QUANTIFYING NICHE EXPANSIONS IN INTRODUCED PLANT SPECIES IN NORTH AMERICA

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Abstract

As introduced plants continue to spread throughout North America, there is an increasing need to understand and predict their invasion patterns. Climatic niche shifts are an important aspect of invasion patterns and occur when the climatic conditions occupied in the introduced range differ from the native range. Neglecting to account for climatic niche shifts reduces the accuracy of predictions of the future distributions of introduced species, limiting our ability to proactively manage and constrain their spread. In this thesis, I examine the frequency and characteristics of climatic niche shifts, and their implications for predicting the distributions of terrestrial introduced plant species in North America. In Chapter 1, I explored how violating a key assumption (niche conservatism) in species distribution modelling affects predictions of the future distributions of invasive plant species using *Vincetoxicum rossicum* as a case study. I found that *V. rossicum* has expanded its niche in North America into wetter climates and climates where precipitation is more evenly distributed throughout the year. As a result, native- and invasive-trained models differed greatly in their predictions of climatic suitability for *V. rossicum* across North America. I also found that a large portion of the climate in North America was non-analogous to the current invaded range. Consequently, the native-trained model generated predictions across a larger area of North America. My study revealed the complementary nature of building both invasive- and native-trained species distribution models. Though the invasive-trained model provides predictions of the species' potential distribution that are more representative of the invasion context (due to the niche shift), the native-trained model is able to make predictions at a much larger geographic scale. In Chapter 2, I evaluated the prevalence of climatic niche shifts in 663 introduced plants species in North America by distinguishing between conditions only occupied in the introduced range (a niche expansion) and conditions only occupied in the native range (which could indicate temporary under-filling) as different types of niche shifts. My results showed that the estimated prevalence of niche shifts more than doubles when considering both under-filling and expansion as types of niche shifts, as opposed to solely expansion. Therefore, it is important to consider under-filling and expansion separately so as to not underestimate introduced plant species' potential distributions in their introduced ranges or overestimate the prevalence of 'true' niche shifts. I also quantified expansion in eight bioclimatic variables to determine under what climatic conditions expansion commonly occurs. I found that introduced plants in North America are primarily expanding into wetter climates and into climates with more seasonally variable temperature and precipitation. By improving our understanding of the niche dynamics of introduced plant species and their implications for model building, we will be able to better predict the spread of these species.

Résumé

À mesure que les plantes introduites continuent de se propager à travers l'Amérique du Nord, il devient de plus en plus nécessaire de comprendre et de prédire leurs dynamiques d'invasion. Les changements de niche climatique constituent un aspect important de ces dynamiques d'invasion et se produisent lorsque les conditions climatiques occupées dans l'aire de répartition introduite diffèrent de celles de l'aire de répartition naturelle. Ignorer les changements de niche climatique réduit la précision des prévisions concernant la répartition future des espèces introduites, ce qui limite notre capacité à gérer et à limiter leur propagation de manière proactive. Dans cette thèse, j'examine la fréquence et les caractéristiques des changements de niche climatique, ainsi que leurs implications pour la prévision de la répartition des espèces végétales terrestres introduites en Amérique du Nord. Dans le chapitre 1, j'ai examiné comment la violation d'une hypothèse clé (le conservatisme de niche) dans la modélisation de la répartition des espèces affecte les prévisions de la répartition future des espèces végétales envahissantes, en utilisant *Vincetoxicum rossicum* comme étude de cas. J'ai constaté que *V. rossicum* a étendu sa niche en Amérique du Nord à des climats plus humides et à des climats où la précipitation est répartie plus uniformément au cours de l'année. En conséquence, les modèles entraînés sur l'aire de répartition naturelle et ceux entraînés sur l'aire de répartition introduite différaient considérablement dans leurs prévisions de l'adéquation climatique pour *V. rossicum* à travers l'Amérique du Nord. J'ai également constaté qu'une grande partie du climat en Amérique du Nord n'était pas analogue à l'aire de répartition envahie actuelle. Par conséquent, le modèle entraîné sur l'aire de répartition naturelle a généré des prévisions sur une plus grande partie de l'Amérique du Nord. Mon étude a révélé la complémentarité des modèles de distribution des espèces entraînées sur l'aire de répartition introduite et sur l'aire de répartition naturelle. Bien que le modèle entraîné sur l'aire de répartition introduite fournisse des prévisions de la distribution potentielle de l'espèce qui sont plus représentatives du contexte d'invasion (en raison du changement de niche), le modèle entraîné sur l'aire de répartition naturelle est capable de faire des prévisions à une échelle géographique beaucoup plus grande. Dans le chapitre 2, j'ai évalué la prévalence des changements de niche climatique chez 663 espèces végétales introduites en Amérique du Nord en distinguant les conditions occupées uniquement dans l'aire de répartition introduite (une expansion de niche) et les conditions occupées uniquement dans l'aire de répartition naturelle (ce qui pourrait indiquer un sous-remplissage temporaire) comme différents types de changements de niche. Mes résultats ont montré que la prévalence estimée des changements de niche est plus que doublée lorsque l'on considère à la fois le sous-remplissage et l'expansion comme des types de changements de niche, comparé à l'expansion uniquement. Il est donc important de considérer séparément le sous-remplissage et l'expansion afin de ne pas sous-estimer les distributions potentielles des espèces végétales introduites dans leur aire de répartition introduite ou de surestimer la prévalence des véritables changements de niche. J'ai également quantifié l'expansion selon huit variables bioclimatiques afin de déterminer dans quelles conditions climatiques l'expansion se produit généralement. J'ai constaté que les plantes introduites en Amérique du Nord s'étendent principalement vers des climats plus humides et vers des climats où la température et la précipitation sont plus variables au cours de l'année. En améliorant notre compréhension de la dynamique des niches des espèces végétales introduites et de leurs implications pour la construction de modèles, nous serons capables de mieux prédire la propagation de ces espèces.

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Table of Contents

List of Tables

List of Figures

List of Appendices

General Introduction

Biological invasions, and plant invasions especially, currently represent a major aspect of global change. As the intensity of international trade and human transport has increased over the past several hundred years, plant introductions (both intentional and accidental) have become increasingly common (Hulme, 2021; Seebens et al., 2022). In particular, North America is home to more introduced plant species than any other continent (Ploughe & Dukes, 2022). Invasive plant species pose a threat to native species as well as to entire ecosystems (Pyšek et al., 2012; Kumar Rai & Singh, 2020). Among other impacts, they can out-compete and displace native plants, alter soil composition, and impact the hydrology of ecosystems (Liao et al., 2008; Vilà et al., 2011; Pyšek et al., 2012; Kumar Rai & Singh, 2020; Ploughe & Dukes, 2022). Predicting the spread of these species is therefore important to enable early detection and increase the likelihood of successfully preventing establishment (Rockwell-Postel et al., 2020; Jarnevich et al., 2023). To do so, it is critical to understand the niche dynamics and invasion patterns of these species.

Understanding what factors predict introduced and invasive species' ranges is a fundamental goal in invasion biology. Species distribution models (SDMs), or ecological niche models, have long been used to predict where an introduced species might spread based on associations between the species' current range and the climatic conditions present there (Peterson, 2003). Therefore, this approach assumes (among other assumptions) that the climatic conditions included in the model are what limit the distribution of the introduced species, and that these species will continue to occupy similar climates over time and across geographic regions (i.e., niche conservatism; Thuiller et al., 2005). To test this latter assumption, previous work has compared introduced plant species' climatic niches in their native and introduced ranges (Petitpierre et al., 2012; Early & Sax, 2014; Atwater et al., 2018; Liu et al., 2020; Bates & Bertelsmeier, 2021; Sychrová et al., 2022; Cao Pinna et al., 2025; Riera et al., 2025). Some studies have concluded that climatic niche shifts are rare in introduced plant species (e.g., Petitpierre et al., 2012; Liu et al., 2020; Riera et al., 2025), while others have determined that they are common (e.g., Early & Sax, 2014; Atwater et al., 2018; Cao Pinna et al., 2025). However, methods and interpretations differ across studies, pointing to a lack of consensus regarding how to define a climatic niche shift (Bates & Bertelsmeier, 2021).

Climatic niche shifts occur in introduced species when the set of environmental conditions occupied in the native range differs in the introduced range (Bates & Bertelsmeier, 2021). Climatic niche shifts in analogous climates can be separated into two types: niche expansions, which occur when a species occupies climates in its introduced range that are present but unoccupied in its native range, and niche unfilling, which occurs when a species occupies climates in its native range but not in its introduced range (Guisan et al., 2014). While a niche expansion represents a 'true' niche shift (e.g., caused by adaptation and/or a change in biological interactions), unfilling may just be a temporary artifact of dispersal limitation (Petitpierre et al., 2012). Though niche unfilling could also reflect a permanent niche contraction, it is difficult to know whether observed unfilling is temporary or permanent, making unfilling an unreliable indicator of niche shift (Petitpierre et al., 2012). When evaluating whether a niche shift has occurred in an introduced species, it is therefore essential to differentiate between expansion and unfilling as the two types of niche shifts. To my knowledge, no study has explored the prevalence of niche expansions for a large group of introduced plant species.

While the question of whether introduced species conserve their climatic niches is fundamental in invasion biology, it also has significant practical implications. SDM predictions vary based on whether a species' native or introduced range is used to train the model, and this difference is most pronounced in cases where a niche shift has occurred (Atwater & Barney, 2021). However, the assumption of climatic niche conservatism often goes untested when building SDMs to forecast introduced species' potential distributions. Though SDMs remain very popular for predicting introduced plant spread (Evans et al., 2016; Srivastava et al., 2019; Jarnevich et al., 2023), there is no standardized method for selecting what set of occurrence data (native or introduced range) to train the models with. It is critical to verify the underlying assumptions of these models (e.g., niche conservatism) and ensure appropriate interpretation to improve the utility of SDM predictions for invasive species management.

In this thesis, I examine the frequency and characteristics of niche shifts, and their implications for predicting the distributions of terrestrial introduced plant species in North America. In Chapter 1, I explore the use of SDMs for predicting invasive plant distributions. I present a case study of *Vincetoxicum rossicum*, an aggressive invasive plant species in eastern North America, and discuss the building and interpreting of SDMs in the context of niche expansion. In Chapter 2, I evaluate the prevalence of climatic niche shifts in 663 introduced plants species in North America by differentiating between expansion and unfilling as different types of niche shift. Furthermore, I investigate climatic patterns of niche expansions and identify regions of North America that contain climates that are frequently expanded into. By improving our understanding of the niche dynamics of introduced plant species and their implications for model building, we will be able to better predict the spread of these species.

Chapter 1: Niche expansion in an invasive plant has significant influence on the modelling of its current and future geographic distributions

Abstract

Species distribution models (SDMs) are commonly used to predict the potential distributions of invasive species; however, these models rely on assumptions that often go untested when applied to invasive species. To determine what climatic conditions may be suitable for invasion using SDMs, it is critical to assess whether the species occupies the same climatic niche in its native and invaded ranges (niche conservatism). If this assumption is not met, current distribution-climate relationships will not be predictive of future climatic suitability. I tested for climatic niche shift and trained SDMs on the native and invaded ranges to forecast the potential distribution of *Vincetoxicum rossicum*, an invasive plant species in North America. I found that *V. rossicum* has expanded its niche in North America into wetter climates and climates where precipitation is more evenly distributed throughout the year compared to its native range. As a result, native- and invasive-trained models differed greatly in their predictions of climatic suitability for *V. rossicum* across North America. Given the niche shift, the invasive-trained models are likely more representative of the invasion context than the native-trained models for assessing where *V. rossicum* could spread. However, my analysis revealed that a large portion of the climate in North America was non-analogous to the current invaded range. Consequently, the native-trained model produced predictions of broader geographic scope, identifying potential climatic suitability for *V. rossicum* across a larger area of North America than the invasive-trained models. My results suggest that the native-trained model could be used to fill gaps in regions outside the geographic scope of the invasive-trained model. Combining predictions from models trained on each range increases confidence where they align. This study provides a

framework for building biologically meaningful SDMs for invasive species, particularly those that have undergone niche shifts.

Introduction

Invasive plants threaten ecosystems and native biodiversity around the world (Vilà et al., 2011; Pyšek et al., 2012). They are known to alter ecosystems in several ways, such as by out-competing native species, altering species interactions, and influencing nutrient cycling processes (Liao et al., 2008; Maron & Marler, 2008; Vilà et al., 2011; Pyšek et al., 2012; Grove et al., 2017). Invasive plant species are expected to shift their ranges as the climate changes (Bellard et al., 2013; Fernández De Castro et al., 2018; Rockwell-Postel et al., 2020; Wang et al., 2022). Consequently, it is critical to understand and forecast the invasion patterns of these plants to inform prevention and control efforts.

Species distribution models (SDMs) are a commonly used tool to predict the potential range of invading species based on associations between species occurrence records and climatic conditions in their native and/or invaded ranges (Václavík & Meentemeyer, 2012; Evans et al., 2016). Two of the key assumptions of SDMs are that (1) the current distribution of a species reflects the full range of suitable habitats for the species (environmental equilibrium) and (2) niches change slowly over timescales relevant to ecological predictions such that species will continue to occupy similar climatic conditions in the future (niche conservatism; Thuiller et al., 2005; Kharouba & Williams, 2024). However, these assumptions are often not valid for invasive species because they could be actively spreading in the invaded range and/or expanding into new climatic conditions, such as through adaptation or a shift in biological interactions (Pearson & Dawson, 2003; Václavík & Meentemeyer, 2012; Sotka et al., 2018; Bates & Bertelsmeier, 2021). If these assumptions are not met, current distribution-climate relationships will not be predictive of future climatic suitability; therefore, invasive-species SDMs must explicitly test both.

Previous work has shown that introduced plant species often occupy different climatic conditions in their native and invaded ranges, which could indicate a niche shift has occurred, violating the second assumption (Atwater et al., 2018; Bates & Bertelsmeier, 2021). Given this potential for niche differences between the native and introduced range, the choice of training range (i.e., whether species occurrence records used in the model come from the native range or the invaded range) for building SDMs should have implications for predictions (Atwater & Barney, 2021). However, there is no standard approach to this range selection; all three possibilities have been previously suggested as the best way to train SDMs: the native range (e.g., Petitpierre et al., 2012; Liu et al., 2020), the invaded range (e.g., Atwater & Barney, 2021; Young et al., 2025), or a combination of both ranges (e.g., Broennimann & Guisan, 2008).

Vincetoxicum rossicum (Kleopow) Barbar., commonly known as dog-strangling vine, is an aggressive invasive species from Ukraine and southwestern Russia that established in southeastern Ontario and the northeastern United States beginning in the late 1890s (Pringle, 1973; Sheeley & Raynal, 1996; DiTommaso et al., 2005). The spread of *V. rossicum* has led to a decrease in plant, insect, and soil biodiversity (Ernst & Cappuccino, 2005; Bugiel et al., 2018; Carboni et al., 2021). Like many other invasives, this species is very difficult to control once it has established in an area (DiTommaso et al., 2005). Consequently, it is important to identify regions that are at risk of future invasion by *V. rossicum*.

V. rossicum appears to be at equilibrium with respect to the climate space it occupies in its invaded range in North America (Foster et al., 2022). As this meets the first assumption of SDMs, there is support for the potential use of SDMs in predicting the future distribution of *V. rossicum*. However, Foster et al. (2022) also found that *V. rossicum* is continuing to expand its geographic range in North America with no indication of how far this expansion could get in the future. This expansion in geographic space could be because of a niche shift (i.e., violating the second assumption of SDMs). If this is the case, the climatic conditions occupied by *V. rossicum* in its native range would not be appropriate to use to forecast the future climatic suitability across North America.

Here, I evaluate the best approach for predicting the future range of invasive plant species using *V. rossicum* as a case study. I do this by: (1) conducting a niche overlap analysis: determining whether this species occupies different climatic conditions in its native and invaded ranges; (2) considering different future climate scenarios, a common approach in forecasting with SDMs; and (3) explicitly identifying areas of North America that are non-analogous to the climates where this species is currently found, as model predictions should not be made in non-analogous areas (Elith et al., 2010). This study demonstrates the importance of niche overlap analyses on forecasts generated by SDMs for invasive species.

Methods

Occurrence data

I collected and cleaned occurrence records for *Vincetoxicum rossicum* from the Global Biodiversity Information Facility (GBIF; www.gbif.org) and the Early Detection and Distribution Mapping System database (EDDMapS; www.eddmaps.org). In total, there were 10,079 records in North America (Canada and the United States) and the native range (Russia and Ukraine). I removed all entries in GBIF that listed iNaturalist as their source, and retained these records as a separate, independent dataset for model evaluation. All other records (i.e., other observations and herbarium records from EDDMapS and GBIF) were used as the training dataset. I thinned the occurrence records to one record per grid cell at 5-minute resolution to reduce the effect of sampling bias in the models (Figure 1.1). For the training dataset, this resulted in 66 records in the native range and 456 records in the invaded range. For the evaluation dataset, this resulted in 640 records (in the invaded range).

I defined the native range with a 500-km buffer around recorded occurrences in Ukraine and Russia, and the invaded range with a 300-km buffer around occurrences in Canada and the United States (Figure 1.1). The buffer sizes were chosen to reflect the geographic areas that *V. rossicum* has had access to over its history in each range (VanDerWal et al., 2009). Consequently, the invaded-range buffer is smaller than the native-range barrier since *V. rossicum* has had less time to disperse and establish in the invaded range. These ranges were used as the background/training areas for the niche overlap analysis, climatic similarity analysis, and SDM building.

Climate data

For the current-day climate, bioclimatic data (averaged from 1970–2000) was obtained from WorldClim (Fick & Hijmans, 2017). Out of the 19 bioclimatic variables available from WorldClim, I identified eight variables that are most biologically relevant for *V. rossicum* based on previous work (Table S1.1; Petitpierre et al., 2017; Foster et al., 2022). Climate data was set to 5-minute resolution and cropped to the regions of interest (the native and invaded ranges, as defined with the buffers, and North America).

