USING INVASION HISTORY TO QUANTIFY EQUILIBRIUM IN OVER 250 INVASIVE PLANT SPECIES IN NORTH AMERICA

MAISY ROACH-KRAJEWSKI

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Department of Biology

Faculty of Science

University of Ottawa

Abstract

Plant invasions pose an increasing global threat to ecosystem function and native biodiversity. Understanding the current and potential future distributions of harmful invaders is the key to developing efficient and effective management strategies. One widely used approach to achieve this is the use of species distribution models. Despite the implications for the predictive accuracy of these models, the assumption that species are in equilibrium with their environment (i.e., they occur in all suitable areas) is poorly tested. This assumption is even more likely to be violated for introduced species that are still in the process of colonizing suitable environments. In the limited cases where this assumption is tested, researchers do not typically incorporate a temporal analysis of an invading species (i.e., invasion history), but rather evaluate the assumption from a snapshot in time.

In this study, I used patterns of expansion in climate space over time to determine if an invading species has reached stable climate distribution (i.e., climatic equilibrium) in its introduced range, and estimated how long this process took relative to its first reported collection in North America. To quantify the expansion pattern of each species, I compared the climates occupied by a species in their native and introduced ranges throughout their invasion history. I found that only a small subset (15.2%) of species were actively expanding at a constant rate, indicated by single-phase, linear pattern on expansion through time. Further, the equilibrium assumption (defined as ≥30 years of no significant change in expansion) was only supported for less than half (42.3%) of the species analyzed. Of these species, the time it took to reach equilibrium varied between 20 and 120 years relative to its first reported collection in North America. I also found that, on average, species at equilibrium only occupy 95% of the suitable climates available in their invaded range. This could indicate that some species may be experiencing temporary equilibria caused by intrinsic or extrinsic barriers in the invaded range. My findings suggest that a temporal approach is necessary to evaluate equilibrium, and that it is possible that many North American plant invaders have not yet stabilized their climatic distribution. The methods outlined in this study lay the groundwork for developing a standardized approach to evaluating equilibrium, and not just in invasive plants. To my knowledge, this study represents one of the first to use a temporal approach to describe the equilibrium status of a large group of introduced species.

Resumé

Les invasions de plantes constituent une menace mondiale croissante pour la fonction des écosystèmes et la biodiversité indigène. La compréhension des distributions actuelles et futures des plantes envahissantes est clé pour le développement de stratégies de gestion efficaces et durables. Une approche largement utilisée pour y parvenir est l'utilisation de la modélisation de la distribution d'espèces, ou SDM. En dépit des divers enjeux liés à l'exactitude prédictive de ces modèles, l'hypothèse selon laquelle les espèces sont en équilibre avec leur environnement (c'est-à-dire qu'elles sont présentes dans toutes les zones qui leur convient) est peu testée. Cette hypothèse est encore plus susceptible de ne pas être respectée pour les espèces introduites qui sont encore en train de coloniser des environnements propices à leur expansion. Dans les rares cas où cette hypothèse est testée, les chercheurs n'intègrent généralement pas d'analyse temporelle de l'espèce envahissante (c'est-à-dire l'historique d'invasion), mais évaluent plutôt cette hypothèse à partir d'un moment précis dans le temps.

J'ai utilisé des modèles d'expansion pour quantifier et décrire l'état d'équilibre de plus de 250 espèces de plantes envahissantes en Amérique du Nord. En comparant les divers climats occupés par ces espèces dans leurs aires de répartition d'origine et d'introduction à travers leur historique d'invasion, j'ai constaté que même si seulement un petit sous-ensemble (15,2 %) d'espèces s'étendaient activement à un taux constant, l'hypothèse qu'elles étaient à l'équilibre, définie par 30 ans de distribution climatique stable, n'était valable que pour moins de la moitié (42,3 %) des espèces analysées. Pour ces espèces, le temps nécessaire pour qu'elles atteignent un état d'équilibre variait entre 20 et 120 ans, calculé à partir de l'introduction initiale de l'espèce dans l'environnement. J'ai également constaté qu'en moyenne, les espèces à l'état d'équilibre n'occupent que 95 % de l'espace disponible dans les zones envahies. Ceci pourrait indiquer que

certaines espèces connaissent des équilibres temporaires causés par des barrières intrinsèques ou extrinsèques dans la zone envahie. Quoi qu'il en soit, ces résultats sont la preuve que la distribution d'état d'équilibre d'une espèce doit être considérée dans le contexte de son historique d'invasion. À ma connaissance, cette étude est l'une des premières à utiliser une approche temporelle pour décrire l'état d'équilibre d'un grand groupe d'espèces introduites.

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1. Introduction

Human-introduced plant invasions have markedly increased in recent centuries, with an exceptional upsurge coinciding with the Industrial Revolution (Hulme, 2009; Seebens et al., 2015). The development of transcontinental travel and trade has played a considerable role in the temporal trends in invasions, with many plant species deliberately introduced for commercial exploitation (e.g., medicinal, agricultural) or ornamental purposes (Hulme et al., 2008; Reichard et al., 2021). Driven by factors associated with global change (e.g., land use change, elevated atmospheric carbon dioxide, increased global trade; Bradley et al., 2012), plant species introductions are predicted to continue increasing in the coming decades (Pysek et al., 2020; Seebens et al., 2021).

Many, but not all, introduced species will become invasive (Van Kleunen et al., 2015; Pysek et al., 2020). Invasive plants are characterised by rapid range expansion, extreme population growth (Richardson et al., 2000), and their negative impacts on native biodiversity (Bezemer et al., 2014; Bellard et al., 2016) and ecosystem functions (Vitousek et al., 2008). For example, they can outcompete native plant species for resources (Vilà et al., 2011), modify soil composition (Weidenhamer & Callaway, 2010), and disrupt plant-animal interactions (Litt et al., 2014). This can result in an overall loss of productivity for invaded ecosystems (Charles & Dukes, 2007; Eviner et al., 2012), making the understanding and control of plant invasions essential to conservation biology.

