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PRIMARY RESEARCH PAPER

Modelling the distribution of a submerged invasive macrophyte and its potential biological control agent in invaded ranges

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Abstract Understanding current and potential geographical distributions of invasive species is an important part of natural resource management. Therefore, the aim of this study was to evaluate the current and future climate suitability of *Lagarosiphon major*, an invasive aquatic weed, and assess establishment potential for *Hydrellia lagarosiphon*, its candidate biological control agent. Using MaxEnt species distribution models, we identified climatically suitable regions for *L. major* invasion under current and projected climates. Additionally, mechanistic modelling was employed to map potential establishment zones for *H. lagarosiphon*, in order to determine overlap. Our findings indicate that more than 90% of New Zealand is currently suitable for *L. major*, with climate change expected to have minimal impact. In contrast, Australia and Europe exhibit limited suitability (8% and 15%, respectively), with future projections showing reduced suitability and a northward shift in Europe. Additionally, no climatic overlap was found between South Africa and invaded ranges. This highlights the adaptability of *L. major* to diverse environmental conditions. For *H. lagarosiphon*, degree-day modelling predicts viable populations across most invaded regions in New Zealand, supporting its potential as a biological control agent. This could help mitigate the impact of *L. major* in invaded sites, provided adaptive strategies are implemented.

Keywords Climate change · Degree-day modelling · *Hydrellia lagarosiphon* · *Lagarosiphon major* · MaxEnt modelling

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Introduction

Lagarosiphon major (Ridl.) Moss (Hydrocharitaceae) is a submerged aquatic plant native to southern Africa and is invasive in many parts of the world, including Europe, New Zealand, the United Kingdom, and Ireland (Wells et al., 1997; Champion & Tanner, 2000; McGregor & Gourlay, 2002). This plant exhibits characteristics of an ecosystem engineer as it can modify its immediate environment by trapping sediment and promoting its own dominance over other co-occurring macrophytes (Clayton, 1996; Caffrey & Acevedo, 2007). Management of *L. major* using

traditional means such as chemical and mechanical removal has proven to be challenging, as this plant can regrow from even small fragments remaining in the system (McGregor & Gourlay, 2002; Caffrey & Acevedo, 2007; Hussner et al., 2017). Because of this, biological control options are being explored, with *Hydrellia lagarosiphon* Deeming, 2012 (Diptera: Ephydridae) and *Polypedilum tuburcinatum* Andersen (Diptera: Chironomidae) showing promising results (Baars et al., 2010; Deeming, 2012).

Novel climates in the introduced range are likely to play an important role in the establishment and efficacy of these biological control agents should permission for release be granted (Fisher et al., 2011). This an important consideration as climate mismatches are especially common in cases where the source population is being transferred from tropical to more temperate or subtropical regions (see review by Harms et al., 2021). Furthermore, *L. major*, like many freshwater plant species, is highly sensitive to temperature change as well as changes in rainfall patterns due to climate change. Thus, making use of climate models and machine learning to predict how changes in temperature will influence the spatial distribution of invasive species over time should form the bases of any management or conservation plan. Such studies aid in prioritising conservation efforts to areas that are identified as the most vulnerable (Kumar et al., 2014).

Biological control programmes may also benefit by predicting ideal deployment locations based on climate matching (Sutton, 2019; Minuti et al., 2022). Indeed, studies have shown that climate incompatibility between native and invaded range may lead to the failure of an otherwise good biological programme (Harms et al., 2021). Desktop studies such as Species Distribution Modelling (SDM) and Ecological Niche Modelling (ENM) provide a cost-effective way of assessing the suitability of a biological control agent, whilst the project is still in the early stages. This is because the development of a biological control programme can cost close to $ 5 000 000 due to the amount of fieldwork and manpower required in the early stages (Paynter, 2015).

The aim of this investigation was to predict how changes in various bioclimatic variables under current climates and future scenarios will affect the distribution of *L. major* in New Zealand, Australia, and Europe (invaded range) through the use of SDMs. We also examined whether this invasive alien plant has reached its full potential distribution in New Zealand and if there are any likely mismatches with its natural enemy and potential biological control agent, *H. lagarosiphon* in that region using a mechanistic modelling approach. Lastly, this study determined the bioclimatic envelope of *L. major* and the associated potential agent and revealed which climatic data best determined the current distribution. These results will be instrumental in the management of *L. major* in the invaded range both under current conditions and future climates as understanding possible changes in the distribution of this species will be vital in the successful implementation of regulations and management plans.

Materials and methods

Species occurrence records

Worldwide occurrence records of *L. major* were downloaded from the Global Biodiversity Information Facility (GBIF) portal (https://www.gbif.org/) and supplemented with data obtained from field surveys carried out by the authors. After extensive data cleaning, removal of duplicate records, cell filtering (one record per 2.5-arc min resolution) and spatial thinning, the final dataset had 803 global occurrence records (Fig. 1). The global distribution of *L. major* was modelled using the cleaned total occurrence dataset and then cropped to the regions of interest for further analysis and evaluation.