Future projections for bioclimatic variables were obtained from the same source (Fick & Hijmans, 2017). I chose two future scenarios for climate projections based on the shared socioeconomic pathways (SSP) framework (IPCC, 2023). These scenarios are SSP2, which represents ‘middle-of-the-road development’, and SSP5, which represents ‘fossil-fueled development’. Future projections were used for the year 2060 (bioclimatic data averaged from 2040–2060) with the HadGEM3-GC3.1 global circulation model (Williams et al., 2018).

Niche overlap analysis

I compared *V. rossicum*’s niches between the native range and invaded range by quantifying the degree of stability, expansion, and unfilling using the ‘ecospat’ package in R (Di Cola et al., 2017). ‘Stability’ here refers to the climate space occupied by *V. rossicum* in both the native and invaded ranges, while ‘expansion’ is space occupied only in the invaded range, and ‘unfilling’ is space occupied only in the native range (Guisan et al., 2014). Using the selected bioclimatic variables (Table S1.1), I performed a principal component analysis (PCA) of *V. rossicum*’s native and invaded ranges. Climate space was defined with the first two axes of this PCA.

To determine which climatic conditions differ between *V. rossicum*’s two ranges, I repeated this niche overlap analysis with each of the eight climate variables individually. Expansion, stability, and unfilling indices were calculated in the same way for each individual climate variable.

Climatic similarity analysis

I used multivariate environmental similarity surface (MESS) analyses to identify non-analogous climates in North America (i.e., climates not found in a training range) with the ‘predicts’ package in R (Elith et al., 2010; Hijmans, 2024). This analysis randomly samples cells in a given background area to generate a range of values for each climate variable. It then compares these background values to corresponding values from each cell of a given projection range to identify non-analogous climates (i.e., climates not found in the background area) in the projection range. MESS values greater than 0 mean these cells are climatically analogous to the training range, whereas values less than 0 reflect non-analogous climate.

I used MESS analyses to compare the two training ranges (native range and invaded range, as defined with the 500-km and 300-km buffers) to three projection ranges (current North America, 2060 North America under SSP2, and 2060 North America under SSP5). Areas in the projection range that had MESS values less than or equal to 0 were considered non-analogous to the training range and were excluded from model projections.

Species distribution models

For the bioclimatic variables (Table S1.1), I evaluated the variance inflation factors (VIF; i.e., correlated if VIF > 10) using the 'usdm' package in R (Naimi et al., 2014) across North America and the native range combined. This process resulted in five bioclimatic variables for use in the SDMs (Table S1.2). The same variables were used in all models.

Using the selected bioclimatic variables, I built SDMs with Maxent. Maxent is a species distribution modelling algorithm designed for use with presence-only data (Phillips et al., 2006). For each cell in the projection area, Maxent generates a 'suitability' value from 0 (low) to 1 (high) representing an estimate of how closely the conditions in the cell correspond to conditions occupied by the species in the training region (Elith et al., 2011). I used the 'ENMeval' package in R (Muscarella et al., 2014) to set model parameters and generate models (Table S1.3).

For background point selection, I used a target-group background approach for each training range that reflected the sampling effort for similar species (Barber et al., 2022). The target group for North America included the rest of the Apocynaceae family and seven invasive forbs that are common and widespread in the region (Table S1.4). The target group for the native range included all records from the genus *Vincetoxicum* (Table S1.4). For each set of models generated (native-trained set and invaded-trained set; Table S1.3), the optimal model parameters were selected by minimizing the Akaike information criterion (AIC; Table S1.3). Each selected model was then projected to the current climate, the 2060 climate under SSP2, and the 2060 climate under SSP5. This generated a total of six maps, with three from each training area (native range and invaded range).

To aid visualization, I partitioned model suitability values into three classes (i.e., bins). To do so, I extracted suitability values for the current time period from cells where *V. rossicum* is present. For this set of suitability values, I defined thresholds for high, moderate, and low suitability as values corresponding to the 50th percentile and above (high), the 5th to 50th percentile (moderate), and the 1st to 5th percentile (low). 'Not suitable' cells had suitability values below the 1st percentile. These thresholds were also applied to the corresponding future models. MESS analysis was used to identify non-analogous climates as described above.

Evaluating model performance

Using the independent evaluation dataset, I calculated a continuous Boyce index for each model with a modified function from the 'ecospat' package (Di Cola et al., 2017). This metric is used to evaluate model performance using presence-only data. It is calculated with a Spearman correlation between classes of predicted suitability and predicted-to-expected ratios of cells in those classes (Hirzel et al., 2006). High predictive accuracy is based on the frequency of presences occurring more often in cells that are predicted to have high suitability. The Boyce index can range from -1 to +1, where a value close to 1 reflects a model with high predictive accuracy, a value near 0 means there is a random distribution of presences with respect to model predictions, and a value near -1 indicates cells with low predictive accuracy (i.e., that presences occur more frequently in cells lower predicted suitability).

Model comparison

To assess the differences in model projections, I generated maps showing the overlap in total suitable areas (low, moderate, and high suitability together) between the native-trained model and the invasive-trained model both projected to (1) the current climate, (2) the 2060 climate under SSP2, and (3) the 2060 climate under SSP5.

Results

Niche overlap analysis

Comparing *Vincetoxicum rossicum*'s invaded niche to its native niche revealed that a large niche shift has occurred (Figure 1.2). Over one third of *V. rossicum*'s current occupied climatic niche in North America was present but not occupied in its native range (expansion = 34.4%), signifying that a niche expansion has happened. A considerable proportion of *V. rossicum*'s current occupied climatic niche (stability = 65.6%) in the invaded range was the same as the native range. Finally, many conditions occupied in the native range (unfilling = 72.4%) were not occupied in the invaded range.

V. rossicum's niche expansion occurred primarily along precipitation gradients, including annual precipitation (expansion = 88.8%), precipitation of wettest quarter (expansion = 42.1%), precipitation of coldest quarter (expansion = 14.9%), and precipitation seasonality (expansion = 13.9%; Figures 1.3E-H). In each case, *V. rossicum* occupied wetter regions in North America than in its native range (Figures 1.3E-H). In contrast, there was little differentiation along temperature gradients (all <1% expansion), other than a narrower set of temperature seasonality conditions being occupied in the introduced range compared to the native range (Figures 1.3A-D).

Climatic similarity analysis

The MESS analyses showed that much of North America was climatically analogous to the current native range (62.0% for the current climate, 56.8% for 2060 under SSP2, and 54.8% for 2060 under SSP5; Figure 1.4A; Table 1.1). In comparison, only a quarter of the climate space in North America was climatically analogous to the current (26.0%) and future (26.9% for 2060 under SSP2, 24.4% for 2060 under SSP5; Figure 1.4B; Table 1.1) invaded range.

Predictors of climatic suitability in species distribution model

Precipitation seasonality and precipitation of wettest quarter were the most important variables in both the native- and invasive-trained models (Table 1.2). The invaded range was associated with lower precipitation seasonality values and higher precipitation of wettest quarter values compared to the native range (Figures 1.3F-G).

All models had very high predictive accuracy (Boyce index ~99%; Figure 1.4).

Model comparison

Overall, there was a greater difference in model predictions between the two training ranges (native vs. invaded) than there was between time periods (current day/2060) or climate scenarios (Figure 1.4). Models trained on the native range (Figure 1.4A) and then projected to the current climate in North America predicted a much larger area (33.3%; Table 1.1) of habitat suitability (low, moderate, or high) than models trained on the invaded range (7.0%; Figure 1.4B; Table 1.1). In particular, the native-trained model predicted that large amounts of area towards the east and west coasts of North America could be suitable for *V. rossicum*. In contrast, given that these areas were climatically non-analogous to the current invaded range, there were no predictions for these areas from the invasive-trained model.

Projections to 2060 also differed by training range. The native-trained models projected to the 2060 climates under SSP2 and SSP5 predicted a decrease in the total amount of suitable area compared to current day (33.3% of North America in current day, 25.5% in 2060 SSP2, and 22.6% in 2060 SSP5; Figure 1.4; Table 1.1). Conversely, the invasive-trained model predicted an increase in the total amount of suitable area under both scenarios compared to the invasive-trained model projected to the current climate (7.0% of North America in current day, 11.5% in 2060 SSP2, and 11.2% in 2060 SSP5; Figure 1.4B); predictions also showed an overall increase in suitability levels (i.e., more high and moderate suitability areas relative to low suitability areas; Table 1.1). For all 2060 models, a northward shift of suitable climates was predicted (Figure 1.4).

Model predictions between the two training ranges shared some overlap in geographic space (Figure 1.4C). Unsurprisingly, the overlap corresponded largely to *V. rossicum*'s current range in North America.

Discussion

In this study, I demonstrated how a niche shift affected SDM predictions of the future range of an invasive plant species. I found that suitability predictions from SDMs varied significantly depending on whether models were trained on the native or invaded range, and that the choice of training range was more influential on the model predictions than differences between time periods or climate scenarios. This difference is consistent with my findings that that *Vincetoxicum rossicum* has undergone a large niche expansion in North America, and that a large portion of the climate in North America (74%) was non-analogous to the current invaded range. As a result, the invasive- and native-trained models provided complementary insights into this species' potential future distribution.

I found that *V. rossicum* had low niche conservatism associated with precipitation variables but high conservatism along temperature axes. *V. rossicum* has expanded its niche in North America into wetter climates and climates where precipitation is more evenly distributed throughout the year. In comparison, it did not expand along temperature axes. This result is consistent with Häkkinen et al. (2022), who found that introduced plants generally expand into wetter climates compared to their native ranges but not into hotter or colder climates. The patterns I observed in *V. rossicum*'s niche expansion suggest that this species could continue to expand into new precipitation conditions as it reaches new climates in North America. The niche expansion suggests that the invasive-trained model is likely to represent a closer approximation of *V. rossicum*'s current climatic niche in North America than the native-trained model, and therefore the future predictions from the invasive-trained models are likely to be more representative of the invasion context compared to the native-trained model.

My analysis revealed that a large portion of the climate in North America (74%) was non-analogous to the current invaded range, whereas only 38% of North American climate was non-analogous compared to the native range. Consequently, the native-trained model produced predictions of broader geographic scope, identifying climatic suitability for *V. rossicum* across a larger area of North America than the invasive-trained models. For example, the native-trained models predicted that large areas in western Canada and the United States could be moderately or even highly suitable for *V. rossicum*, whereas this was an area for which there was insufficient data in the current invaded range to generate predictions. My study suggests that the native and invaded ranges each capture different factors important to modelling and are therefore both necessary for future projections. While the invasive-trained model is likely more representative of the invasion context in the geographic regions for which it can make predictions, the native-trained model serves to fill in the gaps in regions that are beyond the geographic scope of the invasive-trained model. In addition, combining predictions from models trained on each range can provide greater certainty in areas where they align.

I also found that a large portion of conditions occupied in the native range were not occupied in the invaded range. This change may indicate a niche contraction, or that *V. rossicum* has not been able to colonize these locations yet due to a dispersal barrier in North America, such as time or geographic distance (Mainali et al., 2015). *V. rossicum*'s invasion in North America is still relatively recent—this species reached the United States and Canada in the late 1800s and has since spread throughout southern Ontario, the northeastern United States, and nearby regions (Sheeley & Raynal, 1996; DiTommaso et al., 2005). However, when comparing *V. rossicum*'s current geographic distribution to the predictions from the native-trained models, we see that the species has not accessed much of its predicted suitable area in western North America. As a result, it is possible that *V. rossicum*'s geographic range in North America (and also its climatic niche, should *V. rossicum* colonize new climates) could expand if these dispersal barriers are overcome.

I found that the climatic suitability of North America for *V. rossicum* in the future is likely to change in a few ways. Based on the native-trained model, the suitability is predicted to decrease by 2060. This result indicates that areas predicted as currently highly suitable, including western North America, could become less suitable for *V. rossicum* as the climate changes. On the other hand, the invasive-trained models predicted an increase in the total amount of suitable climate by 2060. This finding suggests that the changing climate may facilitate *V. rossicum*'s spread in and around its current invaded range in eastern North America, but not as much towards western North America. Furthermore, the models predict a northward shift of suitable climates in the future, which would allow this species to exploit areas that were previously unsuitable. My results agree with existing studies that have modelled future North American climatic suitability for invasive plants, which show mixed changes in total suitable area but show a general northward shift (Peterson et al., 2008; Banerjee et al., 2020; Wang et al., 2022).

My predictions align with the current potential distribution of *V. rossicum* in northeastern North America modelled by Foster et al. (2022), which also used Maxent models. In contrast, my results differ from Westbrook et al. (2023), which used CLIMEX models and global occurrences (including its native range, invaded range in North America, and introduced ranges elsewhere) to model *V. rossicum*'s current potential distribution. Notably, their models predicted a continuous area of suitable climate across the entire continent from east to west, whereas my models predicted a large area within the interior of the continent as not climatically suitable for *V. rossicum*. This difference could be caused by algorithm choice and variable selection, since these CLIMEX models considered only mean annual temperature and precipitation (Westbrook et al., 2023); however, my models indicated that precipitation seasonality was the most influential variable for *V. rossicum*'s distribution forecasts, and this variable was not included in the CLIMEX models from Westbrook et al. (2023).

A known limitation of correlative SDMs is their reliance solely on bioclimatic variables (Gallien et al., 2010; Peterson et al., 2015). They do not account for differences in biotic interactions between training and projection areas, like competition and herbivory, which could affect *V. rossicum*'s spread or persistence (and therefore decrease the accuracy of SDM projections). For example, in its native range, *V. rossicum* is host to multiple specialist insect herbivores, whereas there is little evidence that any animals native to North America feed on this plant (DiTommaso et al., 2005). Future studies should focus on incorporating biotic interactions into SDMs for this species. This work would further our understanding of how species interactions influence geographic range limits for *V. rossicum* and contribute to more accurate distribution forecasts.

Management implications

The knowledge of future climatic suitability of North America for *V. rossicum* has important implications for management planning. Current areas of North America that have the highest predicted suitability and consequently are most at risk for invasion are Atlantic Canada, the American mid-Atlantic, and western Canada and the United States around the Rocky Mountains. Consequently, these areas should be prioritized for efforts to prevent its establishment (e.g., early detection and removal programs). However, efforts to control *V. rossicum* along the leading edge of the invasion in eastern North America may only succeed in slowing its expansion in that region, as propagule pressure is likely to increase over time. In contrast, the relative isolation of suitable areas in the west suggests that *V. rossicum* invasion will be more dependent on rare long-distance dispersal events and will be more difficult to predict. Nevertheless, early detection and control may prevent *V. rossicum* from establishing a beachhead this far from source populations.

Conclusions

This study provides a framework to build a biologically meaningful SDM for an invasive plant species by (1) testing for a climatic niche shift between the native and invaded range; and (2) quantifying non-analogous climates. When a niche shift has occurred, invasive- and native-trained SDMs can provide complementary insights due to the better representation of the invasion context from the invasive-trained model but larger geographic scope of the native-trained model. This approach to building and interpreting SDMs has the potential to be used in forecasting the spread of other invasive plant species. For *Vincetoxicum rossicum*, predicting its spread in North America in response to changes in climate has significant implications for helping guide prevention and control efforts. These efforts should be focused on the at-risk areas indicated by the models, especially where *V. rossicum* has not yet had an opportunity to establish.

Tables

Table 1.1. Area and percent of North America for each suitability level in models projected to the current climate, the 2060 climate under SSP2 (‘middle-of-the-road development’), and the 2060 climate under SSP5 (‘fossil-fueled development’).

Suitability	Native-trained		Invasive-trained	
	Area (km^2)	% area	Area (km^2)	% area
Current climate				
Not suitable	5,767,775	28.7	3,818,952	19.0
Low	2,685,983	13.4	727,032	3.6
Moderate	2,262,335	11.2	648,633	3.2
High	1,751,567	8.7	41,662	0.2
Non-analogous	7,645,336	38.0	14,876,715	74.0
2060 climate under SSP2				
Not suitable	6,129,176	31.4	3,014,788	15.4
Low	2,374,671	12.2	1,127,578	5.8
Moderate	1,710,442	8.8	1,079,769	5.5
High	887,209	4.5	35,845	0.2
Non-analogous	8,428,834	43.2	14,272,353	73.1
2060 climate under SSP5				
Not suitable	6,297,549	32.2	2,582,315	13.2
Low	2,065,488	10.6	820,954	4.2
Moderate	1,714,794	8.8	1,264,727	6.5
High	620,904	3.2	103,313	0.5
Non-analogous	8,831,598	45.2	14,759,023	75.6

Table 1.2. Percent contribution and rank of climate variables for each model.

Variable	**Native-trained model**		**Invasive-trained model**	
	% Contribution	Rank	% Contribution	Rank
Precipitation seasonality	54.8	1	35.4	1
Precipitation of wettest quarter	19.8	2	34.5	2
Precipitation of coldest quarter	16.9	3	2.1	5
Mean temperature of warmest quarter	5.8	4	8.5	4
Temperature seasonality	2.8	5	19.5	3

Figures

Figure 1.1. Occurrences of *Vincetoxicum rossicum* in the North American invaded range for the evaluation dataset (n=640) and the training dataset (n=456), and occurrences in the native range training dataset (n=66). Range bounds, as defined with buffers (500 km for the native range and 300 km for the invaded range), are shown. Occurrences are shown after thinning to one record per cell at 5-minute resolution.

