EFFECTS OF CLIMATE CHANGE ON THE HABITAT SUITABILITY OF 4 RELATIVELY NEW INVASIVE PLANT SPECIES IN THE PACIFIC NORTHWEST

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Abstract

Invasive species are a substantial threat to biodiversity and ecosystem structure. This threat is exacerbated by the increasingly concerning and urgent outlook of predicted climate change, land cover change, and other human influences. Specifically, an increasing number of invasive plant species are spreading in the Pacific Northwest (PNW), an area of unique natural areas, economic value, and increasing human population. Predicting the potential habitat suitability for invasive plant species that are not yet established in the region is crucial for developing preventative management strategies. To this end, I developed habitat suitability models for four invasive plant species, two terrestrial species: *Geranium lucidum* and *Pilosella officinarum*; and two aquatic species: *Butomus umbellatus* and *Pontederia crassipes*. I initially considered 33 bioclimatic variables, 10 land cover types, and a human influence index as current model predictor variables with location records for each species drawn from the introduced range (North America). I projected each species' current habitat suitability in the PNW region using ensemble modelling of six algorithms to 2050 and 2080, under 3 potential future climate scenarios. The majority of the coastal PNW is predicted to remain potential habitat for *Geranium lucidum* under all future climate scenarios, with some loss of habitat suitability in Oregon. In contrast, *Pilosella officinarum*, while currently suited to most inland regions of the PNW, is predicted to lose suitable habitat by 2050 under all climate scenarios, retaining high elevations as potential habitat. The suitable habitat for *Butomus umbellatus* in the PNW, which is currently moderately suitable, is not predicted to increase substantially in the future. Likewise, potential future habitat suitability remains relatively unchanged for *Pontederia crasipes*, which is currently highly suitable for inland waterways that do not experience freezing temperatures. Overall, the bioclimatic variables and human influence index were more important than land cover variables, suggesting that climate change and human activity are the determining factors for changes in future suitable habitat. My research provides a template to model other concerning species, assisting local land managers and practitioners to inform current and future management strategies and increasing the efficiency of allocating limited resources toward species with expanding ranges.

Lay Summary

The introduction of non-native, or invasive, plant species can negatively impact the functioning of natural areas, causing species extinctions and economic losses. The objective of this study was to predict how the suitability of habitats may change due to climate change, land use, and human influence, for four relatively new invasive plants species in the Pacific Northwest region of North America, a particularly vulnerable area due to its mild climate. Using current climate data and future climate scenarios, changes in suitable habitat were projected to 2050 and 2080. The results of this study suggest that invasive plants will not be impacted by climate change in the same way, with some species gaining and some losing suitable habitat in the future. This research is crucial for local and regional land managers as they assess the risk posed by these species and develop preventative management strategies to implement before invasive species spread.

Preface

This thesis is original, unpublished work by the author, Emma K. Nikkel. Original project proposal and design was initiated by Dr. David R. Clements (Trinity Western University, Biology), while further guidance and supervision for this work was provided by Dr. Jennifer L. Williams (University of British Columbia, Geography) and Dr. David R. Clements. Data retrieval and cleaning, as well as map visualization, was done with the assistance of Delia Anderson, undergraduate research assistant (Trinity Western University). All further research and data analysis was done by Emma K. Nikkel.

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Chapter 1: Introduction

Invasive species are a substantial threat to biodiversity and ecosystem structure (Mack et al. 2000, Hellmann et al. 2008, Whitney and Gabler 2008, Crossman et al. 2011). Introduction of invasive species, defined as species that establish, spread, and negatively impact an area outside of their native range, is the result of human action, whether intentional or not, and introductions are further facilitated by natural factors such as dispersal and environmental conditions (Guo et al. 2020). The spread of invasive species is a major cause of biodiversity loss and can disturb community structure in both natural systems and modified environments or impede the delivery of ecosystem services (Mack et al. 2000, Cordier et al. 2020, Seebens et al. 2020). Not only can the control and management of invasive species be very costly (Mack et al. 2000, Cordier et al. 2020), but damage can extend more broadly to socio-ecological impacts. For example, invasive species can reduce human well-being and livelihoods through reducing incomes, food security, and community adaptive capacity (Shackleton et al. 2019). Threats of invasive species are further exacerbated by the increasingly concerning and urgent outlook of predicted climate change (Bradley et al. 2010, Crossman et al. 2011, Beaury et al. 2020)

The effect of climate change on the distribution of invasive plant species is increasingly concerning. Global climate change is predicted to critically increase invasion risk (Bradley et al. 2010), with increases in non-native distributions predicted to be particularly strong in temperate regions (Bellard et al. 2013, Seebens et al. 2020). A study of the continental USA showed that, while 80% of current invasive plant hotpots were geographically stable with climate change, 20% are shifting northward (Allen and Bradley 2016). Specifically, northwestern North America, including the Pacific Northwest, is currently an invasion hotspot due in part to its temperate climate and is predicted to gain higher numbers of invasive species under future climate conditions, relative to more extreme climates (Bellard et al. 2013). Not only does climate change allow for novel habitats of climatic suitability for invasive species, non-native and invasive species often have an increased ability to adapt to climate change, through their higher growth rates, wider environmental tolerances, and shortened generation time, among other traits, compared to native species (Whitney and Gabler 2008, Willis et al. 2010, Clements and DiTommaso 2011). This adaptive capacity has

the potential to enhance non-native species' ability to invade new areas in response to climate change (Clements and DiTommaso 2011). Furthermore, climate change is allowing for increased and altered pathways for tourism and commerce, which aids the transport and spread of invasive species (Hellmann et al. 2008).

While climatic tolerances are often considered the most influential factor in the distribution of invasive plant species, land use and other human influences are also critical to consider. Land use change can provide a pathway for introduction of new species while altering the types of habitat, increasing disturbances, and rapidly changing species composition (Hobbs 2000). Particularly at a regional scale, the number of invasive species present has been mainly associated with land use change, while climate change is seen to play a role in determining broader scale distribution patterns (Chytrý et al. 2012). For example, land cultivation and disturbances from road and power line installation resulted in a 13-20% increase in the likelihood of cheatgrass expansion in the western USA (Bradley and Mustard 2006). While climatic suitability is necessary to allow a species to establish and spread, human influence on the environment increases the frequency of new introductions (Roura-Pascual et al. 2011). Increased human-mediated dispersal in the introduced range could thus facilitate colonization of new habitats. Along with climatic factors, land use and other human influences are considered to be among the main drivers of plant invasions.

Identifying invasive species that could shift their distributions under the influence of climate change, land use, and other human influences provides an opportunity to target species before they can establish and spread. Many regions assess the risk of invasive species, placing medium to high risk species that have not yet arrived (or are very recently introduced) on an 'early detection and rapid response' (EDRR) list. These risk assessments often do not incorporate climate change or the potential for range shifting in the future (Chai et al. 2016). A recent study of the incorporation of climate change into invasive species management showed that there is a considerable need for more targeted research, accessible science communication, and two-way dialogue between land managers and researchers (Beaury et al. 2020). The use of species distribution models is a cost-effective way to prioritize and focus actions on those species of highest invasion concern (Bellard et al. 2013),

as land managers frequently report that lack of funding and personnel limited their ability to manage invasive species (Beaury et al. 2020). Moreover, if invasive species are given the time to establish and become widespread, eradication can become nearly impossible, leaving costly containment and impact reduction strategies as the only options (Rockwell-Postel et al. 2020). The use of habitat suitability models (HSMs) and EDRR lists can work in tandem to account for shifting invasive species and the risks posed by their spread.

Habitat suitability models (alternatively known as ecological niche, envelope, or species distribution models, depending on the application) are increasingly being used as tools to predict the current potential suitability of an area to invasive species (De Kort et al. 2020). Habitat suitability models (HSMs) develop correlative relationships between species location or occurrence data and the environmental or climatic conditions in which those occurrence points are found (Peterson 2003, Cordier et al. 2020). These models produce predictive approximations of an area's current suitability, and can be used to project these responses into future scenarios or alternate locations. HSMs are widely used for reserve planning for conservation, predicting extinctions or extirpations of species under future climates, and predicting species invasion risk (Bocsi et al. 2016, Barbet-Massin et al. 2018), and can also be used in conjunction with species risk assessments to develop priority lists that account for future climate change projections (Chai et al. 2016). While predictive outcomes are known to be variable across model types (Qiao et al. 2015, Hao et al. 2019), an ensemble modelling approach that results in a consensus model from multiple individual models improves the reliability of species distribution predictions (Marmion et al. 2009). The use of HSMs plays a vital role in our ability to identify areas of high suitability for invasive species before they become established.

While risk assessments have been completed on many species with invasive potential in the Pacific Northwest of North America (PNW), they are often completed without an assessment on the impacts of climate change (Gervais et al. 2020). The PNW is currently considered an invasion hotspot and is predicted to increase with climate change (Bellard et al 2016), however the impacts of climate change on particular invasive plants are generally unknown. The region is increasingly susceptible to the spread of invasive species due to its location in a

temperate zone, its position as highly trafficked ports and tourist destinations, and its vastly heterogeneous landscapes and changing land-use. In a recent review of climate-induced expansions of invasive species present or considered an invasion threat to the PNW, only 6 studies focused specifically on the expansion or abundance of invasive species due to climate change within the PNW region (Gervais et al. 2020). To date, information about the current and future potential habitat suitability of invasive plant species in the PNW is lacking, but critically needed to prioritize the monitoring of species and establishing preventative strategies.

I selected four species with varying habitat requirements and invasion status from the EDRR lists from British Columbia (BC) for this study. Two terrestrial species, *Geranium lucidum* and *Pilosella officinarum*, and two aquatic species, *Butomus umbellatus* and *Pontederia crassipes*, were chosen based on their limited establishment in the PNW and the major impacts they have in their introduced ranges. Using habitat suitability models, I aimed (1) to establish the current potential habitat suitability of four relatively new invasive plant species to the Pacific Northwest region of North America, assessing the relative contributions of climate, land use, and human influence, and (2) to predict the future habitat suitability for these species in the PNW, assessing the potential expansion or contraction of the distribution of these species with climate change.

Chapter 2: Methods

2.1 Study system

In this study, the Pacific Northwest (PNW) of North America includes the province of British Columbia (BC) in Canada and both Oregon (OR) and Washington (WA) State in the USA. While previous studies of the PNW have included the states of Idaho and Montana, I restricted the focal study area to the regions of BC, OR and WA as the initial motivation for this project was to focus on the Metro Vancouver region (BC), a temperate region of approximately 2,880 km^2, west of the Cascade Mountain Range. The PNW has already experienced seasonal warming trends with mean annual temperatures having increased by approximately 0.6-0.8 ºC over the past century (Mote et al. 2003). Regional climate models predict a continuation of these warming trends, especially in summer months, with mean annual temperatures predicted to increase 1.1-4.7 ºC by the 2080s and a 20% increase in growing season length (Mote and Salathé 2010, Mote et al. 2013, Metro Vancouver 2016). Additionally, models project decreases in summer precipitation over the next century, as well as increased frequency of storms, droughts, floods, and wildfires (Mote et al. 2013, Metro Vancouver 2016). Moreover, the human population of the states in the PNW has doubled since 1970 and continues to grow at twice the rate of the national average (Mote et al. 2003), with the human population in Metro Vancouver projected to increase by 1 million by 2050 (Metro Vancouver 2018). This region has high ecological and economic importance and has become a significant tourist destination. While many studies have focused on either Canada or the United States, including the entire region, rather than delineating by country allows for increased targeting of biosecurity efforts and coordination across borders (Seebens et al. 2020).

2.2 Study species

Species were chosen from the British Columbia provincial EDRR (early detection and rapid response) list (Early detection and rapid response 2022), in conjunction with consultation with invasive plant experts from the Invasive Species Council of Metro Vancouver and the Provincial government of BC. Species placed on the EDRR list are identified as not currently present, or present in a limited extent, in BC and assessed as posing a high or medium risk, prompting the development of a response plan with the goal of eradication (IMISWG 2014).

These species likewise pose a threat to other areas of the Pacific Northwest, particularly the areas west of the Cascade Mountain Range in Washington state and Oregon. Four study species were chosen based on the risk they pose and the difference in niche space they occupy. Studies have shown a trend towards stronger expansion of invasive species in aquatic ecosystems, suggesting a particular vulnerability of aquatic systems to climate change (Havel et al. 2015, Gervais et al. 2020), thus two terrestrial and two aquatic species were chosen to compare contrasting ecosystems.

Geranium lucidum L. *(*Geraniaceae*)*, also known as shiny geranium, shining geranium, or shining cranesbill (hereafter referred to as *G. lucidum*), is an annual herbaceous terrestrial plant originating from Europe and temperate Asia (USDA 2013). *Geranium lucidum* is considered invasive in Australia, New Zealand, USA, and Canada, and was first collected in North America in 1971, in Oregon (Dennehy et al. 2011). *Geranium lucidum* spreads by seeds, which are explosively dispersed from an elongated capsule. Seeds can germinate from February to October, leading to up to 5 generations in a single growing season, and create a persistent seed bank (USDA 2013). Long distance dispersal is most often due to spread by the feet of livestock, deer, or hikers (Dennehy et al. 2011), although information on shiny geranium as an invasive species is limited. *Geranium lucidum* can form dense mats and displace native annual species, particularly in oak woodlands, dry conifer forests, riparian forests, and disturbed areas, most often in shaded, moist-to-dry sites (Dennehy et al. 2011).

Pilosella officinarum Vaill. *(*Asteraceae*)*, syn. *Hieracium pilosella*, with the common name mouse-ear hawkweed (hereafter referred to as *P. officinarum*), is a perennial herbaceous terrestrial plant, originating from temperate and sub-arctic Europe (Bishop and Davy 1994). *Pilosella officinarum* is considered invasive in similar climates of New Zealand, Australia, Argentina, USA, and Canada. Its introduction date and pathway in North America is unknown; however, it has been planted as an ornamental species, or spread as a contaminate of agricultural pasture seed (CABI 2022b). *Pilosella officinarum* can spread via seed, which is often wind-dispersed, but more often spreads vegetatively by producing daughter rosettes from stolons and can spread rapidly and create dense mats (Bishop and Davy 1994). While studies on the biology of this species are somewhat lacking, mouse-ear hawkweed seems to

be intolerant of high temperatures, excessive rain or high water-table, and significantly shaded habitats, preferring exposed grassland, heathlands, dunes, rock outcroppings, and pastures (Bishop and Davy 1994). Invasion hotspots include disturbed areas, construction sites, roadsides, degraded pastures, and quarry or mine areas (Cipriotti et al 2010).