Environmental variables

Predictive environmental variables for both current and future climate were sourced from the WorldClim database 2.1 (https://www.worldclim.org/data/worldclim21.html) at a spatial resolution of 2.5 arc minutes (~5 km). This website provides a set of 19 bioclimatic variables which are derived from measures of rainfall, temperature, and altitude from weather stations all around the world, indicative of annual, quarterly, and monthly means, as well as extreme ranges (Fick & Hijmans, 2017). This was supplemented with their elevation data as well as radiation. To project future climate conditions, the CMIP6 (Coupled Model Intercomparison Project Phase 6) dataset was utilised. Specifically, we employed the CNRM-CM6-1 climate

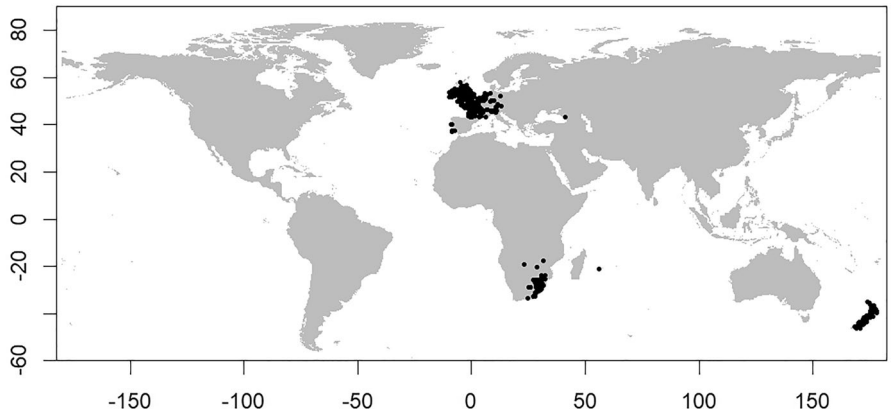

Fig. 1 Worldwide distribution of Lagarosiphon major, with 4181 uncleaned occurrence records. Data cleaning removed 2529 occurrence localities that shared the same grid cell, 6 occurrence points with NA predictor variable values, and spatial thinning removed 1720 records, resulting in 803 remaining occurrence points for modelling

model under the SSP5-8.5 scenario, which represents a high greenhouse gas emissions pathway. The time period for the projections was set from 2061 to 2080.

Due to the unavailability of accurate global water quality data relevant to SDM in freshwater systems, atmospheric variables such as those offered by this database are routinely used as proxies (Khosa et al., 2019; Minuti et al., 2022). These variables are considered effective predictors of macrophyte niche distribution and have been used in similar studies (Coetzee et al., 2007; Hoveka et al., 2016; Luukkonen et al., 2024).

The model outcome of any SDM is determined by the predictive environmental layers used, and the most relevant layers depend on the species under investigation. Thus, including highly correlated predictor variables may lead to model overfitting and overall poor model optimisation (Kass et al., 2021). Therefore, only bioclimatic variables that were found to not be strongly correlated (correlation coefficient < 0.75), predetermined using vifcor (usdm package in R), were used to train the model for current *L. major* distribution (Table 1). In order to determine and visualise niche overlap between the distribution of *L. major* in the native (SA) as well as invaded ranges, a Principal Component Analysis (PCA) was run in R. To do this, the raster package was used to extract bioclimatic data for each occurrence point, and this was then used to produce a niche overlap summary using the first two dimensions of the PCA.

Species distribution modelling

Current climate suitability and projected changes in habitat suitability under future climates were modelled using the Maximum Entropy Species Distribution Modelling (MaxEnt) algorithm. This was implemented using the ENMeval package (v2.03) and the dismo package (v1.3.8) in R. This package offers an automated way of selecting the best model settings to use when running MaxEnt (Kass et al., 2021). This is an important step in SDM as model complexity may lead to overfitting when the default settings are used. The automation of model tuning also allows for transferability and reproducibility of results, which is always an important consideration in any scientific study.

Spatial partitioning and cross-validation using the checkerboard method also reduced the effect of sampling bias and ensured increased spatial extrapolation to novel conditions (Kass et al., 2021). Background points necessary for running the presence-only MaxEnt algorithm were randomly generated from the species-defined background within ENMevaluate during model evaluation and selection. The selection of these background points has a significant influence on the resultant projections (Phillips et al., 2017; Kass et al., 2021), thus the random.seed command in RStudio was used in order to get the same random points each time and ensure duplication.

Model settings from the ENMeval output which best minimised the Akaike Information Criterion corrected for small samples sizes (AICc) were used to select the best-fitting models. The resultant models from this were evaluated for predictive performance using the area under the curve (AUC) scores (Table 2), a comparative metric for assessing discrimination ability. An AUC value of 0.5 indicates a model that is not different from a randomly generated one, whilst values closer to 1 indicate high