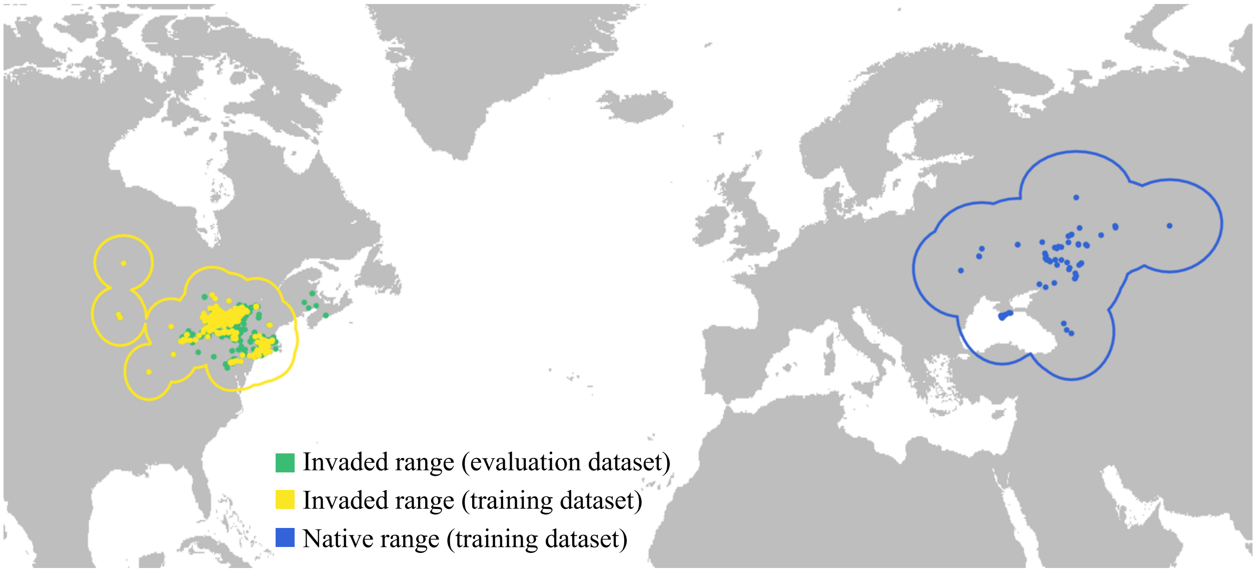


Figure 1.2. Comparison in climate space (A) and in geographic space (B) for *Vincetoxicum rossicum*'s niche in its native range and its invaded range. In (A), PC1 and PC2 represent the first two axes of a principal component analysis of all climate variables (Table S1.1) and together define climate space. The outlines and solid areas represent all climatic conditions present and occupied, respectively, in *V. rossicum*'s native (blue) and invaded (yellow) ranges. Green is their overlap. Density of the invaded-range occurrences is shown with black shading. For this species, 65.6% of climate space is occupied in both the native and invaded ranges (green; stability), compared to 34.4% occupied only in the invaded range (yellow; expansion), and 72.4% occupied only in the native range (blue; unfilling). Note that the darker blue area represents climates that are occupied in the native range but not present in the invaded range. Together, expansion and stability (components of the invaded niche) sum to 100%. The climates that make up the different components of *V. rossicum*'s niche are shown within *V. rossicum*'s geographic range in North America (B), with expansion in yellow, stability in green, and unfilling in blue. *V. rossicum*'s range boundary and occurrences in North America are shown in black.

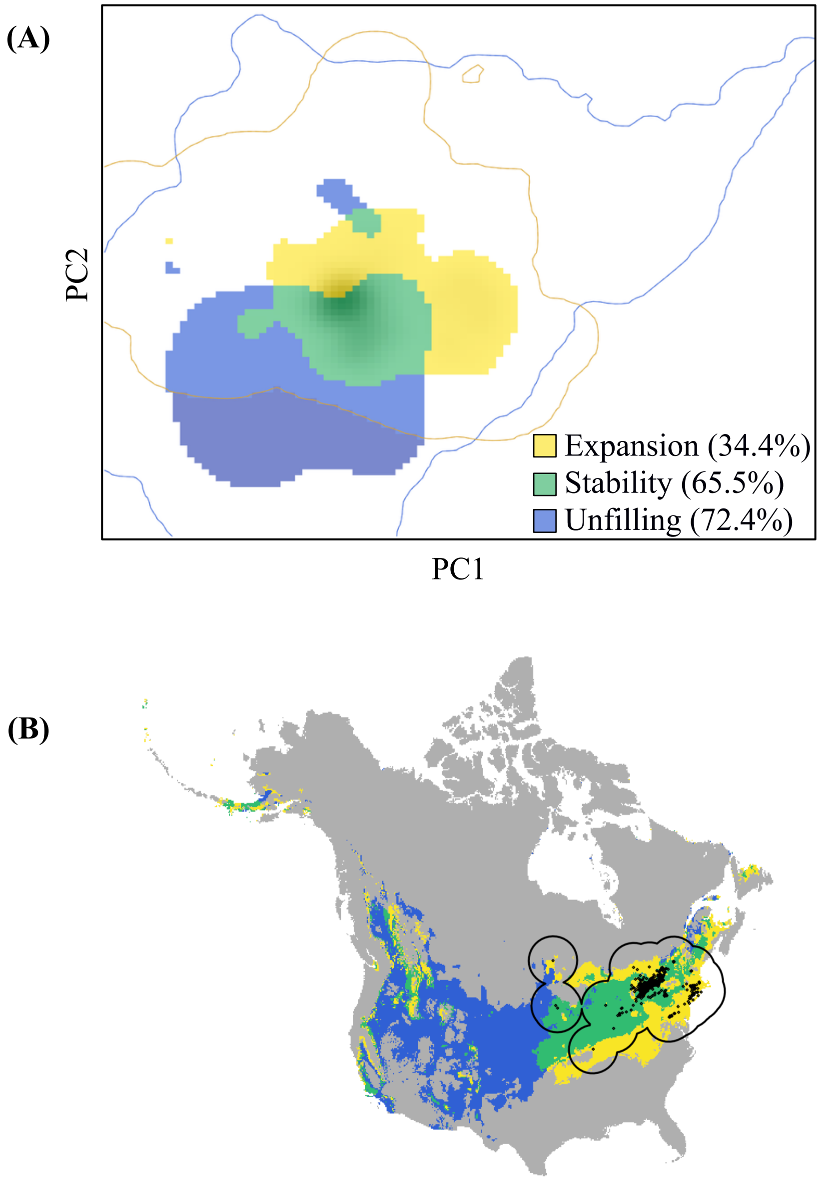


Figure 1.3. Comparison of expansion, stability, and unfilling components for each variable included in quantification of *Vincetoxicum rossicum*'s niche (Table S1.1). The outlines and solid areas represent the frequency of climatic conditions present and occupied, respectively, in *V. rossicum*'s native (blue) and invaded (yellow) ranges. Green is their overlap. The expansion metric is shown for each variable, calculated as the proportion of climate space occupied only in the invaded range (relative to the total size of the invaded range).

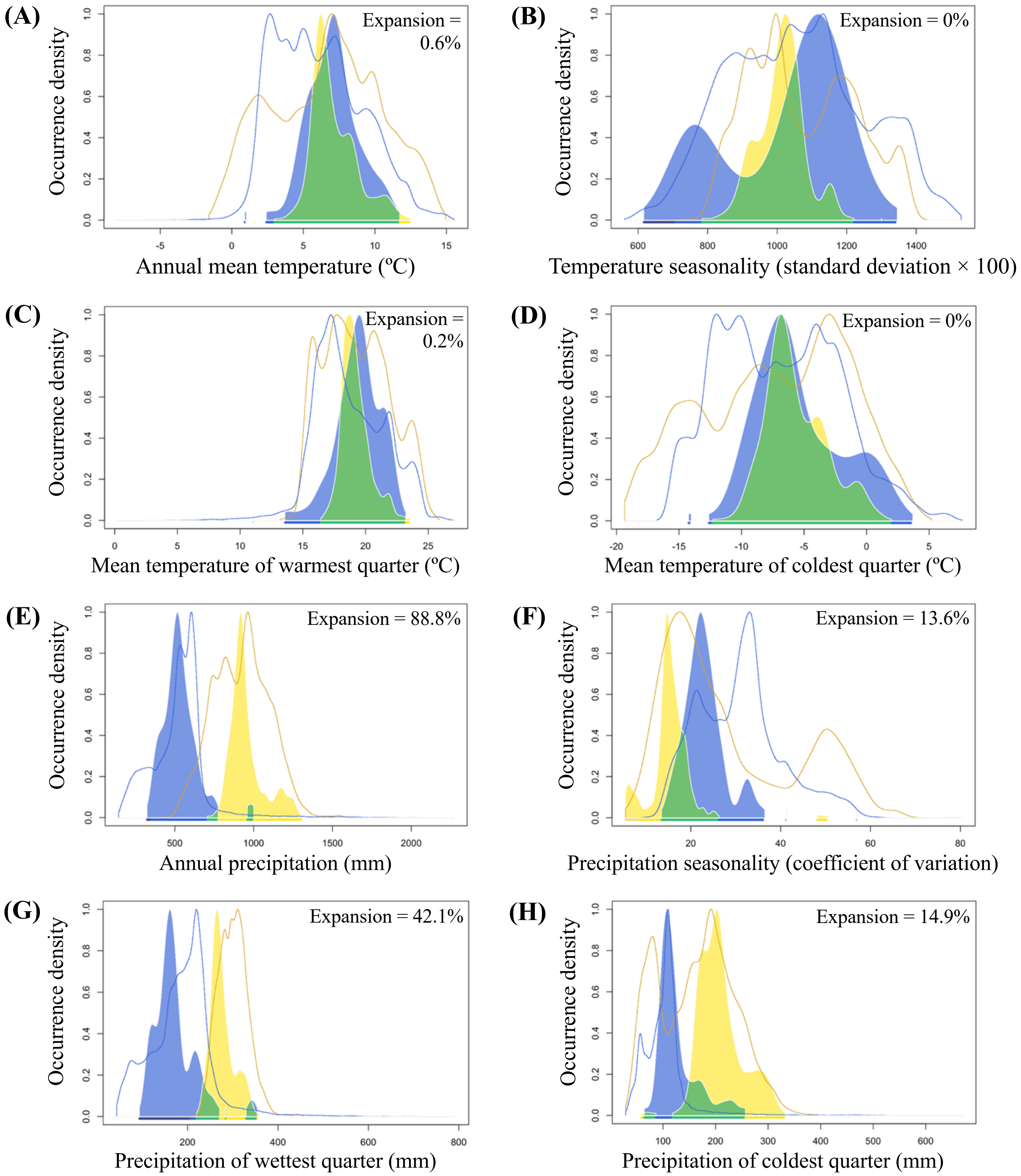
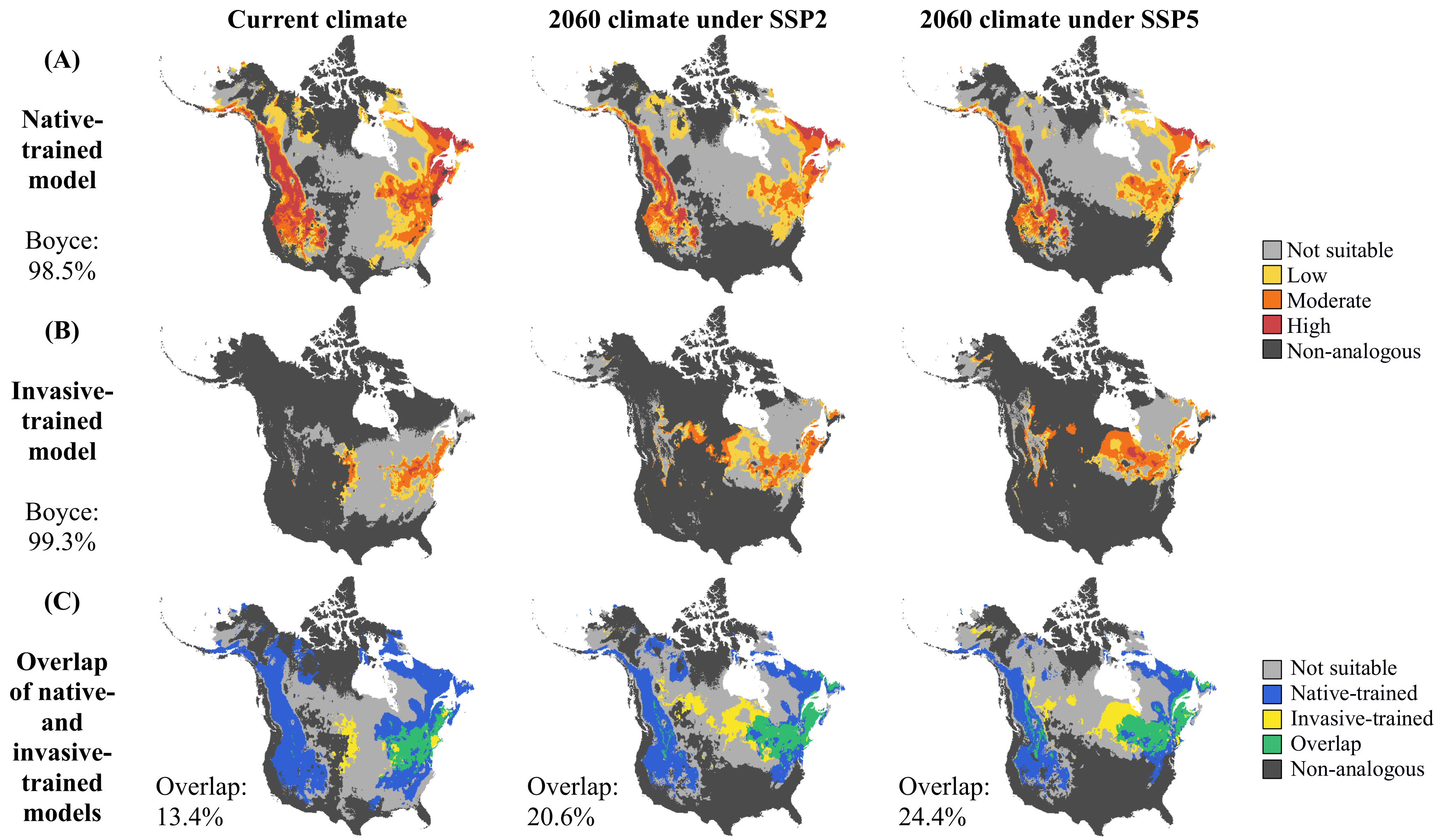


Figure 1.4. Habitat suitability predictions for *Vincetoxicum rossicum* from Maxent, projected to the current climate, 2060 climate under SSP2 (‘middle-of-the-road development’), and 2060 climate under SSP5 (‘fossil-fueled development’) from (A) training on the native range and (B) training on the invaded range. Continuous Boyce indices are shown. Overlap of all suitable areas (C) between the native- and invasive-trained models is shown. The overlap value represents the proportion of overlapping suitable areas (i.e., green areas) relative to the sum of all suitable areas from both models.



Chapter 2: Climatic niche shifts in introduced plant species are driven by niche under-filling

Abstract

As introduced plants continue to spread throughout North America, there is an increasing need to understand and predict their invasion patterns. Climatic niche shifts are an important aspect of invasion patterns and occur when a species occupies different climates in its introduced range than in its native range. Previous work has attempted to evaluate the prevalence of niche shifts in introduced plants in North America but has not distinguished between conditions only occupied in the introduced range (a ‘true’ niche shift) and conditions only occupied in the native range, which could indicate temporary under-filling of the niche rather than an actual niche shift. Using bioclimatic variables, I quantified the degree of niche expansion in climate space for 663 introduced plant species in North America. I found that niche expansions are relatively common; however, my results showed that the prevalence of niche shifts more than doubles when considering both under-filling and expansion as types of niche shifts, as opposed to solely expansion. Therefore, it is important to consider under-filling and expansion separately so as to not underestimate introduced plant species’ potential distributions in their introduced ranges or overestimate the prevalence of ‘true’ niche shifts. I also quantified the degree of expansion in each of the bioclimatic variables to determine under what climatic conditions expansion is occurring. I found that these species are primarily expanding into wetter climates and into climates with higher seasonality for both temperature and precipitation. Therefore, these climatic conditions may be less likely to limit the spread of introduced plant species as would be predicted by distribution forecasts. This study highlights the importance of separating expansion and under-filling when quantifying climatic niche shifts to better understand the invasion patterns of introduced plant species and predict their spread.

Introduction

As introduced plants are expected to continue to spread rapidly across North America under climate change (Bradley et al., 2024), there is an increasing need to understand and predict their potential distributions in their introduced ranges. Early detection and prevention are often more effective at limiting plant invasions than removal efforts after they become established (Rockwell-Postel et al., 2020; Jarnevich et al., 2023). Consequently, forecasting the spread of introduced plants is critical; however, these predictions require an understanding of their dynamics in niche and geographic space.

Methods that quantify a species' climatic niche and project it into geographic space, like correlative species distribution models (SDMs), are frequently used in predicting species' potential geographic distributions (Evans et al., 2016; Srivastava et al., 2019). SDMs assume that a species' niche is static over a given geographic range and ecological time, and therefore that the niche is transferrable across large spatial extents (i.e., niche conservatism; Thuiller et al., 2005). However, this assumption has been contested for introduced plant species when niche shifts have been documented (Early & Sax, 2014; Atwater et al., 2018; Bates & Bertelsmeier, 2021). Climatic niche shifts in introduced species occur when the set of environmental conditions occupied in the native range differs from the introduced range (Bates & Bertelsmeier, 2021). Niche shifts can arise from adaptation, altered biological interactions, or exposure to novel climatic conditions, leading to mismatches between the climatic conditions occupied in the native and introduced ranges (Pearson & Dawson, 2003; Soberon & Peterson, 2005; Petitpierre et al., 2012; Liu et al., 2020; Bates & Bertelsmeier, 2021). When models rely on data from the native range, such mismatches can undermine the accuracy of forecasts for introduced species, limiting our ability to proactively manage and constrain their spread (Atwater & Barney, 2021).