Once established, invasive plants are difficult to eliminate. Successful eradication is costly (Pimentel et al., 2005), and typically only achieved at smaller spatial scales (Corbin & D'Antonio, 2012). Even in cases where local eradication is successful, removal alone is unlikely to restore ecosystem characteristics to pre-invasion conditions. For example, studies have shown that the abundance and composition of native plants species (Heleno et al., 2010) as well as soil nutrients (Hetherington & Wilson, 2019) are permanently altered following plant invasions—even after the plants are removed. Due to the limited success and high costs of eradication efforts, invasion prevention strategies are preferred (Jiménez-Valverde et al., 2011). Ideally managers would be able to accurately predict where invasions are most likely to occur and then protect those areas.

The range expansion of invasive species can be predicted using species distribution models (SDMs), a widely used approach in ecology and conservation biology. SDMs relate georeferenced occurrence records (presence-only or presence/absence) to a set of environmental variables (e.g., climate, land cover) to predict habitat suitability across geographic space (Václavík & Meentemeyer, 2012). SDMs have been used to identify correlations between biotic and/or abiotic factors and a species' geographic range limits (Peterson & Soberón, 2012). These correlations can then be used to predict how future climate change will lead to species' range shifts. For example, a study by Sung et al. (2021) used global-scale occurrence records to model the distribution of the highly invasive *Solenopsis invicta* (red imported fire ant) and then projected their potential distribution in South Korea under a predicted climate change scenario. They found that temperature-related variables were more important than precipitation-related variables for predicting *S. invicta*'s geographic range, and that under predicted climate change scenarios, *S. invicta* is likely to expand its geographic range to new areas, including major coastal cities and airports in South Korea. Given these results, researchers were able to recommend the appropriate quarantine policies in order to minimize the further spread of this harmful invader.

Despite the widespread use of SDMs, producing reliable predictions for the range expansion of invasive species remains challenging. The suitability of SDMs for modelling invasive species has been criticized on the grounds that one of the fundamental assumptions of the approach is often not supported: that the species is at equilibrium with the environment in which it occurs (Gallien et al., 2012). A species is at equilibrium when it has occupied all suitable environments, while unsuitable environments remain unoccupied (Araújo et al., 2005). However, invasive species, particularly those that have been recently introduced, are defined by their rapid and aggressive range expansion (Richardson et al., 2000; Pysek et al., 2020). Studies have shown that an invasive species only nears equilibrium in its final stages of invasion (Václavík & Meentemeyer, 2012; Bradley et al., 2015; Foster et al., 2022). Thus, SDMs based on data collected before this point may not produce accurate predictions (Gallien et al., 2012; Briscoe Runquist et al., 2019).

Despite this potentially wide-reaching implication, relatively few studies have attempted to quantify equilibrium, especially at broad scales. When they do, equilibrium is typically evaluated from a snapshot in time (e.g., Gallien et al. 2012; Bradley et al. 2015; Pili et al., 2020; Goncalves et al., 2022) and does not usually consider the species' invasion history. Instead, these studies evaluate a species' current (i.e., *realized)* distribution compared to its *potential* distribution. If there is a mismatch between the realized and potential distribution, the species is considered to not be at equilibrium. One issue with this approach is how we define the potential distribution. This is often based on the species' niche in its native range. These native niche requirements are then projected onto the invaded range to determine the potential suitable area the species will occupy at equilibrium (Petitpierre et al. 2017).

While this may be the only option for species newly established in a region (and thus lacking distribution data outside of their native range), there are two main issues with this approach. First, it assumes that the species is at equilibrium in its native range, which we cannot always expect to be the case (Early & Sax, 2014). If the species has yet to colonize all suitable environments in its native range, projecting that distribution to the invaded range will underestimate its fundamental niche. Conversely, there may be records from areas in the native range where the species no longer occurs (e.g., due to shifting climate). These data would overestimate its fundamental niche. Second, it assumes that the equilibrium conditions are the same in the invaded range as in the native range—based on biotic interactions (i.e., limitations imposed by predators, parasites, or competitors) or the relative importance of environmental variables (Wisz et al., 2013, Mainali et al. 2015). Furthermore, differing selection pressures in the invaded range may lead to local adaptation of the invading population, leading to a shift in its fundamental niche (Wiens et al. 2005). Thus, the potential distribution in the native range may not truly reflect the potential niche of the species in its invaded range.

Alternatively, equilibrium can be quantified based on trends in the expansion of an introduced species as it invades a novel region. Theoretically, a species should become closer to reaching equilibrium as it proceeds through the stages of invasion (Theoharides & Dukes, 2007; Václavík & Meentemeyer, 2012, Foster et al., 2022). According to classic invasion dynamics, species invasions typically follow a three-phase pattern following introduction: establishment/lag, expansion, equilibrium (Vermeij, 1996; Radosevich et al., 2003) (Figure 1). During the lag phase, the environment occupied by an invasive species represents a small subset of the total available suitable environment (i.e., its equilibrium distribution) (Radosevich et al., 2003). Thus, the species is furthest from equilibrium at this stage, and SDMs are expected to be less accurate (Foster et al., 2022). After the species has become established (i.e., developed self-sustaining local populations), the invading species rapidly expands into previously unoccupied suitable climates. In this framework, the species stops expanding its distribution in environmental space once it has reached its equilibrium distribution. Therefore, in order to know *if* or *when* a species has reached equilibrium, a temporal context is essential (Foster et al. 2022).

Attempting to quantify patterns of expansion for a large dataset of invasive species using historical data is not a new concept. However, past studies – particularly those at a national or continental scale – have looked at patterns of expansion in *geographic* space only (i.e., how occurrences accumulate in physical space). For example, past works have used the cumulative number of geographic grid cells occupied (Aiello-Lammens, 2020; Osunkoya et al., 2021), log-transformed number of records (Williamson et al., 2004), or number of counties/townships occupied (Crawford & Hoagland, 2009; Mosena et al., 2018) by the species over time to evaluate expansion. Patterns of expansion only in geographic space do not allow us to accurately distinguish between expansion that occurs into new (i.e., not occupied in the native range) or similar (i.e., occupied in the native range) environments in the introduced range, thus constraining our ability to predict where expansions might occur in the future. In addition, studies are often designed to evaluate the presence of a lag phase (e.g., Aiello-Lammens, 2020; Osunkoya et al., 2021) and ignore the equilibrium phase. By focusing only on the early stages of an invasion, they overlook the full potential distribution of the invader.