Table 1 Bioclimatic envelope of *Lagarosiphon major* based on occurrence data

Locality	BIOS	N	Mean ± SD
Global	Mean Diurnal Range of Temperature (°C, Bio 2)	801	8.4 ± 2.2
SA	Mean Diurnal Range of Temperature (°C, Bio 2)	73	14.0 ± 1.5
NZ	Mean Diurnal Range of Temperature (°C, Bio 2)	192	9.4 ± 1.2
EU	Mean Diurnal Range of Temperature (°C, Bio 2)	725	7.7 ± 1.2
Global	Max Temperature of Warmest Month (°C, Bio 5)	801	22.1 ± 2.8
SA	Max Temperature of Warmest Month (°C, Bio 5)	73	26.3 ± 2.2
NZ	Max Temperature of Warmest Month (°C, Bio 5)	192	22.3 ± 1.3
EU	Max Temperature of Warmest Month (°C, Bio 5)	725	22.0 ± 2.6
Global	Min Temperature of Coldest Month (°C, Bio 6)	801	1.7 ± 2.0
SA	Min Temperature of Coldest Month (°C, Bio 6)	73	1.6 ± 3.2
NZ	Min Temperature of Coldest Month (°C, Bio 6)	192	2.8 ± 2.2
EU	Min Temperature of Coldest Month (°C, Bio 6)	725	1.1 ± 1.5
Global	Mean Temperature of Wettest Quarter (°C, Bio 8)	801	9.1 ± 4.6
SA	Mean Temperature of Wettest Quarter (°C, Bio 8)	73	19.6 ± 1.9
NZ	Mean Temperature of Wettest Quarter (°C, Bio 8)	192	9.2 ± 2.3
EU	Mean Temperature of Wettest Quarter (°C, Bio 8)	725	8.1 ± 3.6
Global	Mean Temperature of Warmest Quarter (°C, Bio 10)	801	16.6 ± 2.2
SA	Mean Temperature of Warmest Quarter (°C, Bio 10)	73	20.0 ± 1.9
NZ	Mean Temperature of Warmest Quarter (°C, Bio 10)	192	16.6 ± 1.3
EU	Mean Temperature of Warmest Quarter (°C, Bio 10)	725	16.5 ± 2.0
Global	Mean Temperature of Coldest Quarter (°C, Bio 11)	801	5.7 ± 2.7
SA	Mean Temperature of Coldest Quarter (°C, Bio 11)	73	10.7 ± 2.4
NZ	Mean Temperature of Coldest Quarter (°C, Bio 11)	192	7.7 ± 1.9
EU	Mean Temperature of Coldest Quarter (°C, Bio 11)	725	4.5 ± 1.5
Global	Mean solar radiation (kJ $m^{-}2$ day^{-1})	805	11,849.1 ± 2903.4
SA	Mean solar radiation (kJ $m^{-}2$ day^{-1})	73	18,813.9 ± 1100.9
NZ	Mean solar radiation (kJ $m^{-}2$ day^{-1})	192	14,355.0 ± 574.6
EU	Mean solar radiation (kJ $m^{-}2$ day^{-1})	725	10,659.0 ± 1369.7
Global	Elevation (m)	805	251.2 ± 412.0
SA	Elevation (m)	73	1365.0 ± 462.6
NZ	Elevation (m)	192	218.0 ± 207.8
EU	Elevation (m)	725	132.4 ± 128.7

N number of occurrence point, *Glob* global, *SA* South Africa (native range), *NZ* New Zealand, *EU* Europe

Table 2 Best MaxEnt model settings with maximum AUC from the ENMeval package

Species and area	Feature class	RM	AUC	CBI	10p
Global *L. major*	LQH	1	0.991	0.987	0.120

LQH linear quadratic and hinge features, *RM* regularisation multiplier, *AUC* area under the curve, *CBI* Calibration and Bias Index, *10p* 10 percentile training presence threshold

model performance. Additionally, a Calibration and Bias Index (CBI) was used to further evaluate the performance of the model by measuring how well it predicts species distributions and identifying any potential biases. Again, values closer to 1 indicate a well-calibrated model with minimal bias, meaning the model's predictions are accurate and reliable.

The final products from these models were set to produce cloglog-transformed MaxEnt output maps which predict the probability of species occurrences. These maps were also converted into binary maps of presence or absence using 10 Percentile Training Presence threshold, in order to make predictions about actual changes in km^2 and percentages. The output model also includes information about variable importance which according to Phillips (2006) is calculated, whilst the MaxEnt model

is being trained by keeping track of which environmental variables contribute to model fitting.

Degree-day modelling and net reproduction

Due to distribution data limitations, MaxENT modelling could not be performed for the two potential biological control agents associated with *L. major*. Rather, development data from Mangan & Baars (2013) as well as daily minimum and maximum temperatures from local weather stations around invaded areas in New Zealand were used to predict population persistence of *H. lagarosiphon* in those regions, with no similar data available for *P. tuburcinatum*. The weather data were sourced from the Cliflo database (https://cliflo.niwa.co.nz/) which provides access to a variety of climate data from more than 600 stations. Temperature data from the past 10 years (2012–2022) was requested from 18 weather stations across New Zealand and used in the following Eq. (1) to estimate the number of generations this potential agent would be able to complete at the specified sites based on mean accumulated degree days (generation turnover):

$$K = \sum \left(T_{\max} + T_{\min}\right)/2 - t\left(\text{where } T_{\min} < t,\ t \text{ was used}\right), \quad (1)$$

where $T_{\max}$ and $T_{\min}$ represent mean daily minimum and maximum temperatures at each site and t represents the lower development threshold which was determined to be 7.5 °C for *H. lagarosiphon* by Mangan and Baars (2013). Furthermore, the study also determined the net reproductive rate (R_o) to be estimated by the following equation: $R_o = -10.5507 + 01.1995\chi + 0.0035\chi^2$, where χ represents the daily average temperature per site. Using the reduced major axis regression equation (Ikemoto & Takai, 2000), they estimated that *H. lagarosiphon* requires 571-degree days above their development threshold of 7.5 °C (Mangan & Baars, 2013). In this study, χ was substituted by relevant temperatures for New Zealand, and the resultant values were averaged over the entire year to give net reproductive rate per year at each site. As noted previously, a value less than 1 was taken as an indication that population persistence would not be possible. All data analyses and visualisations were done in the R environment (R Core Team, 2023).

