

## Research Article

## Niche dynamics and potential geographic distribution of *Didymosphenia geminata* (Lyngbye) M. Schmidt, an invasive freshwater diatom in Southern Chile

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### Abstract

Aquatic invasive species are a major threat to native freshwater ecosystems and cause enormous ecological and economic damage worldwide. *Didymosphenia geminata* (Lyngbye) M. Schmidt is an emerging invasive aquatic species that is spreading aggressively in Southern South America. Using niche analysis and species distribution models (SDMs), we examined niche requirements of *D. geminata* using climatic, topographic, and biological variables. We compared the realized niche of the species in the United States (US) with the niche in Chile. Within Chile, we also examined the environmental conditions (environmental envelopes) of rivers with and without this alga, to assess whether this species has the potential to colonize more rivers. Finally, we compared the SDMs from the US and Chile projected to Chile. Results showed that the potential distribution of *D. geminata* varied significantly between US and Chile. The US-based model predicted a geographic distribution in Chile which ranged from 32° to 55° S latitude while the Chile-based model predicted suitable habitats only from 36° to 48° S, and not so in the coastal ranges nor in Southern Patagonia (~52–55°S). In Chile, we found no differences in the environmental envelopes of the invaded and uninvaded rivers, thus suggesting that this species has even more suitable habitats to invade. These results can be used for prioritizing survey sites in Southern Chile for an early detection and management of *D. geminata* and for the conservation of native flora and fauna in freshwater ecosystems in Chile.

**Key words:** algal blooms, aquatic invasions, MaxEnt, species distribution models, climatic niche, phytobenthos, phytoplankton, Patagonia

### Introduction

Aquatic invasive plants are a major threat to the biodiversity of native freshwater ecosystems and cause enormous ecological and economic damage worldwide (Mack et al. 2000; Didham et al. 2005; Dudgeon et al. 2006; Connelly et al. 2007; Strayer 2010). Blooms of the diatom *Didymosphenia geminata* (Lyngbye) M. Schmidt, native to boreal streams in the Northern Hemisphere, now pose a threat to pristine, freshwater ecosystems in Chilean and Argentinean Patagonia (Segura 2011). Besides aesthetic changes induced by this species in pristine rivers, it can also modify native benthic communities by increasing organic matter. In Chile, this species has been reported in catchments in Los Lagos and Aysén regions (41°–44° S), the Baker basin (48° S) and Chubut and Neuquen

Provinces, Argentina (Sastre et al. 2010; Segura 2011; POCH and U. Chile 2011a). Although a single record of *D. geminata* was reported in Chile almost five decades ago (Asprey et al. 1964), recent records obtained from 2010 and 2012 show that this species appears to be spreading across catchments, with people being one of the main dispersal vectors (Bothwell et al. 2009; Kilroy and Unwin 2011; Bothwell et al. 2014). Water nutrient chemistry such as low phosphate concentration as well as environmental changes induced by humans have also been regarded important to determine the invasive success of *D. geminata* (Whitton et al. 2009; Kilroy and Bothwell 2011; Bothwell and Kilroy 2011; Bothwell et al. 2014).

Between 2010 and 2012, after *D. geminata* presence was confirmed, it has spread more than 100 km from the Futaleufú River to the Yelcho basin in the Los Lagos Region (43°S) (Montecino

unpublished data). The same dispersal pattern has been documented in New Zealand. *D. geminata* was first recorded in South Island rivers in 2004, and within six years it spread to most of the larger rivers of this island (Kilroy and Unwin 2011). In summary, *D. geminata* constitutes an invasive species (*sensu* Richardson et al. 2000) because it is spreading across rivers. The study of the ecological requirements for the establishment and spread of this species as well as the resulting distribution pattern across watersheds in Southern Chile, is important in order to establish appropriate management practices for the identification of the most invulnerable rivers.

Species Distribution Models (SDMs) have been successful in describing niche requirements and predicting potential distribution of invasive aquatic species (e.g., Kumar et al. 2009; Januchowski-Hartley et al. 2011; Liu et al. 2011; Zengeya et al. 2012). This approach statistically correlates species' presence with environmental variables to identify factors defining the species' niche and, to project the niche back onto the geographic space (Guisan and Thuiller 2005; Colwell and Rangel 2009; Elith and Leathwick 2009). One way to use these models is to project native SDM in the invaded range and to compare it with the SDM obtained from the invaded range (Broennimann et al. 2007; Fitzpatrick et al. 2007). SDMs have also been used in risk assessment by pooling biological and socio-economic information to generate invasive risk maps (Strubbe and Matthysen 2009; Januchowski-Hartley et al. 2011).

In this study, three objectives were proposed to assess the environmental correlates for *D. geminata* presence in Southern Chile jointly with a comparative approach using US potential distribution as a reference point (Kumar et al. 2009). Firstly, we compared whether niche of *D. geminata* in Southern Chile was similar to the niche of this species in the US. This objective was conducted to test whether the niche of this species changes across invaded regions. Secondly, in Chile, we examined the environmental envelope characterizing invaded and un-invaded rivers. This approach takes advantage of the fact that we were able to obtain "true absences" (negative sites) from the field campaigns then, we could discern whether this species has the potential to colonize new rivers. Thirdly, we obtained climatic and biophysical variables at *D. geminata* presence sites in Southern Chile and the US from a global data base in order to compare SDMs projected to Chile. If the niche does not differ between

regions, then the projections of the US and the Southern Chile models will be similar.