Butomus umbellatus L. *(*Butomaceae*)*, known as flowering rush (hereafter referred to as *B. umbellatus*), is a sedge-like perennial aquatic plant, originating from Eurasia (Anderson et al. 1974). *Butomus umbellatus* was first recorded in North America along the St. Lawrence River near Montreal in 1897 and has since spread throughout the Great Lakes region of eastern North America as well as northwestern USA and western Canada (Anderson et al. 1974, Gaskin et al. 2021). Originally, it may have been intentionally planted as an ornamental, however ship's ballast waters have also been suggested as the initial vector of introduction (Cao et al. 2022). *Butomus umbellatus* can grow as an emergent plant in shallow waters (< 3 m) or as a submerged plant in deeper waters (3 - 6 m) (Jacobs et al. 2011). *Butomus umbellatus* spreads by seed, bulbil, and/or rhizome fragments, depending on its ploidy level or genotype (Gaskin et al. 2021). Preferred habitats include lake shores, slow-moving waterways, irrigation ditches, and wetlands, with fluctuating water levels promoting establishment and dispersal (Jacobs et al. 2011). *Butomus umbellatus* establishes quickly in disturbed areas or areas of sparse aquatic vegetation and is tolerant of a wide range of temperatures; however, it is intolerant of salt or brackish waters (Cao et al. 2022).

Pontederia crassipes (Mart.) Solms, formerly *Eichhornia crassipes*, *(*Pontederiaceae*)*, also known as common water hyacinth (hereafter referred to as *P. crassipes*), is a tropical aquatic plant, originating from the Amazon basin of Brazil (CABI 2022a). *Pontederia crassipes* has spread to nearly all tropical and subtropical regions of the globe and has been found seasonally in higher latitudes. Imported as an ornamental pond plant, water hyacinth was introduced to North America in 1884 for an exposition in New Orleans (USDA 2020). As a free-floating, freshwater plant, *P. crassipes* forms dense mats of vegetation that spread horizontally in uncrowded, shallow waters but can elongate to 1 m in height in crowded, deeper waters (Villamagna and Murphy 2010). *Pontederia crassipes* can spread vegetatively or through seeds which are released below water, rooting in mud initially and germinating

immediately or remaining dormant for many years (CABI 2022a). Although highly adaptive in many habitats, increased growth rates are associated with warm, eutrophic, nutrient-rich conditions resulting in the ability to double its biomass within 2 weeks (Zhang and Guo 2017). Growth ceases with extreme pH levels (below 4.5 or above 10) or low temperatures (below 10 °C), although it may tolerate short periods at freezing (CABI 2022a).

2.3 Species data

Species occurrences were collected from three internet databases: Global Biodiversity Information Facility (GBIF; GBIF 2022), Early Detection and Distribution Mapping System (EDDMapS; EDDMapS 2022), and Invasive Alien Plant Program (IAPP; IAPP 2022) (Figure 1; Table A1). Due to high resolution climate data being unavailable at the time of this study, the species records used were from the species' invaded range in North America only. While use of both invasive and native range data is ideal, several studies have shown the use of invasive range data to be sufficient to model the suitability of an invasive species as invaded ranges often encompass both the abiotic range of the native distribution as well as potential novel conditions (Barbet-Massin et al. 2018). While current and future projections were produced for the entirety of North America, mapped results include BC, WA, and OR only, as the future climate projections I used were focused on, and thus most appropriate, for western North America (Mahony et al. 2022). To ensure the species records correspond with the available environmental variables, records before 1980 were removed. To account for spatial bias and avoid model over-fitting, only one record per km² was retained, chosen according to quality of the data source, as sources with greater detail from non-governmental organizations, academic institutions, or government agencies were often higher quality than records sourced from community science, such as iNaturalist. Additionally, occurrence records underwent significant cleaning to keep records with coordinate uncertainty of <1000 m and complete time and place data, while removing duplicate records, country centroid coordinates, or records with inconsistencies in time or place of recording. If species had fewer than 50 occurrence records after cleaning, they would be excluded from further analysis. All filtering and cleaning of occurrence records was done using R 4.1.1 (R Core Team 2021), using additional packages 'CoordinateCleaner' (version 2.0.18; Zizka et al 2019) and 'dplyr' (version 1.0.6; Wickham et al. 2021). Detailed methodology and R scripts

for all data cleaning and species modelling is available in a public GitHub repository accessible at https://github.com/enikkel/PNW-Habitat-Suitability-Modelling.

Table 1 Number of species records before and after data cleaning. The high number of *Pilosella officinarum* and *Pontederia crassipes* records filtered out after cleaning was mainly due to many records being in very close proximity to each other and only 1 record per km^2 was retained. (see Figure 1 for record locations)

Species	**Records before cleaning**	**Records after cleaning**
Geranium lucidum	2,243	583
Pilosella officinarum	12,254	230
Butomus umbellatus	637	515
Pontederia crassipes	26,956	650

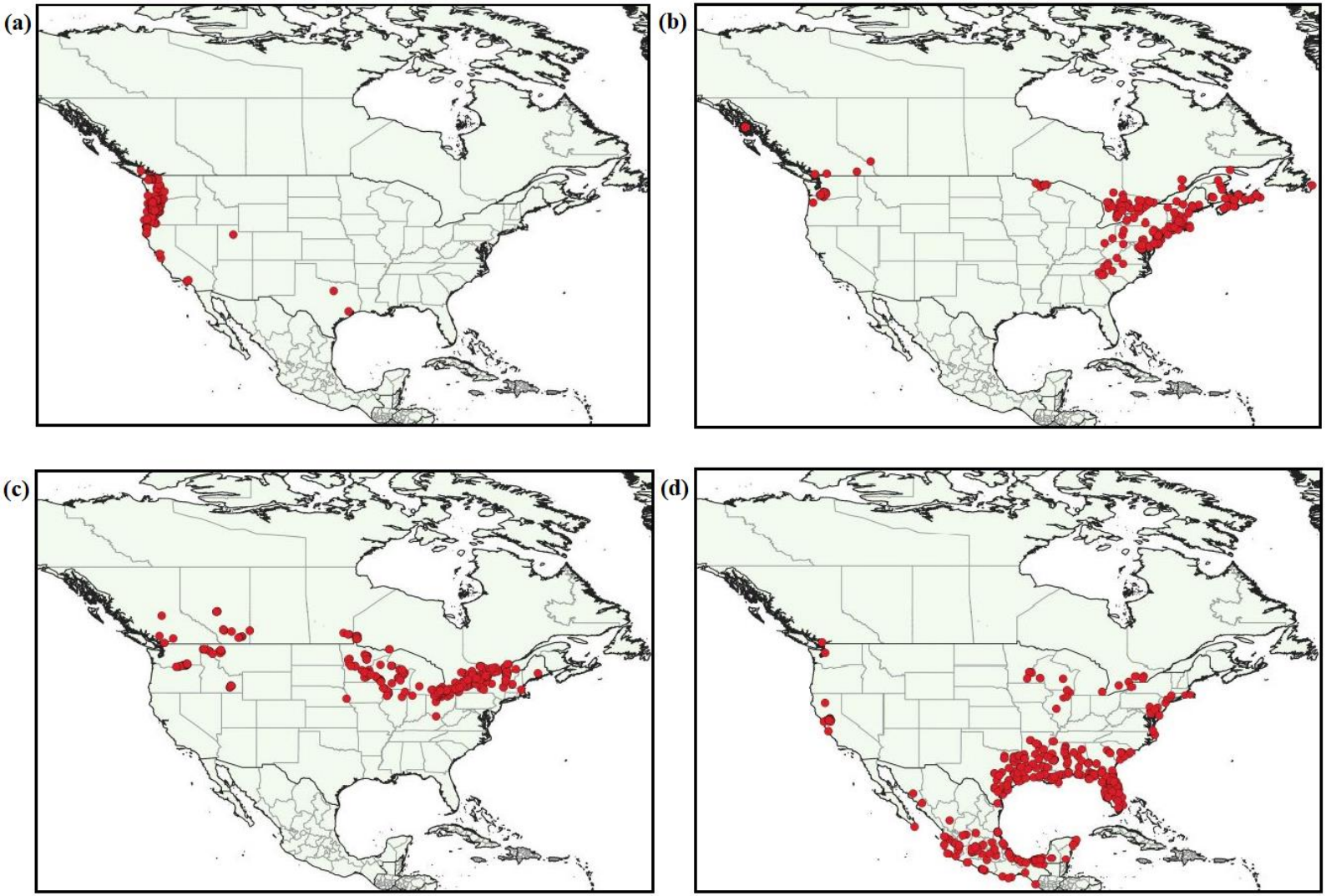

Figure 1 Species presence record locations after data cleaning. (a) *Geranium lucidum* presence records; (b) *Pilosella officinarum* presence records; (c) *Butomus umbellatus* presence records; and (d) *Pontederia crassipes* presence records.

2.4 Environmental variables

To account for variables influencing the distribution of invasive plant species, bioclimatic variables, land cover variables, and a human influence index were considered. I used 33 bioclimatic variables available from ClimateNA (AdaptWest Project 2021), averaged for the 1981 - 2010 period, at a 30 arc-second resolution (approximately 1 km²). These variables consist of biologically relevant means and indices, including seasonal and annual means, extremes, growing and chilling degree days, and drought indices (Wang et al. 2016). I used 10 land cover variables from the Global Land Cover-SHARE database, created by the Land and Water Division of the Food and Agriculture Organization of the United Nations (FAO), at a spatial resolution of 30 arc-seconds (Latham et al. 2014; see Table B1 for a list of all variables considered). The 11th land cover variable available, artificial surfaces, was omitted and, instead, the Human Influence Index provided by NASA's Socioeconomic Data and Applications Center (SEDAC) was used (WCS and CIESIN 2005). This index provides a geographic projection of the anthropogenic impacts on the environment, at 30 arc-second spatial resolution, created from layers including human population density, human land use and infrastructure, and human access (such as roads, railways, or coastlines) (WCS and CIESIN 2005). Anthropogenic variables are increasingly considered an important inclusion in the future predictions of plant invasions (Bellard et al 2016).

To identify collinearity between variables, correlations between all 44 variables (Table B1) were assessed using Pearson's correlation coefficient and those over the threshold of 0.7 were removed, as visualized by a correlation dendrogram (Figures B1-4). Additionally, I assessed multicollinearity by calculating a variance inflation factor (VIF) for each variable (R package 'usdm' version 1.1.18; Naimi et al. 2013). Variables were retained for the HSMs if they had both a Pearson's correlation coefficient under 0.7 and a VIF of less than 5 (Tables B2-5). This process resulted in 12 variables retained for *G. lucidum*, 11 for *P. officinarum*, 7 for *B. umbellatus*, and 8 for *P. crassipes*. I assessed variable contributions to each species' model through the 'variable importance' procedure in the 'biomod2' package (Thuiller et al. 2009). This procedure determines the correlation between fitted values and randomly determined values to assess the importance of a variable to a given model, using a randomization technique to allow for comparisons between models (Thuiller et al. 2009).

This procedure was repeated three times for each variable, finding the mean correlation coefficient over all cross-validation runs, resulting in a ranking of variable importance for each model.

For future climate projections, I considered three representative concentration pathways (RCPs), also corresponding to shared socioeconomic pathways (SSPs) from the 6th assessment report from the Intergovernmental Panel on Climate Change (IPCC 2021). While RCPs convey differing amounts of greenhouse gas concentrations, SSPs couple these projections with varying levels of actions addressing climate change through factors such as population, technological advancements, and/or economic growth (Riahi et al. 2017). To address these varying pathways for future climate, I considered RCP 4.5 (SSP2), RCP 7.0 (SSP4) and RCP 8.5 (SSP5) for the model projections. While CO_2 levels under RCP 4.5 correspond to the current 'middle of the road' scenario, RCP 7.0 and RCP 8.5 follow increasing levels of CO_2 in progressively 'worse' scenarios. Each associated SSP complements the RCP CO_2 level by describing a broad socioeconomic trend spanning plausible futures (Riahi et al. 2017). Three general circulation models (GCMs) were used to account for the spatial variation in climate change responses across the Western North American region (Mahony et al. 2022). Averaged projections for 2050 (2041 - 2060) and 2080 (2061 - 2090) were used from GCMs MRI-ESM2.0 (MRI), UKESMI1.0-LL (UK), and MPI-ESMI1.2-HR (MPI) (see Table A2 for GCM information).

2.5 Modelling process

To predict the potential habitat suitability of each species in the PNW, I performed habitat suitability modelling and ensemble forecasting using the 'biomod2' package (version 3.5.1; Thuiller et al. 2009) with R 4.1.1 (R Core Team 2021). For each species, I used six of the algorithms most commonly used for HSMs (Hao et al. 2019) including: three regression methods, (1) Generalized Linear Model (GLM, McCullagh and Nelder 1989), (2) Generalized Additive Model (GAM, Hastie and Tibshirani 1990), and (3) Multivariate Adaptive Regression Splines (MARS, Friedman 1991); and three machine learning methods (4) Random Forests (RF, Breiman 2001), (5) Generalized Boosted Model (GBM, Ridgeway 1999), and (6) Artificial Neural Network (ANN, Ripley 2007). To predict habitat suitability,

presence and absence data should be used; however, when no true absence data are available, pseudo-absence data must be generated. Ensemble modelling requires that the model accuracy be compared to determine which models to include, therefore the same data must be used by all algorithms to remain unbiased. Thus, I generated the same number of pseudo-absences as presence records, ran pseudo-absence generation 10 times (Barbet-Massin et al. 2012), and randomly selected the pseudo-absences from within a geographic extent based on the species in question (according to the methods described by VanDerWal et al. 2009). For each species, test models were performed at 100 km intervals (from 100 to 500 km from the presence record) to determine the appropriate maximum distance for pseudo-absence selection, based on model evaluation statistics and the number of variables contributing to the model (the number of contributing variables reducing from 3+ to 1-2 variables suggested the distance was too great). Therefore, pseudo-absences were selected from within a minimum 1 km distance from presence records and a maximum 200 km distance from *G. lucidum* presence records, 500 km from *P. officinarum* presences, 400 km from *B. umbellatus* presences, and 400 km from *P. crassipes* presences.

To calibrate and test the models, 70% of the species records were randomly selected as training data, and the other 30% were used as testing data. I used two evaluation metrics: the area under the relative operating characteristic curve (AUC, Fielding and Bell 1997) and the true skill statistic (TSS, Allouche et al. 2006), to assess the model's ability to discriminate between an area of presence or absence. I repeated the cross-validation and evaluation operations five times to obtain an average value of model performance. For each individual model and the final ensemble model, I evaluated the response of the species to environmental predictor variables with the evaluation strip method (Elith et al. 2005), to assess how each variable contributed to the model.

For a robust forecast of current and future habitat suitability, I used the ensemble forecasting method to combine the six modelling techniques (Araujo and New 2007, Thuiller et al. 2009). The use of the ensemble, or consensus, modelling method aims to decrease the predictive uncertainty of single models and has been found to increase the accuracy of species distribution predictions (Marmion et al. 2009, Hao et al. 2019, Čengić et al. 2020).

