2020). Crops and livestock thrive in these milder conditions (Xu *et al*, 2020), fuelling economic success in Europe, large parts of Asia and North America (Hwa, 1989). Global temperature warming will have its strongest effects in these hotspots of global food production, with severe negative knock-on effects on all systems of agriculture and farming. We must therefore study the impact of increasing temperatures on these systems in order to predict future impacts, and forge solutions to the ever-growing issue of food insecurity.

Climate change affects food security and ecosystem services on a global scale, partly by altering disease distribution and transmission among agricultural and natural systems. Reports of disease outbreaks in marine ecosystems are increasing (Ward *et al*, 2004), and the interplay of warming temperature and increasing host density is a likely driver of disease transmission (Rohr & Cohen, 2020). Freshwater systems in particular are under increasing pressure from rising water temperatures, and increasing host densities in aquaculture increase the chances of disease emergence and largescale transmission (Woodward et al, 2010). In freshwater ecosystems, parasite and pathogen transmission, and host distributions may be altered further as river flow regimes are predicted to change in addition to temperature increases (Döll & Zhang, 2010).

In some cases, climate change can provoke disease emergence by driving species range shifts that bring novel hosts and/or pathogens into contact. In other cases, increasing temperatures can alter existing host-parasite interactions, susceptibility and virulence to shift non-pathogenic parasites into disease causing agents (Okamura & Feist, 2011). Climate change can also disrupt pathogen development through temperature dependent effects on parasite survival time, potentially leading to a decrease in disease prevalence (Noden *et al,* 1995). Understanding the temperature dependence of parasite and disease development, and the climate change driven shifts in host and parasite distributions are therefore required in order to understand the possible future impacts of climate change on host-parasite interactions that ultimately impact both wild and managed freshwater species.

Freshwater fish biodiversity is severely threatened (Su *et al*, 2021) mainly through river fragmentation and environmental change and the introduction of invasive species. In addition, disease emergence has contributed to the decline of many fish species of particular conservation interest, such as salmonid fish. The ‘Fischnetz’ project in Switzerland (Burkhardt-Holm, 2007) has identified multiple factors responsible for the declining populations of brown trout (*Salmo trutta),* with Proliferative Kidney Disease (PKD) being one of the main drivers alongside poor habitat quality and increased water temperature. PKD has emerged as one of the major factors of brown trout decline across Europe (Gorgoglione *et al*, 2016; Lewisch *et al,* 2018; Sudhagar *et al*, 2019). In North America, PKD causes outbreaks among native salmonids, including the threatened mountain whitefish *Prosopium williamsoni* (Hutchins *et al,* 2021). Brown trout are native salmonids, widespread in the UK, and heavily reliant on cold-water habitats for their spawning and development. PKD occurs in the UK, with infected fish reported by both the Environment Agency in England and Wales, as well as the Scottish Environment Protection Agency (unpublished, pers. comm. Hartikainen). Although mass mortalities in wild fish due to PKD have not been reported in the UK, the inland aquaculture industry suffers yearly losses of >20% due to PKD (pers. comm. O. Robinson). PKD clearly is a major disease of wild and farmed salmonids in the UK, which can impact the UK’s rapidly expanding fish farming industry. The economic impacts of PKD are estimated to cost around £2.5 million a year (Morris & Adams, 2008).

It is expected that the PKD outbreaks will constitute an increased threat to salmonids in the future, due to climate change and expected increasing water temperatures (Mo & Jørgensen, 2017; Strepparava *et al*, 2017; Sudhagar *et al,* 2019; Tops *et al*, 2006). This is because PKD emergence and spread is largely driven by increasing water temperatures - the disease develops in all species of salmonids across their global distribution range when temperatures increase above 15°C, often resulting in mortality (Okamura & Feist, 2011). The causative agent of PKD is *Tetracapsuloides bryosalmonae,* an endoparasitic cnidarian, which develops within the fish kidney. Spores released in fish urine are infective to freshwater bryozoans, in particular *Fredericella sultana,* its main invertebrate host. *T. bryosalmonae* spores produced in *F. sultana* are infective to salmonid fish, and it is notable that no fish-to-fish transmission takes place. This indicates that the bryozoan host is in a key role in driving the emergence of PKD.

PKD in brown trout *F. sultana (Fs)* *T. bryosalmonae (Tb)*

Figure 1. Images of PKD in brown trout *(Salmo trutta)* kidney, the bryozoan *(Fredericella sultana)* and its parasite *(Tetracapsuloides bryosalmonae).*

With this knowledge, this study will focus on the UK distribution of the bryozoan *Fredericella sultana*, the primary host of *T. bryosalmonae*. *F. sultana* are sessile, aquatic, colonial invertebrates found in cryptic, protected areas and low light conditions (Brown, 1933) (e.g. attached to submerged branches and roots). They reside in freshwater environments and have been recorded in lakes and rivers throughout Europe, north America, Asia, Australia and New Zealand (Kipp *et al*, 2010; Wood & Okamura, 2005). The occurrence of *F. sultana* is correlated with nutrient rich waters at temperatures between 8°C to 15°C, particularly at lower elevations. Surveys in Norway provide evidence of habitat preference in calcium rich, hard water at pH>5.4, and rich vegetation (Økland & Økland, 2001). A recent study in Germany further indicated that coniferous forest and wooded grasslands were negatively correlated with *F. sultana* presence (Ros *et al*, 2021). *F. sultana* reproduces asexually through colony fragmentation, which allows for dispersal along rivers. In temperate regions such as the UK, bryozoan colony growth is highest during warmer months by budding new zooids – each have tentacular crowns used for suspension feeding (Wood & Okamura, 2005).

Figure 2. Drawings and images of *F. sultana* – a) drawing of a branching colony, b) drawing of zooid anatomy, c) photograph of abundant statoblast production within a colony of *Plumatella repens*, d) a hatching statoblast. The newly emerging zooid is called an ancestrula, and will initiate an entirely new colony. Photo credit: H. Hartikainen, drawings Wood and Okamura, 2005).

F. sultana produces dormant overwintering statoblasts (Bushnell, 1966), which enclose germinal tissue and hatch as temperatures rise in spring. This overwintering strategy allows the species to persist during the winter, though they can also survive in the colder months as live colonies in some sites (Raddum & Johnsen, 1983). The bryozoan has a high tolerance for low temperatures (Raddum & Johnsen, 1983) and can survive in fluctuating conditions due to the desiccation resistant statoblasts, providing it a malleable life history strategy. The influence of climate change on *F. sultana* and its parasite *T. bryosalmonae* is therefore a particularly interesting topic of study as the parasite cycles between two developmental stages within the bryozoans, resulting in covert and overt infections. Covert infections are more likely to occur in the cooler months, and have no detectable effect on host growth or their ability to produce statoblasts (Tops *et al*, 2009).

In contrast, overt infections occur at higher temperatures in late spring and autumn when the bryozoan host is in prime condition and is able to support this energetically costly stage (Tops *et al*, 2009). Overt infections are highly virulent, increasing mortality within colonies, reducing growth and statoblast production, as well as promoting overwintering in live colonies. (Tops *et al*, 2009). The process of overt infection involves the development of spores within multicellular sacs that circulate within the body cavity (Tops & Okamura, 2003; McGurk *et al*, 2005) – these are released into river systems and infect the inhabiting salmonids with PKD (Feist *et al*, 2001). In some cases, infection may also lead to difference in overwintering strategy by altering the statoblast production propensity of infected colonies (Tops *et al*, 2009). The effects of climate change may therefore result in adaptation of *F. sultana*'s life history strategy, as warming waters may increase the likelihood of overwintering of a growing number of live colonies in the coming decades. Additionally, warming temperature causes statoblasts to hatch in spring, therefore the effects of anthropogenic climate warming may result in faster production of new bryozoan colonies, and longer seasons of overt infection.

F. sultana is abundant in British rivers, although few studies have systematically recorded their presence. Bryozoans in general are largely missed in macrobenthic surveys, due to their cryptic habitats and sessile life-style, which makes them inaccessible to most, e.g. kick-survey base methods. The new availability of bryozoan records from environmental DNA sampling allows niche models to be developed for bryozoans, and in this study, maximum entropy approaches implemented in the MaxEnt program were used. MaxEnt is a machine-learning algorithm based on principles of maximum entropy (Jaynes, 1957). It builds SDMs by training the algorithm with species occurrence data and their associated environmental variables that influence distribution. The algorithm can then predict other locations of habitat suitability. The central theory behind species distribution modelling lies in ecological niche theory, an idea formulated by Joseph Grinell (1917) and distinguished by G. Evelyn Hutchinson (1957). The fundamental niche describes an 'n' dimensional hypervolume of all abiotic environmental conditions that would permit a species to exist with positive population growth. The realised niche are the parts of a fundamental niche where a species can survive despite biotic factors, for example the presence of competitors. Therefore, the realised niche is smaller than the fundamental niche as a result of negative interspecific interactions. SDM allows us to empirically model a portion of the realised niche that has not yet been sampled, producing vital information describing these dynamic species ranges. This is a particularly powerful novel tool in mapping the distribution of host species to understand the potential future of disease emergence and range shifts under climate change.

In this study, species distribution modelling was employed to extrapolate future climate scenarios, and observe how changes in temperature and precipitation may influence the potential spread of PKD in coming decades, based on the distribution of bryozoa. Research into this host-parasite system is important in improving food security and disease management, especially as global temperatures will inevitably rise in coming years. The specific research questions addressed in this work were: (1) What is the prevalence of the host bryozoan species occurrence in the UK? (2) Through MaxEnt modelling, which environmental variables have the greatest influence on bryozoan survival and fecundity? (3) How will future climate scenarios of changing temperature and precipitation influence the distribution of the bryozoan across the UK, and therefore the potential presence of PKD among salmonid populations?