## Methods

### *Species description*

In the benthos, *D. geminata* may develop long stalks, while cell frustules are 60–140 µm long and between 25–43 µm wide (Cox 1996). Blooms of this species (often termed "rock snot" or "Didymo") are mainly due to high rates of vegetative reproduction. Each cell generates a stalk to attach itself to substrates, and the stalks divide at the time the cell divides, subsequently generating a dense mat formed by extracellular stalk material rich in polysaccharides (Spaulding and Elwell 2007; Kilroy and Bothwell 2011). This mat or "woven fabric" that contains algae, macroinvertebrates, stream debris, and detritus is resistant to fungal and bacterial degradation (Whitton et al. 2009). Didymo has been shown to develop in the rivers under a wide range of hydraulic conditions, from very slow-moving, shallow waters, to greater depths and stronger velocities downstream; however, strong flood events often remove considerable *D. geminata* biomass (Kilroy et al. 2006; Kirkwood 2009; Cullis et al. 2013).

### *Field surveys and D. geminata occurrence data*

From November 2010 to May 2012, surveys to detect *D. geminata* in the phytoplankton and phyto-benthos were conducted in 187 rivers, located within 10 catchments, between 38°23' to 52°12' (Figure 1, Supplementary material Table S1). In addition, data from two other field surveys were used (CIEN Austral 2011a, b; CIEP 2010). The selected rivers were evenly distributed latitudinally along the sampling regions in Southern Chile and covering approximately 14° of latitude including Northern, Central and Southern Patagonia (Aracena et al. 2011). Rivers were also selected according to accessibility. At each river, we sampled once in a stretch between 25 and 50 m long. Phytoplankton and phyto-benthos samples were collected at each river, following procedures proposed by Kilroy and Dale (2006) and standardized for Chile by the Procedures Manual of Díaz et al. (2012).

At each river site, phytoplankton was sampled once. These samples were collected at the subsurface, using a 40 µm net maintained submerged at 1 m depth, for 10 min (Kilroy 2005; Duncan et al. 2007). The collected material was fixed with a 2% Lugol solution. For the phyto-benthos samples, in a

stretch between 25 and 50 m long, three perpendicular sections (transects) of variable length (2–10 m) across the riverbed were surveyed according to accessibility and bottom depth. In each transect, at least three stones were randomly removed, and the outgrowth was scraped (6 cm<sup>2</sup> per stone) with a disposable brush (CHE 2005; Kilroy and Dale 2006; Díaz et al. 2012). The three samples were pooled into a flask and fixed with 4% formalin.

After sampling, biosecurity procedures were conducted to prevent potential *D. geminata* contamination among rivers. All the materials were washed using salt solution (5%), and then dried under the sun. Sampling materials included instruments, boots, vehicle and wheels, including disposable materials in plastic bags (Duncan et al. 2007).

Phytoplankton and phytobenthos fixed samples were first processed for qualitative analysis searching for viable *D. geminata* cells in a homogenized original or diluted drop of sample obtained by a disposable Pasteur pipette ( $\pm$  40  $\mu$ l). Presence was determined if at least one living cell in a sample was encountered. Secondly, presence and absence of *D. geminata* was determined based on accurate taxonomical identification of phytoplankton and phytobenthos samples after acid digestion and preparation of permanent slides (18 $\times$ 18 mm) using Naphrax (1.7 refractive index). These slides were examined using a phase-contrast photonic microscope by checking 65 transects for at least 200 valves (Krammer and Lange-Bertalot 1986; Battarbee 1986; Wetzel and Likens 1991).

The rivers in Southern Chile indicating the presence or absence of *D. geminata* were mapped using ARCGIS 9.3, and supported by AUTOCAD Lt 2010. The map included UTM coordinates, and it was normalized to datum WGS 84 and spindle 18 South. For Southern Chile, a total of 55 presences and 225 absences were recorded (Figure 1). Forty seven spatially unique records were used (one record per 1-km grid cell) for the modeling process; eight duplicate records were excluded because the method requires only one record per grid cell. For the US, a total of 308 presence and 2724 absence locations were used in the analyses (see details in Kumar et al. 2009).