Using the true skills statistic (TSS), models achieving a TSS > 0.7 were included in the ensemble model. The mean weighted by each model's TSS value, rather than equally weighting the mean of all models, was used to produce the final current climate ensemble model, as it has been found to perform better (Marmion et al 2009). Overall, a total of 300 projections of habitat suitability (6 modelling algorithms x 10 pseudo-absence runs x 5 cross-validation runs) were created for each species. One current climate habitat suitability map and three future climate habitat suitability maps per year (2050 and 2080) and per scenario (RCP 4.5, 7.0 and 8.5) were produced per species, after future habitat suitability maps were then averaged per year and per scenario. These maps contain continuous probabilities of species occurrence, transformed into integers from 0 to 1000 by the biomod2 functions. All map visualizations were done in QGIS (version 3.22.3 Białowieża, QGIS Development Team 2022).

Chapter 3: Results

3.1 Model evaluation

Overall, most model iterations performed well with an average TSS value of 0.728 and an average AUC value 0.916, across all species (Table 2). Out of 300 projections run for each species, 300 were included in the final ensemble for *G. lucidum*, 76 for *P. officinarum*, 154 for *B. umbellatus*, and 184 for *P. crassipes*, as only models with TSS scores greater than 0.7 were included. The difference in the relatively high evaluation metrics for *G. lucidum*, compared to the relatively low evaluation metrics for *P. officinarum*, may be due to the *G. lucidum* species records being constrained to fewer regions and the relatively limited number of *P. officinarum* species records available.

Table 2 Model evaluation metrics. Two evaluation metrics were used: area under the relative operating characteristic curve (AUC) and the true skill statistic (TSS).

Species	**Mean values (all models)**		**Ensemble modelling values**	
	AUC	**TSS**	**AUC**	**TSS**
Geranium lucidum	0.96	0.85	0.98	0.87
Pilosella officinarum	0.87	0.65	0.95	0.76
Butomus umbellatus	0.91	0.70	0.98	0.85
Pontederia crassipes	0.92	0.71	0.96	0.77

Response curves generated for each predictor variable showed moderate to strong responses across species (Figure C2, C4, C6, and C8). As the training and testing data contains pseudo-absence data, rather than true absence data, some caution is needed when considering the response curve as showing the ‘probability of presence’. Rather, the response can be viewed as the likelihood of presence, or suitable habitat, compared to random environmental space. Owing to the distinctive habitat preferences of each species, the most limiting factors varied; however, climate variables generally contributed the most to explaining the variation in suitability patterns. For all four species, the most limiting variables on the likelihood of a species presence were bioclimatic factors, particularly temperature related variables (Table

3). Additionally, the response curves of all species showed an increase in the likelihood of suitable habitat with increasing human influence index value.

To determine the effect of land cover variables on all species, I used model iterations that compared model results for each species across three test model sets of variables: (1) climate, human influence index, and all landcover variables (Figure E1); (2) climate and human influence index (Figure C6); and for aquatic species (3) climate, human influence index, and all landcover variables excluding water bodies (Figure E2). The inclusion of water bodies as a landcover variable for the aquatic species resulted in its contribution far exceeding that of all other variables and seemed to reduce the species response to climate variables. In turn, the exclusion of the water bodies variable increased the contribution of other landcover variables, such as croplands, since they became very limiting for a species found in only in aquatic ecosystems. Thus, landcover variables were excluded from the aquatic species models. For the terrestrial species, the inclusion of land cover variables refined the mapped outputs without masking the contributions of climatic variables or causing the models to become overfit, and so they were retained in the final models.

Table 3 Effect of selected environmental variables based on the response curves (Figures C2, C4, C6, and C8). A variable was considered to have a slightly limiting effect when the response was between 0.5 and 0.75 (likelihood of presence) for some values of the variables and a limiting effect when the species response fell below 0.5. Responses showing an increase in the likelihood of presence with increasing variable values is noted as positive, while responses showing a decrease in the likelihood of presence with increasing variable values is noted as negative. (All values are approximate and show the upper and/or lower range value in the units of the associated variable, as determined by the species response curves.)

Variable	***Geranium lucidum***	***Pilosella officinarum***	***Butomus umbellatus***	***Pontederia crassipes***
May to September precipitation (mm)		Slightly limiting <250 and >500 mm		

Variable	***Geranium lucidum***	***Pilosella officinarum***	***Butomus umbellatus***	***Pontederia crassipes***
Annual heat-moisture index		Limiting >20		
Summer heat-moisture index	Slightly limiting (negative)			Limiting <1200 and >1400
Degree-days below 0°C (chilling degree-days)	Limiting >125	Limiting >750 degree-days	Limiting <300 and >1700 degree-days	
Degree-days above 18°C (cooling degree-days)	Slightly limiting (negative)			
Number of frost-free days				Slightly limiting (positive)
Day of the year the frost-free period begins		Slightly limiting <120 and >150		
Precipitation as snow (mm)			Limiting >200 mm	Limiting (negative)
Extreme maximum temperature over 30 years			Limiting <34	
Relative humidity (%)	Slightly limiting <60 and >75%		Limiting <53%	Slightly limiting (positive)
Summer (June, July, and August) precipitation (mm)	Limiting >150 mm		Limiting >350 mm	
Winter (December, January, February) precipitation (mm)			Limiting >250 mm	

3.2 Current potential habitat suitability

The current range of habitat suitability for the terrestrial species *G. lucidum* is predominantly in the sheltered coastal and valley regions of the PNW, west of the Cascade Mountain Range and east of the coastline (Figure 2a). Currently, the highest suitable areas are in and surrounding the Willamette Valley and Portland region of OR. Suitability is predicted to decrease with elevation. The variable importance procedure ranked degree-days below 0°C, degree-days above 18°C, and summer precipitation as the top three bioclimatic variables contributing to this model (Figure C1). Furthermore, these variables are also the most limiting (Table 3) with decreased likelihood of species presence when there is an increased number of days below 0°C, increased number of days above 18°C, and increased amounts of summer precipitation.

The current range of habitat suitability for *P. officinarum*, the second terrestrial species, is found along the Cascade Mountain Range through OR, WA, and south-west BC, as well as in the higher elevations of Olympic National Park and the majority of central to eastern Vancouver Island (Figure 2b). These areas have high potential habitat suitability currently, with low to moderate potential suitability predicted at decreasing elevations. The variable importance procedure ranked degree-days below 0°C, annual heat moisture index, and relative humidity as the top three bioclimatic variables contributing to this model (Figure C3). Additionally, unlike its lower contribution to *G. lucidum*, the human influence index contributed nearly as much as the bioclimatic variables did for *P. officinarum*, suggesting an increase in likelihood of presence in climatically suitable regions with high human activity. Moreover, the bioclimatic variables, annual heat moisture index and degree-days below 0°C, are most limiting with decreased likelihood of species presence with increased heat-moisture and increased number of days below 0°C (Table 3).

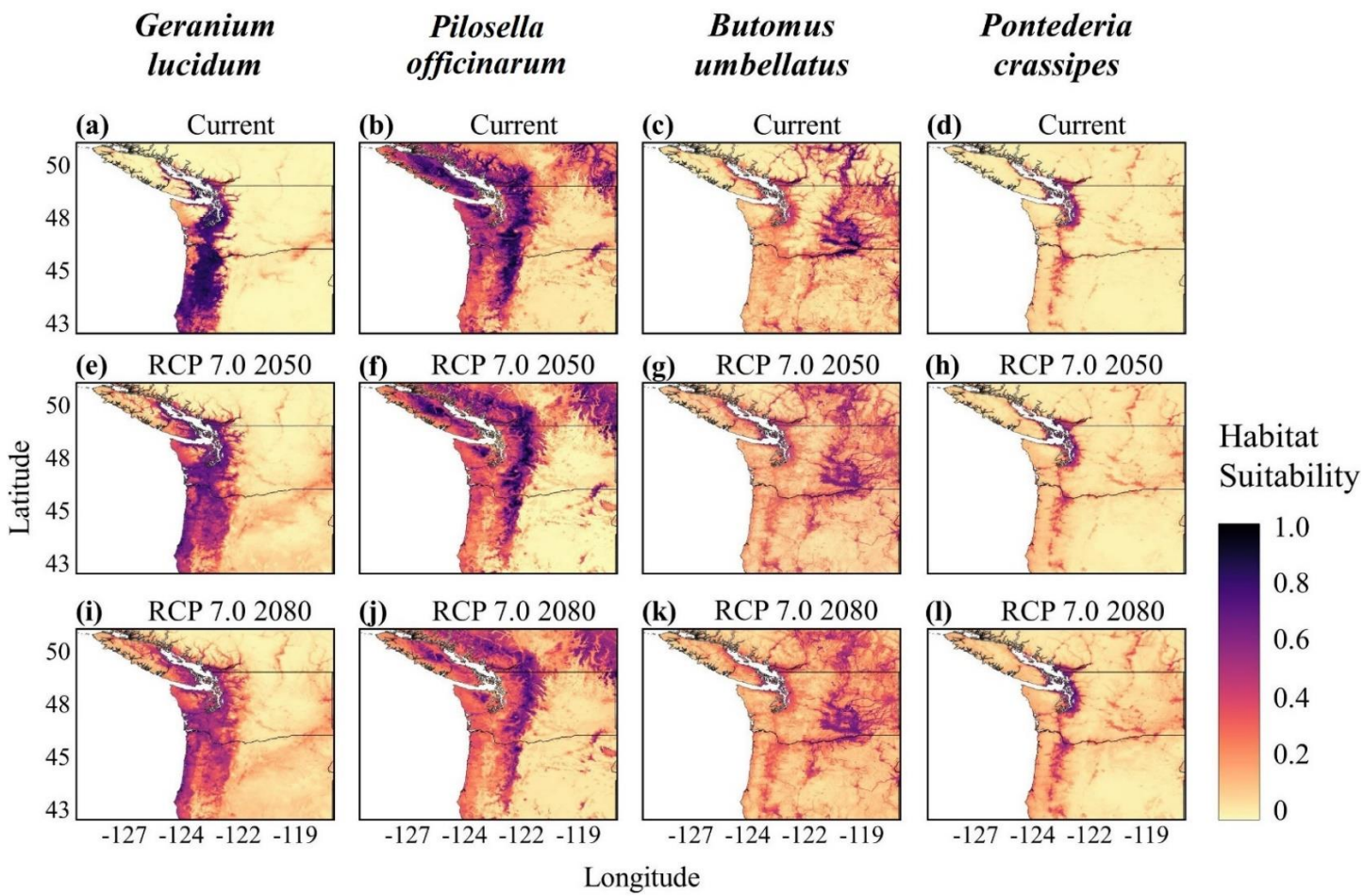

Figure 2 Current and projected future habitat suitability of the PNW for *Geranium lucidum, Pilosella officinarum, Butomus umbellatus,* and *Pontederia crassipes,* according to RCP scenario 7.0. (a - d) Current potential habitat suitability for *Geranium lucidum, Pilosella officinarum, Butomus umbellatus,* and *Pontederia crassipes,* respectively; (e - h) potential habitat suitability under climate scenario RCP 7.0 for the 2050s for *Geranium lucidum, Pilosella officinarum, Butomus umbellatus,* and *Pontederia crassipes,* respectively; (i - l) potential habitat suitability under climate scenario RCP 7.0 for the 2080s for *Geranium lucidum, Pilosella officinarum, Butomus umbellatus,* and *Pontederia crassipes,* respectively.

The current range of potential habitat suitability for the aquatic invasive species *B. umbellatus* is found further inland, compared to *G. lucidum* and *P. officinarum*, in regions experiencing increased continental climates, rather than coastal regions (Figure 2c). These regions are predominately east of the Cascade Mountain Range, although moderate suitability is predicted in sheltered coastal locations around the Seattle and Vancouver areas. The regions with highest suitability have limited summer and winter precipitation and are subject to more extreme maximum temperatures (Table 3). The variable importance procedure ranked extreme maximum temperature over 30 years, relative humidity, and summer precipitation as the top three bioclimatic variables contributing to this model (Figure C5). While increased amounts of summer precipitation is limiting, increased relative humidity and extreme maximum temperatures results in a greater likelihood of *B. umbellatus* presence. In addition, increased human influence increases the likelihood of species presence.

The current range of potential habitat suitability for *P. crassipes*, the second aquatic species, is found along sheltered inland regions west of the Cascade Mountain Range (Figure 2d). These regions reflect the most moderate temperature and precipitation areas of temperate PNW. Very low suitability is predicted in most other areas. The number of frost-free days contributed the most to the model according to the variable importance procedure; however, there is an approximately 50% likelihood that *P. crassipes* is present when the number of frost-free days is greater than 350 (Figure C8). Moreover, the likelihood of its presence drops substantially with any precipitation as snow and with increased winter precipitation. The variable importance procedure ranked these three variables as the top bioclimatic variables contributing to this model (Figure C7). While the response curve shows these variables to be limiting, the highest likelihood of presence under any variable is considerably lower than under limiting variables for *G. lucidum*, *P. officinarum*, or *B. umbellatus*.

3.3 Future potential habitat suitability

The future predictions different substantially across species. Overall, the majority of coastal PNW remains suitable for *G. lucidum* regardless of climate scenario to 2050 or 2080; however, comparatively, suitability increases much more rapidly in RCP 7.0 and 8.5 scenarios compared to RCP 4.5. With climate change, *G. lucidum* habitat suitability is

predicted to increase in higher elevations and higher latitudes, following the coastline poleward, under the ‘middle of the road’ scenario RCP 4.5. Inland southern latitudes show a decrease in suitability by both 2050 and 2080, although most areas remain moderately suitable (Figure 3a and Figure D3). Likewise, the higher CO_2 climate scenario RCP 7.0 leads to a more significant increase in suitability at higher coastal elevations by 2050, with coastal regions and Vancouver Island increasing from low to moderate or high suitability by 2080 (Figure 2e and 2i). Conversely, a greater loss in suitability by 2080 is seen at inland southern latitudes (Figure 2i). Habitat suitability under climate scenario RCP 8.5 follows a similar trend to RCP 7.0 (Figure D2). The increase in coastal suitability toward poleward regions and in higher elevations coincides with decreased suitability at the current southern limits of the range.