Results

The high AUC and CBI scores (0.991 and 0.987, respectively) show that the current *L. major* global distribution was predicted well by the MaxEnt models settings selected from ENMeval compared to random (AUC = 0.5) (Table 2). The PCA showed a separation in the distribution of *L. major* in environmental space between the native range of South Africa and invaded Europe and New Zealand (Fig. 2). The most important bioclimatic contributors to the predicted global suitability of *L. major* were Minimum Temperature of Coldest Month (Bio 6), Mean Temperature of Wettest Quarter (Bio 8), and Mean of Monthly Solar Radiation (S_rad), together contributing more than 65% of the model information (Fig. 3). The response curve for Bio 6 shows *L. major*'s tolerance to cold temperatures (Fig. 4C), whilst Bio 8 suggests that this plant species is not very sensitive to changes in during wetter periods (Fig. 4D). An increase in solar radiation leads to a gradual decline in suitability (Fig. 4H).

Mean Diurnal Range in Temperature varied significantly across the different regions. Globally, the mean diurnal range was 8.4 ± 2.2°C, whilst in the native range, this was notably higher at 14.0 ± 1.5°C (Table 1). New Zealand and Europe exhibited values closer to the global average (Table 1). Interestingly, for the Minimum Temperature of Coldest Month, it was New Zealand which deviated from the global average, having a slightly higher mean of 2.8 ± 2.2°C (Table 1). Lastly, the Mean Temperature of Wettest Quarter showed a similar pattern to the Mean Diurnal Range, with South Africa having the highest reading at 19.6 ± 1.9°C, whilst the other regions were closely matched with the global average (Table 1). The corresponding PCA in Fig. 2 effectively captures the major sources of variation in the dataset (80% for PC1 and PC2), illustrating how localities differ based on their climatic profiles, with South Africa having a distinct climatic envelop.

Lagarosiphon major ecological niche modelling

To make inferences about the actual spatial extent of *L. major* suitability in km^2, the continuous probability of suitability maps were converted to binary maps using the 10 Percentile Training Presence Threshold. This was done for both the total area of each region and also limited to only available freshwater

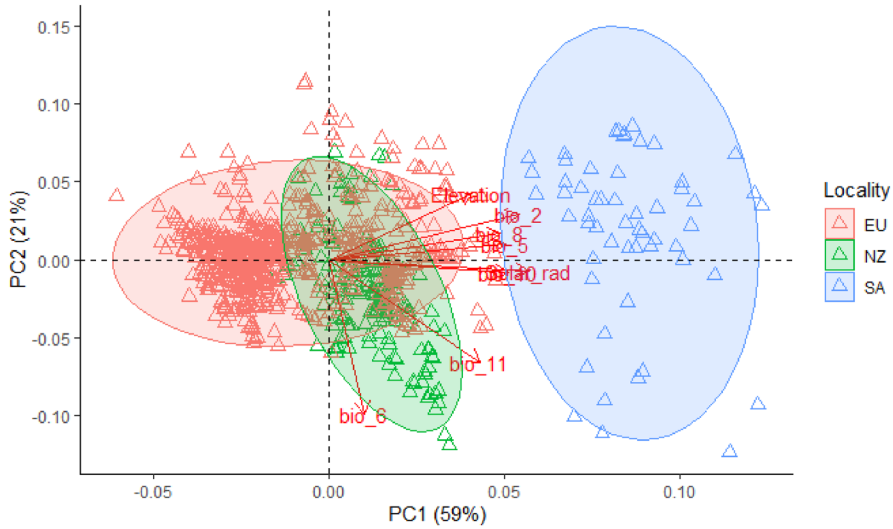

Fig. 2 Principal Component Analysis for Lagarosiphon major occurrence records as separated by bioclimatic variables used to model species distribution (PC1= 59%, PC2= 21%). Ellipses indicate Euclidean Distance, and arrows indicate loadings for the different bioclimatic variables [Bio 2= Mean Diurnal Range in Temp, Bio 5= Max Temperature of Warmest Month, Bio 6= Min Temperature of Coldest Month, Bio 8= Mean Temperature of Wettest Quarter, Bio 10= Mean Temperature of Warmest Quarter, Bio 11= Mean Temperature of Coldest Quarter, S_rad= Mean of Monthly Solar radiation (kJ m-2 day-1), elev= Elevation (m). All temperature data is in ℃]. SA=South Africa, NZ=New Zealand, and EU=Europe