Previous attempts to evaluate niche shifts for introduced plants have led to conflicting results about the prevalence and magnitude of shifts (Petitpierre et al., 2012; Early & Sax, 2014; Atwater et al., 2018; Liu et al., 2020; Bates & Bertelsmeier, 2021; Cao Pinna et al., 2025; Riera et al., 2025). Some studies have concluded that climatic niche shifts are rare in introduced plant species (e.g., Petitpierre et al., 2012; Liu et al., 2020; Riera et al., 2025), while others have concluded that they are common (e.g., Early & Sax, 2014; Atwater et al., 2018; Cao Pinna et al., 2025). One possible cause for this discrepancy could be that to quantify niche shifts, many studies use niche overlap metrics that do not distinguish between permanent niche expansions, the occupation of climatic conditions in the introduced range that are present but unoccupied in the native range, and niche unfilling, the absence from conditions in the introduced range that are occupied in the native range (Atwater et al., 2018; Yin et al., 2021; Cao Pinna et al., 2025).

Though niche unfilling can reflect a permanent niche contraction, and thus a niche shift, it very often represents a niche space that is temporarily under-filled as a result of dispersal limitation (Petitpierre et al., 2012). On the other hand, a niche expansion represents a ‘true’ niche shift, since species have had much more time to spread and explore different climates in their native range compared to their introduced range. Therefore, when species occupy climates in their introduced range that they did not occupy in their native range, this shift is much less likely to be a product of dispersal limitation. Studies that treat both expansion and unfilling components as evidence of a niche shift (e.g., Atwater et al., 2018; Cao Pinna et al., 2025) risk underestimating the potential introduced niche, because currently unoccupied niche space may still be colonized as the invasion proceeds (Petitpierre et al., 2012).

Another potential cause of the variation in the prevalence of climatic niche shifts across studies is that niche shifts can occur in both analogous and non-analogous climates. While a species' climatic niche is often compared between climates that currently exist in their native and introduced ranges (i.e., analogous climates; Petitpierre et al., 2012; Guisan et al., 2014), species also have the potential to expand into novel climates in their introduced ranges that do not exist in their native ranges (i.e., non-analogous climates; Early & Sax, 2014; Atwater et al., 2018). This phenomenon is referred to as 'niche pioneering' (Atwater et al., 2018). Pioneering is distinct from expansion because it reflects a limitation of climatic availability—the climates filled in the introduced range do not exist in the native range—rather than a biological constraint. However, pioneering is not often calculated in studies aiming to quantify niche shifts in introduced plant species. Pioneering has major consequences for forecasting an introduced species' potential distribution, as it provides information about how a species may spread as it encounters novel climates (Early & Sax, 2014).

In this study, my first objective is to quantify climatic niche shifts in 663 terrestrial introduced plant species in North America and assess how frequently they occur. To do so, I distinguish between three processes: 'expansion', the occupation of climatic conditions in the introduced range that are present but unoccupied in the native range (indicating a 'true' niche shift); 'unfilling', the absence from conditions in the introduced range that are occupied in the native range (considered here as not evidence of a 'true' niche shift); and 'pioneering', the establishment in novel climates in the introduced range that are absent in the native range. Here, I define 'niche shift' based on expansion only.

The second objective of this study is to characterize the climatic conditions in which niche expansion is most common and to identify geographic regions of North America that contain these climates. Identifying the climatic patterns of niche expansion is important to understand the niche dynamics of introduced plant species and the climatic conditions that may or may not constrain their spread.

Methods

Occurrence data

Using a list of 815 previously identified introduced plant species at the global scale (Atwater et al., 2018), I compiled occurrence records from the Global Biodiversity Information Facility (GBIF; www.gbif.org) for species introduced to North America. For each species, its native distribution was classified using the World Checklist of Vascular Plants (Govaerts et al., 2021) using the 'rWCVP' package in R (Brown et al., 2023). This process resulted in 673 species. I retained occurrence records that belonged to the introduced range in North America (defined by the extent 180ºW to 40ºW and 20ºN to 90ºN; Figure 2.1) and the native range of each species. I identified native-range occurrences as occurrences within countries (or provinces/states for large countries) where the species has been recorded as native, or within a 500-km buffer of these countries.

To reduce the effect of sampling bias, I thinned the occurrence records to one record per grid cell at 5-minute resolution (~9 km at the equator). I kept species that occupied at least five grid cells in each range (introduced range in North America and native range), which is the minimum number of occurrences required to do a niche overlap analysis. This step resulted in 663 species that were used in all analyses (Table S2.1).

Finally, I used a 500-km buffer around each of the native and introduced sets of occurrences to define the native and introduced ranges respectively.

Climate data

For the climate data, I used eight bioclimatic variables from WorldClim (Table 2.1; Fick & Hijmans, 2017). Out of the full set of variables available from WorldClim, these eight are most biologically relevant and cross-continentally transferrable for plants and are therefore most suitable for this study (Petitpierre et al., 2017). All climate data was used at 5-minute resolution.

Niche overlap analysis

To quantify niche shifts, I compared species' current introduced ranges in North America to their native ranges. Using all eight bioclimatic variables (Table 2.1), I performed a principal component analysis (PCA) of the native and introduced ranges for each species. Climate space was defined using the first two axes of this PCA. To contrast the native and introduced ranges for each species as defined in Guisan et al. (2014), I used the 'ecospat' package in R (Di Cola et al., 2017) and calculated four indices: stability, expansion, unfilling and pioneering. 'Stability' refers to the climate space occupied by a species in both the native and introduced ranges, while 'expansion' in this context refers to climate space occupied by a species only in the introduced range (analogous climate only), and 'unfilling' is the climate space occupied only in the native range (Figure 2.2; Guisan et al., 2014). 'Pioneering' refers to climate space that is occupied in the introduced range but does not exist in the native range (i.e., occupation of novel or non-analogous climate; Figure 2.2). I evaluated what proportion of species had values of ≥5% and ≥10% for the expansion, unfilling, and pioneering indices. The 10% threshold has been widely used in the literature as evidence of a significant niche shift (Petitpierre et al., 2012; Liu et al., 2020; Bates & Bertelsmeier, 2021; Häkkinen et al., 2022; Riera et al., 2025), and I included the

5% threshold as a more sensitive metric to verify that my results are independent of the choice of threshold.

Analysis of high-expansion climates

For each of the eight bioclimatic variables (Table 2.1), I repeated the niche overlap analysis for each species to determine how the species' distribution of occurrence density across a given climate variable shifted from the native range to the introduced range. This step follows the same process as the niche overlap analysis but with a single variable. I calculated stability, expansion, and unfilling indices for each variable. I inspected the set of distribution overlap plots associated with individual climate variables that had average expansion across species ≥5%. I qualitatively categorized the directionality of expansion three different ways for each of these variables based on changes in the variable's upper limit, lower limit, or both limits (Figure 2.3).

Analysis of expansion hot spots of North America

For each species, I projected the climate space (based on the first two axes of the PCA, as described above) only occupied in the introduced range (the 'expansion' portion of its niche) to geographic space across Canada and the United States. This step generated a map of cells that had a value '1' if the climate of that cell was a climate that the species has expanded into, and '0' otherwise. Next, I summed these geographically projected expansion maps for all species to obtain a map of expansion hot spots of North America.

Results

Niche overlap analysis

Niche expansion occurred for the majority of species (92%; 613/663; Figure 2.4A; Table S2.1), though most expansions were small in magnitude. For most species, at least some of the occupied climate space of the introduced range reflected climates that were present but unoccupied in the species' native range (i.e., expansion value >0%; Figure 2.4A; Table S2.1). Of the 663 species analyzed, 30.8% (204/663) expanded into ≥5% of this climate space, and 17.9% (119/663) expanded into ≥10% of this climate space (Figure 2.4A; Table S2.1). The median expansion value across all species was 1.5% (Figure 2.4A).

Niche pioneering (i.e., expansion into non-analogous climates) also occurred in most species (65%; 430/663; Figure 2.4B; Table S2.1), but less frequently than niche expansion into analogous climates. Of the 663 species, ≥5% of the occupied climate space was novel for 15.1% of species (100/662) and ≥10% was novel for 11.9% of species (79/663; Figure 2.4B, Table S2.1). The median pioneering value across all species was 0.1% (Figure 2.4B).

Nearly all species (98%; 650/663) under-filled their introduced niches to some degree (Figure 2.4C; Table S2.1), meaning there was some occupied climate space in the native range that was present but not occupied in the introduced range (i.e., unfilling value >0% for 650/663 species). Of the 663 species, 52.8% (350/663) had ≥5% under-filled niche space and 41.2% (273/663) had ≥10% under-filled niche space (Figure 2.4C; Table S2.1). The median unfilling value across all species was 5.5% (Figure 2.4C).

If we consider both unfilling and expansion as indicators of a niche shift, as previous studies have, there is evidence for niche shift in 68.5% of species based on the ≥5% threshold and 51.9% of species based on the ≥10% threshold. In comparison, there is only evidence for a ‘true’ niche shift (i.e., based solely on expansion) in 30.8% of species based on the ≥5% threshold and 17.9% of species based on the ≥10% threshold.

Description of high-expansion climates

I found that the climate variables with the greatest magnitude and prevalence of expansion across species were precipitation seasonality and temperature seasonality (Table 2.2). For these two variables, the average expansion into these spaces across species was ~6% and the median expansion was 0.1% and 0.4%, respectively (Table 2.2). Of the 663 species, ~15% (precipitation seasonality: 98/663, temperature seasonality:104/663) showed ≥5% expansion for these variables. Expansion occurred primarily in the upper limits of the distribution for precipitation seasonality (i.e., into more seasonally variable precipitation; 8.7% of species; 58/663) and into upper limits (i.e., into more seasonally variable temperature; 6.5% of species; 43/663) or both limits (7.4% of species; 49/663) of the distribution for temperature seasonality (Table 2.2).

I also found expansion was primarily toward wetter climates for both the precipitation of wettest quarter (average expansion across species = 2.6%; median expansion = 0.1%) and precipitation of coldest quarter (average expansion across species = 2.9%; median expansion = 0.2%) variables (Table 2.2). Expansion occurred in upper limits of the distribution for these variables (i.e., into wetter conditions) for 5.3% (35/663) and 8.4% (56/663) of species, respectively. There was little expansion and no pattern in directionality seen with annual precipitation (average expansion across species = 1.5%; median expansion = 0.03%; Table 2.2).

Finally, I found some expansion for the mean temperature of warmest quarter (average expansion across species = 2.2%; median expansion = 0.02%) and mean temperature of coldest quarter (average expansion across species = 2.2%; median expansion = 0.1%) variables, with species tending to expand into warmer summers and colder winters (Table 2.2). There was little expansion and no pattern in directionality seen with annual mean temperature (average expansion across species = 1.4%; median expansion = 0.02%; Table 2.2).

Description of expansion hot spots of North America

The regions predicted to have been most expanded into based on their climates were the Pacific Northwest, the western United States, the Gulf Coast of the United States, southern Ontario and Quebec, and the northeastern United States (Figure 2.5). Of particular note, approximately one third of species showed at least some evidence of expansion into the climates found along the coast of Washington and Oregon.

Discussion

In this study, I quantified climatic niche shifts for 663 terrestrial introduced plant species in North America by distinguishing between niche unfilling (absence in the introduced range from conditions occupied in the native range, possibly a consequence of dispersal limitation) and niche expansion (occupation of climatic conditions in the introduced range that are unoccupied in the native range, a ‘true’ niche shift). My results showed that niche expansions, though generally small in magnitude, occur relatively often in introduced plant species. Therefore, models that aim to predict the potential distributions of introduced plant species based on their native-range niches, such as SDMs, may underestimate the species’ geographic invaded range limits given these species’ potential for niche expansion. Consequently, it is critical to identify niche expansions when building SDMs for introduced plant species to inform modelling decisions (e.g., what occurrence data is best to use in model building).

I demonstrated that unfilling is much more common than expansion, such that the prevalence of niche shifts more than doubled when both unfilling and expansion were considered as types of niche shifts. This result reflects a key difference between my study and those that found niche shifts to be common in introduced plant species but included unfilling as an indicator of niche shift (e.g., Atwater et al., 2018; Cao Pinna et al., 2025). Consistent with my results, previous studies have reported that niche unfilling occurs more frequently than niche expansion in introduced plants (Petitpierre et al., 2012; Sychrová et al., 2022; Cao Pinna et al., 2025; Riera et al., 2025). While it is possible that niche unfilling may be the result of permanent niche contraction, these high levels of observed niche unfilling are likely to be at least partly products of dispersal limitation. Unfilled niche space is highly likely to decrease or even disappear as species spread and reach new climate spaces in their introduced ranges (Petitpierre et al., 2012). Consequently, unfilling cannot be considered a reliable indicator of a ‘true’ or permanent niche shift. Considering unfilling as a niche shift would lead us to underestimate the species’ potential introduced niche (and therefore potential introduced range). On the other hand, niche expansion is always a ‘true’ permanent niche shift, since species do not face the same degree of dispersal limitation in their native range (i.e., because species have had much more time to spread and explore different climates in their native range compared to their introduced range). Therefore, it is important to disentangle unfilling and expansion as different types of niche shifts to avoid (1) inflating the estimates of the prevalence of niche shifts in introduced plant species and (2) underestimating introduced plant species’ potential distributions in their introduced ranges.

Furthermore, I found that niche pioneering (i.e., expansion into non-analogous climates) has been frequent across introduced plants in North America, though small in magnitude. This result supports findings by Atwater et al. (2018), who reported that pioneering in introduced plants globally was small on average but was significant for some species. This finding suggests that non-analogous areas in species' invaded ranges, which are typically not considered by SDMs (Elith et al., 2010), could be suitable for invasion by some introduced plants. This implication applies as well for potential pioneering into non-analogous climatic conditions that are expected to arise under climate change. Therefore, existing forecasts of the potential distributions of introduced plant species could be underestimates. This knowledge is critical for building and interpreting models that aim to forecast the potential distributions of introduced species (e.g., SDMs; Early & Sax, 2014). The 'pioneering' component of a species' introduced niche represents climate that the species may not have been expected to occupy based on its native-range occurrences, which would lead to underestimates in native-trained SDMs. This result emphasizes the importance of explicitly identifying non-analogous climates when forecasting the potential distribution of introduced plant species to better understand the potential for introduced plant spread.

My analysis also revealed that introduced plant species are expanding most into climates with higher seasonality for both temperature and precipitation, as well as into wetter climates overall. This pattern of expansion into wetter climates agrees with findings from Häkkinen et al. (2022), who studied a global set of 606 introduced plants. A possible mechanism underlying this pattern is that a plant species could be more strictly physiologically limited by extreme temperatures or by dry conditions, whereas limits into wetter conditions could be driven by biological interactions (e.g., competition) that may change between a species' native and introduced ranges (Häkkinen et al., 2022).

Another possible explanation for the observed expansion into wetter conditions is that mesophication—a process whereby decreased fire frequency continually creates more favourable, wetter conditions for closed-canopy, shade-tolerant species—has shifted moisture gradients at a local scale in North America, leading to disturbed habitats that are more susceptible to invasion (Nowacki & Abrams, 2008; Alexander et al., 2021). At a regional scale, this process could have increased the precipitation levels of ecosystems, disturbing the precipitation patterns and soil properties of those ecosystems. This disturbance, coupled with the overall higher availability of wetter conditions, could increase the frequency of plant invasions in these climatic conditions. Overall, my findings suggest that as introduced plants spread throughout North America, encountering novel precipitation conditions (and in particular wetter conditions) may be less likely to limit their spread than would be expected from SDM predictions compared to encountering novel temperature conditions (e.g., Chapter 1). Therefore, when interpreting predictions of introduced plant species' distributions, we should be more cautious with regards to spread that is predicted to be constrained by these precipitation conditions.

Finally, my analysis revealed that certain areas of North America contain climates that are predicted to have a higher frequency of niche expansion by introduced plants. For these regions in particular, predictions regarding the spread of introduced plants are likely to have higher uncertainty since these species may have increased potential to expand into these climates. Consequently, this study provides support for prioritizing these regions for early detection efforts to prevent invasive plant establishment.

Despite the popularity of the approach that I used to quantify climatic niche shifts, it has several commonly acknowledged limitations. These analyses rely solely on bioclimatic variables at relatively coarse scales, and do not consider other aspects of environment such as soil conditions, anthropogenic disturbance, or microclimates, limiting the degree to which we can capture the niche of a species. Future work should consider which environmental factors beyond climate are likely to constrain the geographic ranges of introduced plant species, and test whether these species conserve their niches with respect to these additional environmental factors. Furthermore, though inherent to this study's approach, it is only possible to estimate unfilling, stability, and expansion indices within climates that are analogous between a species' native and introduced ranges (Guisan et al., 2014). However, the set of available climates varies greatly between continents. It is therefore challenging to conclude whether perceived patterns in species' niche dynamics can be attributed to an underlying biological process, or whether they are simply the result of differing climatic availability. To address this issue, future studies should continue to analyze niche dynamics in analogous and non-analogous climates separately and correct for climatic availability when possible (Chapter 1). Finally, this study relies largely on community science data, which has many known sampling biases (Geurts et al., 2023). The methods used in this study (e.g., data cleaning and spatial thinning) contribute to minimizing these biases.

Conclusions

This study highlights the importance of separating expansion (a 'true' niche shift) and unfilling (possibly niche contraction or temporary dispersal limitation) as types of climatic niche shifts. I found that unfilling is more common than expansion in introduced plant species in North America. Therefore, niche shifts may not be as common as some studies have reported, as the under-filled parts of these species' niches could shrink as the species continue to spread. Accurately identifying and quantifying climatic niche shifts is critical for predicting the future distribution of introduced species in their introduced ranges (Atwater & Barney, 2021). Better understanding the extent of niche shifts among introduced plants will help to determine the adaptive potential of these species and improve distribution forecasting efforts.

Tables

Table 2.1. Set of bioclimatic variables identified as biologically relevant and transferrable for introduced plants and used for niche quantification (Petitpierre et al., 2017).

Variable
Annual mean temperature
Temperature seasonality
Mean temperature of warmest quarter
Mean temperature of coldest quarter
Annual precipitation
Precipitation seasonality
Precipitation of wettest quarter
Precipitation of coldest quarter

Table 2.2. Average and median expansion across species (n=663), and number of species expanding in each direction for each bioclimatic variable.