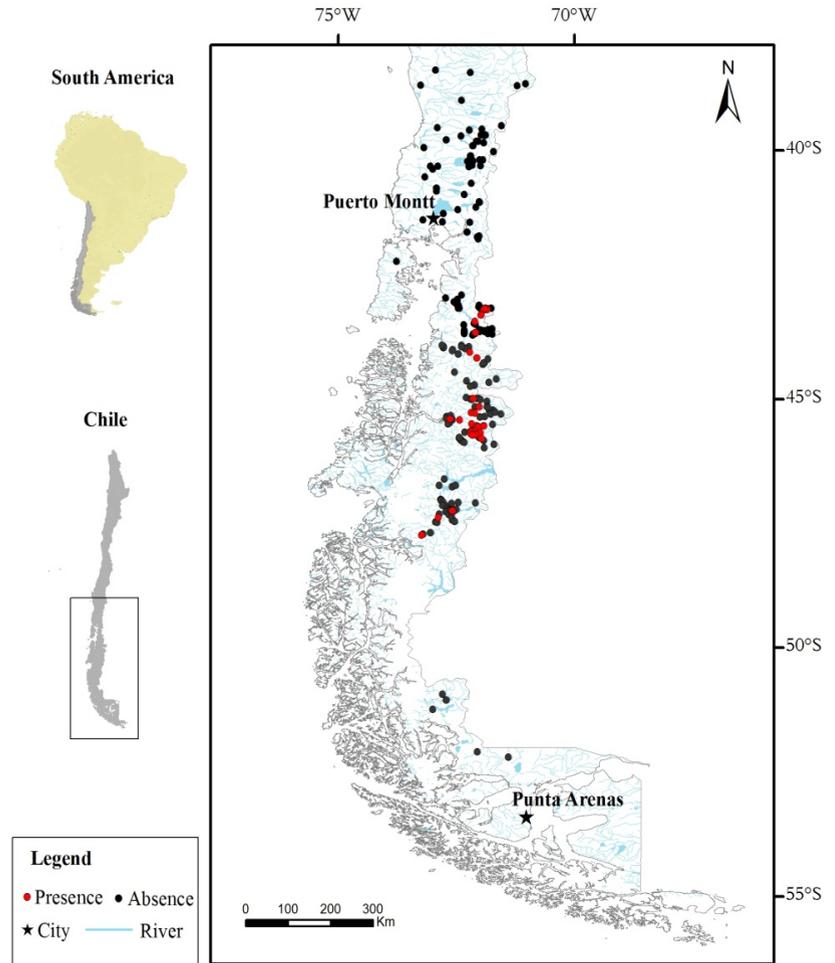
#### Environmental data

Environmental variables for both the US and Southern Chile were obtained from the same databases (Supplementary material Table S2). For Chile, the sources of data and variables considered were slightly different than Kumar et al. (2009);

they used a US specific climatic dataset (Daymet) while for Chile, global WorldClim dataset was used in this study. Initially, a total of 27 variables were included: climatic, topographic, hydrological, geology and remotely sensed variables (see Supplementary material Table S2).

To represent climatic conditions in Southern Chile, nineteen bioclimatic data layers were obtained from the WorldClim dataset (Hijmans et al. 2005) at ~1-km spatial resolution which were generated using altitude and monthly temperature and precipitation records from 1950 to 2000. The 19 bioclimatic variables define general trends, seasonality, and extremes. They are biologically more meaningful than simple monthly or annual averages of temperature and precipitation in defining a species' ecophysiological tolerances (Nix 1986; Kumar et al. 2009). Air-temperature was used as surrogate for water-temperature because air- and water-temperatures have been reported to be highly correlated (Kothandaraman and Evans 1972; Cho and Lee 2012; Johnson et al. 2014). Topographic and hydrological variables included elevation, flow accumulation, flow direction and compound topographic index. These were obtained from the USGS HYDRO1K geographic database developed to provide comprehensive and consistent global coverage of topographically derived data sets, including streams, drainage basins and ancillary layers derived from the USGS' 30 arc-second digital elevation model of the world. Remotely sensed variables (MODIS Vegetation Continuous Field) included percentage tree cover and percentage herbaceous cover. Growing degree days and rock geologic age (a potential surrogate for water chemistry; Koutnik and Padilla 1994) were also included as other environmental predictors (Supplementary material Table S2). All these environmental variables were chosen based on their predictive powers in previous studies on modeling aquatic species distributions (e.g., Kumar et al. 2009 and Poulos et al. 2012 in US; Gallardo and Aldridge 2013, in Great Britain and Ireland). Environmental variables characterizing water chemistry such as alkalinity, pH, phosphorus and iron content would have been ideal for modeling aquatic species distributions, but spatial layers (GIS data files) for these did not exist to be considered in the modeling.

Pixel values for all environmental variables for *D. geminata* survey sites in Chile and the US were extracted and checked for cross-correlations using Pearson correlation coefficient; only one variable from a set of highly correlated variables



**Figure 1.** Presence (red colour circles) and absence (black colour circles) of *Didymosphenia geminata* surveyed sites in Southern Chile from 2010 to 2012. For details see Supplementary material Table S1.

( $r > 0.90$ ) was included in the model. The decision to include or drop a variable was based on its potential biological relevance to *D. geminata* (Kilroy et al. 2006; Kumar et al. 2009). A few variables were dropped because of their low predictive power based on percentage contribution and jackknife training gain in the MaxEnt model. Finally, the best model for Chile included 13 environmental variables (Table 1), whereas the best model for US included eight variables (see Kumar et al. 2009).

#### Niche analysis

Principal Component Analysis (PCA) was used (i) to compare the niche of *D. geminata* between US and Southern Chile, and (ii) to compare the environmental conditions of invaded and uninvaded rivers in Chile. The categorical variable

“rock geologic age” was excluded from the PCA because it requires continuous variables. Following Broennimann et al. (2012), the presence and absence points were converted into occurrence density values using a kernel function to smooth a density distribution. The estimation of densities was conducted by expanding the geographic grid to  $5 \times 5$  km pixels, thus, counting within this grid the number of occurrences. Then, these values were gridded within the environmental envelope obtained by the background points (randomly generated pseudo-absence points) previously selected in the US and in Southern Chile respectively. In this way, three models were constructed: the first, describing the ecological niche of the species in the US; the second, describing the ecological niche of the species in the Southern Chile; the third, describing the environmental space of uninvaded rivers in Chile. Niche similarity was

measured using *Schoener's D* overlap index (Schoener 1970; Warren et al. 2008) which varies between 0 (no overlap) and 1 (complete overlap). The overlap between different niche spaces was tested against chance using resampling procedures (Warren et al. 2008).