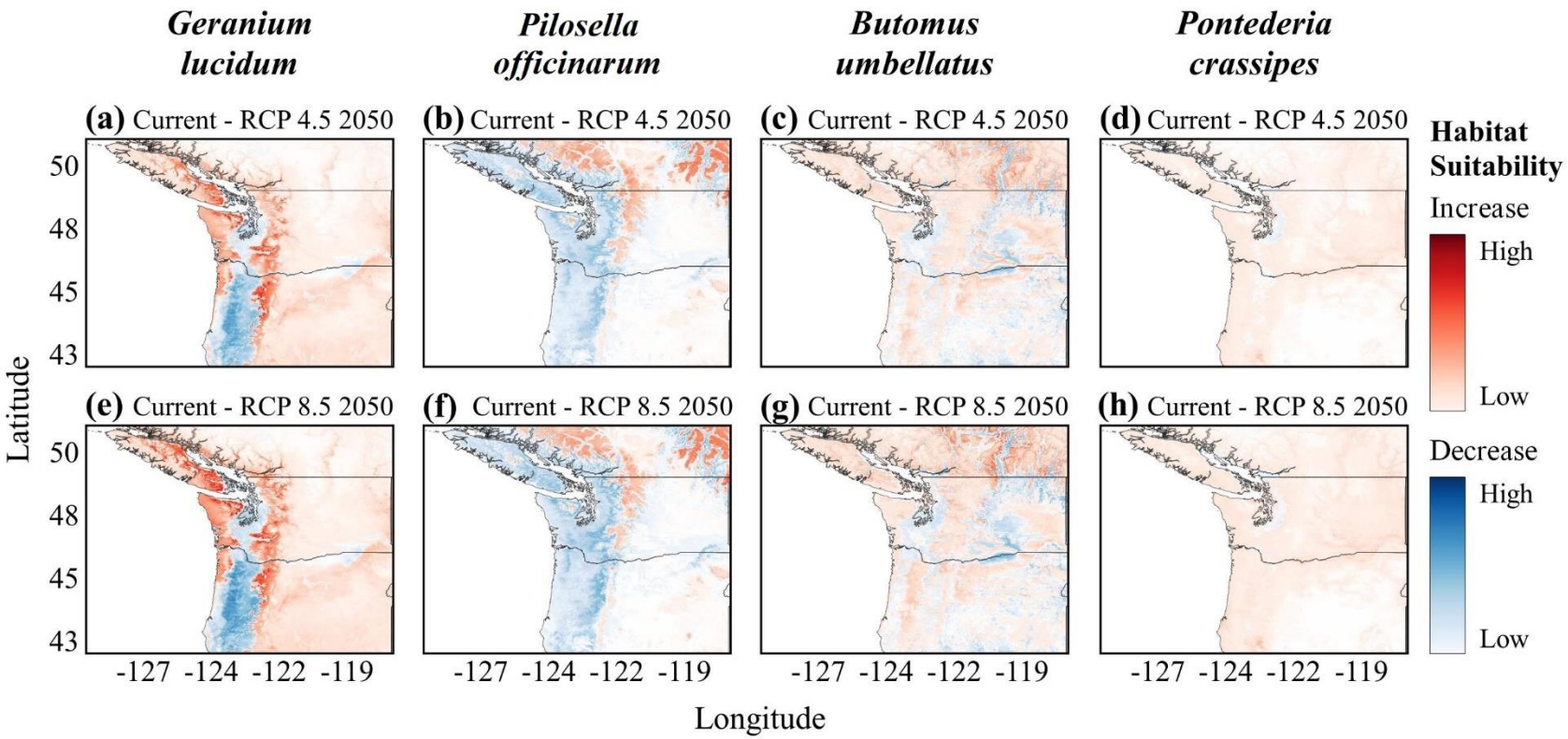

Figure 3 Potential expansion or contraction of habitat suitability under future climate scenarios by 2050. (a – d) Increases and decreases in the predicted habitat suitability of *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively, under climate scenario 4.5 by 2050; (e – h) increases and decreases in the predicted habitat suitability of *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively, under climate scenario 8.5 by 2050.

In contrast to *G. lucidum*, *P. officinarum* habitat suitability under climate scenario RCP 4.5 for 2050 shows a substantial decrease in lower elevations; however, the latitudinal range has low or moderate changes (Figure 3b). Low or moderate increases in suitability are found at higher elevations and in higher latitudes. Additionally, coastal regions lose potential high suitability, but remain low or moderately suitable. While habitat suitability for *P. officinarum* under climate scenario RCP 7.0 in 2050 predicts potential changes similar to RCP 4.5, suitability under RCP 7.0 by 2080 predicts higher decreases in suitability, particularly along coastlines, low or moderate elevations in Olympic National Park in WA, and on Vancouver Island (Figure 2f and 2j). Similarly, *P. officinarum* suitability under higher CO_2 scenario RCP 8.5 for 2050 suggests a decrease in lower elevations and coastal areas, with much higher decreases predicted by 2080 (Figure D2). By 2080, increases in moderate suitability are predicted in higher latitudes and a substantial amount of potential suitability in higher elevations of southern Oregon is lost.

For the aquatic species, *B. umbellatus* and *P. crassipes*, future climate scenarios do not predict as substantial a change in habitat suitability as changes predicted for terrestrial species, *G. lucidum* or *P. officinarum*. Some potential habitat suitability for *B. umbellatus* in the southern regions of the PNW is predicted to be lost under RCP 4.5 and 8.5 by 2050, while some increases in suitability are predicted in the interior of BC (Figure 3c and 3g). Likewise, under RCP 7.0, low and moderate suitability increases by 2050 and 2080 with some potential decreases in southern latitudes (Figure 2g and 2k). Overall, regions of *B. umbellatus* habitat suitability in WA and BC will potentially increase to moderate suitability under all future climate scenarios, with some potential habitat suitability losses occurring in OR. Similarly, future climate scenarios do not predict increases to high suitability for *P. crassipes* in the PNW. Regions of moderate or high suitability under current climate are predicted to remain moderate or highly suitability under all future scenarios (Figure 2h and 2l; Figure D1 and D2). Areas surrounding regions of moderate or high suitability under current climate (Figure 2d) are predicted to increase to low or moderate suitability under climate scenarios 4.5, 7.0, and 8.5 (Figure 2h and 2l, Figure 3d and 3h). Any gains or losses in habitat suitability predicted under scenarios RCP 4.5 or 8.5 by 2050 are minimal and do

not suggest any change to the likelihood of suitable habitat for *P. crassipes* (Figure 3d and 3h).

Chapter 4: Discussion

In this study, I predicted potential changes in habitat suitability driven by climate change for four invasive plant species which have caused economic and ecological impacts in introduced regions: *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*. My results highlight the impact of climate change on invasive plants in the PNW and the variability in response across species when considering the movement of invasive plants. Across the four focal study species, I found that the range of suitable habitat available to each species is not impacted by climate change equally, as some species ranges are predicted to expand or contract, while others may shift in elevation or latitude.

4.1 Impacts of climate change, land cover, and human influence

The impacts of climate change, land cover, and human influence factors on terrestrial species *G. lucidum* and *P. officinarum* differed greatly within the PNW. My results suggest that the impacts of climate change will only moderately reduce the suitable habitat available to *G. lucidum*. While some suitable habitat may be lost in the currently highly suitable regions of Oregon, moderate suitability will remain and may not reduce the growth of already established populations. Furthermore, many areas of low to moderate suitability under current conditions are predicted to increase, especially in higher latitudes and elevations. Conversely, my results suggest that climate change will reduce the area of suitable habitat for *P. officinarum*, relegating it to the higher elevations only. These areas already contain potentially suitable habitat that *P. officinarum* has yet to occupy and would benefit from increased monitoring and implementation of preventative measures. While the highly populated and travelled areas of the PNW may not be as vulnerable to invasion by *P. officinarum* in the long term, many parks or natural areas that attract visitors to the PNW region are located at higher elevations, potentially increasing pathways of spread. Additionally, human influence on landscapes results in a higher likelihood of *P. officinarum* presence than *G. lucidum* presence. Likewise, the presence of croplands increases the potential for *P. officinarum* presence, whereas land cover types does not have a great impact on *G. lucidum*, relative to climate. My results found the only variable to have a limiting effect on *G. lucidum* to be degree-days below 0°C. This may contribute to the limiting of *G. lucidum* in other regions, but climate change scenarios do not predict longer periods of

temperatures below 0°C in the PNW, thus leaving current populations relatively unaffected. However, unlike *G. lucidum*, *P. officinarum* requires more chilling degree-days, which is consistent with its alpine and subalpine range. More limiting is its response to annual heat moisture and, considering the climate change scenarios for the PNW, this contributes to the majority of decreased suitability as temperatures and precipitation are generally predicted to increase over a given year.

While few habitat suitability studies have been done on *G. lucidum* or *P. officinarum*, the models that have been done are consistent with my results although they are at a much larger scale. A USDA weed risk assessment based on three climatic variables estimated that 54% of the United States and 4% of Canada is suitable for the establishment of *G. lucidum*; however, they suggest this estimate is conservative and other variables may limit the suitable range (USDA 2013). My study of *G. lucidum* used 12 variables, covering bioclimatic, land cover, and human influence factors, and while suggesting a more refined area of suitability, the overall results are consistent within the PNW region. While few studies have focused on the invasive nature of *G. lucidum*, *P. officinarum* has become a serious and widespread invasive plant in New Zealand and Argentina, prompting climate modelling in adjacent regions where the species has not become so firmly established yet (Beaumont et al. 2009). Consistent with our model, climate modelling of hawkweed species in Australia predicted that the climatically suitable habitat available to *P. officinarum* will decline overall, with some sub-alpine and alpine areas remaining climatically suitable until 2070 (Beaumont et al. 2009). Large-scale modelling studies are necessary for analysis of large-scale patterns and trends, but regional models are crucial for advising local- and regional-scale management strategies. Regional studies allow local land managers and practitioners to utilize habitat suitability models in every-day conservation or land planning efforts.

While the impact of climate on the terrestrial species differs, the changes in the habitat suitability in the PNW for these species are potentially more dramatic than that of the aquatic species. Nevertheless, several recent studies have called for further studies on invasive aquatic species as freshwater ecosystems are particularly vulnerable to invasion due to a greater number of introduction pathways and being heavily impacted by a variety of human

activities (Havel et al. 2015, Rodríguez-Merino et al. 2018, Gervais et al. 2020). My results suggest that the interior of BC and Washington have a much higher potential habitat suitability for *B. umbellatus* than coastal regions. While some suitability may decrease in regions of WA with high current potential suitability, most areas with current potential suitability remain suitable and surrounding areas increase to moderate suitability in future climate scenarios. Regions of higher elevation remain mostly unsuitable; however, the likelihood of increased suitability is predicted to be stronger in higher latitudes, especially by 2080. Additionally, *B. umbellatus* may have differing climate tolerances based on its ploidy level, and further studies are needed to determine how levels of ploidy affect *B. umbellatus*, as seen in other invasive plant species (Clements and Jones 2021), and how that may result in increased or decreased habitat suitability. The populations of *B. umbellatus* in invaded western North American regions are generally triploids, which are distinct from the earlier invaded eastern North American regions where the majority of populations are diploid (Gaskin et al. 2021). Recent studies have suggested that polyploids exhibit higher invasive capacity and may have a greater tolerance to increasing temperatures and rainfall amounts (Gaskin et al. 2021, Moura et al. 2021), suggesting that projections here may be underestimates of future habitat suitability. For both *B. umbellatus* and *P. crassipes*, the importance of the human influence index on the models suggests a greater impact of human activities on aquatic species, relative to the terrestrial species. On the other hand, as a tropical species, the potential habitat suitability for *P. crassipes* under current climates is less than that of the other species, as suggested by the lower likelihood of presence in the variable response curve. Future climate scenarios suggest some low increases in suitability, but my results suggest that, regardless of scenario, climate change is not likely to increase the habitat suitability of *P. crassipes* substantially. The most moderate climate areas within the PNW are predicted to have some potential suitability; however, this does not necessarily suggest an adequate climate for established populations. For example, *P. crassipes* was discovered at a location in the Metro Vancouver region in 2020 where it persisted over winter, but it did not survive over the winter of 2021 (Brown pers. comm. 2022). In years of few frost days and very limited snow, my model predicts that the sheltered inland regions surrounding Seattle and Portland have the highest potential for suitable habitat although this result also suggests a correlation to human influences.

In response to the increased awareness of aquatic ecosystem vulnerability, recent studies have focused on aquatic invasive plants and their response to changing climate. In a recent study on *B. umbellatus* in North America, it was predicted that an overall decline in distribution may occur under future climate; however, there are currently several regions of potential suitability for *B. umbellatus* where no occurrences have been recorded (Banerjee et al. 2020). Banerjee et al. (2020) suggest that *B. umbellatus* may have undergone a shift in its realized climatic niche and has adapted to environmental conditions in its invasive range. My predictions for potential suitability changes under future climate scenarios in the PNW are consistent with the suitability findings of this study, suggesting that the majority of the PNW will remain suitable with some low to moderate suitability changes. Likewise, a global study on *P. crassipes* using CLIMEX modelling predicts poleward range expansion in the Northern hemisphere; although, populations in the PNW may not persist, potentially dying off each winter (Kriticos and Brunel 2016). As with the terrestrial species, many studies of aquatic species do so at a global scale (e.g., Kriticos and Brunel 2016, Gillard et al. 2017), yet regional-scale modelling provides predictions on a scale that may be more effective for local land managers to target areas for increased management in the PNW.

4.2 Sources of uncertainty

To make predictions about the future habitat suitability of invasive plant species, the methods applied in this study aimed to minimize the uncertainties associated with habitat suitability models (HSMs). The use of multiple algorithms, multiple GCMs, and multiple RCP scenarios, can account for some of the variability in modelled outputs, mitigating some of the associated uncertainty (Thuiller et al. 2019). Algorithm selection can be a large source of uncertainty, as each algorithm contains its own assumptions and limitations (Pearson et al. 2006). While all algorithms I employed make use of presence and pseudo-absence (or background) data, compared to methods that use presence-only data, the combination of regression and machine-learning techniques I employed all have the individual potential to produce equally valid representations of a given system (Araujo and New 2007). Although some finely adjusted single-algorithm models have been shown to perform better than ensemble models (Hao et al. 2020), several studies have found ensemble models perform as

well or better than individual models (Marmion et al. 2009, Hao et al. 2019). Further studies are needed to validate the predictive accuracy of HSMs and, as such, there is no single 'best' method to produce consistently predictive results across any given taxa or application of use (Qiao et al. 2015).