In this study, I compare the climate space occupied in the invaded range over the invasion history of 257 introduced plant species in North America to the climate space currently occupied in their native range. Specifically, at each 5-year time interval, I calculate the proportion of climate space that is occupied by a species in its native range, but not the introduced range. As an invasive species progresses through its invasion, more climate space should become occupied over time in North America. Using this metric, I first quantify the pattern of expansion into climate space over time and test whether invasive plants typically follow a three-phase expansion pattern. Second, I determine if and when a species has reached climatic equilibrium in its introduced range based on the presence of a slowing of expansion in recent decades. Overall, this study will improve our ability to predict where and when expansions of invasive species might occur in the future. To my knowledge, this study represents one of the first to use a temporal approach to describe the equilibrium status of a large group of introduced species.

2. Methods

2.1 Overview

To determine whether these 257 invasive plant species have reached equilibrium in their introduced range, there were three parts to the study. First, I modelled their expansion in climate space at 5-year intervals throughout their invasion history in North America. Second, I determined which pattern best described each species' expansion in climate space (i.e., single-phase, two-phased, or three-phased). Next, I used a moving window approach to determine if and when a species' expansion in climatic space stabilized. All data manipulation and analyses were conducted in R v4.1 (R Core Team, 2022).

2.2 Data

2.2.1 Study species and occurrence records

I created a database of occurrence records for non-native, invasive plant species in North America. To do so, I started with the list of 815 invasive species compiled by Atwater et al. (2018). All species in this list are classified as invasive according to the Centre for Agriculture and Bioscience International (CABI) Invasive Species Compendium (CABI, 2022). From this list, I selected all tree, forb, and shrub species invasive in North America, yielding a list of 651 species. Then, I used a combination of primary and secondary literature (e.g., the CABI Invasive Species Compendium) to classify the approximate native range of each species as one of the following five ranges: Europe, Mediterranean (includes at least one Northern African country and at least one Southern European country), Eurasia, Asia, and South America. Any species where the native range did not fit these classifications, including species with unclear native ranges, as well as species native to parts of North America, were eliminated. This resulted in 320 species.

Next, I downloaded occurrence records from the Global Biodiversity Information Facility (GBIF) online database between December 6th and 12th, 2021. Only records with geographic coordinates were included. To minimize the effect of temporal bias associated with the influx of citizen-science based occurrence records (i.e., iNaturalist observations) in recent decades (di Cecco et al., 2021) and to maintain a consistent type of record across the past century, I only included preserved specimen (i.e., herbarium) records in this study. To ensure a long enough time-series and reasonable sample size for the analysis, I then eliminated species without *i)* at least one occurrence in North America prior to 1990 (i.e., present in North America for less than 30 years), and *ii)* at least 20 total occurrence records in each of their native range and introduced range. This resulted in a final dataset including 257 species from 61 plant families with five native ranges (see Table 1). A full species list with the number of records used is available in the Appendix (Table S1).

Each record was then categorized based on whether it fell within a species' introduced (i.e., North American) or native geographic range (Table S1). To reduce spatial bias associated with GBIF occurrence data (i.e., over-representation of environments in more heavily sampled areas), occurrence records for each species were thinned to match the climate data, such that only one occurrence record was included per 10 km^2 pixel.

2.2.2 Climate data

To define the climate space occupied by each species in their native and invaded (i.e., North American) range, I imported climate data from WorldClim version 2.1 for 1970-2000 (Fick, S.E. and R.J. Hijmans, 2017) at a resolution of 10 km^2. This included 19 variables derived from monthly temperature and rainfall values (variables used are summarized in Appendix, Table S2).

2.3 Quantifying expansion

2.3.1 Overview

For each species, I modelled their expansion in climate space at 5-year intervals throughout their invasion history in North America. To do so, I used the *ecospat* package in R (Di Cola et al. 2017). *ecospat* compares the density of occurrence records between two contexts to see where the occupied environments differ and where they overlap. I used this analysis to compare the climate space occupied in the native and invaded ranges (Eckert et al., 2020; Manzoor et al., 2020; Srivastava et al., 2020). To create a time series for each species, records were accumulated across 5-year time intervals in the introduced range.

2.3.2 Climate space

Climate space for each species' range (both native and introduced) was defined using a combination of the climatic variables. To represent only the climatic combination present in these ranges and to improve the resolution of the *ecospat* analysis, all 19 climate raster layers were cropped into six separate geographic extents: one to match the range extent of the invaded (North American) range extent, and one matched to each of the five different native range extents (Table 1). The climate space for each species was defined by the first two axes of a principal components analysis (PCA) combining the climate data from each native range with the climate data in the invaded North American range. *ecospat* divides each PCA into a 100 x 100 = 10,000 cell grid, and projects each occurrence record in the native and invaded range onto the grid. Thus, I used five different climate grids to capture the environments occupied by species from each of the five different native ranges (see Figure S1).

2.3.3 ecospat details

To measure expansion in climate space over a species' invasion history, I used the 'unfilling' metric in *ecospat.* This metric represents the proportion of climate space that is occupied by a species in its native range, but not in the introduced range. Unfilling is calculated as the number of grid cells occupied only in the native range, divided by the total number of cells occupied in the native range (i.e., including those shared with the introduced range), and weighted according to the occupancy density estimate for cells in the native range. The final value is multiplied by 100, yielding an index that ranges from 0 (all grid cells occupied in the native range are also occupied in the invaded range) to 100 (none of the grid cells occupied in the native range are occupied in the invaded range). If invaders expand their range over the course of their invasion, and thus expand in climate space, unfilling should decline over time.