Following Petitpierre et al. (2012), three regions of the niches of the native and invaded range can be identified, giving clues about niche dynamics of invasive species: (1) stability zone (S), the area that is shared between the US niche vs Southern Chile niche; it is an estimate of niche conservatism (Petitpierre et al. 2012); in our study S was estimated dividing the number of occurrences in the Southern Chile niche, which are included in the US niche, by the total number of occurrences of the species in Southern Chile; (2) the expanded zone (E) is the niche zone in Southern Chile that is not shared with the US niche; E is estimated dividing the number of occurrences in the invaded range, which are not included in the US niche, by the total number of occurrences of the species in the invaded range; in our study, E is an indication of the colonization to new environments and by definition  $S + E = 1$ ; and (3) the unfilling zone (U), the zone in the US niche, not shared with the Southern Chile niche; U is estimated dividing the number of occurrences in the US niche, which are not included in the Southern Chile niche, by the total occurrences in the US range; U indicates the potential environments of the US niche not shared by the invasive species in the Southern Chile. All calculations were performed in R (version 2.15.1; R Development Core Team 2012) using functions provided by Broennimann et al. (2012) and Petitpierre et al. (2012).

#### *Potential distribution modeling*

Maximum entropy modeling or MaxEnt algorithm (version 3.3.3k; Phillips et al. 2006) was used for mapping the potential distribution of *D. geminata* in Chile and US. MaxEnt was chosen because: (1) it performs relatively better than other SDMs (Elith et al. 2006; Kumar et al. 2009); and (2) it is relatively robust to small sample sizes (Pearson et al. 2007; Kumar and Stohlgren 2009). MaxEnt estimates the probability of presence of a species based on presence records and random background points (or pseudo-absences) by finding the maximum entropy distribution (Phillips et al. 2006). Overfitting in MaxEnt is controlled by a regularization parameter beta. It can handle both categorical and continuous variables and non-linearity in species response to different environmental

predictors. It also defines five different features (linear, quadratic, product, threshold and hinge) to constrain the geographical distribution of a species. MaxEnt randomly selects 10,000 background points from the landscape and provides an estimate of probability of presence of a species that varies from 0 to 1. Default settings in MaxEnt were used to run models for *D. geminata*. MaxEnt model was constructed for the southern parts of Chile covering areas within 200 km of the current sampling locations for *D. geminata* (i.e., areas that have been available to the species for dispersal during past 50 years). Then, the model was transferred to the entire country to identify potentially suitable habitat. MaxEnt predictions were brought into a Geographic Information System and the map of potential habitat distribution was generated using ARC Map (version 9.3, ESRI, Redlands, CA, US). A similar methodology as described earlier to run the Chilean model was used to run MaxEnt model for the US range; except the 10,000 background points in MaxEnt were generated randomly from the entire contiguous United States. The geology variable was not used in the US model because of the differences in Chilean and US Geology data layers (US layer had finer resolution and different classes than the Chilean data base).

#### *Model evaluation and validation*

The area under the receiver operating characteristic (ROC) Curve known as AUC (Swets 1988) is one of the most commonly used metrics to evaluate the performance of SDMs. Since relatively true absences were available from the field surveys, it was possible to use 'Presence-Absence' package in R, version 2.15.1 (R Development Core Team 2012), to calculate AUC value. Since the use of AUC has been recently criticized (Lobo et al. 2008), further threshold-dependent measures of model performance were calculated including: sensitivity (i.e. fraction of all presences correctly predicted as presences), specificity (i.e. fraction of all absences correctly predicted as absences), Cohen's Kappa, and Pearson Correlation coefficient between observed presence-absence and predicted probabilities (Fielding and Bell 1997; Elith et al. 2006). To calculate threshold-dependent metrics, a threshold that maximized the sum of specificity and sensitivity was selected (Liu et al. 2005) and 10-fold cross-validation procedure for model validation in MaxEnt was used. Presence (47) and absence data (225) were split into 10 subsets (maintaining equal prevalence) and 90% of the data were used for training the model and

remaining 10% for model validation or testing. Ten replicates were run and AUC and other evaluation metrics values were averaged across the replicates. The final model was run using all presence (47) locations. Relative importance of different environmental variables was judged using ‘percentage variable contributions’ and ‘jackknife’ results from MaxEnt. Relationships between different environmental variables and the predicted probability of occurrence of *D. geminata* were examined using MaxEnt generated response curves. Similar validation procedures were conducted for the US model as detailed in Kumar et al. (2009), given that they also included rivers with presence ( $n = 308$ ) and absence ( $n = 2,724$ ) of *D. geminata*.