HSMs are a useful tool to provide general predictions of potential expansions or contractions in the habitat suitability of invasive species, and at the same time these methods contain assumptions and limitations that can cause models to over-estimate suitability. One assumption is that the species in question is at equilibrium in its environment; however, this is often not the case when considering invasive species (Gallien et al. 2012, Barbet-Massin et al. 2018). Invasive species in their introduced range may not currently be found in the entire current potentially suitable habitat and may never fully realize the current or future projected range of suitable habitat due to potential barriers to dispersal, resulting in predictions under- or over-estimating potential suitable habitat. Likewise, the current climate associated with species records locations used in HSMs may not reflect the current climate in new regions and/or with future climates in the same or new regions, leading to model predictions that also under- or over-estimate potential suitable habitat. In future studies, a Multivariate Environmental Similarity Surfaces (MESS) analysis could be used to assess the extent of extrapolation between current and future climates and the environmental similarity between regions, and suggest more caution where extrapoloation is large. Second, due to data constraints, our models consider abiotic factors only, even as biotic factors, including species interactions and dispersal ability, may increase or decrease the amount of suitable habitat available to a given species. Third, climate change may cause stochastic events, such as flooding or heat waves, which are difficult to accounted for within HSMs. Finally, while modelling terrestrial invasive species comes with challenges, the potential suitability predicted for aquatic invasive species may benefit from the inclusion of water-specific variables such as flow rate, pH, or oxygen levels, although climatic and anthropogenic variables have been most often used and found to contribute substantially to the suitability of freshwater aquatic plants (Rodríguez-Merino et al. 2018, Gillard et al. 2020). While these limitations or data constraints may result in models that tend towards over-prediction, this can often be more valuable when considering the distribution of invasive species (Jiménez-

Valverde et al. 2011). Therefore, while the predicted impacts of climate change on a given species through these modelling techniques can only be considered an initial approximation (Beaumont et al. 2009), HSMs can still effectively project the geographic areas most likely to be invaded next, which is often the most vital information for land managers (Jiménez-Valverde et al. 2011, Barbet-Massin et al. 2018, Cordier et al. 2020).

4.3 Implications for management strategies

Our results provide information necessary to focus management strategies targeting known invasive species that have not yet become established. While risk assessments are critical to determine preventative measures, not all invasive species will be affected by climate change equally. Under all climate change scenarios, our models predict either the maintenance of moderate suitability or the potential increase in suitability for *G. lucidum* in most areas of the PNW. Current strategies to eradicate current populations, or prevent future establishment, should be continued as the species is not predicted to be deterred by climate change. Conversely, the current suitable habitat of *P. officinarum* is predicted to contract into higher elevations and some higher latitudes. While strategies should be put in place to prevent the spread of *P. officinarum* to higher elevations, management strategies focused on the most sensitive ecosystems may be adequate.

While terrestrial ecosystems have often been the focus, freshwater ecosystems are predicted to experience even greater pressure from invasive species under climate change (Havel et al. 2015). Species from tropical and subtropical native ranges, such as *P. crassipes*, show a greater potential for increased suitability in temperate regions under climate change. While our models show moderate suitability increases for *P. crassipes* in the PNW, further studies are necessary to determine whether *P. crassipes* is consistently able to overwinter. While the regions of moderate to high suitability may not be consistently suitable for the persistence of *P. crassipes* over winter, our model can suggest the regions in which increased monitoring may be necessary to prevent the future establishment of this species. Overall, *P. crassipes* has had detrimental impacts throughout its introduced range (Villamagna and Murphy 2010) and our results suggest the PNW has the potential for greater suitability under climate change scenarios. Alternatively, *B. umbellatus* is not predicted to increase in suitability along coastal

regions, but habitat suitability may increase with climate change in regions that experience continental climates, such as east of the Cascade Mountain Range in Washington as well as the interior of BC. Nevertheless, due to the variable nature of water body size and depth, localized coastal regions that experience more extreme conditions and are highly influenced by human activity may satisfy suitability requirements compared to surrounding areas. Furthermore, regions of current habitat suitability are predicted to remain suitable, suggesting current eradication plans should continue in order to prevent further spread of *B. umbellatus* in the PNW.

Chapter 5: Conclusion

Climate change has become an urgent issue in the PNW as, increasingly, summers are drier, winters are wetter, and extreme weather events resulting in flooding or wildfires become more prevalent. These events, along with changing land use and increasing human influences on the landscape, may facilitate the spread of previously unknown invasive species to the region. While habitat suitability models have been used extensively to assess global trends regarding species movement, my results at the regional scale show that invasive plant species are not impacted by climate change equally. The terrestrial species *G. lucidum* has the potential to expand poleward, gaining suitable habitat, while *P. officinarum* will potentially lose habitat suitability and remain mostly in higher elevations in the future. Additionally, the aquatic species *B. umbellatus* will potentially gain moderately suitable habitat in the future, but only in inland regions. Conversely, *P. crassipes* is currently suitable in more coastal, mild climates and is not predicted to gain any substantial suitable habitat beyond those regions in the future. These terrestrial and aquatic species provide an initial sampling of differences seen between species as they respond to future climate scenarios, suggesting that not all invasive species will become worse with climate change. Therefore, my research provides a working template for the necessary modelling of additional species of concern in the PNW. While modelling species on a global scale provides useful information for over-arching trends and patterns, species need to be assessed individually at a localized scale to determine how climate change may impact their spread. My research provides regional-scale models necessary for local land managers to develop targeted, preventative management strategies as they couple climate change models with their local invasive species risk assessments. This study provides valuable insight into the impact of climate change and human influences on relatively new invasive plant species in the PNW and contributes to accessible predictive modelling for land managers and practitioners focusing on preventing the establishment of potentially detrimental invasive plant species.

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Appendices

Appendix A Species record and general circulation model data sources. Detailed methods for species record collection, cleaning protocol, and R code for correlation analysis and Biomod2 modelling is available in an open access repository, found at https://github.com/enikkel/PNW-Habitat-Suitability-Modelling.

Table A1 Species record data sources and citations.

Species	**Data source and citatation**
Geranium lucidum L.	GBIF. 2022. GBIF Occurrence. https://doi.org/10.15468/dl.g7xuqd Retrieved 08/19/2021.
	EDDMapS. 2022. *Geranium lucidum* L. [Dataset]. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. https://bugwoodcloud.org/eddmaps/shp/32876.zip Retrieved 06/29/2021.
	IAPP. 2022. Invasive Alien Plant Program. http://maps.gov.bc.ca/ess/hm/iapp/ Retrieved 04/07/2022.
Pilosella officinarum Vaill.	GBIF. 2022. GBIF Occurrence https://doi.org/10.15468/dl.86h3gy Retrieved 08/19/2021.
	EDDMapS. 2022. *Hieracium pilosella* L. [Dataset]. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. https://bugwoodcloud.org/eddmaps/shp/32962.zip. Retrieved 07/15/2021.
	IAPP. 2022. Invasive Alien Plant Program. http://maps.gov.bc.ca/ess/hm/iapp/ Retrieved 04/07/2022.

Species	Data source and citatation
Butomus umbellatus L.	GBIF. 2022. GBIF Occurrence https://doi.org/10.15468/dl.b7dtg3 Retrieved 08/19/2021.
	EDDMapS. 2022. *Butmous umbellatus* L. [Dataset]. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. https://bugwoodcloud.org/eddmaps/shp/32963.zip. Retrieved 07/15/2021.
	IAPP. 2022. Invasive Alien Plant Program. http://maps.gov.bc.ca/ess/hm/iapp/ Retrieved 04/07/2022.
Pontederia crassipes Mart.	GBIF. 2022. GBIF Occurrence https://doi.org/10.15468/dl.m2fjgj Retrieved 08/19/2021.
	EDDMapS. 2022. *Eichhornia crassipes* Mart. [Dataset]. Early Detection & Distribution Mapping System. The University of Georgia - Center for Invasive Species and Ecosystem Health. https://bugwoodcloud.org/eddmaps/shp/32880.zip. Retrieved 06/29/2021.
	IAPP. 2022. Invasive Alien Plant Program. http://maps.gov.bc.ca/ess/hm/iapp/ Retrieved 04/07/2022.

Table A2 General circulation models and associated references.

Model	Institution	Citation
MRI-ESM2.0	Meteorological Research Institute (Japan)	Yukimoto, S., H. Kawai, T. Koshiro, N. Oshima, K. Yoshida, S. Urakawa, et al. 2019. The meteorological research institute Earth system model version 2.0, MRI-ESM2.0: description and basic evaluation of the physical component. Journal of the Meteorological Society of Japan 97:931–965. https://doi.org/10.2151/jmsj.2019-051

Model	Institution	Citation
UKESMI1.0-LL	Met Office Hadley Centre and Natural Environment Research Council (UK)	Sellar, A. A., C. G. Jones, J. P. Mulcahy, Y. Tang, A. Yool, A. Wiltshire, et al. 2019. UKESM1: description andevaluation of the U.K. earth system model. Journal of Advances in Modeling Earth Systems 11:4513–4558. https://doi.org/10.1029/2019MS001739
MPI-ESM1.2-HR	Max Planck Institute for Meteorology (Germany)	Müller, W. A., J. H., Jungclaus, T. Mauritsen, J. Baehr, M. Bittner, R. Budich, et al. 2018. A higher-resolution version of the MaxPlanck Institute earth system model (MPI-ESM1.2-HR). Journal of Advances in Modeling Earth Systems 10:1383–1413. doi: 10.1029/2017MS001217

Appendix B Environmental variable selection and correlation analyses

Table B1 Environmental variables and acronyms. See Methods (Chapter 2) for descriptions of sources of variables.

Variable	**Acronym**
Mean annual temperature (°C)	MAT
Mean warmest month temperature (°C)	MWMT
Mean coldest month temperature (°C)	MCMT
Temperature difference between MWMT and MCMT, or continentality (°C)	TD
Mean annual precipitation (mm)	MAP
May to September precipitation (mm)	MSP
Annual heat-moisture index (MAT+10)/(MAP/1000))	AHM
Summer heat-moisture index ((MWMT)/(MSP/1000))	SHM
Degree-days below 0°C (chilling degree-days)	DD_0
Degree-days above 5°C (growing degree-days)	DD5
Degree-days below 18°C (heating degree-days)	DD_18
Degree-days above 18°C (cooling degree-days)	DD18
The number of frost-free days	NFFD
Frost-free period (FFP)	FFP
Day of the year on which FFP begins	bFFP
Day of the year on which FFP ends	eFFP
Precipitation as snow (mm) between August in previous year and July in current year	PAS
Extreme minimum temperature over 30 years	EMT
Extreme maximum temperature over 30 years	EXT
Hargreaves reference evaporation (mm)	Eref
Hargreaves climatic moisture deficit (mm)	CMD
Mean annual relative humidity (%)	RH
Hogg's climate moisture index (mm)	CMI
Degree-days above 10°C and below 40°C	DD1040
Winter mean temperature (°C) (Dec – Feb)	Tave_wt
Spring mean temperature (°C) (Mar – May)	Tave_sp

Variable	**Acronym**
Summer mean temperature (°C) (Jun – Aug)	Tave_sm
Autumn mean temperature (°C) (Sept – Nov)	Tave_at
Winter precipitation (mm) (Dec – Feb)	PPT_wt
Spring precipitation (mm) (Mar – May)	PPT_sp
Summer precipitation (mm) (Jun – Aug)	PPT_sm
Autumn precipitation (mm) (Sept – Nov)	PPT_at
Cropland (% cover/km^2)	cropland
Grassland (% cover/km^2)	grassland
Tree-covered areas (% cover/km^2)	forest
Shrub-covered areas (% cover/km^2)	shrub
Herbaceous vegetation (% cover/km^2)	herb_veg
Mangroves (% cover/km^2)	mangroves
Sparse vegetation (% cover/km^2)	sparse
Bare soil (% cover/km^2)	bare
Snow and glaciers (% cover/km^2)	snow_glaciers
Water bodies (% cover/km^2)	water_bodies
Human influence index	HII

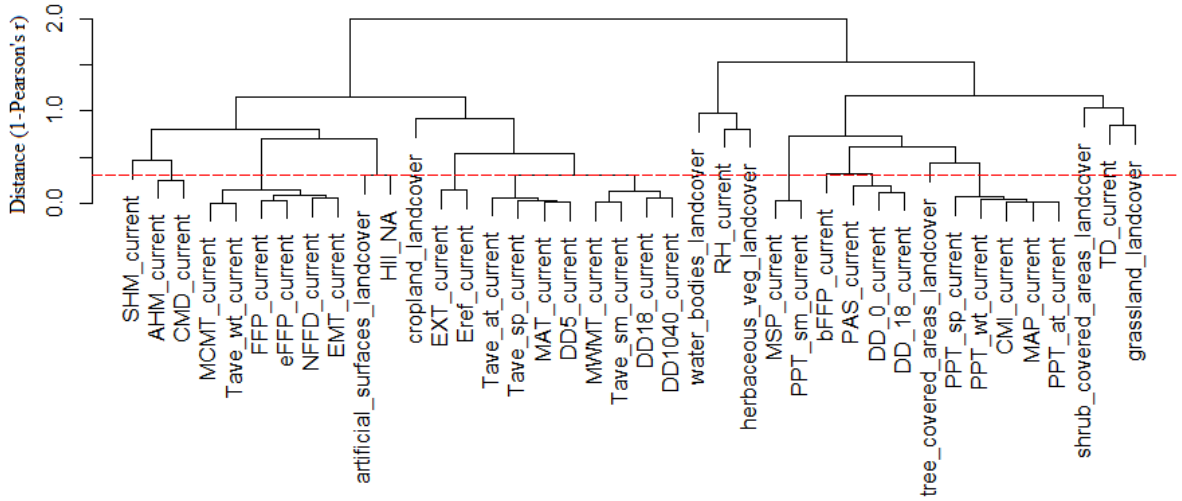

Figure B1 Dendrogram of the environmental variables assessed for *Geranium lucidum*. The threshold used to identify intercorrelated variables was a Pearson's correlation coefficient of 0.7, i.e a distance of <0.3.

Table B2 *Geranium lucidum* variable VIF scores below the threshold of 5.

Environmental variable	**VIF score**
Human influence index	3.45
Summer precipitation	3.14
Degree-days above 18°C	2.39
Winter precipitation	2.34
Degree-days below 0°C	1.91
Summer heat moisture index	1.63
Cropland	1.62
Relative humidity	1.54
Herbaceous vegetation	1.35
Shrub-covered areas	1.33
Grassland	1.17
Water bodies	1.13

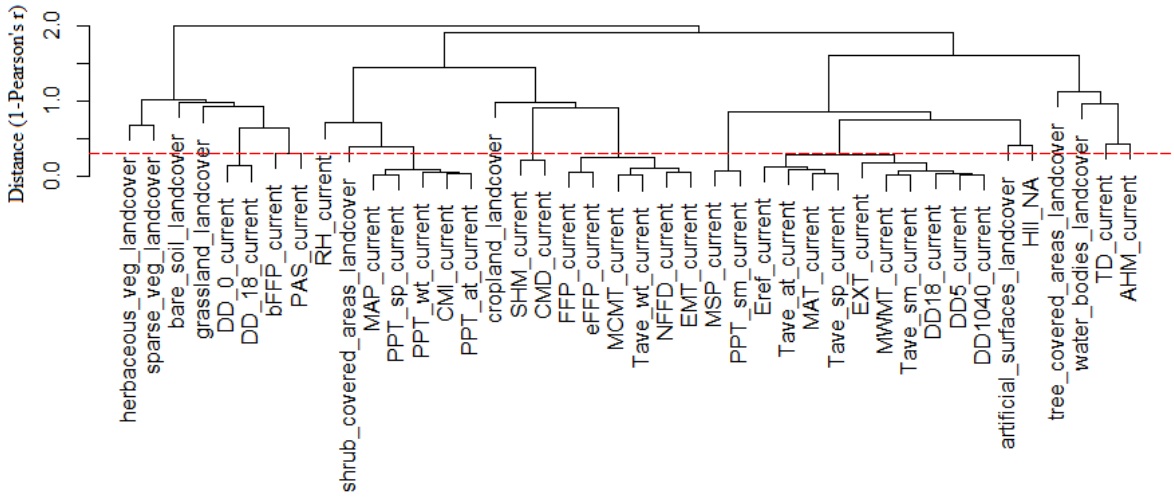

Figure B2 Dendrogram of the environmental variables assessed for *Pilosella officinarum*. The threshold used to identify intercorrelated variables was a Pearson's correlation coefficient of 0.7, i.e a distance of <0.3.