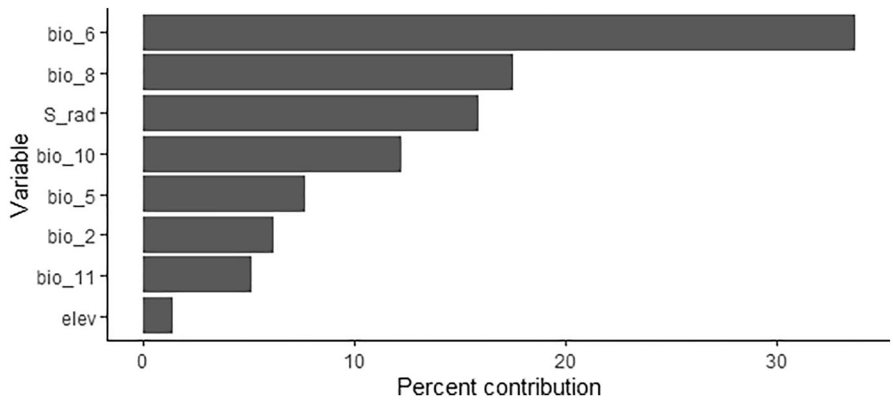

Fig. 3 Percentage contribution of each variable to the current model prediction for global climate suitability of Lagarosiphon major. Bio 2= Mean Diurnal Range in Temp, Bio 5= Max Temperature of Warmest Month, Bio 6= Min Temperature of Coldest Month, Bio 8= Mean Temperature of Wettest Quarter, Bio 10= Mean Temperature of Warmest Quarter, Bio 11= Mean Temperature of Coldest Quarter, S_rad= Mean of Monthly Solar radiation (kJ m-2 day-1), elev= Elevation (m). All temperature data is in °C

ecosystems. According to these maps, the total currently suitable area for *L. major* growth in New Zealand is 255 407 km^2 (Fig. 6A, indicated by green and blue), around 90% of the total available area or ~ 97% of all waterbodies (Fig. 5). This is projected to increase to about 95% under future climates (Fig. 5A, indicated by red and green), but not for freshwater ecosystems (Fig. 5).

In Australia, the total currently suitable niche for *L. major* invasion is predicted to be around 596 803 km^2 (indicated by green and blue in Fig. 6B), representing only about 8% of the country (Fig. 5).

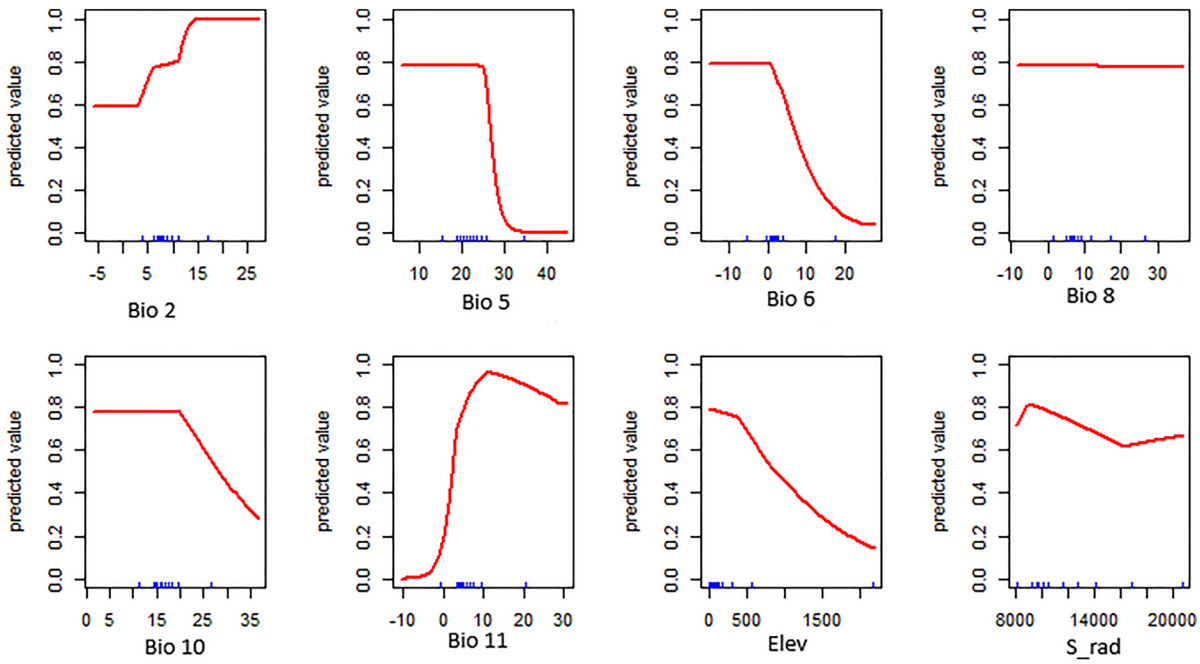

Fig. 4 Bioclimatic variable response curves for current Lagarosiphon major global suitability model. Bio 2= Mean Diurnal Range in Temp, Bio 5= Max Temperature of Warmest Month, Bio 6= Min Temperature of Coldest Month, Bio 8= Mean Temperature of Wettest Quarter, Bio 10= Mean Temperature of Warmest Quarter, Bio 11= Mean Temperature of Coldest Quarter, S_rad= Mean of Monthly Solar radiation (kJ m-2 day-1), elev= Elevation (m). All temperature data is in °C