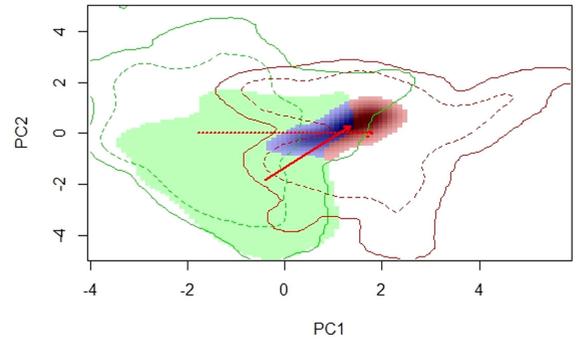
## Results

### Niche analysis using PCA

The similarity between the realized niche of *D. geminata* in the US and Southern Chile was extremely low  $D = 0.06$  (Figure 2). While this index was not statistically significant from the US niche perspective ( $P = 0.16$ ), it was significant from the Southern Chile niche perspective ( $P = 0.04$ ). In fact, over half of the Southern Chile niche was included within the US niche ( $S = 0.59$ ), and an important proportion of environment of the US niche was not shared with the Southern Chile niche ( $U = 0.91$ ; Figure 2). In addition, there is some niche space exclusive to the species in Southern Chile ( $E = 0.41$ ;  $S + E = 1$ ). Finally, in Southern Chile, the similarity between the *D. geminata* niche and the environmental space of the absences was significantly high ( $D = 0.57$ ;  $P = 0.03$ ; Figure 3).

### Species Distribution Models for *D. geminata*

The SDM of *D. geminata* constructed in Chile performed well with an average test AUC ( $\pm$ SD) value of 0.85 ( $\pm 0.06$ ). The model also had a high classification rate ( $Kappa = 0.64$ ) and it performed well in correctly predicting presences (sensitivity = 0.90) and absences (specificity = 0.84). The Pearson correlation coefficient between observed presence-absence and predicted values was also significant ( $r = 0.53$ ;  $P < 0.0001$ ). The areas of higher probability of presence were scattered and located only in rivers of the Andean mountain range (Figure 4A). No suitable habitats were predicted along rivers of the coastal mountain ranges. The areas of maximal probability of



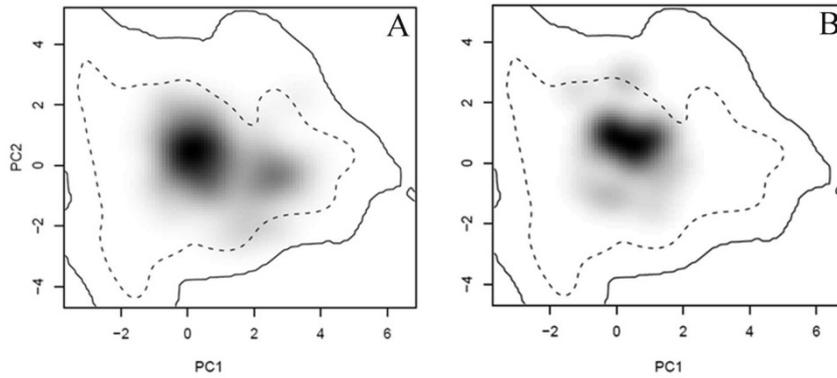
**Figure 2.** Multivariate *Dydymosphenia geminata* niche in the US (green) and Chile (red), obtained with Principal Component Analysis (PCA); blue shows the niche overlap between two geographic regions. Solid and dashed contour lines show 100% and 75% of the environmental envelope for US (green lines) and Southern Chile (red lines). Arrows indicate niche shift considering 75% (dotted) and 100% (continuous) of the environmental envelopes. The PC1 explained 33.42% of the total variability of data while PC2 explained 14.55%. For PC1, temperature seasonality (Bio4) contributed with 20% and mean temperature of the warmest quarter (Bio10) contributed with 16.3%. For PC2 elevation contributed with 30% and growing degree days contributed with 23%.

**Table 1.** Relative percentage contribution of different environmental variables of the potential habitat distribution for *Didymosphenia geminata*. Bold represents the top variables in the SDM.