Table B3 *Pilosella officinarum* variable VIF scores below the threshold of 5.

Environmental variable	**VIF score**
Day of the year on which the frost-free period begins	3.49
Annual heat moisture index	2.89
Degree-days below 0°C	2.65
Human influence index	2.07
Relative humidity	1.74
Shrub-covered areas	1.56
May to September precipitation	1.41
Herbaceous vegetation	1.21
Cropland	1.12
Grassland	1.10
Water bodies	1.09

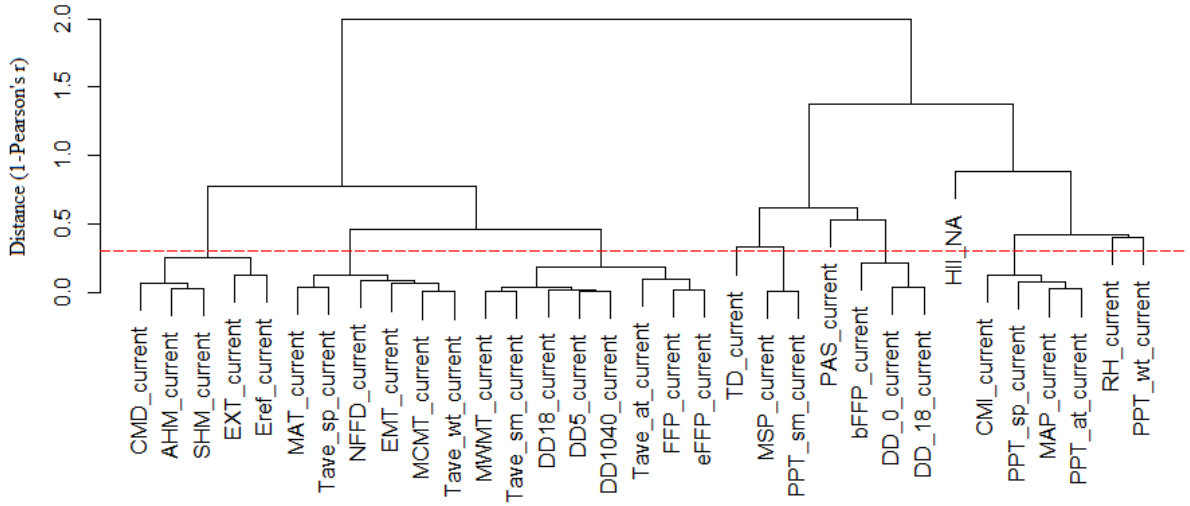

Figure B3 Dendrogram of the environmental variables assessed for *Butomus umbellatus*. The threshold used to identify intercorrelated variables was a Pearson's correlation coefficient of 0.7, i.e a distance of <0.3.

Table B4 *Butomus umbellatus* variable VIF scores below the threshold of 5.

Environmental variable	**VIF score**
Degree-days below 0°C	4.86
Winter precipitation	4.15
Precipitation as snow	3.37
Relative humidity	2.53
Extreme maximum temperature over 30 years	2.43
Summer precipitation	2.39
Human influence index	1.16

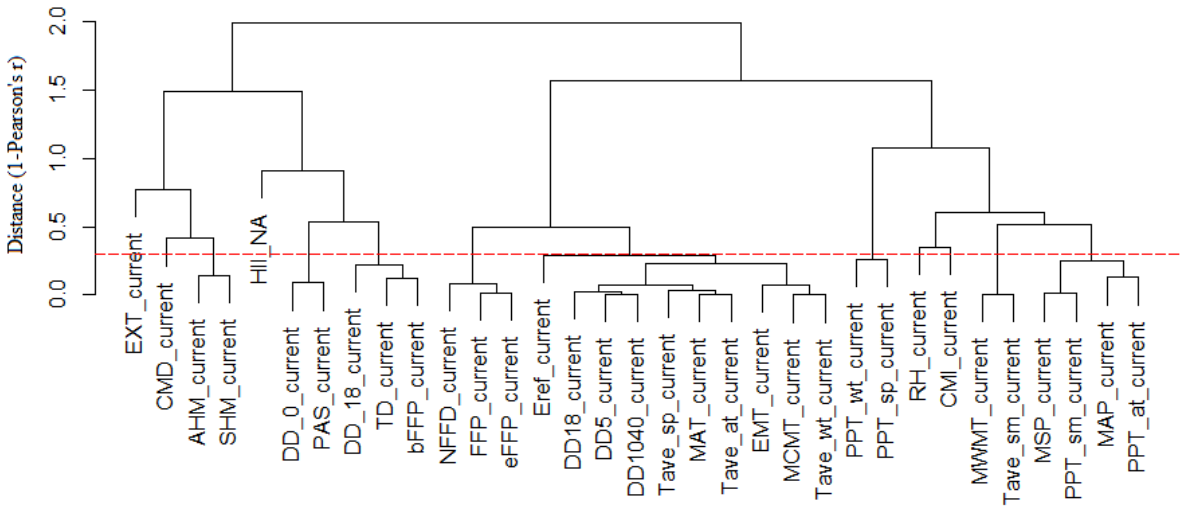

Figure B4 Dendrogram of the environmental variables assessed for *Pontederia crassipes*. The threshold used to identify intercorrelated variables was a Pearson's correlation coefficient of 0.7, i.e a distance of <0.3.

Table B5 *Pontederia crassipes* variable VIF scores below the threshold of 5.

Environmental variable	**VIF score**
Number of frost-free days	3.41
Precipitation as snow	3.18
Autumn precipitation	2.56
Relative humidity	1.99
Summer heat moisture index	1.71
Extreme maximum temperature over 30 years	1.63
Winter precipitation	1.45
Human influence index	1.07

Appendix C Variable importance and response curves. The weighted mean (shown in purple), rather than the mean (shown in blue), of all included models was used to produce the final current climate ensemble model, according to Marmion et al. (2009).

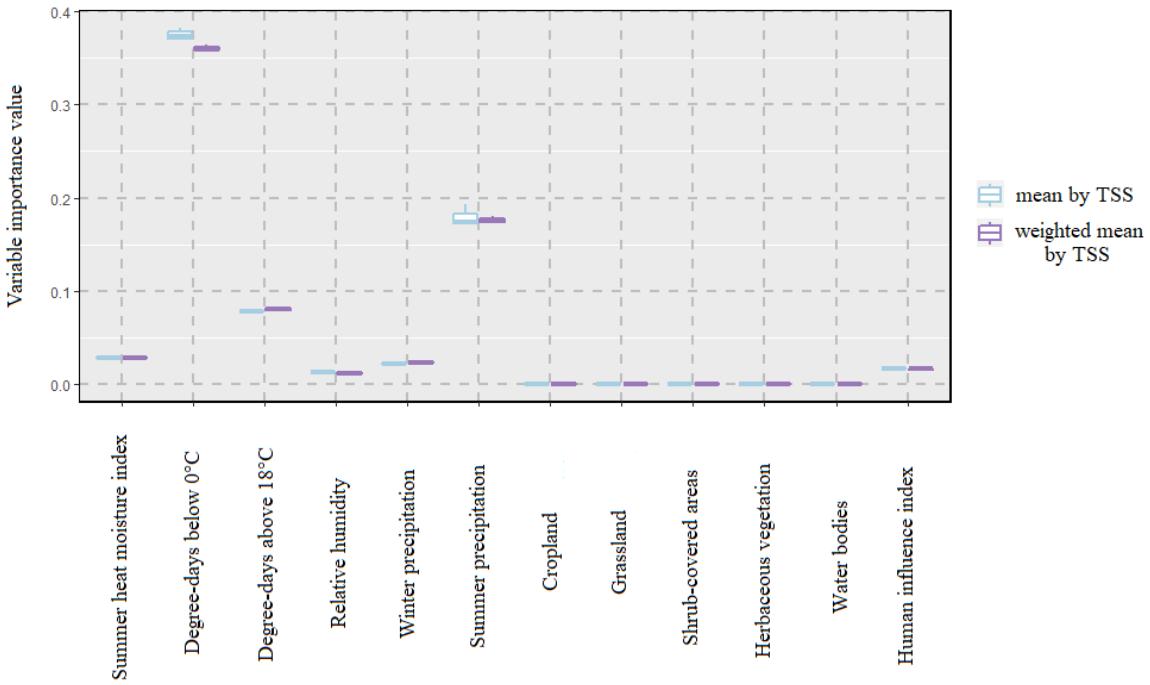

Figure C1 Variable importance of variables selected for the *Geranium lucidum* model, according to the variable importance procedure in Biomod2 (Thuiller et al. 2009).

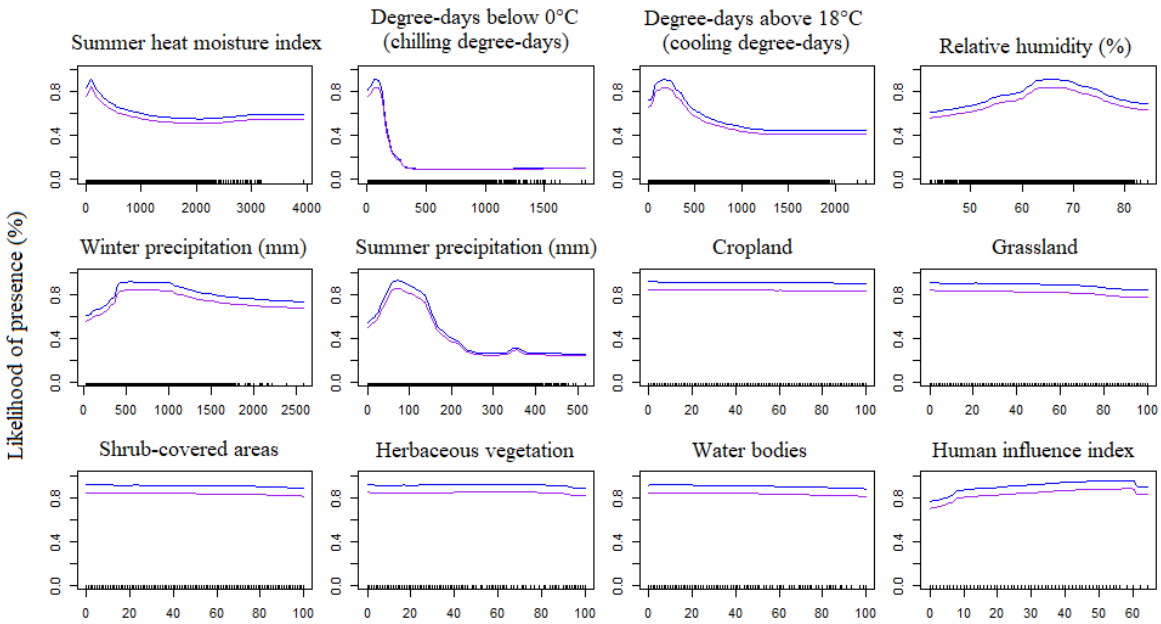

Figure C2 Response curve of *Geranium lucidum* to the selected environmental predictor variables. Blue lines indicate mean values, while purple lines indicted the weighted mean values.

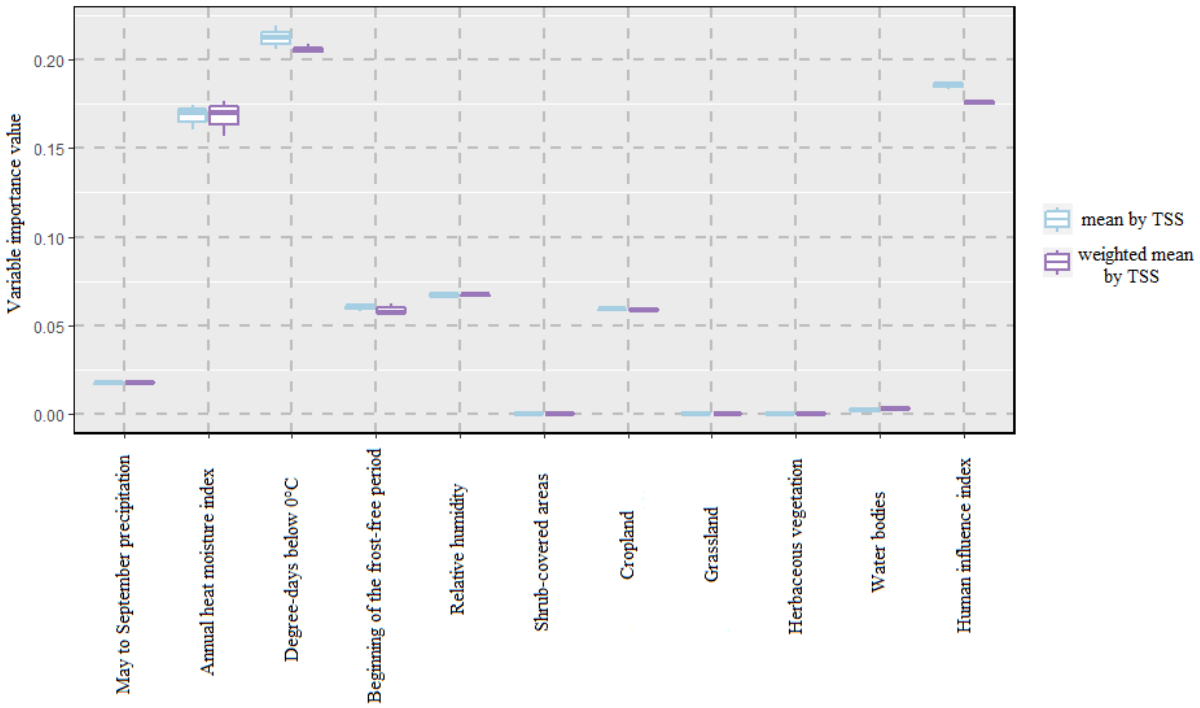

Figure C3 Variable importance of variables selected for the *Pilosella officinarum* model, according to the variable importance procedure in Biomod2 (Thuiller et al. 2009).