As *ecospat* cannot be run with fewer than five observations, the earliest time period for each species was defined as the first 5-year time interval with at least five occurrences in the introduced range (Figure S2). From this point onwards, occurrence records from subsequent 5-year intervals were added cumulatively, with the final interval being 2015-2020. Unfilling was calculated based on the climate space occupied in the introduced range at each 5-year time interval and was compared to the space occupied in the native range based on all records available up to the year 2020 in the native range. For the purpose of plotting invasion patterns, I used the inverse of the unfilling value at each time interval, such that as a species expands its range over the course of its invasion, we would expect to see a positive relationship with time. Hereafter, this inverted unfilling metric will be referred to as 'expansion'.

2.4 Analysis

2.4.1 Patterns of expansion in climate space over the invasion history

To determine which pattern best described each species' expansion in climate space, I compared three model types that described the relationship between expansion and time. From an initial list of model types typically used to quantify growth patterns, I determined that these three models resulted in the best fit for the greatest number of species. To represent a single-, two-, and three-phase pattern in expansion, I considered a linear, asymptotic, and sigmoidal model, respectively. The simple linear model best represents expansion patterns with a constant rate of change, whereas the asymptotic and sigmoidal models best represent expansion patterns with two or three distinct phases in rate of change, respectively (Figure 2). Here, a linear relationship between expansion and time suggests that the species is expanding into available climate space at a constant and continuous rate, with no evidence of slowing (Figure 2A). In contrast, the other two model options describe a nonlinear relationship (Figure 2B-C), suggesting that there is a change in the rate at which a species is filling available climate space. The two-phase model (asymptotic) is characteristic of an initial rapid filling of climate space, followed by a declining rate towards an asymptote (Figure 2B). The three-phase model (sigmoidal) is characteristic of an initial lag phase where the rate of filling is slow in the years after introduction, followed by expansion occurring more rapidly, and then slowing again (Figure 2C).

Both the linear and asymptotic regression models were fit using the R *stats* package (version 3.6.2), using the built-in linear and nonlinear regression fitting functions *lm()* and *nls()*, respectively. The sigmoidal regression model was fit using the maximum and minimum expansion values, and the inflection point of the curve (Ni, 2022) (see formula in Figure 2).

I compared models using multi-model inference. I used the Akaike Information Criterion (AIC) to determine the model of best fit (i.e., model with lowest AIC). I used the *aictab()* function in R (*stats* package, V3.6.2) to calculate the delta AIC (ΔAIC) among models. To discriminate among competing models, we used an $\Delta AIC > 2$ between the best model and the model with the next smallest AIC (Burnham and Anderson, 2003). When more than one model had a $\Delta AIC < 2$ (i.e., models were indistinguishable), the most parsimonious model was selected (i.e., linear was most parsimonious over asymptotic over sigmoidal).

Species with a single-phase (i.e., linear) pattern of expansion were further analyzed to determine if the rate of change was more indicative of a species in active expansion (i.e., expanding into climate space at a constant rate over time) or of a species in a lag phase (i.e., climate space occupied remains stable over time). To distinguish between these two scenarios, I determined if the rate of change in expansion, ß, was significantly different from zero. If ß was less than 0±0.6%/year, the species was classified as being in lag phase, otherwise I classified it as expansion. This is the same threshold used in the equilibrium analysis, explained in section 2.4.2.

2.4.2 Equilibrium analysis

For each species, I determined if they have reached climatic equilibrium, and if so, how long it took them to reach it. I defined equilibrium as a period of no change in expansion for at least 30 years in the last phase of invasion (i.e., excluding any initial lag phase). For the equilibrium analysis, only species previously determined to have a nonlinear expansion pattern (i.e., two-phase and three-phase species) were included.

First, to determine if equilibrium has occurred in the last 30 years (i.e., 1990-2020), I fit a linear model with expansion as a function of year for this time period. If the rate of change in expansion, ß, was less than 0±0.6 %/year, I categorized this species as having reached equilibrium. This threshold was based on the correspondence between the distribution of ß across species and the visual representation of this relationship (i.e., expansion over time). Effectively, this threshold encompassed all species showing stability in expansion. The resolution for estimating time of equilibrium was +/- 5 years based on the time-intervals used. Species with a nonlinear pattern of expansion but that did *not* reach equilibrium before 1990 (i.e., ß > 0±0.6 %/year) were categorized as 'approaching equilibrium'.

Second, for species which were in equilibrium from 1990-2020, I used a backwards 30-year moving window approach to estimate when equilibrium was first reached (Figure 3). To do this, I shifted the window back in time by five year-time intervals and ran a linear model within each window until ß > 0±0.6 %/year (Figure 3). I used the first year of the earliest five-year time interval of the window to estimate how long it took the species to reach equilibrium relative to its first recorded occurrence in North America.

Finally, to assess how much unoccupied climate space remains in the introduced range for a species at equilibrium, I recorded the final expansion values for each species determined to have reached equilibrium.

3. Results

3.1 Patterns of expansion

For the majority of species, the expansion in climate space in their invaded range over their invasion history is slowing or has slowed. There was a non-linear relationship between expansion and time for 84.8% (218/257; Figure 4) of species, suggesting that the rate of expansion into climate space has slowed at least once in these species' invasion history. The pattern of change in expansion for 52.3% (114/218; Figure 4) of these species fit a two-phase model (Figure 2B), indicating a pattern consistent with early rapid expansion followed by a declining rate of expansion (Figure 5B). The remaining 47.7% (104/218; Figure 4) of species with a nonlinear pattern of change in expansion fit a three-phase model (Figure 2C), indicating the presence of a lag phase prior to rapid expansion and then a subsequent phase of slowing expansion (Figure 5C).

For a smaller group of species, the expansion in climate space has not slowed. For 15.2% (39/257; Figure 4), changes in expansion were best described by a linear model (Figure 2A), indicating a constant filling of available suitable climate in the introduced range, with no indication of slowing to equilibrium (Figure 5A). Of these species, 2 had a rate of change close enough to 0 (i.e., $ß < 0 \pm 0.6$), that they were classified as being in lag phase, with the rest of the species (37/257) in active expansion (Figure 4; Figure 5A).