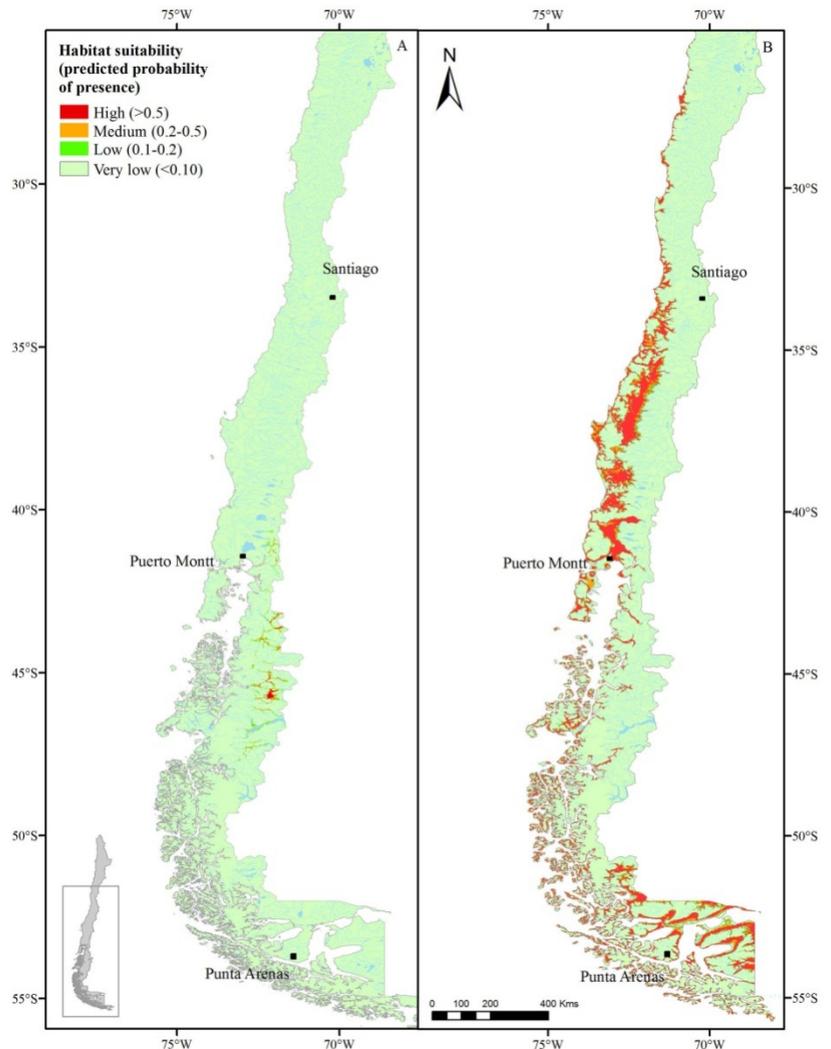
Variable	Percentage contribution
Flow accumulation	<b>26.6</b>
Geologic age	<b>25.4</b>
Growing degree days	<b>10.5</b>
Precipitation seasonality (Bio15)	<b>7.0</b>
Isothermality (Bio3)	<b>5.9</b>
Percentage herbaceous cover	5.8
Precipitation of driest month (Bio14, mm)	4.7
Precipitation of wettest month (Bio13, mm)	4.5
Temperature seasonality (Bio4)	2.3
Mean temp. of warmest quarter (Bio10)(°C)	2.3
Flow direction	2.0
Percentage tree cover	1.9
Elevation (m)	1.1

presence were located between 39° to 48° S from Los Ríos to the Aysén Regions (Baker River). No potential habitats for *D. geminata* were predicted in Southern Patagonia (Figure 4A).

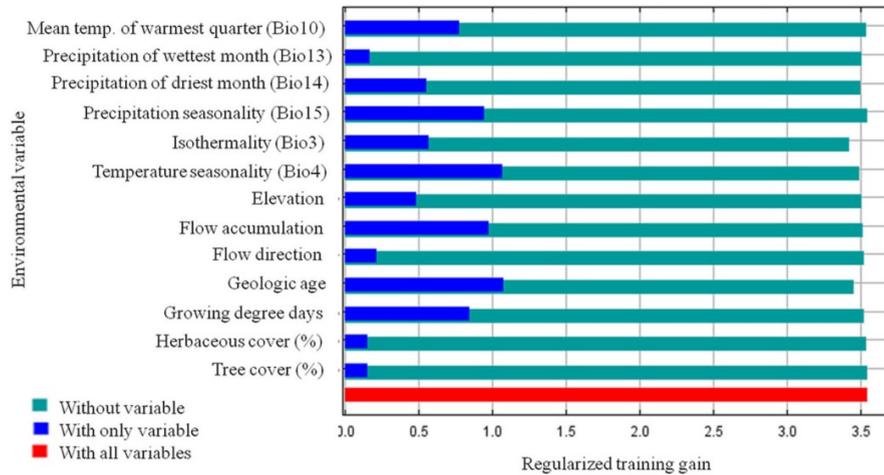
Flow accumulation, rock geological age, growing degree days, and precipitation seasonality were the strongest predictors of *D. geminata* distribution in Southern Chile (Table 1), and all were among the variables with the highest training gain when