Variable	Average % Expansion	Median % Expansion	Number of expanding species			
			Upper limit	Lower limit	Both limits	Total
Precipitation seasonality	6.2	0.1	58	25	15	98
Temperature seasonality	5.9	0.4	43	12	49	104
Precipitation of coldest quarter	2.9	0.2	56	1	26	83
Precipitation of wettest quarter	2.6	0.1	35	12	21	68
Mean temperature of coldest quarter	2.2	0.1	10	33	18	61
Mean temperature of warmest quarter	2.2	0.02	33	8	13	54
Annual precipitation	1.5	0.03	14	17	18	49
Annual mean temperature	1.4	0.02	17	19	12	48

Figures

Figure 2.1. Map of extent of North America considered for this study (180ºW to 40ºW and 20ºN to 90ºN), used to identify occurrence records belonging to a species' North American introduced range.

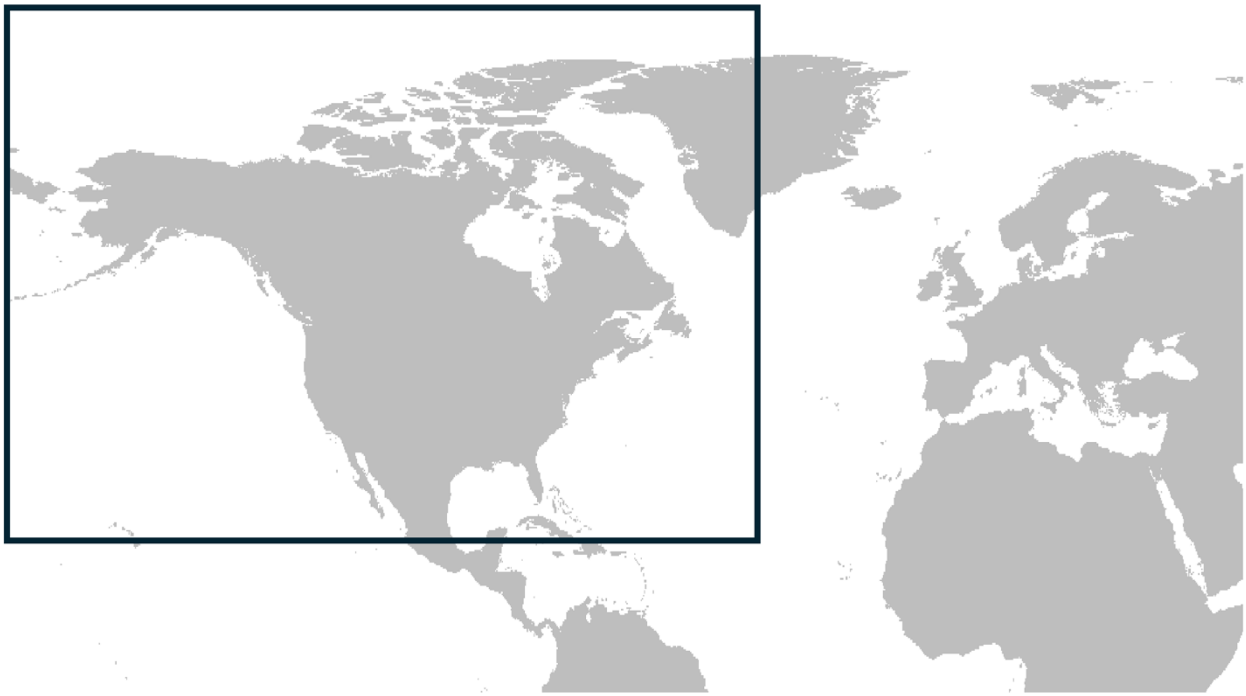


Figure 2.2. Example in climate space of an introduced plant species' niche in its native and introduced ranges. PC1 and PC2 represent the first two axes of a principal component analysis of all climate variables (Table 2.1) and together define climate space. The outlines and solid areas represent all climatic conditions available and occupied, respectively, in this species' native (blue) and introduced (yellow) ranges. Stability (green) refers to climate space occupied by the species in both the native and introduced ranges, expansion (yellow) is occupied only in the introduced range, and unfilling (blue) is occupied only in the native range. Pioneering (pale yellow) is climate space occupied in the introduced range in climates that do not exist in the native range (i.e., non-analogous climates; outside the blue outline), and abandonment (pale blue), not considered here, is climate spaces occupied in the native range in climates that do not exist in the introduced range (outside the yellow outline). Together, expansion and stability make up the entire introduced niche that is analogous to climates within the native range (i.e., inside the blue outline). The arrow shows the direction of niche shift.

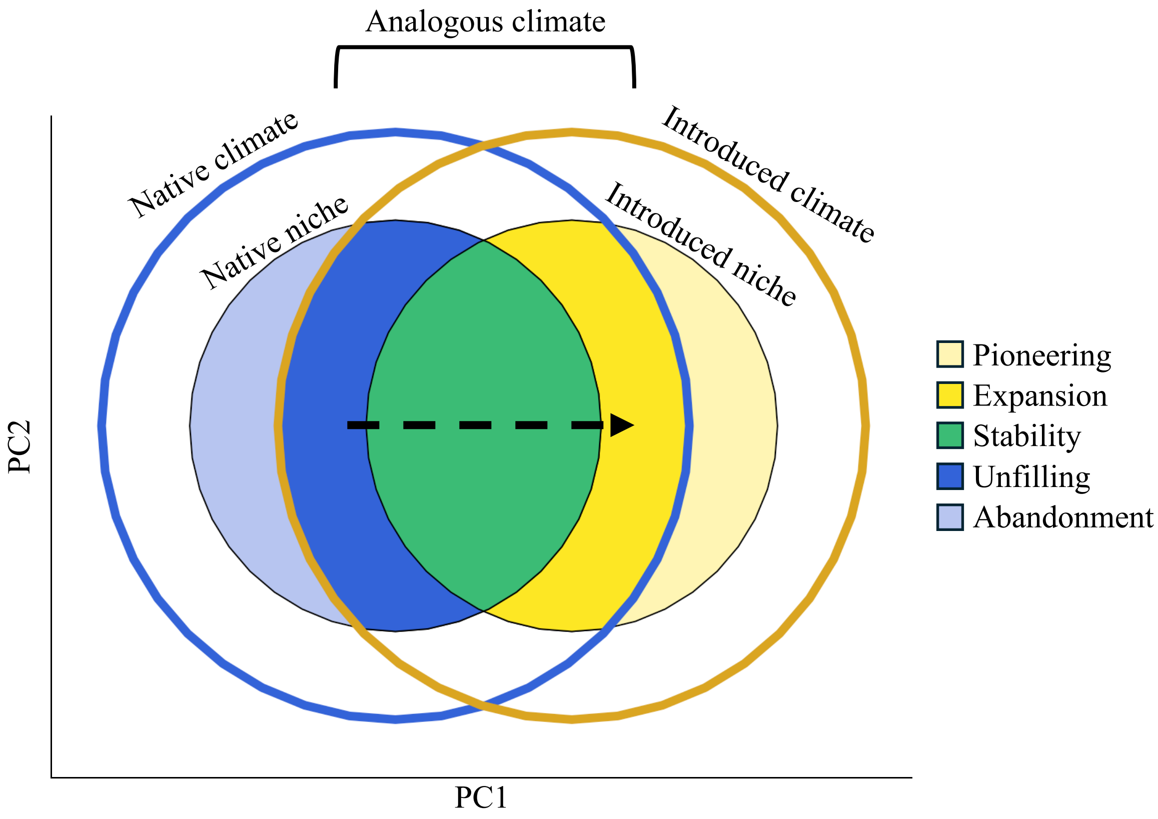


Figure 2.3. Examples of patterns in overlap plots used to categorize the directionality of expansion for individual climate variables from the native range to the introduced range. For each species, the directionality of expansion (yellow area) was categorized based on whether there was expansion in the variable's (A) upper limit, (B) lower limit, or (C) both limits. (D) shows an example of a climate variable with no expansion. The solid areas represent the density of species occurrences across climatic conditions in the species' native (blue) and introduced (yellow) ranges. Green is their overlap. 'Climate variable' represents any of the eight climate variables used in this study (Table 2.1). The arrows show the direction of niche expansion.

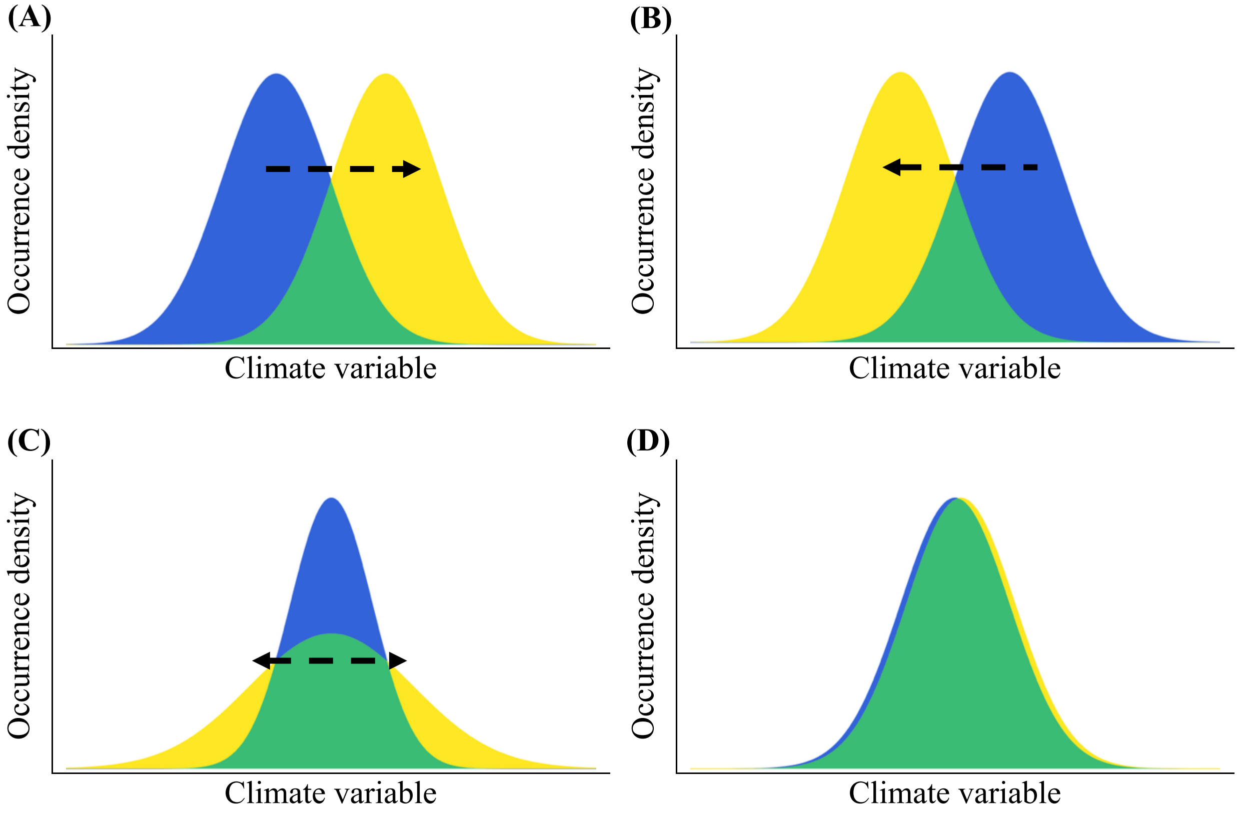


Figure 2.4. Histograms showing the values across all species (n=663) of (A) expansion, the proportion of the introduced niche corresponding to climates occupied only in the introduced range; (B) pioneering, the proportion of the introduced niche corresponding to climates occupied in the introduced range that do not exist in the native range; and (C) unfilling, the proportion of the native niche corresponding to climates only occupied in the native range. The dashed lines show the median for each index. The purple and blue lines represent 5% and 10% thresholds.

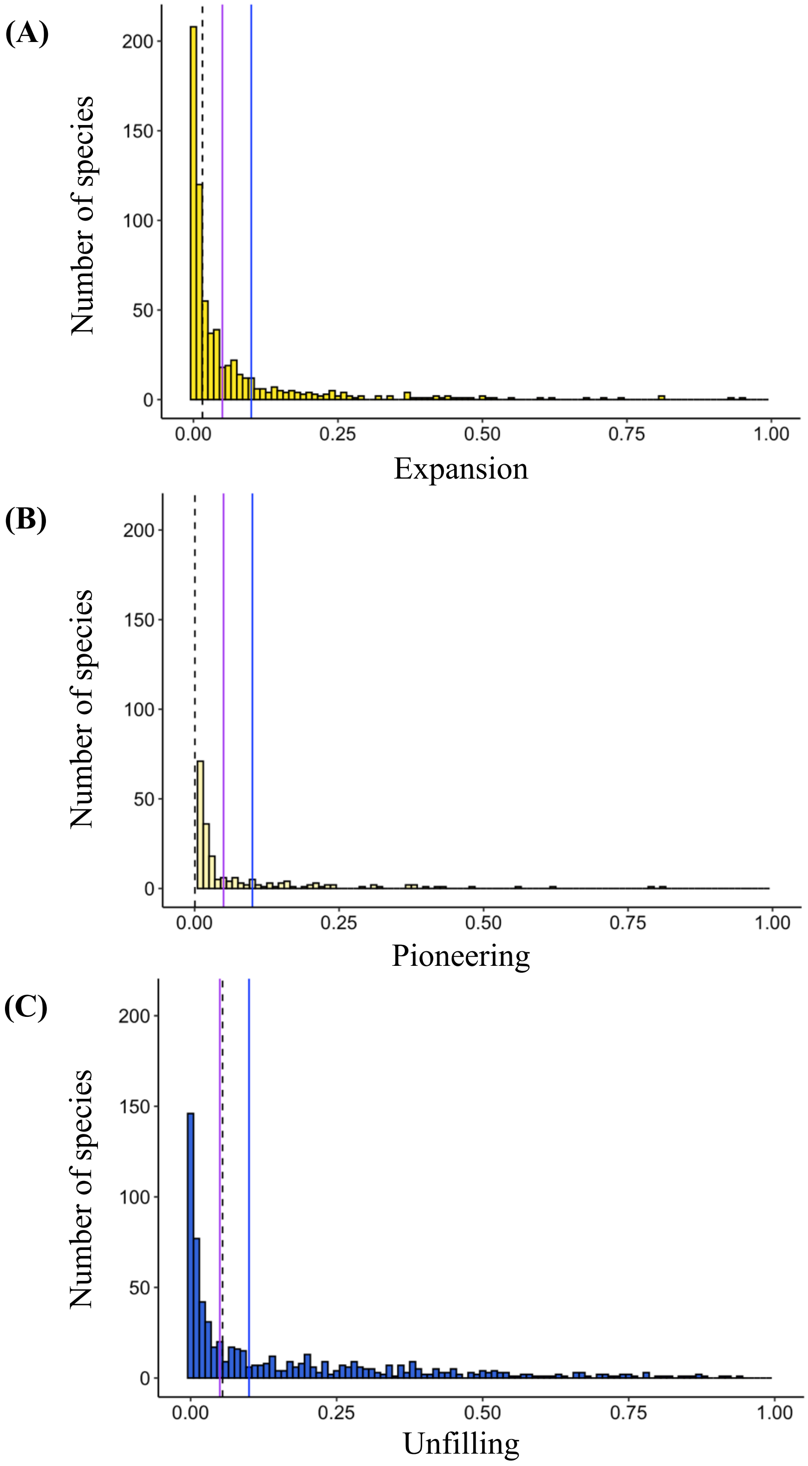
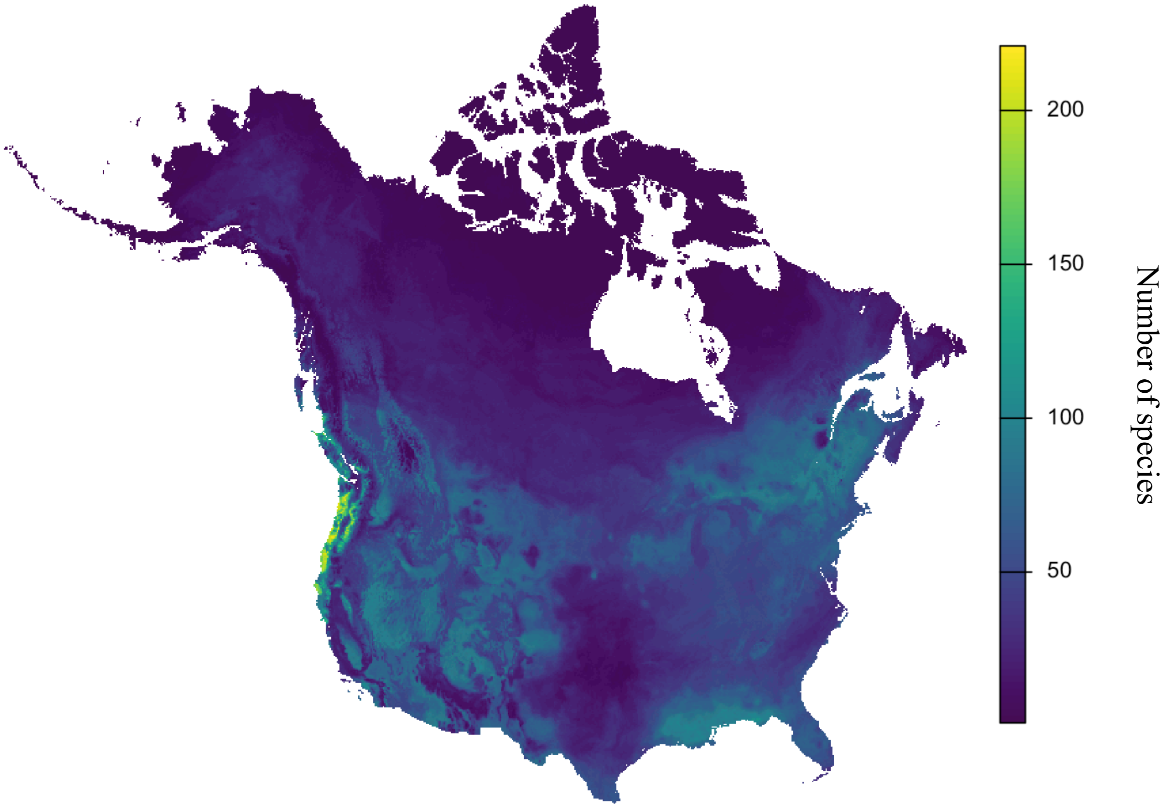


Figure 2.5. Expansion hot spots across North America. The 'expansion' portion of each species' niche was projected to geographic space across Canada and the United States. This step generated a map with cells that had a value '1' if the climate of that cell was a climate that the species is expanding into, and '0' otherwise. These geographically projected expansion layers were summed across all species to obtain a map of expansion hot spots of North America, where the value in each cell reflects the number of species (out of the 663 included in this study) that showed evidence of niche expansion in the type of climate found in that cell.