Based on existing literature, it was hypothesised that: (1) *F. sultana* occurrence would correlate with warmer temperature environments; (2) future *F. sultana* distribution would expand into areas of higher temperature and precipitation in the coming decades; (3) predicted climate change would foster a spread of the bryozoan host, and therefore potentially amplify the prevalence of PKD across the UK.

Methods

F. sultana occurrence was derived from primary sources, following a search of published literature (Supplementary Table 1). The main data source was Fontes (2015), where bryozoan presence was recorded using a visual search during a survey conducted by wading, and via environmental DNA sampling. Briefly, the presence and abundance of *F. sultana* was assessed by searching a stretch of river between 30-50 metres for a period of 20 minutes by two people. Areas with structures suitable for bryozoan colonisation were especially searched, for example tree roots, dead wood, and boulders. In addition, 1L of river water was collected on each site using methods described in Fontes (2015). The bryozoan detection used a *F. sultana* specific qPCR in the DNA extracted from the water sample, supplementing the visual search records. To search for occurrence records in the literature, a Google Scholar search using the terms "*Fredericella*", *"F. sultana*", and "*Fredericella sultana"* were used. Additionally, non-indexed literature were searched manually, focussing on monographs of phylactolaemate species, obtained from the Natural History Museum (pers. comm. Mary Spencer-Jones).

The collection of environmental variables assessed with respect to bryozoan distribution was conducted through literature searches, and implemented in the software ArcGIS (version 10.8.1). ArcGIS is a geographic information system for working with interactive maps to connect locations and data.

The occurrence points must all be mapped in the same coordinate system, to define the location of species presences with precision. Therefore, all coordinates were transformed in ArcGIS from the most common coordinate system, WGS84 (World Geodetic System 1984), to OSGB36 (British National Grid). This is a local coordinate reference system that will more accurately fit the Geoid at the smaller, more local scale of just the United Kingdom. This ensured that all species occurrence points were projected in their precise locations in the same coordinate reference system for later analysis and processing tasks. The coordinates of 102 species presence records were taken from ArcGIS in 'shapefile' format, and inputted into R (version R-4.0.3) via the RStudio interface (version 1.1.463) – this number of records was high enough to reduce sample size effects in later modelling. The study area is defined as mainland UK, excluding Ireland and Northern Ireland.

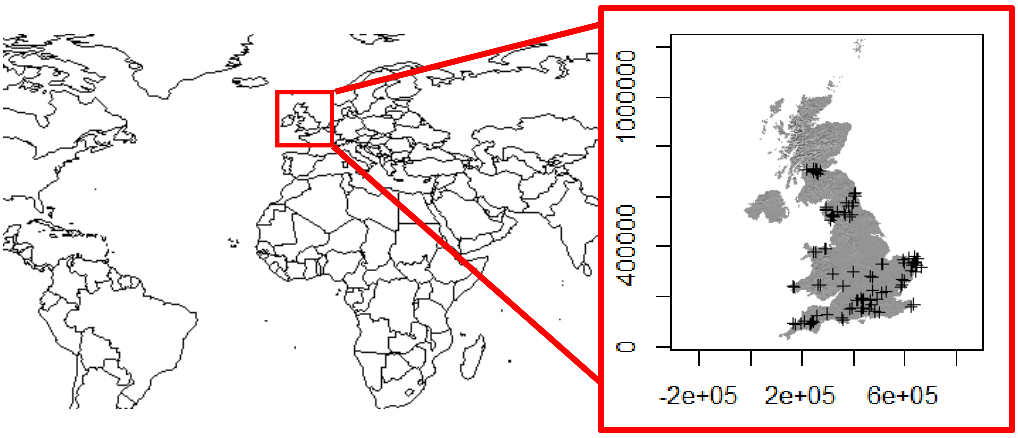


Figure 3. The study area of this project is the United Kingdom. Crosses are plotted on an elevation map of the UK, indicating *F. sultana* occurrence records across the landscape. Map created in R via the RStudio interface, using package ‘rworldmap’.

The final variables selected for niche modelling were bioclimatic variables available on the WorldClim website (http://www.worldclim.org, Hijmans *et al*, 2005) and Human Influence Index (HII) (Last of the Wild Data Version 2, 2005). HII is a composite measure of anthropogenic impacts on the environment, providing a gradient from near-natural to disturbed environments. A number of other environmental variables were considered for inclusion, particularly carbon and elevation (see Supplementary Document). Carbon represented carbon dioxide, emitted compiled from 11 different sectors. Carbon highly skewed results when included in the models, perhaps due to its correlation with HII, which represents similar emissions as anthropogenic influence. Elevation was highly correlated with bioclimatic variables relating to cooler temperatures, therefore this was removed from the final dataset to avoid skewed results due to high levels of intercorrelation. Elevation is known to be an important explanatory variable for PKD presence in other studies. Therefore, for comparison, a model including elevation was run alongside the final model. The results of this can be found in the supplementary documentation (Supplementary Figure 2).

To assess levels of collinearity among environmental variables, a Pearson’s correlation was run in R with package ‘ggplot2’ (Wickham *et al*, 2016) (Fig.4). This was set to a cutoff of 0.7, where 1 represents perfect correlation and 0 represents the absence of any correlation (positive or negative). The most relevant environmental variable to bryozoan survival was chosen from each intercorrelated group, and was included in the final raster stack. This minimised collinearity among variables to ensure model accuracy. The final uncorrelated 10 bioclimatic variables were selected and bound into a rasterstack with HII, including: annual mean temperature (bio1), mean diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4), mean temperature of wettest quarter (bio8), mean temperature of driest quarter (bio9), mean temperature of warmest quarter (bio10), mean temperature of coldest quarter (bio11), annual precipitation (bio12), and precipitation of warmest quarter (bio18). All variables in the final raster stack had a resolution of 2670, 4640 (x, y) and extent of -87855.11, 686444.9, -18027.31, 1248693 (xmin, xmax, ymin, ymax). Bio1 and bio11 were reported to be correlated, however both were included in the study as they both describe important and slightly different aspects of climate.

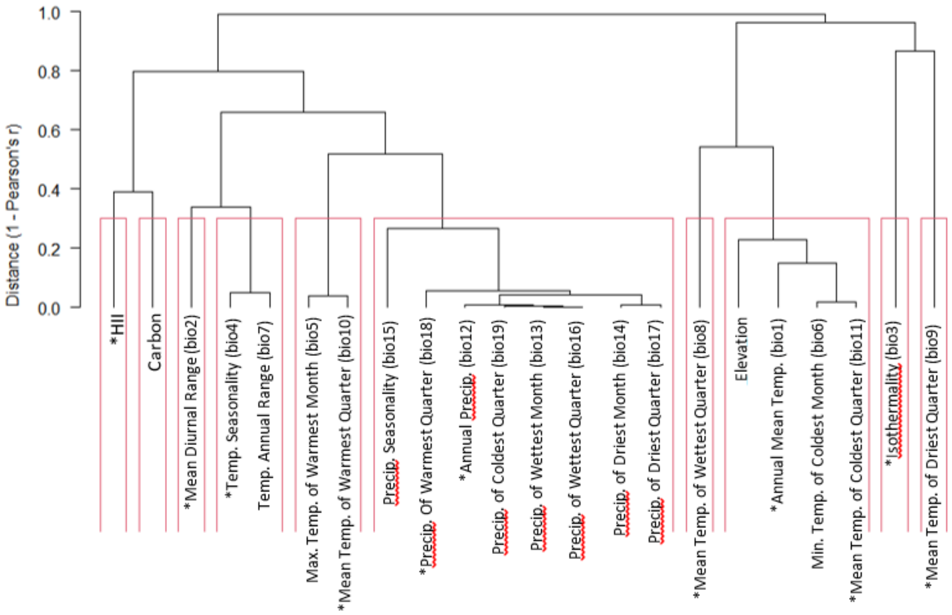

* = implemented in final MaxEnt raster stack

Figure 4. Tree diagram depicting results from the Pearson's correlation, constructed in R via the RStudio interface, with package 'ggplot2'. With a 0.7 cut off, groups of intercorrelated variables are indicated by red boxes. Variables included in the final model are indicated by '*'.

To assess the potential distribution in the fundamental niche (Hutchinson, 1957) of *F. sultana*, background samples were created and bound into a data frame to employ a presence-background density estimation method (Phillips *et al*, 2009) in the R package 'dismo' (Hijmans *et al*, 2013). The K-fold was set to 5, with the data in 75/25 split for training/testing. The background samples are useful in assessing whether the organism occurs in environments at rates either more or less frequently than the environments themselves occur in the landscape. For example, the method can be used to assess if areas with higher precipitation are more common across the landscape. These can then be compared against the 102 species occurrence records to determine the weight of influence of each environmental variable relative to their density across the landscape.

Mahalanobis distance based methods were employed in the package ‘raster’ (Hijmans *et al*, 2013) in R. This was implemented to measure the mean conditions of the location a species occurs to all other locations in an area, finding suitable similar environments where the bryozoan could also occur. This ordination method accounts for correlation between variables and distances in scale, reducing collinearity between environmental variables to a further extent. The Mahalanobis probability of species presence was then converted to a p-value, and graphically displayed at presence >0.5, >0.7 and >0.95.