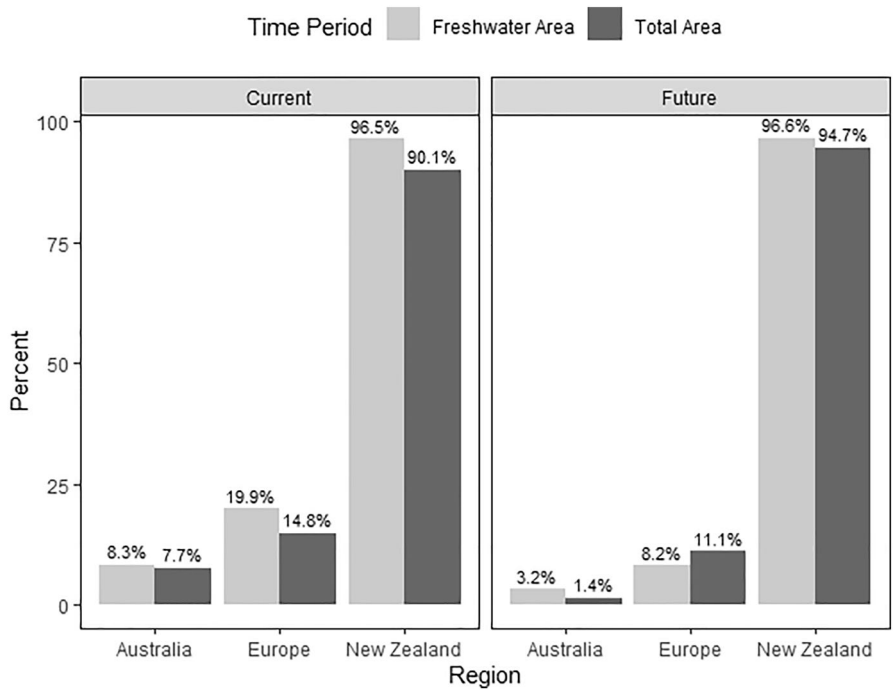

Fig. 5 Percentage of predicted suitable areas for Lagarosiphon major invasion different regions under current and future scenarios (2061-2080). Calculations were done for both the total area and also limited to only freshwater ecosystems