General Conclusions

In Chapter 1 of this thesis, I showed that when using SDMs to forecast the potential distribution of an invasive plant species, it is important to consider whether the species has undergone a niche shift from its native range to its invaded range. My results also showed that the choice of range for model training has implications for the geographic scope of the model projections (i.e., the amount of analogous climate in the desired projection range). My study reveals the complementary nature of building both native- and invasive-trained SDMs. Though the invasive-trained model provides predictions that are likely more accurate, the native-trained model might be able to make predictions at a much larger geographic scale (since many species have larger native ranges that reflect a wider variety of climates, especially for species that are not widespread in their introduced ranges). My findings also suggest that it is worthwhile to establish early detection programs for *Vincetoxicum rossicum* in areas that are (1) geographically separated from *V. rossicum*'s current range in North America and (2) predicted to be highly climatically suitable now and in the future.

In Chapter 2, I found that while climatic niche expansion does occur to some degree in the majority of the 663 introduced plant species included in this study, high magnitudes of expansion are not very common. My results showed that niche unfilling is a larger driver for observed niche shifts than niche expansion. Though unfilling could possibly reflect a permanent niche contraction, it is difficult to know whether observed unfilling is temporary (due to dispersal limitation) or permanent. Introduced species have the potential to spread into the currently under-filled parts of their introduced niches, making unfilling an unreliable indicator of niche shift (Petitpierre et al., 2012). Consequently, modelling species' potential distributions based solely on their current introduced niches would result in underpredictions of the species' true potential distributions in North America. Additionally, by considering introduced plant species' niche dynamics in non-analogous climates (pioneering), my work revealed that spread into non-analogous climates occurs frequently across species, but does not represent a large proportion of introduced plant species' niches generally. I also identified climatic conditions and regions of North America where there is a higher frequency of niche expansion across the 663 study species. To my knowledge, this work represents the first study to report the frequency of niche expansions versus niche unfilling when quantifying niche shifts in a large group of introduced plant species.

Taken together, these results underscore the significance of considering niche expansions and non-analogous climates when building SDMs for introduced species and quantifying the niche dynamics of these species. Since niche expansions can greatly impact SDM results (Chapter 1) and are quite common (though often small in magnitude; Chapter 2), these findings provide support for testing for niche shifts when building SDMs to forecast the spread of introduced species. Additionally, non-analogous climates in a species' introduced range should be explicitly identified (1) to assess the difference in the amount of non-analogous climate between native range- and introduced range-trained SDM predictions (Chapter 1) and (2) due to the potential for niche pioneering across introduced plant species (Chapter 2). Quantifying non-analogous climates in these contexts can therefore help distinguish between true low suitability conditions and novel climates where introduced species could have the potential to spread. These considerations will improve the predictive accuracy of distribution forecasts for introduced plant species, thereby providing better guidance in managing and preventing their spread.

The approaches used in my thesis have several limitations. The species occurrence data used in these two studies came from GBIF and community science sources. These sources have known sampling biases (Geurts et al., 2023) and provide presence-only data. Though I attempted to minimize these biases, it is impossible to eliminate bias or to completely fill in data gaps (e.g., under-sampled regions or taxa) when working at a macroecological scale. However, future work could apply more sophisticated bias correction methods. Furthermore, the SDMs and niche overlap analyses I conducted rely on correlations between species occurrence records and climatic conditions (Peterson et al., 2015). They did not consider anthropogenic disturbance, soil conditions, or other non-climatic aspects that could contribute to a species' niche. In particular, incorporating biological interactions like competition or herbivory into SDMs for invasive plant species like *V. rossicum* would be a strong step in improving the accuracy of predicted distributions (Gallien et al., 2010; Peterson et al., 2015; Srivastava et al., 2019). Finally, when comparing species' niches across continents, it can be difficult to know whether patterns that arise are related to the biological phenomenon we want to understand (in this case, niche conservatism/niche shift) or whether they are driven largely by climatic availability. Though the niche overlap analyses that I used corrected for climatic availability to an extent (Di Cola et al., 2017), the approach used in this study will never be able to fully define the complete set of a species' climatic tolerances, since the species may always be limited by climatic availability to some degree (Bates & Bertelsmeier, 2021). For this reason, it is important that studies continue to separate niche dynamics that occur in analogous and non-analogous climate spaces. Future work should continue to quantify niche dynamics in non-analogous climates (especially niche pioneering) so as to not underestimate the full extent of species' introduced niches.

Overall, the results from my thesis suggest that we can increase our understanding of the potential spread of introduced plant species by studying niche expansions and unfilling, and additionally niche dynamics in non-analogous climates (i.e., niche pioneering). This approach to forecasting the potential distributions of introduced plant species will help guide management and control efforts against the significant threat posed by these species.

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Appendices

Table S1.1. Full set of bioclimatic variables. Variables marked with an asterisk were identified as biologically relevant for *Vincetoxicum rossicum* and were used for niche overlap quantification (Petitpierre et al., 2017).

Variable
Annual mean temperature *
Mean diurnal temperature range
Isothermality
Temperature seasonality *
Max temperature of warmest month
Min temperature of coldest month
Temperature annual range
Mean temperature of wettest quarter
Mean temperature of driest quarter
Mean temperature of warmest quarter *
Mean temperature of coldest quarter *
Annual precipitation *
Precipitation of wettest month
Precipitation of driest month
Precipitation seasonality *
Precipitation of wettest quarter *
Precipitation of driest quarter
Precipitation of warmest quarter
Precipitation of coldest quarter *

Table S1.2. Reduced set of bioclimatic variables for Maxent models chosen by biological relevance and collinearity analysis.

Variable
Temperature seasonality
Mean temperature of warmest quarter
Precipitation seasonality
Precipitation of wettest quarter
Precipitation of coldest quarter

Table S1.3. Selected values for Maxent parameters within the ‘ENMeval’ package.

Parameter	**Selected value**
Background points	Selection of 10,000 points via target-group background
Regularization multipliers	Values from 0.5 to 8 by increments of 0.5
Feature classes	Linear, Linear-Quadratic, Hinge, Linear-Quadratic-Hinge, Linear-Quadratic-Hinge-Product, and Linear-Quadratic-Product-Threshold
Data partitioning method for k-fold cross validation	Spatial hierarchical checkerboard (‘checkerboard’) with aggregation factors (2, 4)
Output type	Complementary log-log
Maximum number of iterations	5000

Table S1.4. List of taxa and species used for target-group backgrounds for the native range and invaded range to select background points for Maxent models.

Training area	**Taxon/species**
Invaded range	Family Apocynaceae
	Alliaria officinalis
	Hesperis matronalis
	Celastrus orbiculatus
	Centaurea stoebe
	Melilotus alba
	Impatiens glandulifera
	Heracleum mantegazzianum
Native range	Genus *Vincetoxicum*

Table S2.1. List of plant species introduced to North America included in this study (n=663), and their indices of niche expansion, unfilling, stability, and pioneering. Expansion and stability sum to 100% of the introduced niche. Expansion was calculated as the proportion of the introduced niche corresponding to climates occupied only in the introduced range. Pioneering was calculated as the proportion of the introduced niche corresponding to climates occupied in the introduced range that do not exist in the native range. Unfilling was calculated as the proportion of the native niche corresponding to climates only occupied in the native range.

Family	**Species**	**Expansion (%)**	**Unfilling (%)**	**Stability (%)**	**Pioneer-ing (%)**
Acanthaceae	*Asystasia gangetica*	0.8	43.2	99.2	0.0
	Ruellia blechum	0.0	36.0	100.0	0.0
Aizoaceae	*Carpobrotus edulis*	29.0	9.1	71.0	10.4
	Mesembryanthemum crystallinum	5.5	20.3	94.5	21.7
Amaranthaceae	*Alternanthera philoxeroides*	0.6	26.7	99.4	5.1
	Alternanthera sessilis	0.0	44.2	100.0	1.2
	Amaranthus palmeri	0.8	0.2	99.2	1.1
	Amaranthus retroflexus	36.8	1.8	63.2	0.2
	Atriplex semibaccata	9.6	3.1	90.4	0.0
	Bassia hyssopifolia	4.9	10.6	95.1	0.0
	Bassia scoparia	1.6	5.8	98.4	0.0
	Dysphania ambrosioides	0.0	7.3	100.0	0.5
	Halogeton glomeratus	9.3	55.1	90.7	0.1
	Salsola collina	5.2	26.1	94.8	0.0
	Salsola kali	23.7	1.6	76.3	1.2
	Salsola paulsenii	33.8	28.4	66.2	0.0
	Salsola tragus	1.6	3.2	98.4	0.0
Amaryllidaceae	*Allium vineale*	0.7	2.4	99.3	0.0
	Leucojum aestivum	26.0	0.6	74.0	3.2
	Nothoscordum gracile	14.0	5.3	86.0	0.1
Anacardiaceae	*Pistacia chinensis*	4.7	34.0	95.3	0.1
	Schinus molle	2.5	30.4	97.5	3.7
	Toxicodendron radicans	0.0	0.1	100.0	1.0
Apiaceae	*Aegopodium podagraria*	0.3	1.2	99.7	0.0
	Anthriscus sylvestris	0.8	5.3	99.2	0.0
	Bupleurum rotundifolium	8.2	8.8	91.8	0.0
	Carum carvi	0.1	3.7	99.9	0.0
	Conium maculatum	1.5	0.8	98.5	0.1
	Daucus carota	1.4	0.5	98.6	0.1
	Falcaria vulgaris	0.3	21.2	99.7	0.0
	Foeniculum vulgare	4.8	0.4	95.2	2.8
	Pastinaca sativa	0.4	1.3	99.6	1.8
	Torilis arvensis	1.7	2.1	98.3	0.5

	Torilis japonica	0.2	7.8	99.8	6.4
Apocynaceae	*Cryptostegia grandiflora*	27.1	3.0	72.9	0.0
	Cryptostegia madagascariensis	92.6	78.3	7.4	0.0
	Vinca major	7.8	0.5	92.2	0.0
	Vinca minor	3.5	0.2	96.5	8.3
	Vincetoxicum nigrum	26.2	73.7	73.8	0.0
Aquifoliaceae	*Ilex aquifolium*	4.3	0.5	95.7	0.0
	Ilex crenata	0.0	62.6	100.0	0.0
Araceae	*Arum italicum*	3.2	0.8	96.8	0.0
	Pistia stratiotes	5.9	20.1	94.1	0.0
	Syngonium podophyllum	0.6	46.2	99.4	0.1
	Xanthosoma sagittifolium	11.1	51.9	88.9	0.0
	Zantedeschia aethiopica	17.2	0.2	82.8	0.4
Araliaceae	*Hedera helix*	1.7	0.4	98.3	0.9
	Hedera hibernica	5.6	0.1	94.4	3.2
	Hydrocotyle sibthorpioides	0.5	18.7	99.5	0.1
	Kalopanax septemlobus	0.0	64.0	100.0	0.0
Arecaceae	*Cocos nucifera*	7.4	31.5	92.6	0.1
	Phoenix canariensis	9.9	3.1	90.1	0.0
	Phoenix reclinata	0.0	55.5	100.0	0.2
	Syagrus romanzoffiana	2.3	49.3	97.7	37.8
Asparagaceae	*Asparagus aethiopicus*	44.4	2.4	55.6	0.0
	Asparagus asparagoides	4.9	25.0	95.1	0.0
	Asparagus officinalis	5.7	0.2	94.3	1.6
	Convallaria majalis	0.2	3.1	99.8	0.0
	Hyacinthoides hispanica	14.5	6.5	85.5	0.0
	Liriope spicata	81.4	87.0	18.6	0.0
	Muscari botryoides	7.2	1.8	92.8	1.5
	Muscari neglectum	1.6	2.0	98.4	0.0
	Ornithogalum nutans	1.4	26.5	98.6	42.5
	Ornithogalum umbellatum	1.2	1.2	98.8	0.0
Asphodelaceae	*Asphodelus fistulosus*	0.3	29.5	99.7	0.0
	Hemerocallis fulva	6.1	13.3	93.9	0.1
	Phormium tenax	0.5	11.7	99.5	0.0
Asteraceae	*Ageratina adenophora*	16.2	1.8	83.8	0.8
	Ambrosia artemisiifolia	0.0	0.0	100.0	0.9
	Anthemis arvensis	0.7	7.9	99.3	0.0
	Anthemis cotula	9.2	0.2	90.8	0.0
	Arctium minus	2.3	0.6	97.7	0.0
	Arctotheca calendula	29.1	37.9	70.9	0.0
	Artemisia absinthium	0.7	1.3	99.3	0.0
	Artemisia vulgaris	0.6	1.9	99.4	0.4

Bidens pilosa	0.6	9.0	99.4	0.0
Carduus acanthoides	0.7	5.2	99.3	6.1
Carduus nutans	1.0	4.6	99.0	0.0
Carduus pycnocephalus	5.8	4.2	94.2	0.0
Carduus tenuiflorus	15.3	57.9	84.7	0.0
Carthamus creticus	7.1	38.6	92.9	0.0
Centaurea benedicta	3.4	2.2	96.6	0.0
Centaurea calcitrapa	8.7	13.7	91.3	0.0
Centaurea cyanus	14.6	0.1	85.4	0.0
Centaurea iberica	0.0	37.8	100.0	13.3
Centaurea melitensis	7.1	0.3	92.9	0.0
Centaurea montana	17.9	0.0	82.1	0.0
Centaurea nigra	6.7	13.3	93.3	0.5
Centaurea nigrescens	0.2	21.9	99.8	1.9
Centaurea solstitialis	7.9	0.6	92.1	1.0
Centaurea stoebe	7.4	0.1	92.6	0.0
Centaurea sulphurea	26.9	14.8	73.1	0.0
Chondrilla juncea	2.2	1.1	97.8	0.2
Cichorium intybus	0.3	1.4	99.7	0.1
Cirsium arvense	1.0	0.4	99.0	0.2
Cirsium palustre	0.0	22.9	100.0	1.1
Cirsium vulgare	0.6	0.1	99.4	1.1
Cosmos bipinnatus	51.7	0.9	48.3	0.0
Cosmos sulphureus	45.1	17.7	54.9	0.0
Cotula coronopifolia	20.0	0.2	80.0	0.2
Crepis tectorum	0.7	1.0	99.3	8.8
Crupina vulgaris	7.0	51.4	93.0	42.6
Cynara cardunculus	8.8	23.0	91.2	0.0
Delairea odorata	39.6	0.0	60.4	0.0
Dittrichia graveolens	8.8	23.3	91.2	0.0
Gaillardia pulchella	6.6	0.0	93.4	1.1
Galinsoga parviflora	22.5	5.3	77.5	20.2
Galinsoga quadriradiata	9.0	20.0	91.0	1.3
Glebionis coronaria	1.1	13.6	98.9	9.6
Helianthus annuus	1.5	0.4	98.5	0.0
Helichrysum petiolare	60.3	17.1	39.7	0.0
Helminthotheca echioides	9.9	13.6	90.1	0.0
Hieracium sabaudum	7.4	1.7	92.6	0.0
Hypochaeris glabra	3.6	1.2	96.4	0.0
Hypochaeris radicata	3.4	0.1	96.6	0.0
Jacobaea vulgaris	3.7	2.3	96.3	0.8
Lactuca saligna	4.2	2.2	95.8	5.6
Lactuca serriola	0.8	0.3	99.2	0.1
Lapsana communis	1.0	0.1	99.0	23.5
Leucanthemum vulgare	1.1	0.0	98.9	0.0