To deal with spatial sampling bias, a raster reflecting the sampling density of *F. sultana* in the study region was created using kernel density estimation (KDE), using the package ‘sm’ (Bowman & Azzalini (1997) (Fig. 5). A final MaxEnt model was decided through trialling combinations of a number of different model settings, including linear, quadratic, hinge and product features, as well as thresholds. These were all run in MaxEnt through the package ‘dismo’ in R, via R studio interface. The final decided model includes linear and quadratic features, with a bias corrected background from the KDE. Model suitability and reliability was determined through formal model comparison of AUC values. Hinge and product features were turned off in the final model for simplicity of results by removing any background noise that may arise and skew results in highly complex models. 10,000 iterations were selected using probabilistic target-group sampling from the KDE bias surface. These were run through 5 folds of the K-Fold cross validation, and were further replicated 5 times to allow us to maximise the use of our data sample and reduce the effects of overfitting and sampling bias.

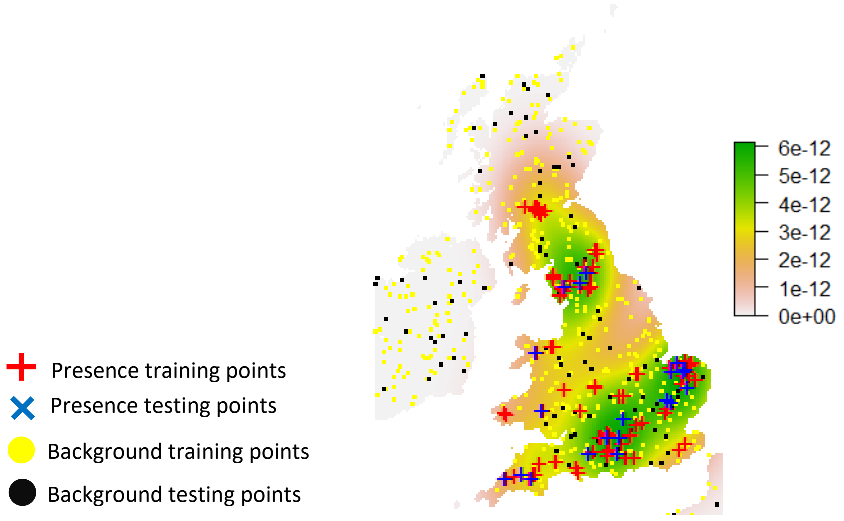


Figure 5. Kernel density estimation (KDE) with background and presence training and testing points. KDE reflects the sampling density bias of the occurrence data, with green being the highest density, orange as intermediate, and grey being the lowest. Created in R via the RStudio interface, package ‘sp’.

To determine feature complexity, a beta regularization coefficient was employed in MaxEnt. It is designed to limit overfitting – values nearer to 1 reduce the complexity, creating a linear curve to show the organism's response to the environment. A number of different AUC values were trialled, including: 0.25, 0.5, 0.75, and 1. These were then compared to select one final model.

To forecast probable future bryozoan distributions, the final models were projected to the years 2041-2060, according to predicted climate predictions from WorldClim. A way to combat the uncertainty of future climate change projections, is through mapping multiple climate scenarios with alternatives that span a range of future possibilities, therefore three different scenarios were modelled in this project. Climate models are constantly updated to incorporate finer spatial resolutions and Earth system processes to improve the accuracy of projections (Eyring *et al*, 2019). The 6th phase of the Coupled Model Intercomparison Project (CMIP6) of future climate scenarios consists of model results from around 100 distinct climate models, produced across 49 different modelling groups. CMIP6 uses socioeconomic pathways (SSPs), with the scenario premises of the previous CMIP5 version (O' Neill *et al*, 2014), to ensure more realistic future scenarios – therefore this method of climate modelling was implemented in this project.

The MaxEnt model was projected onto these three climate scenarios, including: SSP2-4.5 as an optimistic scenario of 3°C by 2100, SSP3-7.0 as a 'middle of the road' scenario, and SSP5-8.5 as a worst case emissions scenario among all other possible 'no climate policy' outcomes. These three were selected to provide a clear range of possible outcomes of *F. sultana*'s future distribution, ranging from optimistic to pessimistic. In line with the study of Ros *et al*, 2021, the bioclimatic variables from the MRI-ESM2-0 model were used in this project. This is to allow comparability of results for future studies, and hopefully compile similarly analysed data to the literature.

MaxEnt was run using the exact same methods, model settings, and parameters as the current environmental variables. The model was then projected onto SSP2-4.5, SSP3-7.0 and SSP5-8.5 individually to produce the final results for analysis.

Results

The Mahalanobis model suggested that large areas of the UK contain suitable climatic conditions for the presence of F. sultana, representing p-values of probability of presence along a scale of 0-1 (Fig. 6). All AUC values ranged above 0.7, inferring high model performance. Probability of presence plotted at >0.5, >0.7, and >0.95 (Fig. 7), indicated that the areas of highest habitat suitability and probability of presence occur in the East of England, as well as at the border of Wales, and in some areas near the Yorkshire Dales and Lake District. This is most likely due to the lack of industrialisation, and the abundance of freshwater river systems in these rural areas, as identified in the HII layer of the raster stack. Conversely, areas identified as currently unsuitable for bryozoans were located around Scotland. This area is therefore an interesting target of observation, as it is the clearest area to distinguish obvious species range shifts.

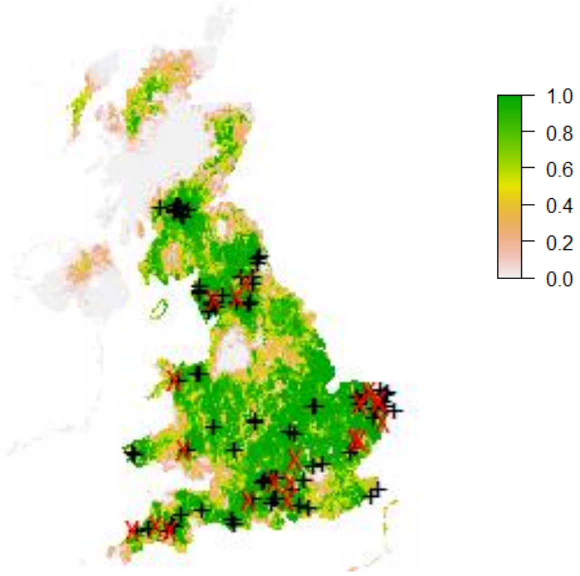


Figure 6. Probability of *F. sultana* presence along a scale to 1, calculated using mahalanobis distance modelling in R via the RStudio interface, package ‘raster’. Zero or lower probability of presence (white and pink) indicates areas less suitable. Higher probability of presence (green) indicates areas of highest suitability. Presence testing (red) and training (black) points indicate species occurrence records. Prediction of probability of presence is based on current UK climatic conditions.

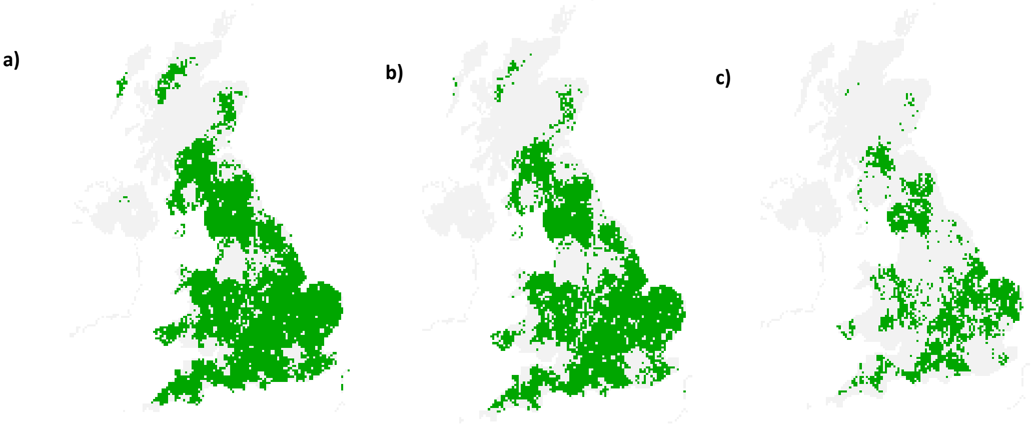


Figure 7. Presence-absence maps, at values of presence a) >0.5, b) >0.7, and c) >0.95. Green indicates presence of *F. sultana*, while grey indicates no presence at these probabilities. Prediction of probability of presence is based on current UK climatic conditions.

A final model of quadratic and linear features with a sampling bias background was implemented in MaxEnt. A raw output format was used to visualise maps, as this is under less strong assumptions than the cloglog format and therefore produces more accurate and probable predictions. The RAW format is presented in log scale in the figures for easier viewing and interpretation of the graphs. After trialling a number of different beta values, a value of 0.5 was decided for this model due to its relatively high AUC value of 0.751. Further, it had a low standard deviation, and the results of variable contribution most fit the observable trend, increasing confidence in this beta value being an appropriate complexity. The MaxEnt algorithm identified the environmental variables that contribute most to the survival and fecundity of *F. sultana*, displayed in Figure 8. The model identified four main contributors that determine probability of *F. sultana* presence, with mean temperature of the coldest quarter (bio11) at 21.3%, mean temperature of the driest quarter (bio9) at 19.6%, precipitation of the warmest quarter (bio18) at 19.6%, and mean temperature of the wettest quarter (bio8) at 13.6%.