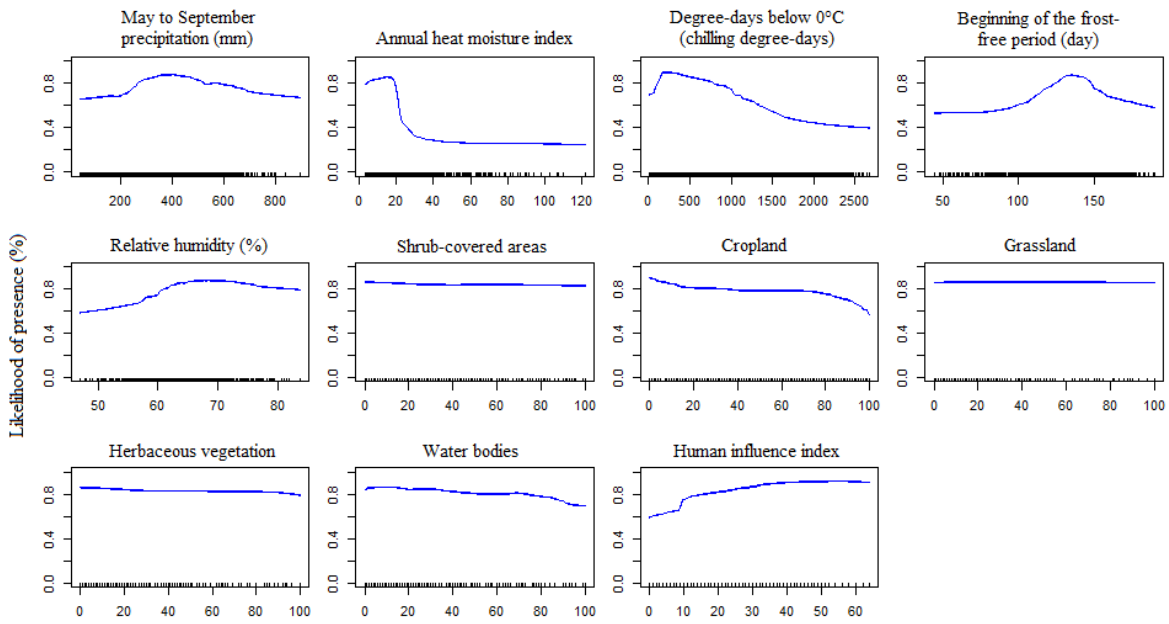

Figure C4 Response curve of *Pilosella officinarum* to the selected environmental predictor variables. Both the weighted mean and mean resulted in the same values and, thus, are shown as one line.

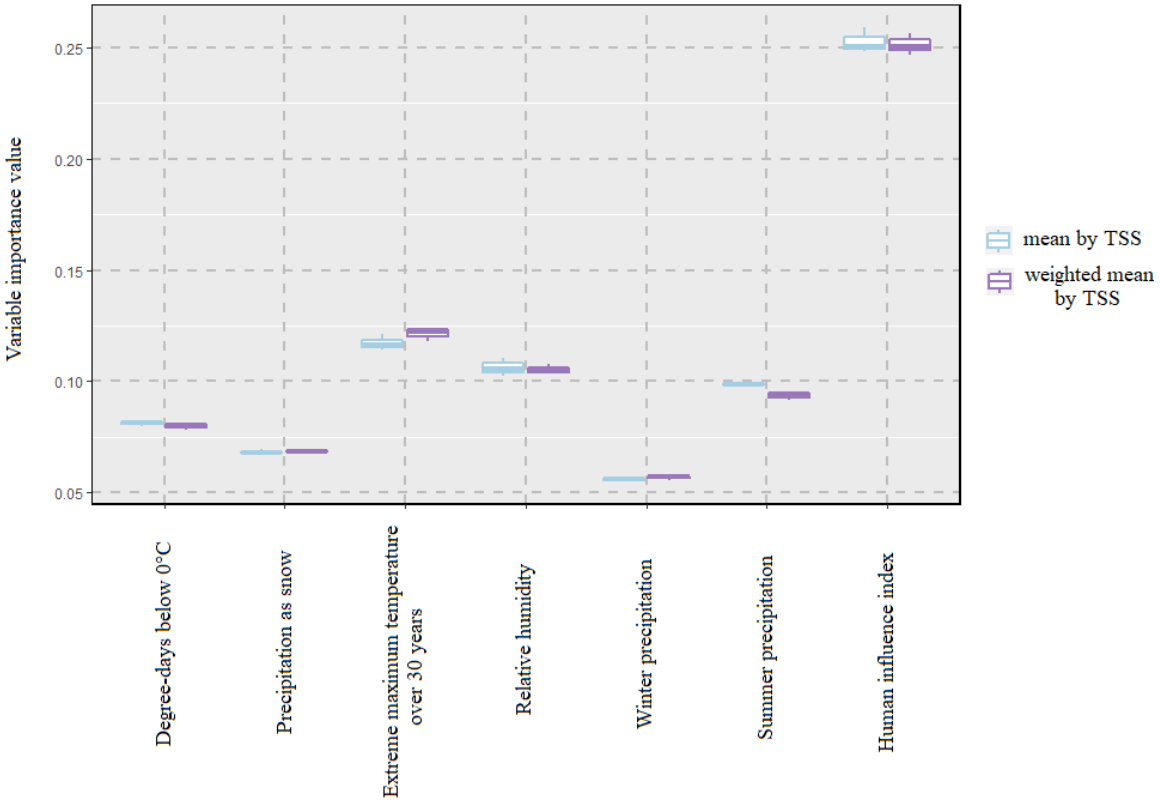

Figure C5 Variable importance of variables selected for the *Butomus umbellatus* model, according to the variable importance procedure in Biomod2 (Thuiller et al. 2009).

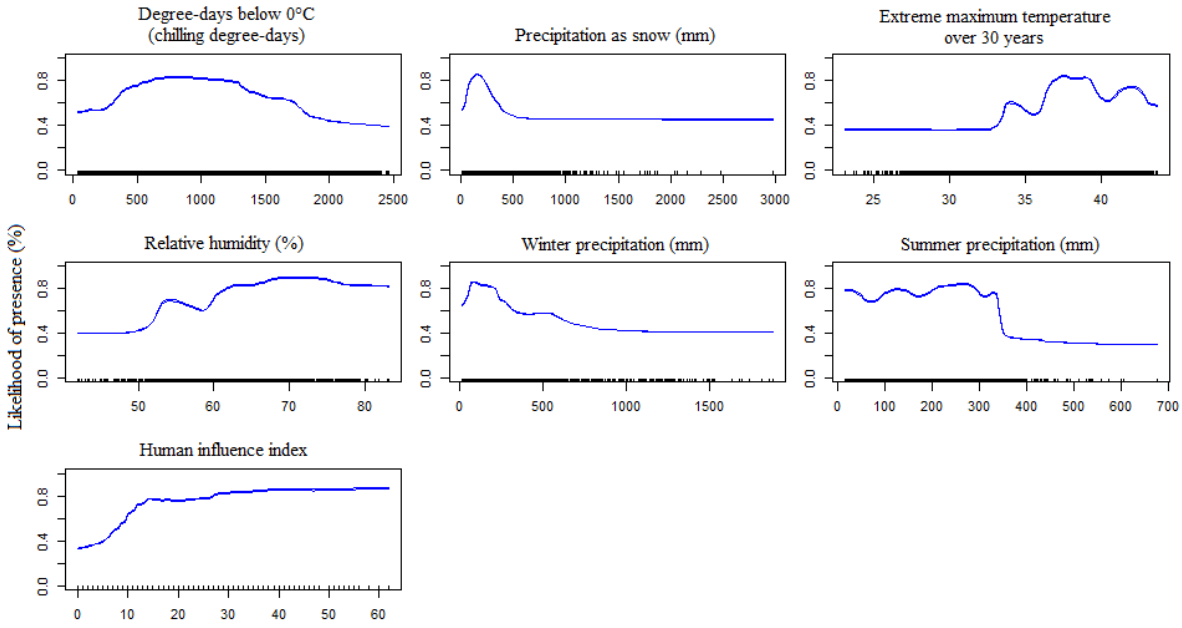

Figure C6 Response curve of *Butomus umbellatus* to the selected environmental predictor variables.

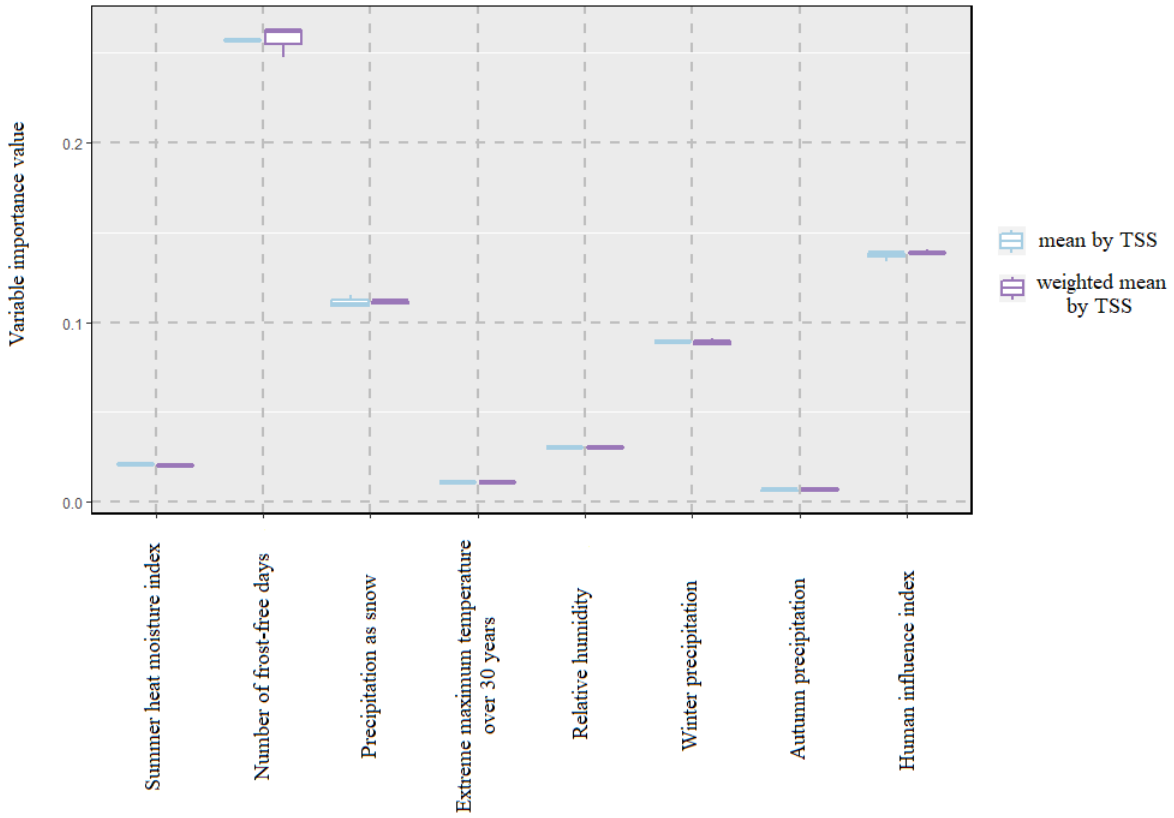

Figure C7 Variable importance of variables selected for the *Pontederia crassipes* model, according to the variable importance procedure in Biomod2 (Thuiller et al. 2009).

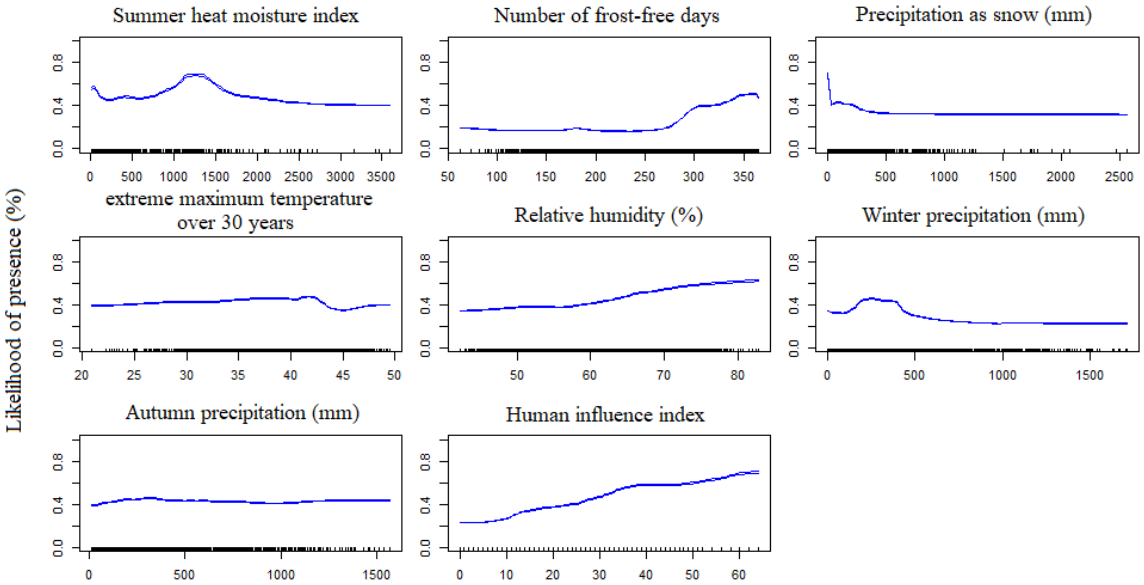

Figure C8 Response curve of *Pontederia crassipes* to the selected environmental predictor variables.