3.2 Quantifying equilibrium

Despite the fact that expansion in climate space is slowing or has slowed for the majority of species, not all of these species have reached equilibrium (i.e., at least 30 years of stability in expansion). There was an equal number of species that have reached equilibrium in the past 30 years than as that are approaching it (42.4% (109/257) in each category, Figure 4).

For those species that reached equilibrium prior to 1990, time to equilibrium relative to the first recorded occurrence in North America ranged from 20 to 120 years, with an average of 82 years across species, and a median of 85 years (Figure 6).

The distribution of percentage of climate space that remained unoccupied when a species reached equilibrium was right-skewed and varied from 0 to 59.8% across species, with a median of 3.13% (i.e., when equilibrium was reached, ~3% of suitable climate space was still unoccupied; Figure 7). One species, *Glebionis coronaria*, had an unusually high percentage of space that remained unoccupied (59.8%; Figure 7). If this outlier is removed, the median percentage of unoccupied climate space remained the same (3.12%).

4. Discussion

Although widely recognized as an important assumption in predictive distribution modelling, evaluating whether or not a species has reached equilibrium with their environment is rarely done, especially at broad scales. This assumption is particularly critical for recently introduced invasive species that are characterized by rapid expansion in their introduced range. By comparing the climates occupied by species in their native and introduced ranges throughout their invasion history, I used patterns in expansion to quantify and describe equilibrium for over 250 invasive plants species. I found that: *i*) invasive species do not always follow the typical three-phase invasion pattern; *ii*) less than half of the species analyzed appear to have reached equilibrium; *iii*) there is a large variation in the time it takes for a species to reach equilibrium; and *iv*) species at equilibrium occupied only 95% of the suitable climates available in their invaded range. These findings serve as evidence that the equilibrium distribution of a species must be considered in the context of its invasion history.

4.1 Patterns of expansion

I found substantial variation in the pattern of expansion across species. To start, there was no detectable lag phase in 41.2% (106/257) of species. This indicates that these species started expanding in environmental space immediately after detection in North America. My results are consistent with previous studies that also reported large amounts of variation in expansion patterns across plant species. For instance, Osunkoya et al. (2021) reported a lag phase in 59% of 91 introduced plant species in Australia. Another study found that a lag phase could only be documented in 28% of introduced plant species in New Zealand and 40% in the mid-West

United States (Hyndman et al., 2015). This variation in results across studies is not surprising considering that the specific drivers of lag phases are still poorly understood. There is some evidence that lag times in plants differ across taxonomic groups and native range (Larkin, 2012). Genetic diversity present in founding populations and the time required to adapt to novel climatic conditions (i.e., niche shifts) likely also plays a significant role in the length of the lag period, if any (Williamson et al., 2005).

Alternatively, it could be that I underestimated the number of species with a lag phase. With the use of herbarium specimens as occurrence data for this study, it is possible that these species did in fact go through a lag phase, but remained undetected until after their populations increased during the expansion phase. The management implications are the same in either case: by the time these species were discovered in North America, they were already aggressively colonizing the region. Given that my approach was retrospective, time since invasion could also be important as some species may not have been here long enough for me to detect a lag phase.

Regardless, clarifying this issue will require a more granular assessment of the traits associated with different invasion patterns as well as the quantification of niche shifts. For example, we would expect species with high dispersal, rapid growth rates, and broad habitat tolerances to require little or no lag period prior to expansion. In contrast, traits contributing to density-dependent fitness (i.e., allele effects) such as self-incompatibility, or dependence on specialist pollinators or mycorrhizae could constrain species to a protracted lag period. The nature and frequency of a species' method of introduction, coupled with features of the introduced landscape (i.e., the presence or absence of geographic barriers) could also contribute to the initial rate of spread (Radosevich et al., 2003; Williamson et al., 2005; Larkin, 2012). Similarly, traits such as plant size, phenology and similarity to co-occurring native taxa may contribute to variation in how extensive a newly arrived species needs to be before it is detected and reflected in herbarium collections (Daru et al. 2018). Quantifying the extent of niche shifts that could have occurred in the invaded range could help to disentangle the role of local adaptation and other traits as the factors underlying the variation in the presence—and length—of the lag phase in newly introduced species.

I also found that a small proportion of species (14.4%, 37/257) are currently actively expanding into unoccupied climate space (i.e., linear expansion patterns). On average, these species were introduced to North America 36 years later than species that had non-linear patterns of expansion (linear species: mean=1930 ±31 SD; vs. nonlinear species: mean=1894 ±26.5 SD; Appendix Table S7). This could indicate that species that are currently in an expansion phase have not experienced enough residency time to reach equilibrium. My findings are identical to another study that found that the average difference in time since arrival between species that are actively expanding vs. those with a nonlinear pattern of expansion was 37 years (Osunkoya et al., 2021). However, given the importance of residency time in determining whether species are actively expanding or not makes it difficult to directly compare the percentage of species in different patterns of expansions with other studies. Nonetheless, given that these species are in active expansion, they could be aggressive invaders and efficient eradication strategies should be considered for these species.

4.2 Quantifying equilibrium

I found that less than half (42.2%) of the invasive plant species analyzed in this study have reached equilibrium in their introduced North American range. This result is difficult to compare to other studies—based on how rarely equilibrium is assessed, differences in methodologies, definitions of equilibrium, etc. For example, Osunkoya et al., 2021 reported that only 2% (2/91) of introduced plant species in Australia showed evidence of having reached a stable equilibrium (as indicated by a period of stabilized number of grid cells occupied) but they measured equilibrium in geographic space. In contrast, another recent study (Ni, 2022) evaluated the relationship between residency time and invasion range (i.e., log number of counties occupied) in eight introduced plants in China using fitted segmented models. They found that 100% of their study species displayed a recent slowing of expansion indicative of reaching equilibrium, determined by a breakpoint in the segmented model.