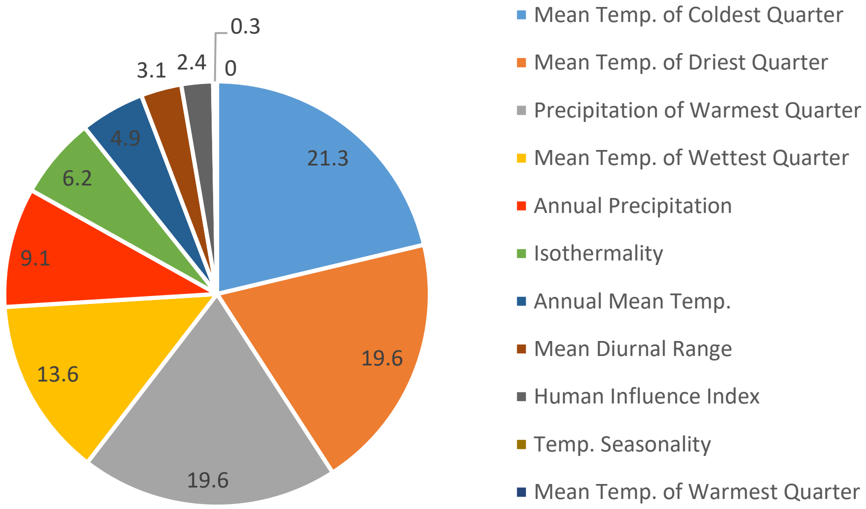


Figure 8. Environmental variable contribution to the bryozoan distribution, based on MaxEnt modelling. Mean temp. of coldest quarter (21.3%), mean temp. of driest quarter (19.6%), precipitation of warmest quarter (19.6%) and mean temp. of wettest quarter (13.6%) had the greatest contribution to species distribution.

A jackknife model (Fig. 9) identified the variables of greatest importance in *F. sultana* distribution. Jackknife procedure systematically removes each observation from the dataset, calculates the estimate, and then finds the average of all these calculations. The environmental variable with the highest gain when used in isolation is mean temperature of the coldest quarter (bio11), therefore appearing to have the most useful information in determining habitat suitability alone. The environmental variable that decreases gain the most when omitted was also mean temperature of the coldest quarter (bio11), appearing to have the most information that is not present in other variables. Of the four highest contributing variables (bio8, 9, 11 and 18), mean temperature of wettest quarter (bio8) is the only one with a negative test gain. It also has a relatively low AUC, suggesting high variance in this predictor (see supplementary document). The overall model gain suggests a relatively good fit between the model and the data.

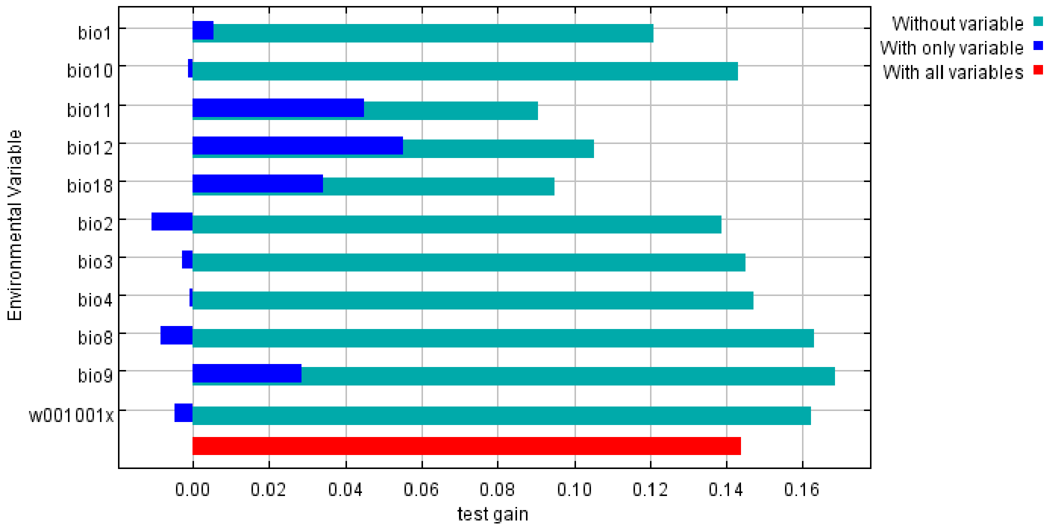


Figure 9. Jackknife testing data gain of variable importance, produced by MaxEnt in package ‘dismo’, in R via the RStudio interface. Values shown are averages over replicate runs. The red bar is the model gain with all variables included.

The five folds of the K-Fold cross validation were replicated five times, and produced sixteen species distribution maps of the 10,000 iterations. All of these maps highlight similar areas of likely bryozoan abundance, with varying intensities (data not shown). The mean of the 16 habitat suitability estimates (Fig. 10a) highlight the areas of highest habitat suitability across the current climatic landscape. This mean map corresponds with the current presence coordinate records within our dataset (Fig. 3) - areas with observed presences are also highlighted to have greater environmental suitability. The standard deviation appears low as the map is mostly dark blue, indicating that the replicates all produce similar and therefore generally reliable results. There are a few areas in the North and East of the UK with a higher standard deviation, which should be treated with caution in interpretation of these maps (Fig. 10b). Predictions of habitat suitability are generally highest in the South and around the Welsh border (indicated by dark red areas), most likely due to the warmer climate. It is notable that areas in the North are predicted to have low habitat suitability, indicated by the dark blue. Further, the areas of highest suitability in the MaxEnt species distribution model correlate with the mahalanobis maps of predicted presence (Fig. 6,7), with areas in the South of England being most prevalent across all maps.

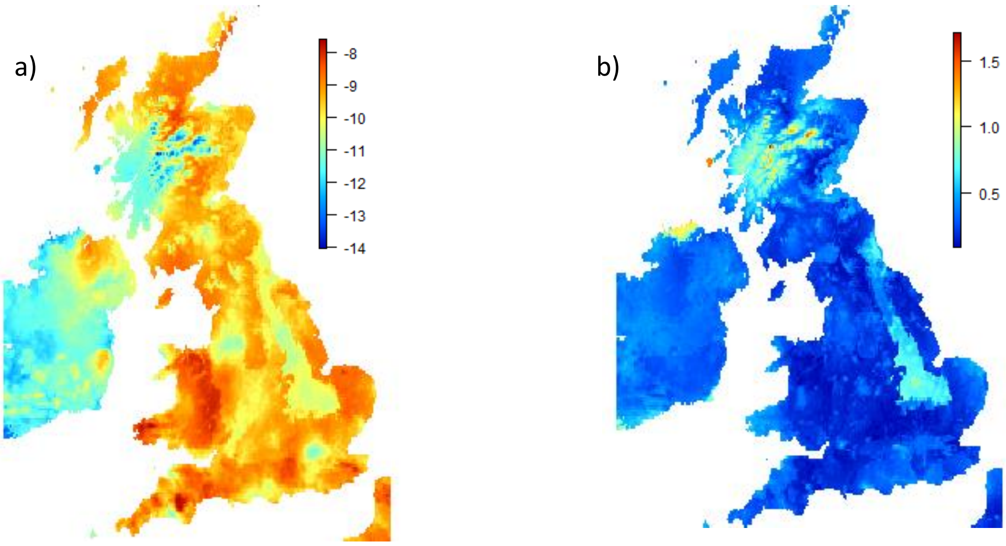


Figure 10. Ecological niche models showing areas of high habitat suitability of *F. sultana*. Models were projected for the period 1996-2018 (current climatic conditions). Fig 3 (a) shows the mean RAW output of all 16 models, with areas in red indicating highest suitability, and blue indicating lowest suitability. Fig 3 (b) is the standard deviation of these 16 models. Presented in log scale for easier interpretation. Created using Maxent in R, using package 'sdm' via the RStudio interface.

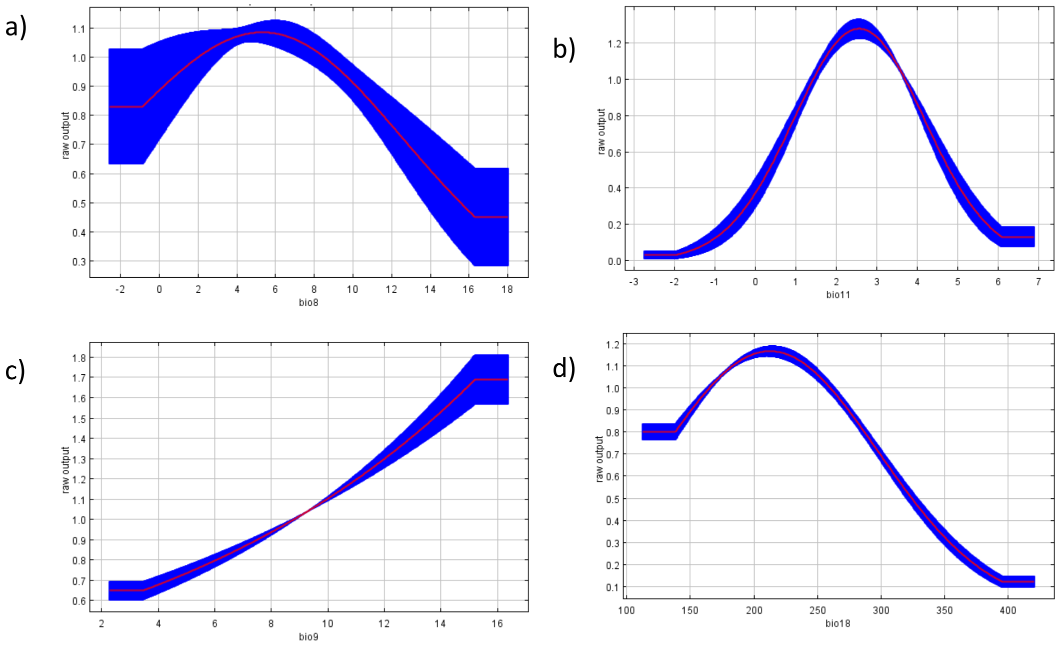
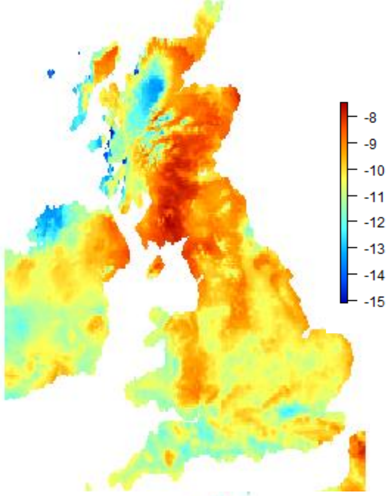


Figure 11. Relationships between four highest contributing environmental variables and their effects on the MaxEnt prediction- a) mean temperature of wettest quarter (bio8), b) mean temperature of the coldest quarter (bio11), c) mean temperature of the driest quarter (bio9), d) precipitation of the warmest quarter (bio18). Curves show how the predicted probability of presence changes as each environmental variable is varied, keeping all other variables at their average sample value. The curves show the mean response of the 5 replicate MaxEnt runs (red) and the mean +/- one standard deviation (blue). Created using Maxent in R, using package 'sdm' via the RStudio interface.