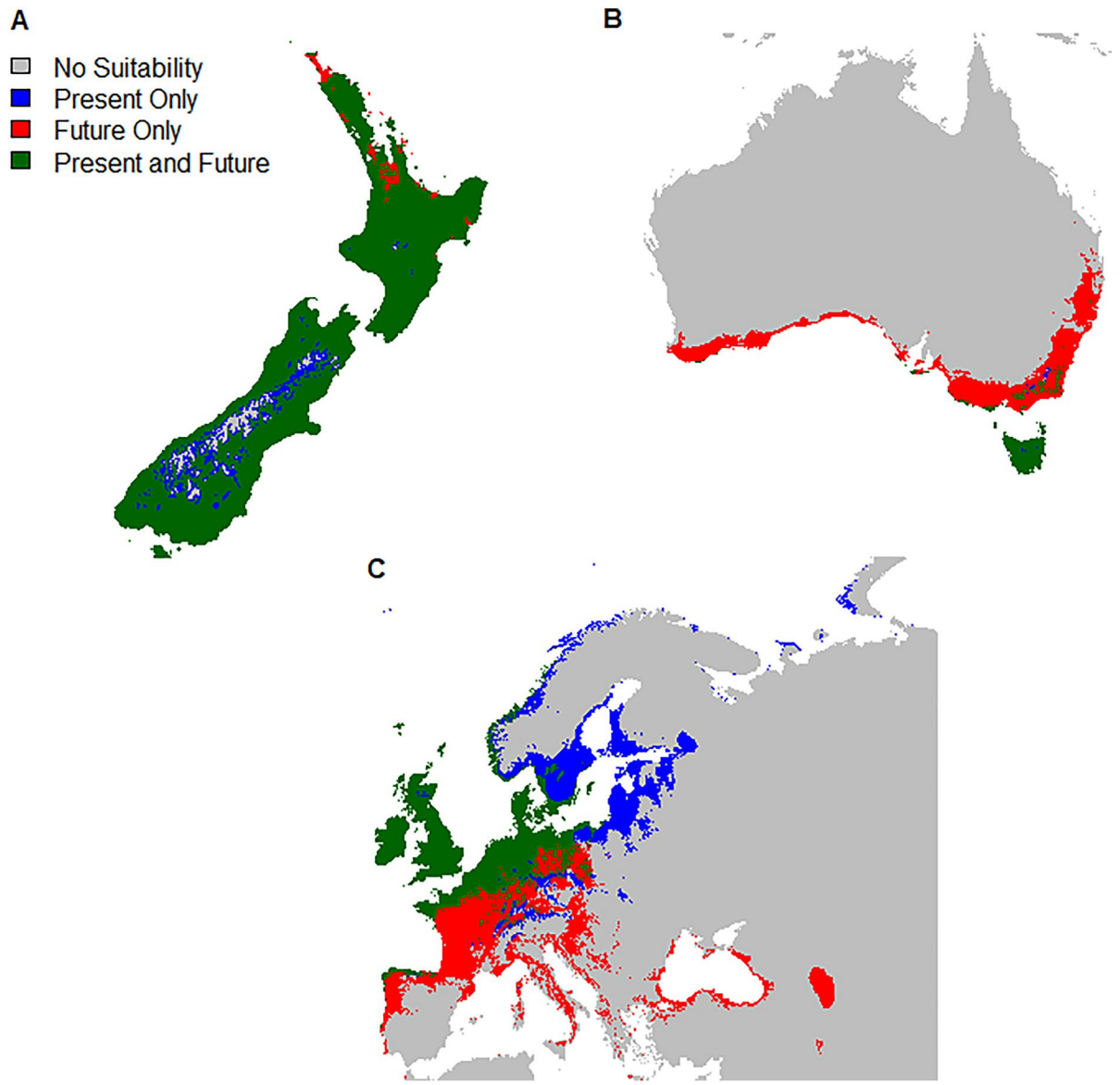

Fig. 6 Binary maps of Lagarosiphon major climate suitability change for (A) New Zealand, (B) Australia and (C) Europe. Grey= not suitable, Green= currently suitable, and Red= future suitability

This is projected to decrease to 3.2% or 1.4% of all freshwater bodies between the years 2061 and 2080 (Fig. 6B; indicated by red and green,). In Europe, the total currently suitable area for *L. major* invasion is approximately 15% or 20% of all freshwater ecosystems (Fig. 6C), and this is projected to decrease to 8% or 11% under future climate scenarios (Fig. 5). Suitability in freshwater ecosystems generally followed the same trend as calculations conducted on whole regions.

Degree-day modelling

According to degree-day modelling, *H. lagarosiphon* was predicted to produce between 4.5 and 9.3 generations per year in New Zealand, depending on

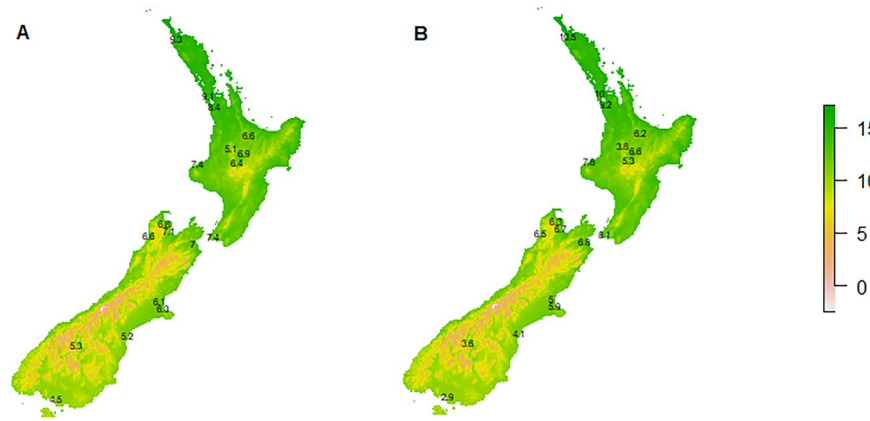

Fig. 7 **A** Number of *Hydrellia lagarosiphon* generations per year and **B** Net reproductive rate (Ro) per year estimated from Mangan & Baars (2013) reduced major axis regression model and New Zealand historical temperature data (Years=2012–2020)

temperature variations between sites (Fig. 7A). The lowest generation turnover was at the lower parts of the Southland region in the South Island, whilst the highest turnover was predicted in the Northland region of the North Island (Fig. 7A). A similar pattern was observed with regard to net reproductive rate (Ro). Here, Ro ranged between 2.9 and 10.5, with no sites having a value less than 1 (Fig. 7B).

Discussion

SDMs are an important part of natural resource management and conservation as they offer valuable information about the habitat suitability of both problematic invaders and endangered species (Coetzee et al., 2007; Khanum et al., 2013; Sutton, 2019). Climate compatibility is one of the primary requirements which determines the geographic distribution of most plants and animal species (Fisher et al., 2011; Khosa et al., 2019). Thus, this study modelled current and future climate suitability for *L. major* based on the highly adaptable MaxEnt algorithm. Model predictions were good, offering high AIC values, and were transferable to areas outside the native range since model training was done using the global occurrence data.

South Africa generally exhibited higher-temperature ranges and means in several bioclimatic variables, setting it apart from New Zealand and Europe, which showed more moderate and similar climatic conditions. Specifically, the lack of climatic overlap between South Africa and invaded ranges seen in this study could be interpreted as an adaptation to a wide variety of environmental conditions (Rodríguez-Merino et al., 2019). *Lagarosiphon major* has successfully invaded many parts of New Zealand and Europe, despite this supposed climate mismatch. According to Mooney and Cleland (2001), climatic niche separation between native and invaded ranges is not uncommon as the invader population usually has the added advantage of release from top-down constraints. This suggest that absence of competition also plays an important role and warrants active investigation in the future studies.