For the species that were estimated to have reached equilibrium, it took 83 years on average to reach it. Again, it is difficult to compare these results to other studies given how rarely time to equilibrium has been quantified. Of the past studies that are most comparable, equilibrium analyses are either limited to only one species (e.g., Václavík & Meentemeyer, 2012; Briscoe Runquist et al., 2019; Foster et al., 2022), or they evaluate whether or not species could be at equilibrium without measuring how long it took to do so (e.g., Gallien et al., 2012). My results align with Foster et al. (2022) who compared the historic and current distribution of an invasive vine, *Vincetoxicum rossicum*, throughout its invasion history and inferred equilibrium from when its distribution remained stable for 50 years. They found that it took approximately 80 years after its introduction for *V. rossicum* to reach environmental equilibrium. My findings, and the lack of comparable studies, reinforce the perspective that a temporal context is necessary to determine if–and especially *when*–a species has reached climatic equilibrium.

I found a large range in the time it took species to reach equilibrium—20 to 120 years (Figure 6). It remains unclear whether it will be possible to predict how long it will take for a newly introduced invasive species to reach equilibrium. Future research should look into which functional traits, if any, could be associated with different rates of climatic expansion. Past studies have demonstrated clear differences between invasive and non-invasive species in traits related to physiology, shoot allocation, growth rate, size, and fitness (Van Kleunen et al., 2012), but it remains unclear if these traits can help predict how quickly a species reaches equilibrium. In the context of invasive species management, this information is useful in order to predict the invasion patterns of early-stage invaders before eradication efforts become too difficult and costly.

4.3 Comparing native and invaded climates occupied at equilibrium

The proportion of native climate space that remained unoccupied in the introduced range at equilibrium was highly variable (0 to 59.8%) with a median of 3.1% (Figure 7). This suggests that, besides a few outliers, most species that have reached equilibrium in their invaded range occupy almost all of the suitable climate space that they occupy in their native range. There is a lack of studies with comparable results, but the most comparable study to mine found that, despite being stable for almost 50 years, 15.4% of the environmental space occupied by *Vincetoxicum rossicum* in its native range remains unoccupied in eastern North America (Foster et al., 2022).

The unoccupied suitable climate space remaining for most species at equilibrium could indicate the presence of dispersal barriers preventing the species from reaching all suitable environments, or altered biotic interactions or species-environment relationships in the invaded range reducing their potential distribution relative to their native range (Mainali et al. 2015). This could result in a temporary equilibria-type state until these barriers are overcome. If this is the case, the results of this study may overestimate the proportion of invasive plants at *true* climatic equilibrium. Determining whether these limitations are due to dispersal barriers, biotic or abiotic factors, or a combination of both, would require in-depth species-specific analyses. Evaluating how the amount of unoccupied suitable climate space translates to geographic space would also help to determine the biological significance of the remaining unoccupied space and the degree to which barriers are likely to be surpassed.

Past studies may have been too quick to classify any invading species with remaining suitable climate space as not being at equilibrium (e.g., Goncalves et al., 2022). Identifying phases of potentially temporary equilibrium is still valuable in the context of invasive species management, and only possible when considering expansion over time. For example, temporary equilibria could present a window of opportunity for efficient management, similar to lag phases (Coutts et al., 2018). Further, if a species is stable but has a larger amount (e.g., >15%) of unoccupied climate space (as defined by the native distribution) remaining in the introduced range, this presents an opportunity to identify the factors preventing the species from fully occupying these apparently suitable locations. The results of such studies, which could include biotic interactions or additional environmental factors (e.g., soil or habitat conditions), could inform further management or biological control initiatives.

4.4 Implications

My findings have a number of implications for modeling the geographic distribution of invasive species and predicting where expansions are likely to occur next. Given the potential ecological and economic consequences of incorrect predictions, I am conservative in the assessment of these implications. First, I found the majority (65%) of species have not yet reached equilibrium. Given the demonstrations by previous studies (Elith *et al.*, 2006; Bradley *et* *al.*, 2015; Briscoe Runquist et al. 2019; Foster et al. 2022), it is likely that SDMs constructed for these species would produce unreliable results. For example, by underestimating the species' potential range by falsely considering unoccupied space as being unsuitable.

In contrast, for the 35% of species that have reached equilibrium, it is likely appropriate to construct SDMs from occurrence data in their invaded range. Foster et al. (2022) demonstrated that once the expansion of an invading species plateaus at equilibrium, adequate data is available to satisfy the equilibrium assumption of SDMs. For species with a slowing, but not yet stabilized distribution, SDMs may still be useful, but will require caution in their interpretation.

For the minority of species that were in the expansion phase, SDMs are likely to be unreliable and alternative assessment methods should be developed. This is a potentially critical issue, as until a species begins to slow its invasion rate (i.e., moves from a single phase to a two-phase pattern), the extent of its final distribution will remain highly uncertain.

4.5 Next steps

Because the metric I used (i.e., unfilling) considers only expansion into climates that are occupied in the native range, any expansion into novel climate conditions (i.e., a niche shift) is not represented. Many past works did not make this distinction, and thus combine two different types of dissimilarity between native and invaded ranges: climate conditions that are suitable in the native range, but unoccupied in the new range (i.e., unfilling), and climate conditions that are unsuitable in the native range but have become suitable in the newly invaded range (i.e., niche shift). In general, studies that find a large proportion of niche shifts among invading species use methods that consider unfilling to be evidence of a niche shift (e.g., Atwater et al, 2018).

However, my analysis suggests that unfilling is more likely due to time since introduction and dispersal rate in the introduced range, rather than an actual niche shift.

Distinguishing between these dissimilarities would be useful in the ongoing dispute of whether or not an invasive species' fundamental niche is conserved from its native to introduced range (e.g., Petitpierre et al., 2012; Atwater et al., 2018; Liu et al., 2020). My method takes a first step at making this distinction by measuring one of these types of dissimilarities (i.e., unfilling). In doing so, I assume the invading species is genetically homogenous and not adapting to new climate conditions in its introduced range that are outside of its native fundamental niche. Future studies should measure niche shifts in these species to get the full picture of the invasive species' fundamental niche. Future studies that aim to measure niche shifts for introduced species should focus on whether the difference in conditions between the native and introduced ranges are due to time constraints or a true niche shift. If a large portion of niche differences between the invaded and native ranges are actually due to processes related to time constraints, it is possible that past work may have overestimated the incidence of true niche shifts among plant invaders (i.e., underestimated niche conservatism). In the context of this study, the use of unfilling as a metric to track species expansion provides a unique perspective into understanding how an invading species spreads without the confounding effects of adaptation.