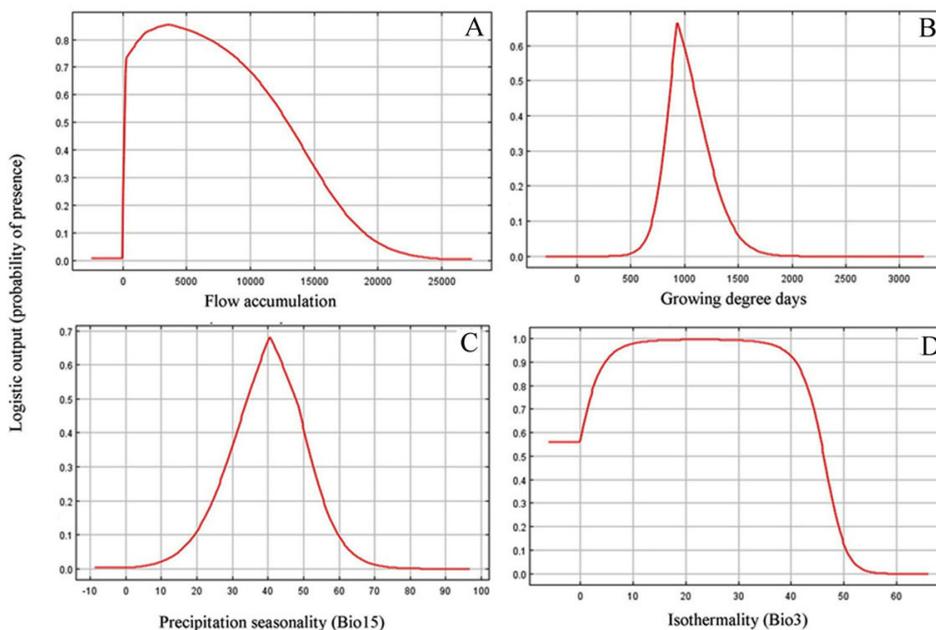
**Figure 3.** Multivariate ecological spaces obtained from Principal Component Analysis (PCA) for *Didymosphenia geminata* (A) Space of the absences (i.e. un-invaded rivers); (B) the ecological niche of *D. geminata* (places where *D. geminata* was detected). Solid and dashed contour lines show 100% and 75% of the existing environment envelopes respectively. The PC1 explained 25.63% of the total variability of data while PC2 explained 18.29%. For PC1 precipitation seasonality (Bio15) contributed with 30% and the percentage of tree cover contributed with 22.7 %. For PC2 precipitation of the wettest month (Bio13) contributed with 29% and precipitation of the driest month (Bio14) contributed with 16.5%



**Figure 4.** Potential distribution of *Didymosphenia geminata* in rivers of Chile. **A**, SDM projected from Southern Chile; **B**, SDM projected from the US. Colours represent different values of probabilities of presence of this species (blue lines and stains represent rivers and lakes respectively).



**Figure 5.** Relative importance of the environmental variables for the SDM of *Didymosphenia geminata* in Chile based on the Jackknife test. The figure shows each environmental variable's contribution to 'training gain' which is a measure of model's predictive ability.



**Figure 6.** Relationships between four strongest environmental predictors and probability of presence of *Didymosphenia geminata* in Chile: (A) Flow accumulation, (B) Growing degree days, (C) Precipitation seasonality, and (D) Isothermality. Although the geological age of rocks was one of the top variables (see Table 1), it is not presented here.

used in isolation (Figure 5). The probability of *D. geminata* presence was higher at lower levels of flow accumulation and declined gradually with an increase of this variable (Figure 6A). For growing degree days (Figure 6B) and precipitation seasonality (Figure 6C), *D. geminata* showed a unimodal response. Higher probability of *D. geminata*

presence was associated with Cretaceous-Tertiary Volcanic rock (age: 145 to 2.7 Million years ago), Precambrian-Devonian, and Silurian period geologic rock types (not shown in Figure 6).

The US model with 10-fold cross validation was excellent in predicting current *D. geminata* occurrences in the US, with an average test AUC

value of 0.92 ( $\pm$  0.02). Mean temperature of warmest quarter, flow accumulation, and isothermality were the strongest predictors of *D. geminata* in the US (see Kumar et al. 2009). When the most important variables that explain SDM in Chile and US were compared, two factors were important in both models: flow accumulation and isothermality. Rock age, growing degree days and precipitation seasonality were important in Chile, while the temperature of the warmest quarter was important for the US model. It is interesting to note that the US-based model predicted the presence of *D. geminata* in the extreme Southern Patagonia ( $\sim$  52–55°S) and in the coastal Central Chile (Figure 4B), while these regions were not predicted by the Chile-based model. Overall, the US model included most of the regions predicted by the Chile model.

## Discussion

The low similarity in the *D. geminata* niche between Southern Chile and US ranges, suggests significant niche differentiation in Southern Chile. The relatively high fraction of niche space observed only in Southern Chile is consistent with the colonization to environments not colonized or non-existing in the US (Figure 2). This differentiation, especially in those non-existing in US, can be explained by local adaptation, as it has been well documented in some invasive plant species (Maron et al. 2004; Hulme and Barrett 2013). Nevertheless, another possibility cannot be discarded: in the US this species could be spatially constrained by biotic interactions, thus preventing its colonization to suitable environments shared between the two regions. In Southern Chile, these constraints could be non-existent, so this species can colonize the suitable environments. This seems to be the first study to document niche differentiation in unicellular species, a poorly understood group with serious invasive potential (Litchman 2010).

The predictions of suitable habitats for *D. geminata* differed significantly between the US and the Chile SDM, suggesting that the distribution of this species in Chile might not be in a geographic equilibrium, i.e. there are more suitable habitats (colonized in US) yet to be colonized by this species in Southern Chile. This idea is reinforced with the significant similarities between the niche of this species in Southern Chile, and the environmental envelopes observed in un-invaded rivers (Figure 3).