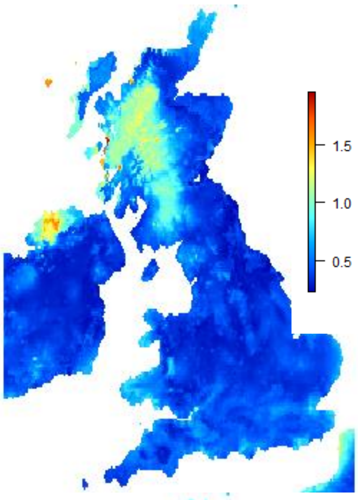
The four highest contributing bioclimatic variables to habitat were the mean temperatures of the wettest, coldest, and driest quarters of the year, as well as the precipitation of the warmest quarter (bio8, 11, 9, and 18) (Fig. 11). The wettest and coldest quarters in the UK largely coincide during the last and the first few months of the year. Mean temperature during the months with highest precipitation (bio8) and lowest temperatures (bio11) thus both have similarly shaped response curves, with an optimal mean temperature for bryozoans at 2-4°C.

In addition, data on precipitation of the warmest quarter (bio18) and mean temperature of the driest quarter (bio9) climatic conditions during the summer are also important factors in determining habitat suitability. The habitat suitability response curve is bell-shaped relative to summer precipitation, showing lower habitat suitability particularly in areas with higher summer precipitation. During the warmest quarter, high positive correlation infers that habitats with higher mean temperatures (bio9) are further predicted to be favoured by *F. sultana* (Fig. 11c). This suggests that the bryozoan generally prefers habitats with warmer summer temperatures, which in the UK tend to co-occur with modest summer precipitation conditions (demonstrated by the bell-shaped bio18 curve in Fig. 11d). These predictions remained the same throughout modelling both current and future climate scenarios.

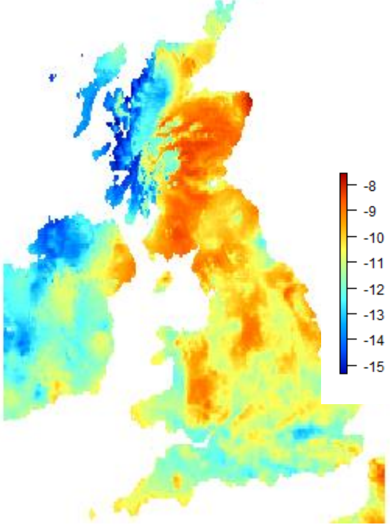
a)



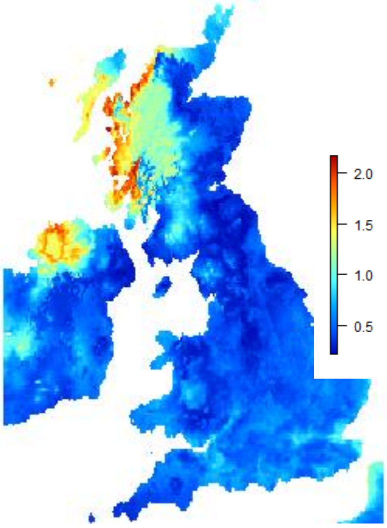
a) i)



b)



b) i)



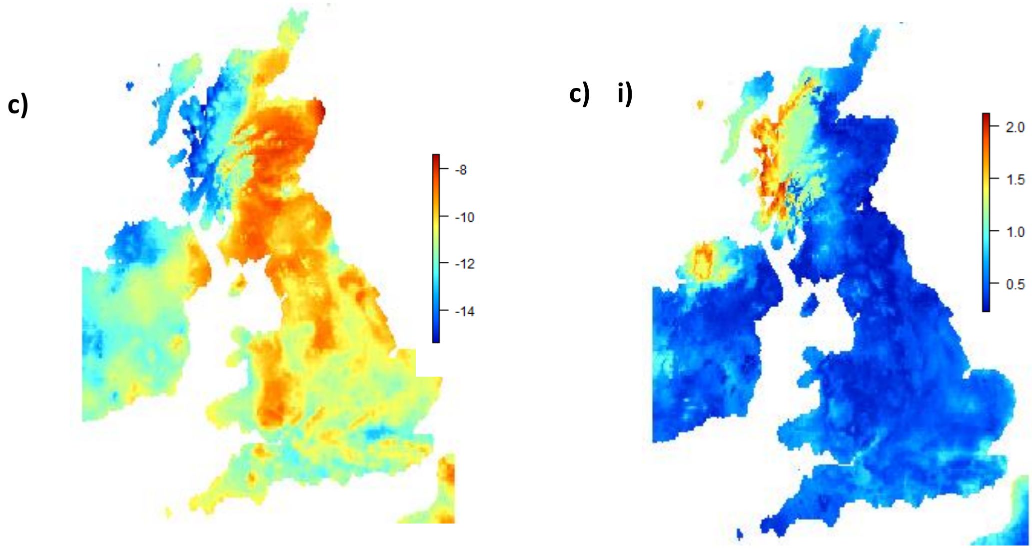


Figure 12. Ecological niche models showing areas of high habitat suitability of *F. sultana*. Models were projected for the period 2041-2060, under three climatic scenarios: a) SSP2-4.5, b) SSP3-7.0, and c) SSP5-8.5. All figures on the right show the RAW output of all 16 models, with areas in red indicating highest suitability, and dark blue indicating lowest suitability. Presented in log scale for easier interpretation. Figures on the right (i) show the standard deviations of each model. Created using Maxent in R, using package ‘sdm’ via the RStudio interface.

The MaxEnt model produced results for all three future climate scenarios: SSP2-4.5, SSP3-7.0, and SSP5-8.5. These are displayed in Figure 12, along with their standard deviations. Habitats with suitable climatic conditions will be increasingly found in more northerly parts of the UK. Suitability appears to expand from the South to the North, indicated by red colours. Three maps were produced to clearly display areas where novel habitat emerges (Fig. 13). Areas in red indicate novel habitats, which are focussed around the North of the United Kingdom. Darker blue areas indicate areas where habitat suitability will decrease, and green areas indicate no change in suitability.

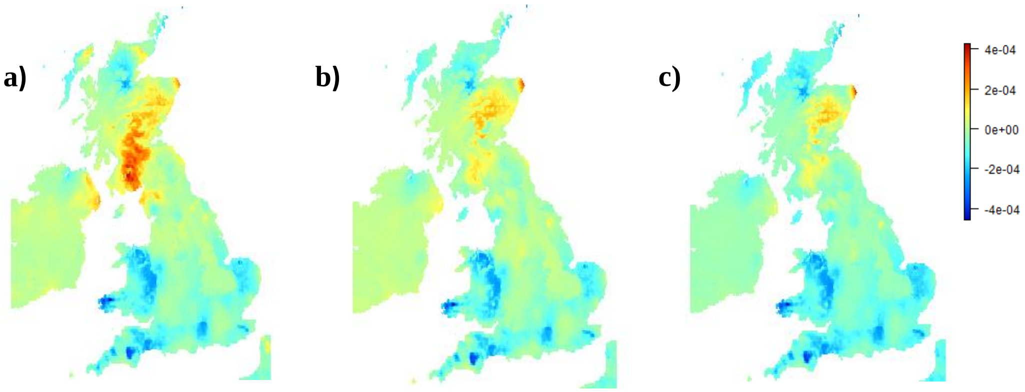


Figure 13. Maps to indicate the emergence of novel habitats. Areas in red indicate high novel emergence, whereas darker blue indicates little change in habitat suitability between the two climatic scenarios. a) difference between current and SSP2-4.5 climatic conditions, b) difference between current and SSP3-7.0, c) difference between current and SSP5-8.5. Created using Maxent in R, using package 'sdm' via the RStudio interface.

Discussion

Current distribution:

Climate change driven temperature increases have a profound effect on species distributions and may impact the dynamics of disease emergence through the occurrence of disease vectors and reservoir hosts, such as bryozoans. The results of this study indicate that under current climatic conditions, most parts of England and Wales are suitable habitats for the PKD reservoir host *F. sultana*. The models indicate that presence is most likely in the south of England, in areas of warmer summer climates and with optimal winter temperatures of around 2-4°C. The models predict highest incidence of occurrence particularly in locations around the border of Wales, indicated by redder colours. In support of these results, it is apparent that PKD has the highest incidence in southern England, where it presents a major economic constraint in the trout farming industry (Morris *et al*, 2008*). F. sultana* preference for lower elevation, and by correlation, warmer sites was also reported in a survey in Norway by Økland & Økland (2001).