5. Conclusion

Plant invasions pose an increasing global threat to ecosystem function and native biodiversity (Vilà et al., 2011; Van Kleunen et al., 2015). In an attempt to control and predict these invasions, researchers use a variety of methods, including tracking geographic spread over time (e.g., Aiello-Lammens, 2020; Osunkoya et al., 2021) and building predictive species distribution models (Kariyawasam et al., 2019). However, these studies often ignore a very important consideration: how long does it take an invading species to reach climatic equilibrium in its introduced range? Knowing if and when a species reaches equilibrium is a crucial, yet consistently understudied, aspect of invasion biology. In this study, I used patterns of expansion in climate space over time to determine if an invading species has reached a point of stable climate distribution (i.e., climatic equilibrium), and estimated how long this process takes relative to its first reported collection in North America.

My findings suggest that a temporal approach is necessary in evaluating equilibrium, and that it is possible that many North American plant invaders have not yet stabilized their climatic distribution. Researchers must consider the implications of nonequilibrium in their studies of invasive species, especially in the context of building reliable distribution models with the purpose of predicting potential suitable habitat. Future directions for this work include investigating the biotic and abiotic factors that could potentially be associated with different equilibrium patterns, as well as looking into how niche shifts between the native and invaded range affect equilibrium distribution. The methods outlined in this study lay the groundwork for developing a standardized approach to evaluating equilibrium, and not just in invasive plants. This approach should be tested in other taxa with available historical occurrence data for both their native and invaded ranges, highlighting the importance of accessible natural history collections.

Tables

Table 1. Breakdown of the native geographic ranges and number of species from each range included in this study. Geographic extent is represented by the white area on the maps for each native range.

Native Range	Geographic Extent	Number of Species
Mediterranean		73 (28.4%)
Eurasia		98 (38.1%)
Europe		46 (17.9%)

Asia		29 (11.3%)
South America		11 (4.3%)
	Total:	**257**

Figures

Figure 1. Theoretical curve depicting the three phases of the invasion process: lag/establishment phase, expansion phase, and equilibrium phase.

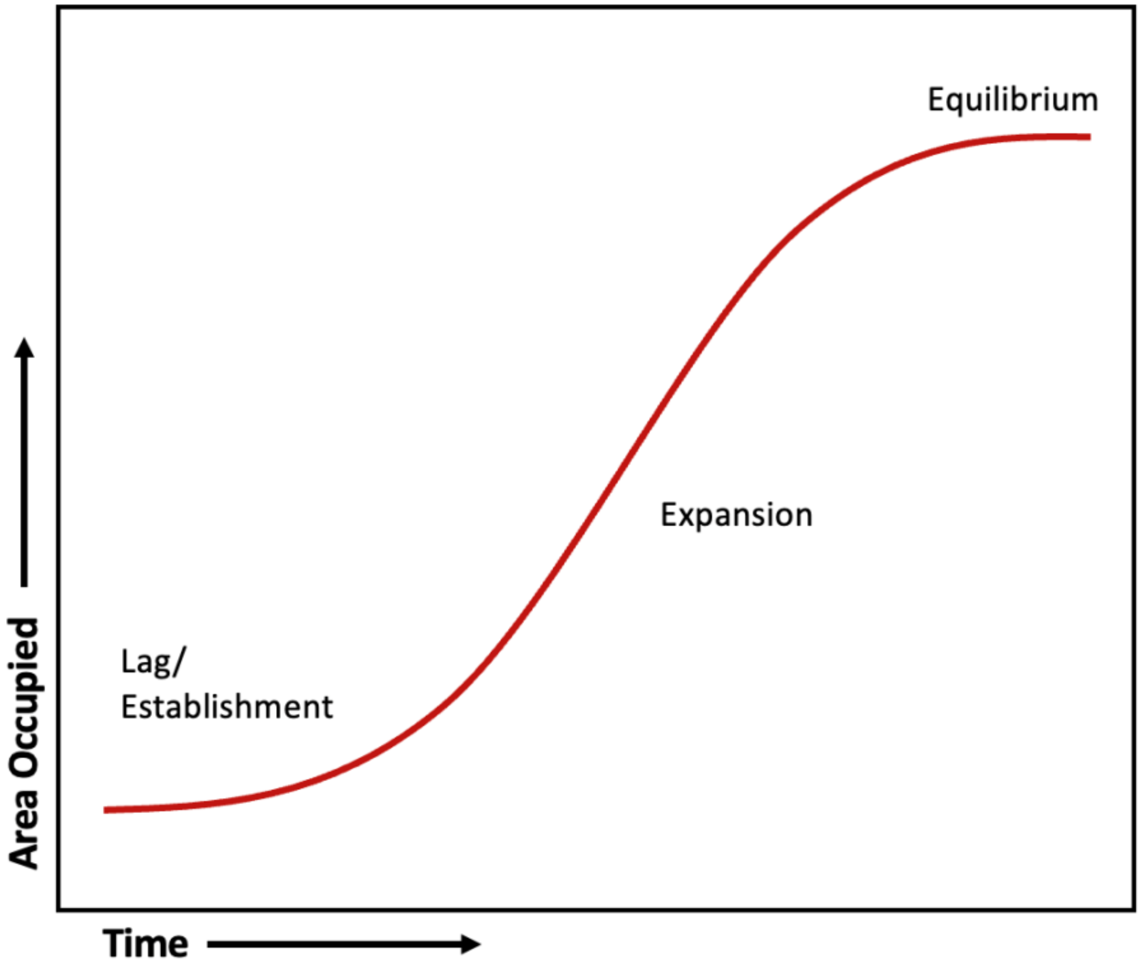


Figure 2. Overview of the three models used to describe patterns in expansion (*E*) in climate space across species. Expansion (%) was calculated as 100 – unfilling. Unfilling was calculated as the number of grid cells occupied only in the native range, divided by the total number of cells occupied in the native range. Time is measured in years since first North American record.