Minimum Temperature of Coldest Month was the most significant contributor to model performance. This is crucial as it determines the plant's ability to survive in regions with harsh winters. The ability to withstand low-temperatures allows *L. major* to establish and persist in a wider range of climatic conditions, enhancing its invasive potential (Caffrey & Acevedo, 2007). The importance of Mean Temperature of Wettest Quarter highlights the species' preference for specific thermal conditions during the wettest part of the year. This variable is particularly relevant in regions with distinct wet seasons, as it affects the growth and reproductive cycles of *L. major* and other similar species (Harms et al., 2021; Luukkonen et al., 2024). The higher mean temperature of the wettest quarter in South Africa compared to other regions suggests that *L. major* may find optimal conditions for growth in warmer, wetter climates (Baars et al., 2010). These variables also reflect and highlight that the submerged nature of this species means that these conditions provide optimum growth opportunities (Harms et al., 2021; Luukkonen et al., 2024).

The SDMs revealed that the majority of waterbodies in New Zealand (90% and above) are suitable for *L. major* growth, and climate change will not result

in any major changes in suitability. It is possible that this invaders already near its optimum range, since New Zealand has many clear oligotrophic freshwater systems which are ideal for *L. major* growth (Caffrey & Acevedo, 2007; Caffrey et al., 2010). Furthermore, this plant is also known to prefer cooler regions in its native range (Clayton, 1996; Martin et al., 2013). Indeed, there are many localities in New Zealand where *L. major* forms large dense mats that negatively impact those ecosystems, thus reducing overall functioning and ecosystem services (Baso et al., 2024). Therefore, future habitat suitability is still concerning as it indicates that this species will continue to be a problem in many parts of New Zealand.

For Australia, model predictions only showed 8% area of current suitability, with future climate conditions expected to reduce suitability even further. Suitability was shown to be restricted to the most southern parts of New South Wales, Victoria, and Tasmania. These are mostly temperate to cool temperate regions, with only mild seasonality (Duursma et al., 2013), mirroring native range distribution (Martin et al., 2013). There are currently no naturalised populations of *L. major* in Australia and previous infestations were successfully eradicated (CHAH, 2020). This absence of problematic infestations might be due to differences in climatic requirements or other barriers of entry, such as the listing of *L. major* amongst prohibited species in Australia (CHAH, 2020). Additionally, competition from native or established aquatic plants may further limit the establishment of *L. major* in Australia through biotic resistance. Species such as *Vallisneria australis* S.W.L. Jacobs & Les, *Potamogeton* spp., and *Myriophyllum crispatum* Orchard, which are common in temperate regions, could outcompete *L. major* by dominating available resources, including light, nutrients, and space (Strange, 2017). Investigating the role of these biotic interactions alongside climatic factors could provide valuable insights into the barriers preventing *L. major*'s establishment in Australia.

In Europe, 15% of all waterbodies are projected to be suitable for *L. major* invasion, and this is mainly in the western region, including Ireland and the UK. This is in line with the current known localities of *L. major* in this region, where Mediterranean climate provides favourable conditions for this species (Baso et al., 2024). Future climates are projected to result in a range reduction to about 11% and a shift towards Northern Europe. Whilst *L. major* thrives in cooler temperate conditions, the warming trends in Northern Europe may render previously unsuitable cooler regions more favourable by bringing them closer to its optimal climatic range (Hoveka et al., 2016). Conversely, areas in southern Europe that are currently suitable may become less favourable due to temperatures exceeding the species' tolerance thresholds. Factors such as temperature, humidity, and precipitation patterns play a crucial role in determining habitat suitability, and these are all expected to change under future climates (Harms et al., 2021).

Mechanistic modelling informed by insect biology from Mangan and Baars (2013), as well as this study, showed that *H. lagarosiphon* would be able to complete at least two generations in Ireland, and even more in New Zealand, especially in areas where mean annual temperature is above 15 °C. Microclimatic conditions within macrophyte weed beds play an important role in the establishment and distribution success of *L. major* and associated natural enemies. These beds tend to maintain higher minimum temperatures relative to the surrounding open waters, which may create more favourable microhabitats for the species (Wheeler & Center, 2001; Mangan, 2012). This buffering effect, caused by reduced water movement and shading, can help *L. major* and the biocontrol agents establish themselves even in regions with cooler ambient temperatures (Smith et al., 2019). Therefore, beyond these two desktop modelling approaches discussed here, ground truthing studies are still a fundamental part of any successful management strategy as they can be used to help build adaptive strategies in order to maximise biological control efforts (Muskett et al. 2020; Smith et al., 2022).

MaxEnt modelling showed that future climates are likely to reduce suitable habitat for *L. major* across the different regions. These results however deserve some circumspection as they are based on atmospheric data, with no available comprehensive layers for freshwater systems (Khosa et al., 2019). Furthermore, the influence of background selection and model parameters should also be considered in this regard, as results are highly dependent on model tuning (Phillips et al., 2017; Kass et al., 2021). Nevertheless, these models still offer valuable information about the current and future suitability of the different modelled regions for *L. major* invasion, and this can be used to simplify monitoring efforts by focusing

resources on those areas that have predicted higher suitability. Degree-day modelling showed that *H. lagarosiphon* would be able to sustain viable populations throughout New Zealand. Therefore, if approved for release in New Zealand, this natural enemy could help reduce the impact of this weed in invaded localities.

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Declarations

Conflict of interest None.

Data availability Data will be made available on request.

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