An ecological niche model was run including elevation, to compare the outcome of its inclusion and exclusion from the final models (see Supplementary Document). Elevation was highly correlated with cooler temperatures (bio6, 8, 11), which are concentrated in few spots around the UK where elevation is increased. The results (Supplementary Figure 2) illustrate that when elevation is included, the model results in an artificially high prediction of probability of presence. This may be because the high unsuitability of colder areas in higher elevation would in comparison make the rest of landscape seem to be of relative higher suitability. In addition, the model may predict under stronger assumptions if there is interference between these highly correlated variables. Upon analysis of results the decision was made to remove elevation from the final raster stack used in MaxEnt modelling.

Our presence data was limited to 102 records, mainly located in south of England, with conspicuous absence of records in Scotland. This means that some areas identified as high habitat suitability were not sampled. Although standard deviations of the model were generally low, interpretation of the climatic aspects of habitat suitability in these areas should be done with caution, especially around North-West Scotland where standard deviation is high. However, the information from these maps may be useful in predicting locations of *F. sultana* and potentially *T. bryosalmonae* occurrence for follow-up studies to investigate and sample further. For example, areas around the border of Wales should be sampled more extensively in future, as it has been predicted to have high bryozoan habitat suitability, although little occurrence data is available. It may also be useful for fisheries managers, and fish conservation programs to investigate the likelihood of bryozoan presence in the specific areas identified by the model. This knowledge would allow disease management on farms using pre-exposure and vaccination programs, and help with PKD specific surveillance during conservation efforts.

Response to bioclimatic predictors:

The results of the niche models revealed that bryozoan distribution at the scale of the UK is mostly driven by four main bioclimatic variables. These included: mean temperature of the coldest quarter (bio11), mean temperature of the driest quarter (bio9), precipitation of the warmest quarter (bio18), and mean temperature of the wettest quarter (bio8). These remained consistent throughout current and future climate scenarios, suggesting that these climatic variables are essential predictors in bryozoan habitat suitability.

Analysis of the jackknife procedure for model evaluation revealed differing results between the training and testing gain. In particular, the mean temperature of the wettest quarter (bio8) had a negative testing gain, despite having high training gain and percentage of variable contribution. This indicates a high variance in the predictions involving bio8. Compared to the other three highest contributing variables, bio8 has large error envelopes around its response curves, suggesting inconsistency in the results produced by this variable. It also had an average AUC gain of 0.67(see supplementary doc). This suggest a good model fit, though not perfect – therefore bio8 and the overall model should be treated with more caution than bio9, bio11, and bio18 when interpreting results.

F. sultana has a strongly seasonal life-cycle, with rapid budding growth of adult colonies during summer, and the regression into overwintering statoblast stages during winter (Raddum and Johnsen, 1983). Thus, the winter and summer climates, their variation and seasonality may determine the climatic suitability of certain areas of the UK for bryozoans. The mean temperature of the coldest quarter (bio11) and the mean temperature of the wettest quarter (bio8) both decreased in probability of *F. sultana* presence with rising temperatures when modelled jointly with the other variables included. When their relevance for explaining habitat suitability in absence of other variables was assessed, a temperature range of 2-4°C was found as optimal. Particularly bio11 indicated that as winter temperatures rise past a mean of 2.5°C, habitat suitability begins to decrease. This winter temperature range was extrapolated from the results of bio11, as it had greater generalisability than the high variance of bio8. Despite our model predicting highest habitat suitability based on these optimal winter temperatures of 2-4°C, it should be noted that there are a number of other biotic and abiotic factors that influence bryozoan habitat preference that we were not able to model in this study (some of the data explored for inclusions, and potentially useful for future work are detailed in the Supplementary Document). However, the results from this study confirm the strong role of bioclimatic variables for bryozoan occurrence, and the temperature niche is a good basis of understanding one of the many broad factors that influence habitat suitability.

The two variables mostly related to summer climates (the mean temperature of the driest quarter (bio9) and the mean precipitation of the warmest quarter (bio18)) indicated that localities with warmer summers and moderate levels of rainfall would provide the optimal summer climates for habitats suitable for bryozoans. The strongly declining marginal response curve for bio18 suggests that habitat suitability decreases when summer precipitation increases. The mean temperature of the driest quarter (bio9) is positively correlated with probability of presence, suggesting that habitat suitability will increase as summer temperatures increase in the coming decades. The model shows that this correlation begins to plateau at around 16°C, suggesting that there is a temperature threshold after which increasing temperature has a negative impact on habitat suitability. This could be due to intrinsic thermal tolerance limits of *F. sultana*, where the combination of increased growth rate and thermal stress may be metabolically demanding on the bryozoan, leading to oxidative damage to essential biomolecules (Burraco *et al,* 2020). An alternative explanation may arise from altered biotic interactions, such as temperature correlated changes in substrate availability and resource competition. This latter scenario would also be supported by the analysis of variables bio9 and bio18, which suggest that habitats experiencing wetter and colder summers are less likely to provide suitable habitat for bryozoans. *F. sultana* thus prefers warmer environments to a certain threshold, with lower levels of rainfall.

The responses to these four predictors together suggest that habitat suitability is highest when climatic conditions promote warm, moderately dry summers, and temperate conditions during the winter at a 2-4°C mean temperature. This further suggests that *F. sultana* is highly sensitive to seasonality and temperature (Tops *et al,* 2009). Positive effects of temperature on *F. sultana* growth have been reported in laboratory studies, with highest per capita growth in both infected and uninfected colonies observed at 20°C, as opposed to 10°C and 14°C (Tops *et al,* 2009). The production of statoblasts was observed to show an opposite trend, with more statoblasts produced at 10°C and 14°C than at 20°C (Tops *et al*, 2009). It thus appears that bryozoans are well adapted to fluctuating conditions, with statoblast production enabling an overwintering strategy that makes them particularly suited to seasonal habitats. This makes the temperate environment of the UK a suitable environment for *F. sultana*. Therefore, despite possible changes is seasonality in both current and future climatic conditions, the bryozoa will have the ability to persist throughout these possible changes due to their malleable overwintering and statoblast production strategy.

The results indicate that bio8 and bio11 describe a winter temperature tolerance zone between 2-4°C for *F. sultana*, however this zone can vary as a result of phenotypic plasticity (Bowler & Terblanche, 2008). *F. sultana* has the ability to reproduce clonally, and selection may favour colony genotypes with particularly high temperature tolerance range as temperatures continue to rise. Alternatively, clonally reproducing populations may be unable to adapt rapidly, and become extinct as their thermal limits are reached. Although the current results indicate that bryozoan habitat suitability is temperature related, with clear optimal bioclimatic conditions, the limited knowledge of their phenotypic plasticity may bias these predictions. Further, it is currently unclear if clonally and sexually reproducing bryozoan populations differ in their thermal tolerance and thermal optima. In general, thermal tolerance and temperature-dependent effects on performance can shape the distribution patterns of ectotherms. Performance, such as growth or reproductive rate often increases with temperature, reaches a maximum at an intermediate temperature, then rapidly decreases (Huey & Stevenson, 1979; Huey & Kingsolver, 1989; Angilletta *et al*, 2002). An organism's thermal response curve is typically assessed under constant temperature regimes in the lab, therefore, they can be unreliable when predicting thermal responses in the wild where temperature fluctuates both diurnally and seasonally (Khelifa *et al*, 2019). In the case of F. sultana, any future measurements of thermal tolerance should incorporate both reproductive strategy of the colonies, as well as their infection status to better understand the potential of climatic variation to influence PKD emergence in the UK.

Climatic conditions which show seasonality may indicate suitable habitats for bryozoans. Seasonality is also described by isothermality (bio3) and temperature seasonality (bio4). Both of these variables were included in the final model, and would be expected to have a large contribution to bryozoan presence as we predict that seasonality is an important driver in suitability. Isothermality had a relatively large contribution of 6.2% to habitat suitability, describing the size of oscillation between day and night temperatures. However, temperature seasonality had only a small contribution of 0.3% to habitat suitability. Temperature seasonality is described as the amount of temperature variation over a given year based on the standard deviation (variation) of monthly temperature averages. It may have a small percentage of contribution to habitat suitability as it is highly correlated with mean diurnal range (bio2), and therefore made redundant. Additionally, although it is not explicitly correlated, the effects of bio8, 9, 11, and 18 are all very similar, and may produce conflicting results for bio4.

Based on these four bioclimatic variables (bio8, 9, 11, and 18) with the highest percentage contribution to probability of bryozoan presence, we can conclude that temperature seasonality is a great driver of distribution. The mechanism for the influence of seasonality cannot be inferred from the variables included in this study, but would perhaps arise from competitive interactions with other benthic species that compete for substrate and resources in aquatic habitats. Thus, bryozoans may particularly prefer habitats where winters are sufficiently harsh to reduce the abundance of aquatic plants, mosses, sponges, mussels, and other substrate occupying organisms during winter. Bryozoans can also rely on the rapid hatching of statoblasts already present on suitable substrates to reproduce and undertake extensive clonal growth during the early summer. Therefore, as temperatures rise in the coming decades, bryozoan distributions across the UK may change, and thus influence PKD emergence.

Future climate scenarios:

The MaxEnt model was projected onto three future climate scenarios from the years 2041-2060 to determine the future of *F. sultana* distribution. These included: SSP2-4.5 optimistically predicting warming of around 3°C by 2100, SSP3-7.0 as a ‘middle of the road’ scenario, and SSP5-8.5 as a worst case emissions scenario among all possible ‘no climate policy’ outcomes. Across all three future scenarios, habitat suitability expands to distributions beyond its current range, especially in the North of the UK. This is a clear change in potential distribution, as the predicted rising temperatures increase suitability across the entire country, demonstrated by areas of light blue, yellow and red on the map.