	Matricaria discoidea	0.0	0.0	100.0	0.0
	Onopordum acanthium	0.4	3.1	99.6	0.4
	Onopordum illyricum	0.0	0.0	0.0	0.0
	Parthenium hysterophorus	3.8	3.7	96.2	3.2
	Picris hieracioides	0.6	20.3	99.4	0.1
	Pilosella aurantiaca	1.4	0.6	98.6	61.7
	Pilosella caespitosa	7.2	0.2	92.8	0.0
	Pilosella officinarum	0.1	13.3	99.9	0.0
	Pilosella piloselloides	2.7	4.3	97.3	0.0
	Rhaponticum repens	0.0	0.0	0.0	0.3
	Scolymus hispanicus	0.0	71.5	100.0	2.3
	Senecio elegans	43.9	0.1	56.1	1.7
	Senecio inaequidens	4.4	29.5	95.6	0.0
	Senecio minimus	7.8	4.0	92.2	0.5
	Senecio squalidus	0.0	0.0	0.0	3.0
	Senecio sylvaticus	10.3	0.0	89.7	0.3
	Senecio vulgaris	1.3	0.2	98.7	0.1
	Silybum marianum	1.6	0.6	98.4	1.1
	Soliva sessilis	12.8	3.1	87.2	0.3
	Sonchus arvensis	0.1	0.4	99.9	2.0
	Sonchus asper	2.1	0.3	97.9	0.0
	Sonchus oleraceus	5.0	0.2	95.0	0.0
	Sphagneticola trilobata	0.2	26.4	99.8	0.0
	Tagetes minuta	24.2	21.0	75.8	0.0
	Tanacetum vulgare	0.4	0.5	99.6	0.0
	Taraxacum erythrospermum	13.0	0.3	87.0	0.3
	Tragopogon dubius	1.8	0.7	98.2	0.2
	Tridax procumbens	0.2	14.3	99.8	0.1
	Tripleurospermum inodorum	1.6	0.2	98.4	1.5
	Tussilago farfara	0.0	13.4	100.0	0.0
	Youngia japonica	0.1	17.0	99.9	0.0
Athyriaceae	*Deparia petersenii*	1.0	20.4	99.0	3.5
Balsaminaceae	*Impatiens glandulifera*	2.5	13.7	97.5	0.0
Basellaceae	*Anredera cordifolia*	7.3	9.1	92.7	0.0
Begoniaceae	*Begonia cucullata*	1.6	6.6	98.4	0.0
Berberidaceae	*Berberis thunbergii*	19.7	17.5	80.3	0.0
	Berberis vulgaris	0.2	7.5	99.8	0.0
	Nandina domestica	11.9	6.8	88.1	0.4
Betulaceae	*Alnus glutinosa*	0.4	17.9	99.6	0.0
	Betula pendula	0.8	0.3	99.2	0.0
Bignoniaceae	*Catalpa bignonioides*	3.8	0.1	96.2	0.1
	Catalpa ovata	81.1	87.3	18.9	0.1
Boraginaceae	*Anchusa arvensis*	0.0	0.0	0.0	0.9

	Anchusa officinalis	7.9	3.6	92.1	0.0
	Buglossoides arvensis	0.6	1.5	99.4	37.1
	Cynoglossum officinale	0.3	4.8	99.7	2.2
	Echium plantagineum	4.4	2.4	95.6	0.0
	Echium vulgare	0.2	4.5	99.8	0.0
	Lappula occidentalis	0.0	0.0	100.0	9.0
	Lappula squarrosa	0.2	5.6	99.8	4.8
	Myosotis scorpioides	1.5	1.0	98.5	0.0
	Symphytum officinale	4.2	0.1	95.8	3.4
Brassicaceae	*Alliaria petiolata*	0.1	2.7	99.9	0.0
	Arabidopsis thaliana	0.8	3.1	99.2	8.2
	Barbarea vulgaris	0.3	1.6	99.7	0.1
	Berteroa incana	0.1	2.1	99.9	0.0
	Cakile maritima	4.5	2.6	95.5	0.4
	Capsella bursa-pastoris	0.1	0.7	99.9	0.0
	Cardamine impatiens	0.0	27.5	100.0	0.3
	Chorispora tenella	3.0	8.3	97.0	0.7
	Descurainia sophia	0.2	1.7	99.8	31.4
	Draba verna	1.0	0.5	99.0	0.2
	Hesperis matronalis	3.2	0.3	96.8	0.0
	Hirschfeldia incana	5.7	1.7	94.3	0.0
	Isatis tinctoria	16.6	5.1	83.4	4.6
	Lepidium campestre	5.9	0.2	94.1	0.3
	Lepidium coronopus	24.5	2.6	75.5	36.9
	Lepidium densiflorum	0.0	0.0	100.0	0.0
	Lepidium draba	0.3	1.6	99.7	0.0
	Lepidium latifolium	1.5	4.3	98.5	0.0
	Lobularia maritima	5.5	0.3	94.5	0.6
	Nasturtium officinale	4.0	0.2	96.0	0.0
	Raphanus raphanistrum	2.1	0.2	97.9	0.0
	Rapistrum rugosum	1.5	48.4	98.5	13.2
	Rorippa amphibia	19.6	73.6	80.4	0.0
	Rorippa austriaca	3.0	5.4	97.0	0.0
	Rorippa sylvestris	1.0	3.3	99.0	0.0
	Sisymbrium altissimum	10.4	0.1	89.6	0.0
	Sisymbrium irio	0.0	12.3	100.0	0.0
	Thlaspi arvense	0.3	0.7	99.7	0.0
Butomaceae	*Butomus umbellatus*	3.0	8.8	97.0	1.1
Buxaceae	*Pachysandra terminalis*	0.3	25.6	99.7	0.0
Cabombaceae	*Cabomba caroliniana*	0.8	1.2	99.2	16.7
Campanulaceae	*Campanula rapunculoides*	0.3	0.8	99.7	0.6
Caprifoliaceae	*Dipsacus fullonum*	4.1	0.2	95.9	0.5
	Dipsacus laciniatus	1.0	6.9	99.0	0.0
	Dipsacus sativus	94.5	67.5	5.5	0.0
	Lonicera japonica	0.6	12.6	99.4	0.5

	Lonicera xylosteum	0.3	3.5	99.7	0.0
	Scabiosa atropurpurea	0.0	0.0	0.0	4.6
	Valeriana officinalis	0.1	9.8	99.9	0.0
Caryophyllaceae	*Agrostemma githago*	2.8	2.8	97.2	0.0
	Arenaria serpyllifolia	0.3	1.1	99.7	0.0
	Cerastium glomeratum	2.5	0.5	97.5	0.0
	Dianthus armeria	4.3	0.2	95.7	0.0
	Drymaria cordata	0.0	34.4	100.0	0.0
	Gypsophila paniculata	6.1	1.2	93.9	0.0
	Lepyrodiclis holosteoides	0.0	0.0	0.0	0.1
	Sagina procumbens	1.8	0.1	98.2	0.0
	Saponaria officinalis	1.1	0.2	98.9	0.0
	Silene dioica	2.7	1.1	97.3	0.0
	Silene flos-cuculi	0.0	23.4	100.0	0.3
	Silene latifolia	0.6	1.8	99.4	2.7
	Silene noctiflora	7.1	0.3	92.9	14.4
	Silene vulgaris	0.2	4.5	99.8	0.0
	Spergula arvensis	4.5	0.4	95.5	0.0
	Spergularia rubra	5.4	0.0	94.6	0.2
	Stellaria media	0.2	0.5	99.8	19.7
Casuarinaceae	*Casuarina cunninghamiana*	1.1	31.3	98.9	0.8
	Casuarina equisetifolia	2.4	36.2	97.6	0.0
	Casuarina glauca	47.6	70.6	52.4	0.0
Celastraceae	*Celastrus orbiculatus*	0.0	36.2	100.0	0.0
	Euonymus alatus	0.0	27.1	100.0	0.1
	Euonymus europaeus	0.3	5.4	99.7	0.0
	Euonymus fortunei	0.1	19.1	99.9	0.3
Combretaceae	*Terminalia catappa*	0.2	37.3	99.8	0.0
Commelinaceae	*Callisia fragrans*	1.9	5.5	98.1	1.1
	Commelina benghalensis	0.0	34.5	100.0	15.7
	Commelina communis	0.1	43.2	99.9	0.2
	Gibasis pellucida	4.8	3.9	95.2	2.2
	Murdannia keisak	0.1	76.2	99.9	0.0
	Tradescantia fluminensis	5.8	2.8	94.2	0.0
	Tradescantia spathacea	3.3	19.9	96.7	0.0
Convolvulaceae	*Convolvulus arvensis*	0.3	0.7	99.7	0.1
	Ipomoea aquatica	7.7	42.1	92.3	0.2
	Ipomoea carnea	0.2	17.3	99.8	0.0
	Ipomoea hederacea	5.2	3.2	94.8	0.1
	Ipomoea lacunosa	0.2	0.0	99.8	1.5
	Jacquemontia tamnifolia	0.0	25.5	100.0	0.0
Crassulaceae	*Kalanchoe pinnata*	4.2	21.5	95.8	0.0
Cucurbitaceae	*Bryonia alba*	3.8	20.0	96.2	0.1

	Coccinia grandis	6.1	27.9	93.9	0.0
	Cucumis myriocarpus	0.0	0.0	0.0	0.0
Cyperaceae	*Carex kobomugi*	0.0	44.8	100.0	0.0
	Cyperus entrerianus	1.4	8.0	98.6	0.0
	Cyperus iria	0.0	42.4	100.0	0.0
	Cyperus prolifer	4.7	49.1	95.3	0.0
	Cyperus rotundus	0.0	15.3	100.0	0.0
	Schoenoplectiella mucronata	0.0	31.4	100.0	12.2
Dioscoreaceae	*Dioscorea bulbifera*	0.0	60.7	100.0	0.0
	Dioscorea polystachya	2.6	88.2	97.4	1.7
Dryopteridaceae	*Cyrtomium falcatum*	9.3	20.0	90.7	2.4
Elaeagnaceae	*Elaeagnus angustifolia*	4.3	3.1	95.7	15.2
	Elaeagnus pungens	2.9	11.4	97.1	0.0
	Elaeagnus umbellata	0.1	30.7	99.9	0.0
Ericaceae	*Erica lusitanica*	36.8	33.0	63.2	0.0
Euphorbiaceae	*Euphorbia cyparissias*	1.0	1.6	99.0	0.0
	Euphorbia esula	1.0	5.0	99.0	0.0
	Euphorbia graminea	4.5	9.2	95.5	0.2
	Euphorbia heterophylla	0.0	6.6	100.0	3.8
	Euphorbia myrsinites	11.0	2.7	89.0	0.1
	Euphorbia oblongata	50.2	7.8	49.8	0.0
	Euphorbia terracina	0.4	80.5	99.6	0.0
	Ricinus communis	12.3	0.0	87.7	2.0
	Triadica sebifera	16.5	30.3	83.5	16.3
	Vernicia fordii	42.0	90.9	58.0	0.0
Fabaceae	*Abrus precatorius*	0.5	78.1	99.5	30.7
	Acacia dealbata	23.6	34.0	76.4	2.9
	Acacia mearnsii	42.2	39.7	57.8	0.0
	Acacia melanoxylon	1.9	51.6	98.1	0.0
	Acacia paradoxa	42.6	51.5	57.4	0.2
	Adenanthera pavonina	4.2	22.7	95.8	38.2
	Aeschynomene indica	0.3	49.8	99.7	0.0
	Albizia julibrissin	0.1	7.0	99.9	1.5
	Alhagi maurorum	0.0	38.5	100.0	1.3
	Alysicarpus vaginalis	0.0	52.7	100.0	7.6
	Amorpha fruticosa	0.0	0.0	100.0	18.5
	Cytisus scoparius	10.1	0.0	89.9	0.0
	Cytisus striatus	20.7	28.1	79.3	2.5
	Dalbergia sissoo	0.1	42.0	99.9	0.4
	Galega officinalis	17.4	8.9	82.6	0.2
	Genista monspessulana	28.2	31.6	71.8	0.1
	Genista tinctoria	0.0	29.0	100.0	3.4
	Indigofera hirsuta	0.0	63.4	100.0	0.0
	Kummerowia stipulacea	3.4	73.2	96.6	0.1
	Kummerowia striata	0.2	69.9	99.8	0.0

	Lathyrus latifolius	12.2	0.1	87.8	0.0
	Lespedeza bicolor	0.1	65.8	99.9	0.0
	Lespedeza cuneata	0.0	24.3	100.0	0.1
	Leucaena leucocephala	1.8	6.6	98.2	0.7
	Lotus corniculatus	0.3	0.6	99.7	1.5
	Lupinus arboreus	12.4	0.0	87.6	7.3
	Lupinus polyphyllus	0.0	0.0	100.0	16.0
	Medicago lupulina	1.1	0.2	98.9	0.0
	Medicago polymorpha	1.3	1.4	98.7	10.2
	Medicago sativa	1.1	0.1	98.9	2.6
	Melilotus officinalis	1.4	0.3	98.6	0.0
	Pueraria montana	0.0	42.7	100.0	0.0
	Robinia hispida	14.6	0.0	85.4	0.0
	Robinia pseudoacacia	11.0	0.0	89.0	0.0
	Senna obtusifolia	0.0	15.7	100.0	0.0
	Senna occidentalis	4.4	15.5	95.6	0.0
	Senna pendula	0.1	13.8	99.9	0.0
	Sesbania punicea	0.5	4.3	99.5	1.8
	Spartium junceum	6.8	13.1	93.2	1.9
	Trifolium aureum	1.5	1.7	98.5	0.0
	Trifolium campestre	0.8	1.3	99.2	7.4
	Trifolium dubium	3.7	0.1	96.3	0.0
	Trifolium hirtum	14.5	12.0	85.5	0.1
	Trifolium hybridum	4.9	0.0	95.1	10.7
	Trifolium pratense	0.4	0.2	99.6	0.0
	Trifolium repens	0.7	0.2	99.3	0.8
	Ulex europaeus	8.8	0.7	91.2	0.8
	Vachellia nilotica	0.2	5.2	99.8	0.0
	Vicia cracca	0.2	1.4	99.8	0.0
	Vicia sativa	1.7	0.7	98.3	0.4
	Vicia villosa	0.9	0.3	99.1	0.1
	Wisteria floribunda	14.2	24.0	85.8	0.0
Fagaceae	*Quercus acutissima*	2.4	56.8	97.6	0.0
Geraniaceae	*Erodium cicutarium*	0.8	0.3	99.2	2.6
	Geranium columbinum	3.1	3.4	96.9	0.1
	Geranium dissectum	1.9	0.5	98.1	0.0
	Geranium lucidum	6.2	8.1	93.8	0.0
	Geranium robertianum	0.3	0.2	99.7	3.0
Goodeniaceae	*Scaevola taccada*	0.1	45.9	99.9	2.1
Grossulariaceae	*Ribes rubrum*	4.1	2.8	95.9	0.0
Haloragaceae	*Myriophyllum aquaticum*	4.3	7.0	95.7	0.2
	Myriophyllum heterophyllum	0.4	0.6	99.6	0.0
	Myriophyllum spicatum	1.0	1.2	99.0	0.0
Hydrangeaceae	*Philadelphus coronarius*	3.3	21.3	96.7	0.1

Hydrocharitaceae	*Hydrilla verticillata*	0.0	32.8	100.0	0.0
	Hydrocharis morsus-ranae	3.9	38.8	96.1	0.2
	Najas minor	1.5	10.0	98.5	0.0
	Ottelia alismoides	0.0	59.2	100.0	0.0
Hypericaceae	*Hypericum perforatum*	1.8	0.2	98.2	0.9
Iridaceae	*Iris domestica*	1.3	29.7	98.7	0.3
	Iris pseudacorus	1.4	0.1	98.6	0.0
Juncaceae	*Luzula luzuloides*	5.8	1.8	94.2	1.3
Lamiaceae	*Ajuga reptans*	0.7	0.3	99.3	0.4
	Elsholtzia ciliata	0.6	82.3	99.4	0.0
	Galeopsis bifida	0.3	0.7	99.7	0.0
	Galeopsis tetrahit	0.5	3.5	99.5	0.0
	Glechoma hederacea	1.1	0.5	98.9	0.1
	Lamium album	0.0	7.2	100.0	2.1
	Lamium amplexicaule	0.1	0.8	99.9	1.1
	Lamium galeobdolon	1.7	0.3	98.3	0.0
	Lamium maculatum	2.0	4.1	98.0	0.0
	Leonurus cardiaca	1.2	1.3	98.8	0.0
	Marrubium vulgare	0.9	0.8	99.1	0.5
	Melissa officinalis	2.0	0.4	98.0	0.2
	Mentha pulegium	5.5	0.7	94.5	0.0
	Mentha spicata	9.3	0.4	90.7	0.0
	Mosla dianthera	0.0	84.0	100.0	0.4
	Nepeta cataria	0.9	0.9	99.1	0.0
	Perilla frutescens	0.3	27.1	99.7	0.3
	Salvia aethiopis	1.7	20.9	98.3	0.0
	Salvia pratensis	3.6	7.5	96.4	1.2
	Salvia sclarea	6.3	2.8	93.7	0.1
	Vitex agnus-castus	1.2	0.6	98.8	0.0
	Vitex rotundifolia	0.6	27.8	99.4	0.0
	Vitex trifolia	0.0	35.9	100.0	0.0
Lardizabalaceae	*Akebia quinata*	11.8	17.5	88.2	0.0
Lygodiaceae	*Lygodium microphyllum*	0.1	75.1	99.9	0.0
Lythraceae	*Lythrum hyssopifolia*	8.2	0.2	91.8	0.0
	Lythrum salicaria	0.3	0.4	99.7	0.0
	Trapa natans	0.0	42.2	100.0	0.5
Malvaceae	*Abutilon theophrasti*	7.3	17.3	92.7	0.1
	Anoda cristata	3.4	4.8	96.6	0.4
	Firmiana simplex	0.0	50.1	100.0	0.0
	Hibiscus syriacus	36.6	20.0	63.4	0.0
	Hibiscus tiliaceus	0.0	0.0	0.0	0.1
	Hibiscus trionum	0.6	1.5	99.4	0.5
	Sida spinosa	4.2	9.5	95.8	0.1
	Thespesia populnea	0.1	37.3	99.9	0.6
	Urena lobata	0.0	48.0	100.0	12.6