Further support for the validity of the MaxEnt model stems from its “eco-plausibility” (*sensu* Rodda et al. 2011) in that the output makes sense in ecological terms, bearing in mind what is known about the species’ traits and tolerances. The relevance of growing degree days in the models is indicative of the importance of water temperature- accumulation. The unimodal relationship is consistent with *D. geminata* cell division and stalk formation being limited by low and high temperatures (Kilroy and Bothwell 2011). Geologic age of rocks may reflect the chemical composition of different types of river basin rocks in the currently infested areas (Gallardo and Aldridge 2013). The linking of micronutrient requirements of algae with the geology of rocks is an issue that deserves serious attention. For instance, calcium concentration and alkalinity are high in sedimentary rocks and low in igneous and metamorphic rocks (Salminen et al. 2005; Rost et al. 2011). A more detailed and comprehensive knowledge about water chemistry (e.g., pH and phosphorus), and the physical properties of river waters and rocks are critical for more accurate prediction of the invasive spread of this species. Knowledge of water quality will be also be useful for the control and management of other alien aquatic plants as well, such as *Egeria densa*, *Eichornia crassipes*, *Limnobium laevigatum* and *Nymphaea alba* that are also becoming invasive in Southern Chile rivers (Pauchard et al. 2006). Unfortunately, for Chile, there is no long-term, comprehensive database of river characteristics and water quality.

Flow accumulation was a good predictor of the potential distribution of *D. geminata* in Chile. SDM predicted higher probability of presence at lower values of flow accumulation (Figure 6A). Flow accumulation, an estimation of the volume of water transported by the river, makes biological sense given the light requirements for photosynthetic activity (Cullis et al. 2012). At low to intermediate flow volumes, *D. geminata* mats can establish because light penetrates deeper into the waterbed. At high flow volumes, light does not penetrate deeper in the water column and no mat establishment will be possible.

Although the spatial models for *D. geminata* performed well, there are some limitations and uncertainties that deserve consideration. Firstly, there are sampling limitations that ought to be considered. Surveys were likely incomplete, especially when we couldn’t sample inaccessible rivers. We recognize that adding more sample sites, more transects at each site, and sampling

more rocks along each transect may have yielded more “presence” locations, therefore an increase of the performance of the models. However, economic constraints, safety, and sampling efficiency came into play. Then alternatively, as the best case, we offered a “snapshot” of the current invasion patterns of *D. geminata* in Chile. Secondly, the SDM trained for US was different from that trained for Chile. This was inevitable given that it was not possible to get exactly comparable environmental databases for both regions.

Additionally, these models cannot be compared because each one reflects their own environmental conditions. Which model is “better”? Our results indicate that both models have an excellent performance in their respective regions based on diverse estimators (AUC, Kappa, etc.). One alternative could be to construct a new model for the US, considering the same variables used for Chile; however, this alternative was discarded given the excellent performance of the US model (Kumar et al. 2009). Thirdly, the resolution of the models was relatively coarse (1km<sup>2</sup> pixel) especially since a stretch of river would occupy only a fraction of each pixel. Nevertheless, the variables selected for inclusion in the models were consistent with physiological studies of *D. geminata*, and our results may indicate the biophysical characteristics of river basins at the larger scale. Fourthly, dispersal limitation, by training the models, was included for the southern parts of Chile, covering areas within 200 km of the current sampling locations. This is a conservative approach, because when dispersal limitation was not included (results not presented), the model projected its distribution to Tierra del Fuego, in the same way the US model predicted. It is likely that humans unintentionally dispersed this species over longer distances on footwear or water sports equipment (Kilroy and Unwin 2011). In this case, the Chile model could be under-predicting potential distribution. The construction of a SDM, considering the occurrence points of US, Southern Chile and other regions (e.g., New Zealand) together, along with data on human recreation patterns, could give a more complete prediction of the potential geographic distribution of this species in Chile (Gallien et al. 2012).

Both the predictions of potential distribution using SDM and the similarity of the niche of this species in Southern Chile with un-invaded environments indicate that most of the sampled

rivers constitute suitable habitats for *D. geminata*. If dispersal of this species is not constrained (Kilroy and Unwin 2011), the colonization to these other rivers is just a matter of time. This is supported by the high predictive power of the MaxEnt model projected from US that highlighted considerable areas suitable for future colonization. This can be a serious conservation problem, given that *D. geminata* can affect the structure and composition of native benthic communities (Kilroy et al. 2009).

Recreational activities are regarded as the main source of dispersal of *D. geminata* across watersheds (Kilroy and Unwin 2011). However, while cells arrival is a prerequisite, a successful establishment necessitates that the river has suitable conditions for cell survival and blooming. Recent investigations have documented that extremely low concentration of soluble reactive phosphorus (below ~2 ppb) is the main environmental factor for bloom formation in rivers (Bothwell and Kilroy 2011). In southern Chile, freshwater ecosystems are oligotrophic (Soto and Stockner 1996; Soto 2002) and therefore suitable for invasion.

Continuous long-term monitoring of rivers in Southern and Central Chile will be necessary to test the distribution models, and to monitor the geographic expansion of this species. Fortunately, the Chilean government is aware of this problem, and is investing funds to accomplish this important task. This database will be made public and available in the future for basic research and decision-making. In the meantime, it is imperative that consideration is given to limiting spread by banning felt-soled waders, implementing strict biosecurity measures (disinfection stations) at popular sites for water sports (including fishing), and raising public awareness to properly check, clean and dry equipment used in waterways.

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The following supplementary material is available for this article:

**Table S1.** Location of sites surveyed for *Didymosphenia geminata* in Southern Chile from November 2010 to May 2012.

**Table S2.** Environmental variables considered for the SDMs for *Didymosphenia geminata*.

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