Interestingly, the standard deviation of all three of these climate scenarios are quite high in the North. This suggests that the 16 repeats of the 10,000 iteration models all produced slightly different results, and disagree on a final map of habitat suitability. This could be because the projections of the future scenarios are very different from the current climate scenarios that our occurrence records are trained on, so MaxEnt is unfamiliar with how the future environmental variables will interact with each other. As temperature rises, the bioclimatic variables may become more highly correlated, which would cause interference in MaxEnt and result in conflicting results. To address this concern, future studies should run a correlation analysis on the future climatic predictors, and run the model again removing highly correlated variables. Alternately, this problem can be addressed by using multiple algorithms and parameters to fit potentially hundreds of models to produce a final outcome. Different species distribution modelling algorithms may respond differently in the areas where MaxEnt becomes inaccurate, and therefore an exploration of this possibility is imperative for future studies.

To have a clearer understanding of how species distribution will evolve in the coming decades, further data is required to improve model accuracy. Our future predictions remain somewhat uncertain due to the limited data available, therefore the models should be continually trained with updated data over the coming years. Further, the future will remain uncertain with unprecedented distribution changes, as this is all dependent on the species' biological adaptation to the changing abiotic environment which MaxEnt cannot predict. For example, bryozoans may rapidly adapt their overwintering strategy, and increasingly persist as adult colonies. This is a likely scenario as declining temperatures in the autumn are suggested to act as a cue for statoblast production (Tops *et al*, 2009). The PKD parasite *T. bryosalmnoae* has been observed to be released from adult bryozoans during winter (Gay *et al*, 2001), however, no parasite spores are produced during overwintering as statoblasts. Therefore, we can only make inferences on how distribution will change based on the MaxEnt model, as *F. sultana's* biological response will also play a role in distribution that MaxEnt cannot predict.

This can be further understood with analysis of the results. Models show that the SSP3-7.0 scenario has greatest habitat suitability for bryozoans, with the reddest surface area on the map. Suitability decreases with the SSP5-8.5 scenario, suggesting that even higher rising temperatures result in an increasingly unsuitable environment for *F. sultana*. Though some studies suggest that species' and their associated parasites may face extinction under climate change (Lafferty & Mordecai, 2016), we can expect the bryozoan to persist throughout these environments due to their overwintering and life history strategies. Moreover, the dynamic environment of freshwater rivers means that the species will still be able to persist in cooler micro-environments, especially as they enter statoblast phase. The effects of climate change may increase the likelihood of overwintering of live colonies, and result in *F. sultana* generating statoblasts quicker and earlier within the growing season. Such life- history changes in the bryozoan host would generate a longer season of *T. bryosalmonae* transmission, with a possible increase in overt infection.

As global mean temperatures continue to rise as a result of anthropogenic influence, few ecosystems will be able to adapt to these new climatic conditions (Fischlin *et al*, 2007). Paleogeological data from past period of rapid climate change indicate that species and ecosystems need time to adapt to new environmental conditions (Warren *et al*, 2011). Interactions in host-parasite systems will not be able to keep up with this pace of adaptation, and *T. bryosalmonae* may disproportionately benefit from anthropogenic warming at a rate that salmonid populations cannot sustain. Symptoms of PKD are known to exacerbate with increasing temperature (Ros *et al*, 2021), therefore, upon analysis of these results we can expect higher rates of fish mortality in the coming decades.

Caveats and future directions

A number of caveats must be kept in mind when interpreting the species distribution models generated in this study. The number of presence records for *F. sultana* was limited to 102 occurrence points, and resultantly the MaxEnt model may not have been utilised to its fullest potential. Model performance and accuracy may have improved with a greater number of species presence points, however data on our target species is limited within the UK, and this study paves the way in highlighting these issues.

A practical method of improving the species sampling through environmental DNA (eDNA) could be implemented. This is a sampling method where DNA is extracted from water samples and the target species DNA is amplified and sequenced using general or universal primers in polymerase chain reaction (PCR). Such methods have been shown to be effective for *F. sultana* (Carraro *et al*, 2017, 2018). Through this, more extensive sampling can be achieved by identifying possible presences in the environment that may otherwise be missed by human error. The technique brings together traditional field-based ecology and in-depth molecular methods to allow biomonitoring without actually requiring the collection of the organism – a non-invasive practice to reduce anthropogenic stress. Further, eDNA sampling is often more cost-effective than the traditional sampling methods employed in this study (Qu *et al*, 2019).

The statistical analysis of this data was also limited by the lacking knowledge and limited information regarding river networks and connectivity. Covid-19 impacted our ability to execute field work, including validation sampling, and therefore the data used in this study is heavily reliant on online resources. With more computing resources, an improvement to this study would be to mask the raster stack of variables using a UK river network. The current model investigates the climatic conditions on the UK scale that are indicative of bryozoan habitat suitability – however, it also includes many areas where no freshwater is present. Further, no catchment level approaches were employed, and could be conducted in follow up work. The biodiversity of river systems can be sensitive to longitudinal connectivity, and other network-like properties of river systems such as climatic or human alterations (McCluney *et al*, 2014). Therefore, explicitly including connections between river stretches, and the upstream contributing area would refine the estimates proposed here. This could allow the incorporation of salmonid records in future records - salmonid distribution is known to be impacted by river connectivity, as their distributions are highly influenced by variables that change along upstream-downstream gradients. For example, water flow, turbidity, nutrient levels (Bjornn & Reisner, 1991) and anthropogenic influences such as pollution (Arkoosh *et al*, 1998).

Further, information on river temperature is difficult to ascertain due to the complex nature of river connectivity. Therefore, the bioclimatic variables used in this study are in reference to air temperature. We can only use this information to infer river temperature, though it is not an entirely precise method of prediction. With scarce information regarding river connectivity and river temperature available online, this aspect of the study is limited to the resources at hand. This investigation, and similar studies concerning river systems would greatly benefit from an online accessible database where researchers can share the data they have collected - for example of river connectivity, temperature, eDNA results, and pollution. Shared knowledge would result in greater potential for accurate and extensive statistical analysis and mapping to characterise rivers across the landscape.

Alongside adjusting modelling approaches, empirical work could complement this area of study. The adaptive potential of bryozoans to changing temperatures could be measured experimentally, and gene expression studies used to find genetic loci under greatest selection for adaptation to changing biotic and abiotic pressures. Understanding the genetic basis of thermal adaptation in host-parasite systems in general could aid in mitigation and preparing for the climate change driven disease emergence in freshwater systems. *F. sultana* are clonal species, with sexual reproduction observed only in some populations. Many clonally production populations may be lacking in genetic diversity leading to an evolutionary dead end and higher probability of population extinctions (Stebbins, 1957). Our current understanding of the mechanisms that underlie *F. sultana*'s response to temperature change is still limited, therefore further investigation into population genetic diversity, life-history strategies and phenotypic plasticity are required to understand adaptation across different timescales in a rapidly changing global climate.

Summary

The aims of this study were to find the greatest environmental variable contributors to *F. sultana* habitat suitability, and build a species distribution map to infer the areas at highest risk of PKD among trout populations. Utilising primary data gathered from a range of sources, this study provides empirical evidence regarding the current and projected distribution of our host species *F. sultana*, inferring the possible locations at risk of PKD outbreak.

This study employs first-hand primary presence records of *F. sultana* across the UK. This is the first study utilising this data in analysis, to provide us a better understanding of the primary host of *T. bryosalmonae*, and its distribution across the UK landscape. The results suggested an optimal winter temperature range for bryozoan habitat suitability at 2-4°C, and a possible summer threshold of 16°C. Predictions based on future climate models suggest potential range shifts of bryozoan distribution, increasing habitat suitability in the North, and fewer optimally suited locations in the South. It can be inferred that the spread of PKD could follow these distribution trends of its primary host in the following decades, especially as the severity of PKD in fish increases with temperature.

The threat of PKD for inland trout aquaculture continues to increase as the fish farming industry expands to meet growing food demand globally. With rapidly emerging research and attention to climate change science, the results of this study are yet another warning of the possible detriments of a warming planet. Following the latest IPCC report (IPCC, 2021), the threat of food insecurity and economic loss is growing blaringly urgent – the impacts of PKD in the UK is just a small scale example of a macroscale problem.

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List of Supplementary Materials:

1. Supplementary Table 1: Environmental variables considered for inclusion in ecological niche modelling, along with their sources.

2. Supplementary Figure 1: Diagnostic plots for MaxEnt model, showing jackknife evaluation of variable contributions of *Fredericella sultana* habitat suitability.