Appendix D Mapped outputs

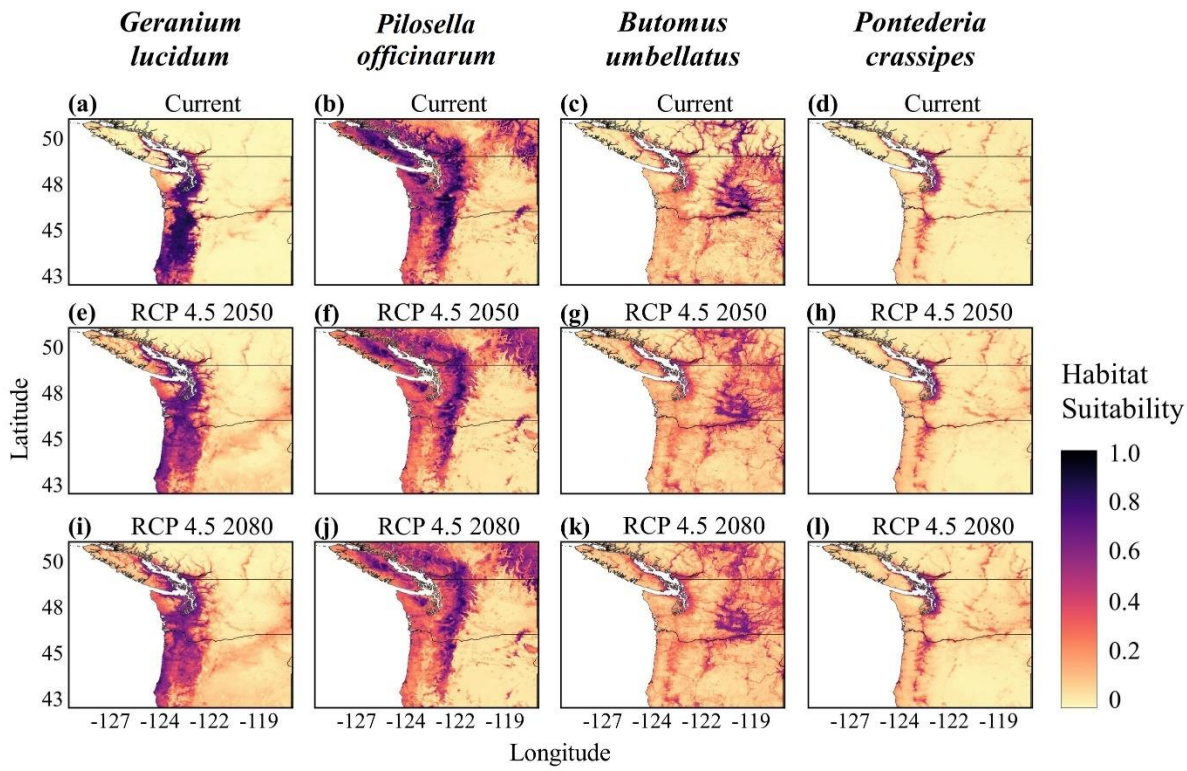

Figure D1 Current and projected future habitat suitability of the PNW for *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, according to RCP scenario 4.5. (a - d) Current potential habitat suitability for *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively; (e - h) potential habitat suitability under climate scenario RCP 4.5 for the 2050s for *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively; (i - l) potential habitat suitability under climate scenario RCP 4.5 for the 2080s for *Geranium lucidum*, *Pilosella officinarum*, *Butomus crassipes*, and *Pontederia crassipes*, respectively.

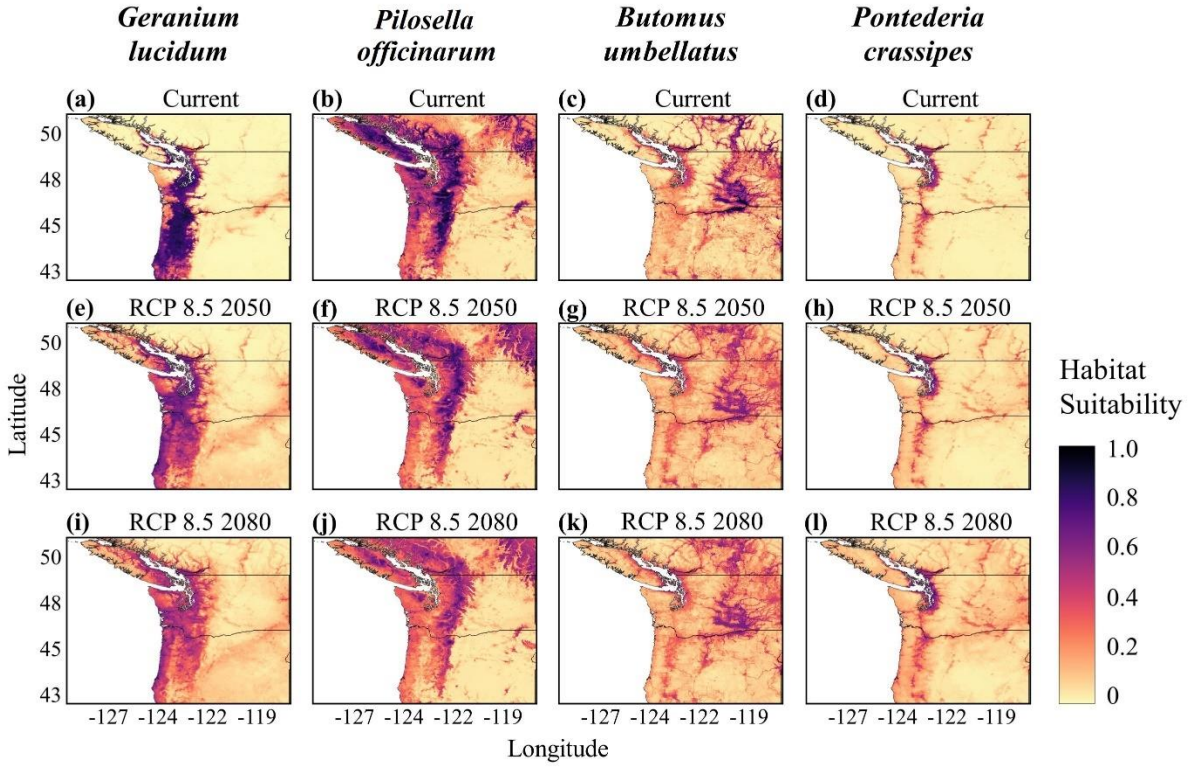

Figure D2 Current and projected future habitat suitability of the PNW for *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, according to RCP scenario 8.5. (a - d) Current potential habitat suitability for *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively; (e - h) potential habitat suitability under climate scenario RCP 8.5 for the 2050s for *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively; (i - l) potential habitat suitability under climate scenario RCP 8.5 for the 2080s for *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively.

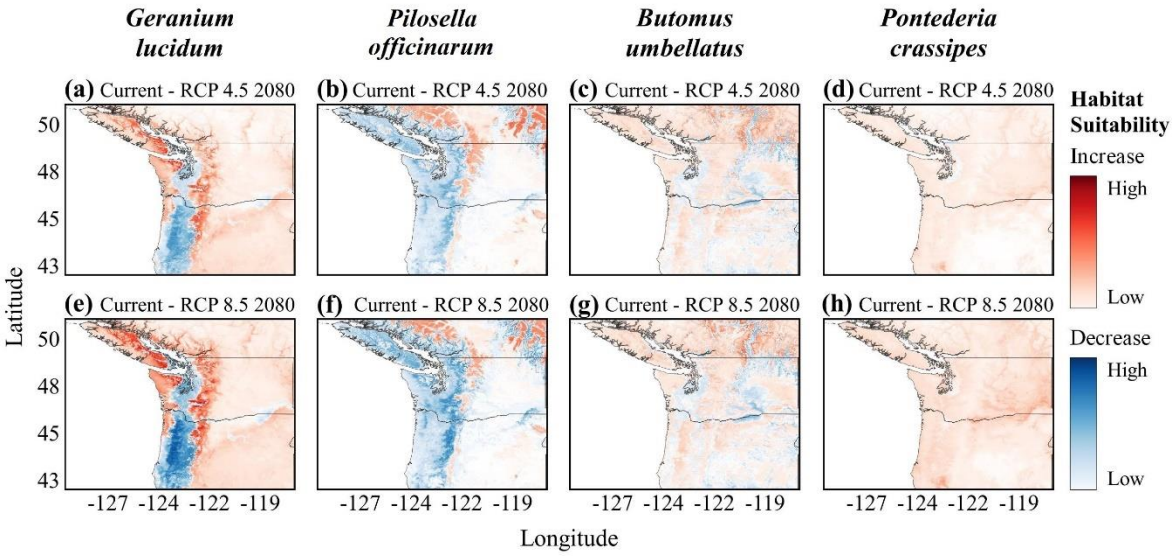

Figure D3 Potential expansion or contraction of habitat suitability under future climate scenarios by 2080. (a – d) Increases and decreases in the predicted habitat suitability of *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively, under climate scenario 4.5 by 2080; (e – h) increases and decreases in the predicted habitat suitability of *Geranium lucidum*, *Pilosella officinarum*, *Butomus umbellatus*, and *Pontederia crassipes*, respectively, under climate scenario 8.5 by 2080.

Appendix E Test model results for *Butomus umbellatus*

The inclusion of landcover variables resulted in limited variable response, as seen by flattened response curves, conveying minimal importance of most predictor variables (Figure E1). The steep increase in likelihood in response to the water bodies variables resulted in nearly half of all variable importance being allocated to water bodies, as may be expected with an aquatic species; however, this resulted in less importance assigned to climatic variables, relative to the other test models. Furthermore, the inclusion of a water bodies variable for an aquatic species resulted in the mapped outputs showing high suitability in areas where water is present and low suitability in nearby surrounding areas, yet the water bodies variable is not exhaustive and may be missing smaller water bodies. Thus, the results when including the water bodies variable may be misleading and under-representative of the suitable habitats for *B. umbellatus*.

Additionally, the exclusion of the water bodies variable was tested to determine its effect on the other variables (Figure E2). While the species response to climatic variables is somewhat stronger without the water bodies variable, the species response to particular land cover variables is much stronger. For example, the likelihood of species presence decreases nearly 80% in response to increasing proportions of cropland. This substantial decrease resulted in high variable importance being attributed to cropland in particular, which again resulted in minimizing the importance of climatic variables relative to the climate test model. As *B. umbellatus* is an aquatic species, the very high importance placed on other land cover variables, such as cropland, may be misleading causing inaccurate mapped outputs.

The response curves of the model using climate and human influence index variables only show moderate or highly predictive variables (Figure C6), compared to the other test model response curves. Variable importance is much more even across predictor variables, with no single variable contributing substantially more than another. With the results of the other test models (Figures E1 and E2) and the consideration of *B. umbellatus* as an aquatic species (and therefore the inclusion of terrestrial land cover types having less biological relevance), I retained the model including climate variables and the human influence index as the final model.

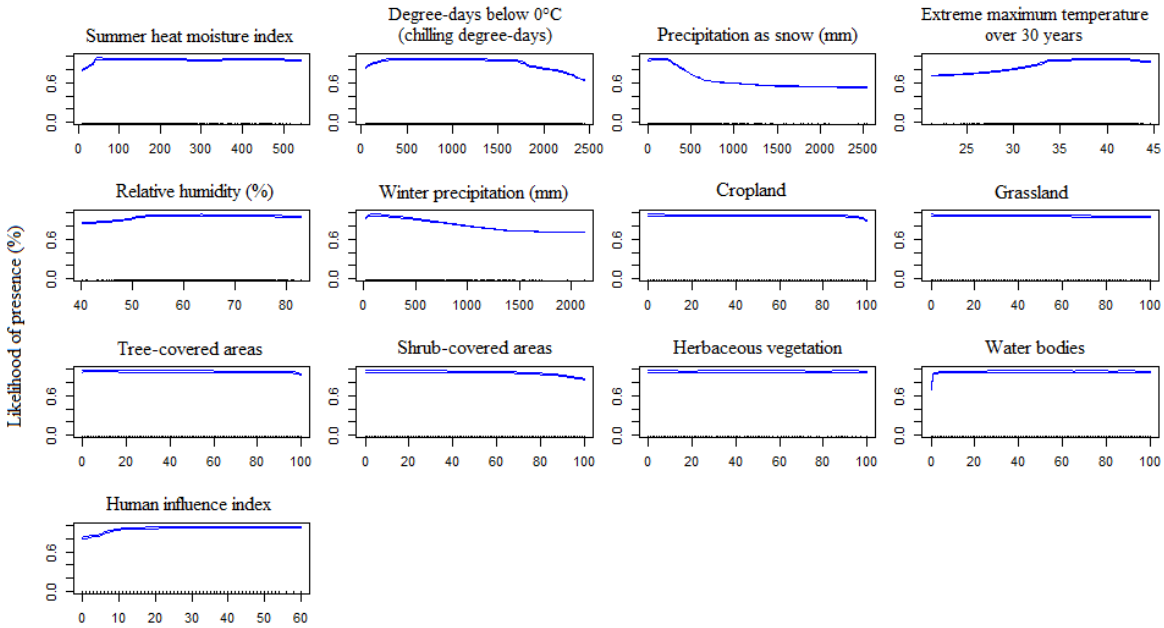

Figure E1 Response curve for the *Butomus umbellatus* test model using climate, land cover, and human influence index variables.

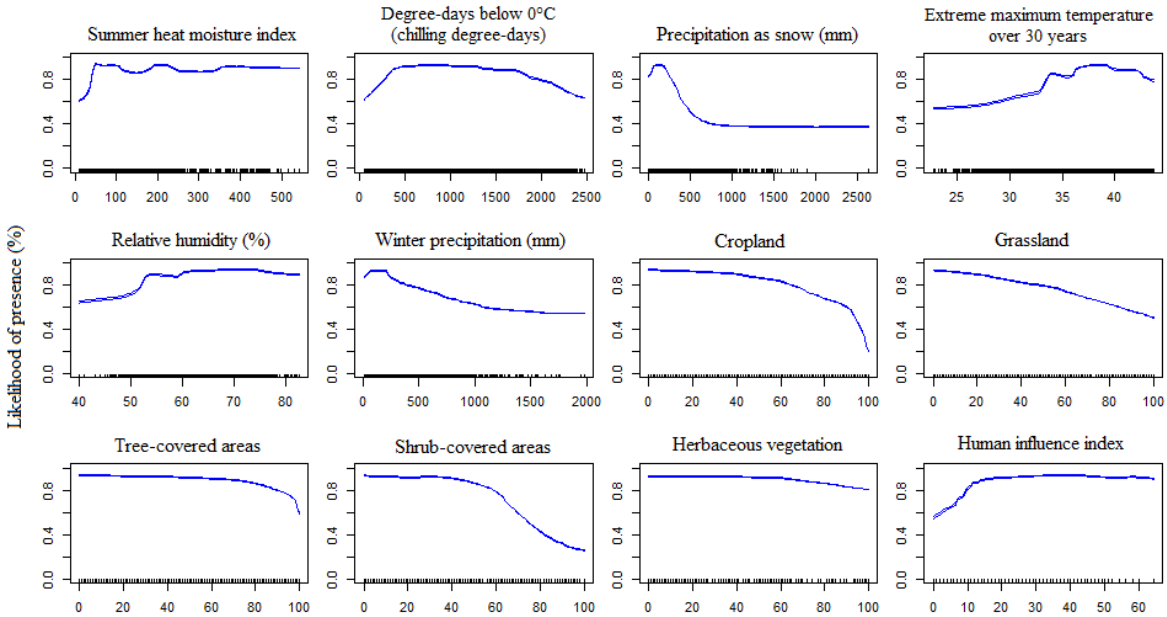

Figure E2 Response curve for the *Butomus umbellatus* test model using climate, land cover, and human influence index variables, but excluding the water bodies variable.