Marsileaceae	*Marsilea quadrifolia*	0.7	28.2	99.3	0.1
Martyniaceae	*Proboscidea louisianica*	0.1	0.9	99.9	1.6
Meliaceae	*Melia azedarach*	0.0	13.7	100.0	0.0
Menyanthaceae	*Nymphoides peltata*	4.2	8.3	95.8	0.0
Molluginaceae	*Mollugo verticillata*	0.0	5.4	100.0	0.0
Moraceae	*Broussonetia papyrifera*	0.2	20.6	99.8	0.0
	Fatoua villosa	0.3	18.7	99.7	10.7
	Ficus carica	1.9	3.6	98.1	0.0
	Ficus microcarpa	1.7	20.4	98.3	0.1
	Morus alba	50.5	6.7	49.5	0.0
Myrtaceae	*Eucalyptus camaldulensis*	3.1	33.9	96.9	0.0
	Eucalyptus globulus	50.2	49.8	49.8	0.1
	Eugenia uniflora	0.5	27.3	99.5	79.2
	Melaleuca quinquenervia	3.6	26.3	96.4	0.5
	Psidium guajava	0.2	15.7	99.8	0.0
Nephrolepidaceae	*Nephrolepis cordifolia*	0.0	28.1	100.0	0.6
Nymphaeaceae	*Nymphaea mexicana*	2.8	0.3	97.2	0.0
	Nymphaea odorata	1.4	0.3	98.6	0.0
Oleaceae	*Jasminum fluminense*	3.4	53.7	96.6	0.2
	Ligustrum obtusifolium	3.1	23.3	96.9	0.0
	Ligustrum ovalifolium	22.4	10.3	77.6	0.5
	Ligustrum vulgare	1.7	0.9	98.3	0.0
	Olea europaea	0.6	9.7	99.4	0.0
Onagraceae	*Epilobium hirsutum*	0.2	12.0	99.8	2.5
	Ludwigia peruviana	1.1	37.7	98.9	1.1
Orchidaceae	*Epipactis helleborine*	0.2	1.9	99.8	1.5
Orobanchaceae	*Euphrasia nemorosa*	8.1	1.3	91.9	0.0
	Orobanche minor	8.0	5.6	92.0	0.0
Oxalidaceae	*Oxalis pes-caprae*	14.2	1.4	85.8	0.0
	Oxalis stricta	0.0	0.2	100.0	0.0
Papaveraceae	*Chelidonium majus*	0.1	5.9	99.9	0.0
	Eschscholzia californica	0.2	0.0	99.8	0.0
	Glaucium corniculatum	0.8	23.3	99.2	0.1
	Glaucium flavum	5.0	38.4	95.0	1.6
	Macleaya cordata	36.9	71.2	63.1	0.0
	Papaver dubium	0.9	9.7	99.1	0.0
Passifloraceae	*Passiflora foetida*	0.0	17.0	100.0	20.8
Paulowniaceae	*Paulownia tomentosa*	2.0	12.1	98.0	0.0
Phyllanthaceae	*Phyllanthus urinaria*	0.0	45.1	100.0	0.0
Pinaceae	*Picea abies*	0.2	14.3	99.8	0.0
	Pinus radiata	0.4	0.0	99.6	1.0
	Pinus thunbergii	2.9	36.6	97.1	0.0
Pittosporaceae	*Pittosporum undulatum*	8.1	27.9	91.9	0.0
Plantaginaceae	*Bacopa monnieri*	0.0	7.7	100.0	0.0

	Callitriche stagnalis	3.6	0.2	96.4	0.2
	Digitalis lanata	8.0	57.2	92.0	1.4
	Digitalis purpurea	2.4	0.0	97.6	0.0
	Kickxia elatine	11.1	0.3	88.9	0.0
	Limnophila sessiliflora	0.0	66.6	100.0	6.9
	Linaria genistifolia	0.5	15.9	99.5	0.0
	Linaria vulgaris	0.2	0.3	99.8	0.0
	Plantago lanceolata	1.9	0.3	98.1	0.1
	Plantago major	1.5	0.1	98.5	0.0
	Veronica arvensis	0.8	0.4	99.2	0.0
	Veronica beccabunga	0.2	8.6	99.8	0.0
	Veronica hederifolia	0.4	4.4	99.6	0.1
Poaceae	*Aegilops cylindrica*	1.4	3.2	98.6	0.0
	Aegilops triuncialis	13.1	19.1	86.9	0.0
	Agropyron cristatum	1.3	10.5	98.7	1.4
	Agrostis avenacea	0.4	44.3	99.6	0.0
	Agrostis capillaris	3.8	0.0	96.2	0.2
	Agrostis gigantea	1.5	0.7	98.5	0.3
	Aira caryophyllea	6.7	0.3	93.3	32.1
	Alopecurus arundinaceus	0.0	28.3	100.0	0.1
	Alopecurus geniculatus	12.6	0.1	87.4	56.4
	Alopecurus myosuroides	21.4	0.6	78.6	0.6
	Alopecurus pratensis	3.0	0.1	97.0	0.0
	Amelichloa brachychaeta	47.2	12.8	52.8	0.0
	Andropogon virginicus	0.2	1.2	99.8	0.0
	Anthoxanthum odoratum	0.2	1.2	99.8	0.0
	Apera interrupta	34.2	1.9	65.8	0.3
	Arrhenatherum elatius	1.8	0.9	98.2	0.0
	Arthraxon hispidus	0.0	54.1	100.0	0.0
	Arundo donax	0.0	10.5	100.0	0.2
	Avena barbata	5.7	1.6	94.3	0.5
	Avena fatua	2.3	0.4	97.7	5.4
	Avena sterilis	2.1	14.4	97.9	0.0
	Bothriochloa bladhii	0.6	52.0	99.4	0.0
	Bothriochloa ischaemum	4.0	17.5	96.0	4.8
	Briza maxima	6.2	0.3	93.8	0.4
	Bromus arvensis	23.4	2.8	76.6	0.4
	Bromus catharticus	0.2	5.7	99.8	0.1
	Bromus commutatus	9.2	0.1	90.8	0.3
	Bromus diandrus	12.1	0.3	87.9	0.0
	Bromus hordeaceus	3.9	0.2	96.1	0.0
	Bromus inermis	0.7	1.1	99.3	0.5
	Bromus japonicus	0.0	4.7	100.0	0.0
	Bromus madritensis	2.9	19.3	97.1	0.0

Bromus racemosus	25.9	0.1	74.1	0.5
Bromus rubens	11.1	0.8	88.9	0.0
Bromus secalinus	18.2	0.3	81.8	0.0
Bromus sterilis	6.6	0.9	93.4	0.0
Bromus tectorum	1.3	0.6	98.7	1.1
Cenchrus echinatus	0.1	6.0	99.9	2.2
Cenchrus spinifex	0.0	1.9	100.0	0.0
Chrysopogon aciculatus	1.0	25.0	99.0	0.0
Cortaderia jubata	14.5	8.0	85.5	21.4
Cortaderia selloana	3.0	0.9	97.0	0.0
Cynosurus echinatus	5.4	3.1	94.6	0.0
Dactylis glomerata	1.1	0.3	98.9	0.0
Dactyloctenium aegyptium	0.8	24.8	99.2	0.7
Deschampsia elongata	0.0	0.2	100.0	0.8
Dichanthium annulatum	0.3	28.9	99.7	0.7
Digitaria abyssinica	0.0	67.1	100.0	0.3
Digitaria ciliaris	0.0	15.4	100.0	0.0
Digitaria sanguinalis	0.9	1.7	99.1	0.3
Ehrharta calycina	7.5	53.0	92.5	0.0
Ehrharta erecta	1.3	11.5	98.7	3.5
Ehrharta longiflora	1.4	77.6	98.6	1.5
Eleusine indica	0.1	17.5	99.9	0.1
Elymus repens	0.6	0.4	99.4	1.4
Eragrostis cilianensis	0.2	7.8	99.8	0.0
Eragrostis curvula	24.2	2.0	75.8	1.0
Eragrostis lehmanniana	3.2	22.0	96.8	16.2
Festuca filiformis	1.0	9.3	99.0	1.3
Glyceria declinata	17.0	2.2	83.0	1.8
Glyceria maxima	14.7	0.3	85.3	0.0
Hemarthria altissima	0.0	34.1	100.0	0.0
Holcus lanatus	2.1	0.2	97.9	0.2
Holcus mollis	7.4	1.8	92.6	0.0
Hordeum jubatum	0.0	0.3	100.0	0.8
Hordeum marinum	10.7	0.1	89.3	0.2
Hordeum murinum	1.1	0.4	98.9	2.9
Hordeum vulgare	1.2	4.2	98.8	2.2
Hymenachne amplexicaulis	0.6	45.1	99.4	0.0
Hyparrhenia rufa	0.7	37.9	99.3	14.7
Imperata brasiliensis	7.5	20.3	92.5	22.6
Imperata cylindrica	0.0	70.2	100.0	1.7
Ischaemum rugosum	0.2	59.7	99.8	0.0
Lolium multiflorum	9.9	0.2	90.1	7.3
Lolium perenne	3.9	0.2	96.1	22.9
Megathyrsus maximus	0.8	9.2	99.2	0.0

Melinis minutiflora	0.7	11.0	99.3	0.3
Melinis repens	0.4	5.4	99.6	0.0
Microstegium vimineum	0.0	49.8	100.0	0.1
Miscanthus sacchariflorus	25.2	79.9	74.8	2.6
Miscanthus sinensis	0.0	35.6	100.0	0.0
Nassella tenuissima	6.7	0.7	93.3	2.0
Nassella trichotoma	0.0	0.0	0.0	0.3
Oryza rufipogon	2.5	2.2	97.5	0.0
Panicum miliaceum	4.6	17.4	95.4	0.0
Panicum repens	0.1	52.9	99.9	0.2
Paspalum dilatatum	9.4	3.6	90.6	0.0
Paspalum notatum	0.9	7.7	99.1	3.4
Paspalum quadrifarium	37.9	67.2	62.1	0.2
Paspalum scrobiculatum	4.0	52.3	96.0	0.0
Paspalum urvillei	3.5	7.0	96.5	0.0
Phalaris aquatica	19.1	1.2	80.9	0.0
Phleum pratense	0.8	0.1	99.2	0.1
Phragmites australis	0.0	1.9	100.0	0.4
Poa annua	0.4	0.3	99.6	0.4
Poa bulbosa	2.6	2.5	97.4	0.0
Poa compressa	5.8	0.2	94.2	0.4
Poa pratensis	0.1	0.1	99.9	0.0
Poa trivialis	1.9	0.2	98.1	0.0
Polypogon monspeliensis	1.7	1.4	98.3	0.0
Pseudosasa japonica	23.8	0.0	76.2	0.0
Rottboellia cochinchinensis	0.0	66.2	100.0	1.9
Saccharum spontaneum	0.0	32.0	100.0	47.7
Schismus arabicus	1.1	32.2	98.9	3.4
Schismus barbatus	2.6	2.9	97.4	6.9
Secale cereale	16.4	0.0	83.6	21.0
Setaria faberi	0.1	25.3	99.9	0.1
Setaria italica	16.2	22.9	83.8	0.0
Setaria pumila	0.0	7.0	100.0	0.0
Setaria verticillata	1.6	1.6	98.4	0.0
Sorghum bicolor	38.9	18.8	61.1	0.1
Sorghum halepense	0.3	1.7	99.7	0.0
Taeniatherum caput-medusae	8.0	0.6	92.0	10.1
Thinopyrum intermedium	6.7	2.2	93.3	0.0
Tribolium obliterum	0.0	0.0	0.0	0.0
Urochloa mutica	5.0	20.3	95.0	0.0
Urochloa panicoides	0.1	29.9	99.9	1.1

Polygonaceae	*Antigonon leptopus*	2.1	7.8	97.9	0.0
	Fallopia convolvulus	1.0	0.5	99.0	0.1
	Persicaria longiseta	0.0	40.9	100.0	0.2
	Persicaria maculosa	2.2	0.5	97.8	0.1
	Persicaria orientalis	1.2	58.0	98.8	0.5
	Persicaria perfoliata	0.0	85.9	100.0	0.1
	Polygonum aviculare	0.2	0.3	99.8	0.0
	Reynoutria japonica	2.0	12.2	98.0	0.0
	Rumex acetosella	0.8	0.3	99.2	0.0
	Rumex crispus	1.2	0.5	98.8	0.0
	Rumex longifolius	0.5	3.1	99.5	0.0
	Rumex obtusifolius	1.4	0.2	98.6	0.0
Potamogetonaceae	*Potamogeton crispus*	0.7	1.8	99.3	1.6
Primulaceae	*Ardisia crenata*	0.8	38.0	99.2	0.1
	Lysimachia nummularia	1.0	0.6	99.0	0.0
	Lysimachia vulgaris	0.2	6.3	99.8	14.5
Pteridaceae	*Pteris vittata*	0.0	37.5	100.0	1.8
Ranunculaceae	*Clematis orientalis*	0.2	30.1	99.8	0.0
	Clematis terniflora	0.6	19.7	99.4	0.0
	Clematis vitalba	9.6	5.7	90.4	0.0
	Ranunculus acris	0.2	0.5	99.8	0.1
	Ranunculus bulbosus	0.0	8.8	100.0	0.1
	Ranunculus repens	2.8	0.2	97.2	0.0
Rhamnaceae	*Colubrina asiatica*	0.0	51.3	100.0	0.7
	Frangula alnus	0.0	9.3	100.0	0.9
	Rhamnus cathartica	0.1	5.5	99.9	0.2
Rosaceae	*Crataegus monogyna*	2.1	0.2	97.9	0.0
	Fragaria vesca	0.2	0.1	99.8	1.2
	Kerria japonica	6.9	30.7	93.1	0.8
	Photinia serratifolia	2.8	34.9	97.2	0.7
	Potentilla recta	0.9	1.4	99.1	0.0
	Prunus avium	1.5	1.0	98.5	0.2
	Prunus cerasifera	9.3	0.5	90.7	0.0
	Prunus mahaleb	1.6	3.1	98.4	0.0
	Prunus padus	0.5	1.3	99.5	1.1
	Pyracantha coccinea	17.2	0.5	82.8	0.0
	Pyracantha crenulata	25.8	14.4	74.2	0.7
	Pyrus calleryana	41.3	16.8	58.7	9.5
	Pyrus communis	3.6	0.4	96.4	0.0
	Rosa gallica	9.8	7.2	90.2	6.1
	Rosa laevigata	23.4	36.0	76.6	6.7
	Rosa multiflora	3.1	13.6	96.9	0.7
	Rosa rubiginosa	13.6	0.9	86.4	0.1
	Rosa rugosa	2.0	7.9	98.0	1.9
	Rubus bifrons	73.9	0.1	26.1	0.2
	Rubus illecebrosus	20.0	92.2	80.0	0.0

	Rubus niveus	0.0	37.6	100.0	0.0
	Rubus phoenicolasius	0.1	12.7	99.9	0.6
	Rubus ulmifolius	18.8	0.4	81.2	0.0
	Rubus vestitus	70.9	1.8	29.1	0.4
	Sorbus aucuparia	0.8	0.2	99.2	0.0
	Spiraea japonica	4.8	27.2	95.2	0.0
Rubiaceae	*Diodia virginiana*	0.0	0.0	100.0	0.0
	Galium mollugo	0.0	14.1	100.0	0.5
	Galium verum	0.0	6.9	100.0	0.0
	Paederia foetida	0.0	66.4	100.0	0.0
Rutaceae	*Murraya paniculata*	0.2	38.4	99.8	0.0
	Phellodendron amurense	0.0	48.3	100.0	0.0
Salicaceae	*Populus alba*	1.6	0.1	98.4	0.0
	Salix caprea	0.2	16.8	99.8	0.0
	Salix cinerea	0.0	27.1	100.0	0.0
	Salix pentandra	2.4	4.9	97.6	0.1
	Salix purpurea	0.7	9.5	99.3	4.3
Salviniaceae	*Azolla pinnata*	0.2	61.6	99.8	1.5
	Salvinia minima	1.1	44.2	98.9	0.7
Sapindaceae	*Acer palmatum*	10.5	17.3	89.5	0.4
	Acer platanoides	0.6	0.8	99.4	0.3
	Acer tataricum	1.4	0.7	98.6	0.1
	Cardiospermum halicacabum	1.6	26.3	98.4	0.0
	Cupaniopsis anacardioides	0.0	44.6	100.0	0.0
Sapotaceae	*Manilkara zapota*	0.5	33.6	99.5	28.5
Saururaceae	*Houttuynia cordata*	0.1	22.3	99.9	1.6
Scrophulariaceae	*Buddleja davidii*	54.8	3.7	45.2	0.0
	Buddleja madagascariensis	19.1	3.4	80.9	1.2
	Myoporum laetum	21.9	74.6	78.1	0.0
	Verbascum blattaria	3.4	0.6	96.6	0.2
	Verbascum thapsus	0.8	0.5	99.2	0.0
Simaroubaceae	*Ailanthus altissima*	4.9	10.8	95.1	0.0
Solanaceae	*Hyoscyamus niger*	0.1	15.7	99.9	0.5
	Nicandra physalodes	31.5	1.0	68.5	0.1
	Nicotiana glauca	3.5	6.8	96.5	0.8
	Solanum carolinense	0.0	0.0	100.0	0.0
	Solanum diphyllum	0.1	41.3	99.9	0.0
	Solanum dulcamara	0.7	1.4	99.3	81.1
	Solanum lanceolatum	4.4	29.1	95.6	0.6
	Solanum nigrum	0.6	0.9	99.4	0.0
	Solanum physalifolium	68.1	28.7	31.9	0.0
	Solanum pseudocapsicum	10.2	3.5	89.8	0.0

	Solanum rostratum	0.0	0.2	100.0	0.4
	Solanum sarrachoides	61.9	45.1	38.1	24.0
	Solanum sisymbriifolium	5.1	9.4	94.9	0.1
	Solanum tampicense	0.4	38.6	99.6	0.1
	Solanum torvum	0.2	18.9	99.8	0.4
	Solanum viarum	0.3	35.9	99.7	1.8
Tamaricaceae	*Tamarix aphylla*	1.5	7.4	98.5	0.7
	Tamarix gallica	17.9	1.6	82.1	0.0
	Tamarix parviflora	21.2	0.4	78.8	0.1
	Tamarix ramosissima	10.0	3.3	90.0	0.0
Taxaceae	*Taxus cuspidata*	3.6	54.4	96.4	0.0
Tetradiclidaceae	*Peganum harmala*	0.1	38.7	99.9	0.0
Thelypteridaceae	*Macrothelypteris torresiana*	0.1	39.7	99.9	2.5
Thymelaeaceae	*Daphne laureola*	31.6	11.4	68.4	3.8
Typhaceae	*Typha latifolia*	0.2	0.1	99.8	0.0
Ulmaceae	*Ulmus parvifolia*	2.7	7.7	97.3	39.9
Urticaceae	*Urtica dioica*	0.5	0.1	99.5	0.0