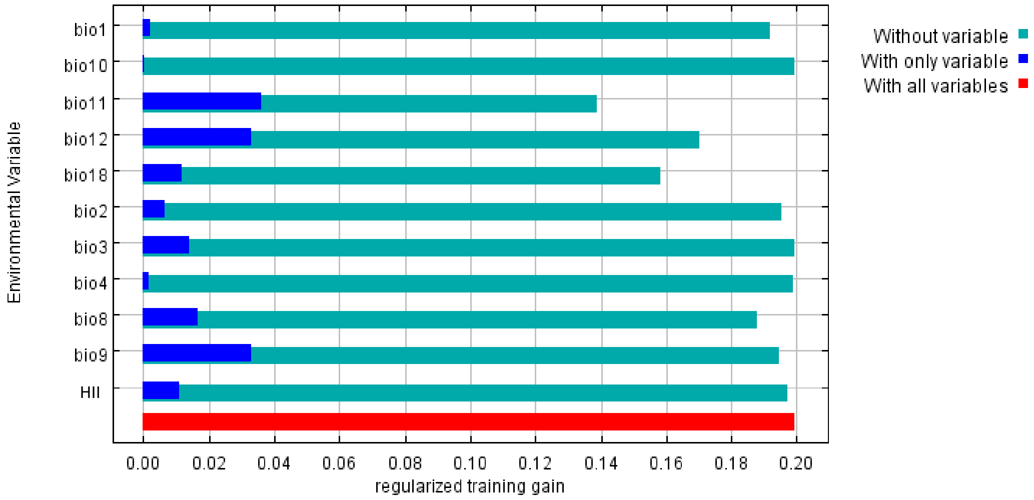
3. Supplementary Figure 2: Ecological niche models including elevation added as an explanatory variable.

Supplementary Table 1. Environmental variables considered for inclusion in ecological niche modelling. Time constraints and Covid-limited access to computers with higher processing power meant that they were removed from final raster stack. Variables were selected based on the literature and field data. Variable name, file type and source link are provided for follow-up studies to access.

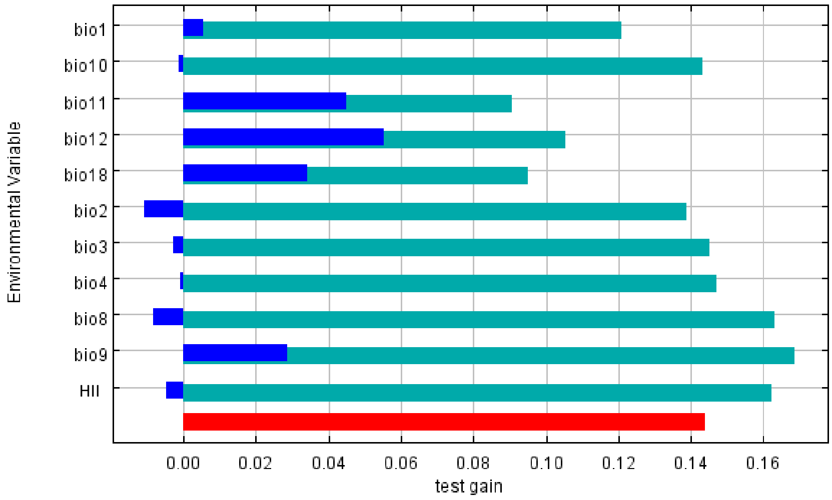
Environmental variable	**File type**	**Source link**
Ammonia	ASCII Grid	National Atmospheric Emissions Inventory: https://naei.beis.gov.uk/data/map-uk-das?pollutant_id=21&emiss_maps_submit=naei-20210830163051
Carbon dioxide as Carbon	ASCII Grid	National Atmospheric Emissions Inventory: https://naei.beis.gov.uk/data/map-uk-das?pollutant_id=2&emiss_maps_submit=naei-20210830163051
Copper	ASCII Grid	National Atmospheric Emissions Inventory: https://naei.beis.gov.uk/data/map-uk-das?pollutant_id=13&emiss_maps_submit=naei-20210830163051
Elevation (Digital Terrain Model at 50cm spatial resolution)	Shapefile	Digimap: https://digimap.edina.ac.uk/lidar
Fertiliser (2010-2015): including nitrogen, phosphorous and potassium	TIFF	Digimap: https://digimap.edina.ac.uk/environment

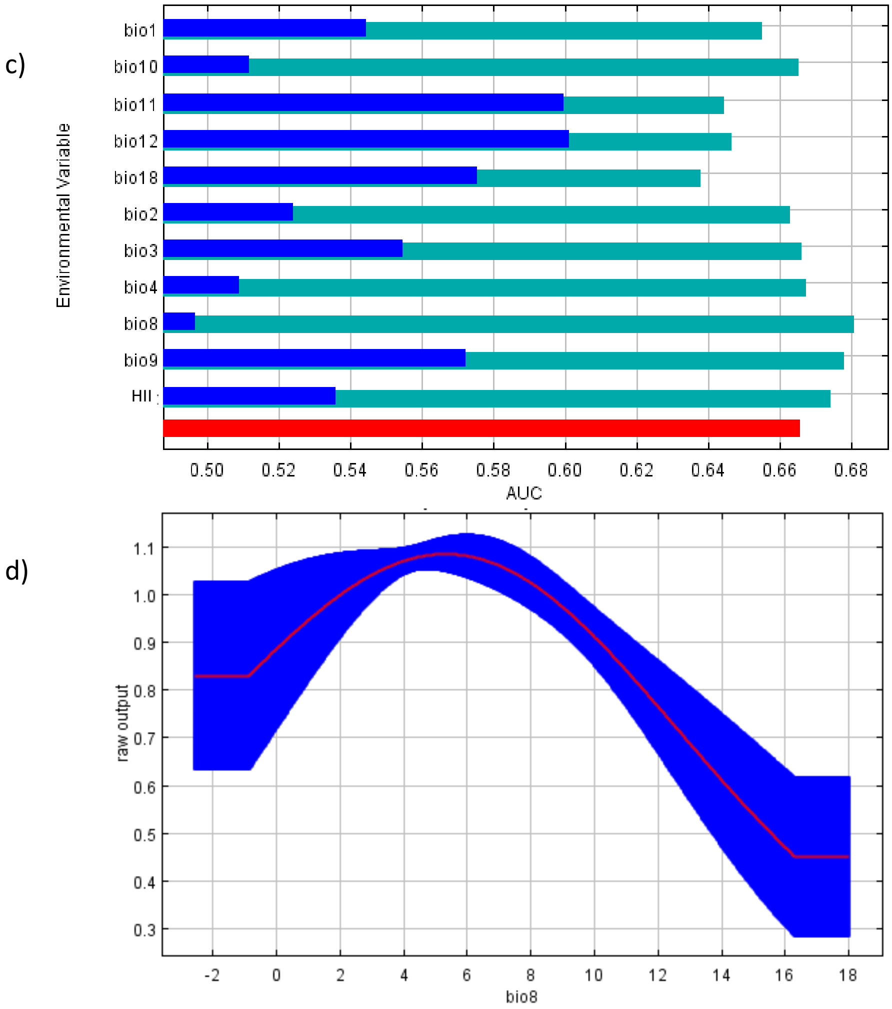
Geological indicators of flooding	Shapefile	Digimap: https://digimap.edina.ac.uk/geology
Land cover plus crops	ESRI Shapefile	UK Centre for Ecology and Hydrology: https://www.ceh.ac.uk/services/ceh-land-cover-plus-crops-2015
Lead	ASCII Grid	National Atmospheric Emissions Inventory: https://naei.beis.gov.uk/data/map-uk-das?pollutant_id=17&emiss_maps_submit=naei-20210830163051
Nitrogen oxides (NOx as NO2)	ASCII Grid	National Atmospheric Emissions Inventory: https://naei.beis.gov.uk/data/map-uk-das?pollutant_id=6&emiss_maps_submit=naei-20210830163051
Soil parent material model	Shapefile	Digimap: https://digimap.edina.ac.uk/geology

a)

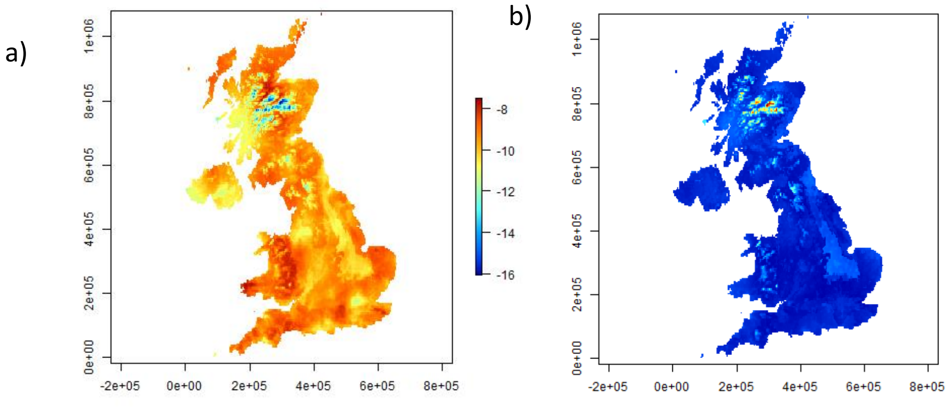


b)





Supplementary Figure 6. Jackknife output of variable importance, produced by MaxEnt in the R package ‘dismo’, version 3.4.1 via the RStudio interface. a) training gain for species, b) testing gain for species, c) AUC to reveal model fit, d) marginal response curve with error envelope (in blue) of mean temperature of the wettest quarter (bio8). Values shown are averages over replicate runs. The x axis is the model gain, suggesting how much ‘better-than-random’ the model fit is. A high model gain therefore suggests greater predicted value of the variable/model. The red bar is the model gain with all variables included – a 0.67 gain of the AUC is just above average, indicating a good model fit, though not perfect. This suggests some variability in the model runs and the bioclimatic variables. Results should therefore be treated with caution.



Supplementary Figure 7. Ecological niche models showing areas of high habitat suitability of F. sultana including elevation in the final raster stack. Models were projected for the period 1996-2018 (current climatic conditions). Supplementary Figure 2 (a) shows the mean RAW output of all 16 models, with areas in red indicating highest suitability, and blue indicating lowest suitability. Supplementary Figure 2 (b) is the standard deviation of these 16 models. Presented in log scale for easier interpretation. Created using Maxent in R, using package ‘sdm’ via the RStudio interface.