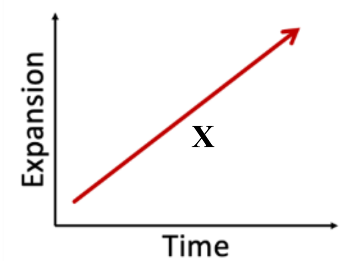
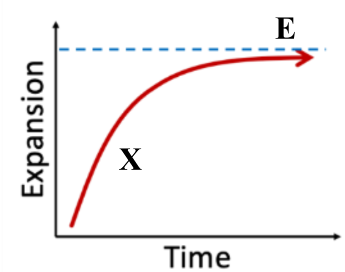
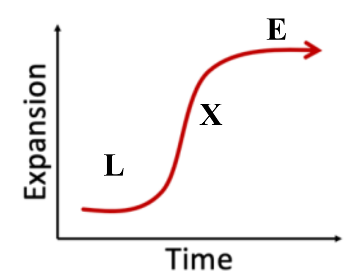
Panel	Model	Formula	Shape	Number of phases	Description
A.	Linear	$E = 1 - (b + ßx)$ Where *b* is the y-intercept, ß is the slope, and *x* is time.		Single	Expansion is increasing at a constant rate (expansion phase, **X**); no slowing.
B.	Asymptotic	$E = 1 - (a + (b - a)e^{-ecx})$ Where *a* is the asymptote, *b* is the y-intercept, *c* is the rate constant, and *x* is time.		Two	Expansion begins by increasing at a constant rate (expansion phase, **X**), but then the rate slows to an asymptote (blue dashed line) representative of equilibrium (**E**).
C.	Sigmoidal	$E = 1 - (S + \frac{U_{max} - S}{1 + e^{(-c(x-\tau))}})$ Where S is the minimum value of unfilling, U_{max} is the maximum value of unfilling, *c* is the rate constant, τ is the inflection point, and *x* is time.		Three	Expansion stays stable for a number of years (lag phase, **L**), then increases at a constant rate (expansion phase, **X**), then the rate slows again (equilibrium phase, **E**).

Figure 3. Demonstration of the backwards 30-year moving window approach used to estimate when equilibrium occurred using *Glechoma hederacea* as an example. For each window (here identified by iteration: orange, green, blue and yellow brackets), a linear model with expansion as a function of year was fit until ß > 0±0.6 %/year (here, 1970). Each black datapoint represents cumulative expansion at 5-year intervals, with expansion (%) equal to 100 – unfilling.

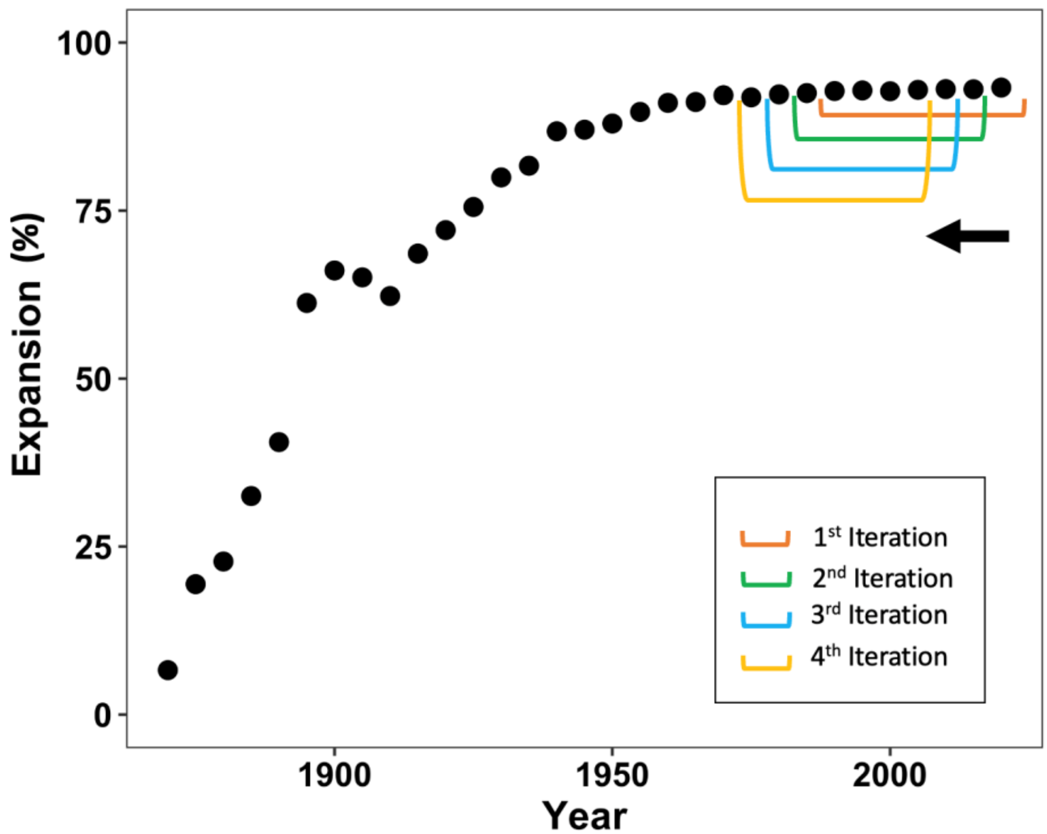


Figure 4. Flow chart summarizing results. Expansion data for all species (n = 257) were input into the model fitting analysis (red), yielding 39 species with a linear pattern over time (green), 218 with a nonlinear pattern over time (blue). All linear species were classified as 'single-phase', and then categorized as 'expanding' (n=37) or 'lag' (n=2). The 218 nonlinear species were further classified as either 'two-phase' (n=114) or 'three-phase' (n=104). Both the two and three phase species (all nonlinear) were input into the equilibrium analysis (red), yielding 109 species classified as approaching equilibrium, and 109 species classified as having reached equilibrium. For visualizations of phases, see Figure 2. For an overview of which species are in each classification, see Appendix Tables S3, S4 and S5.

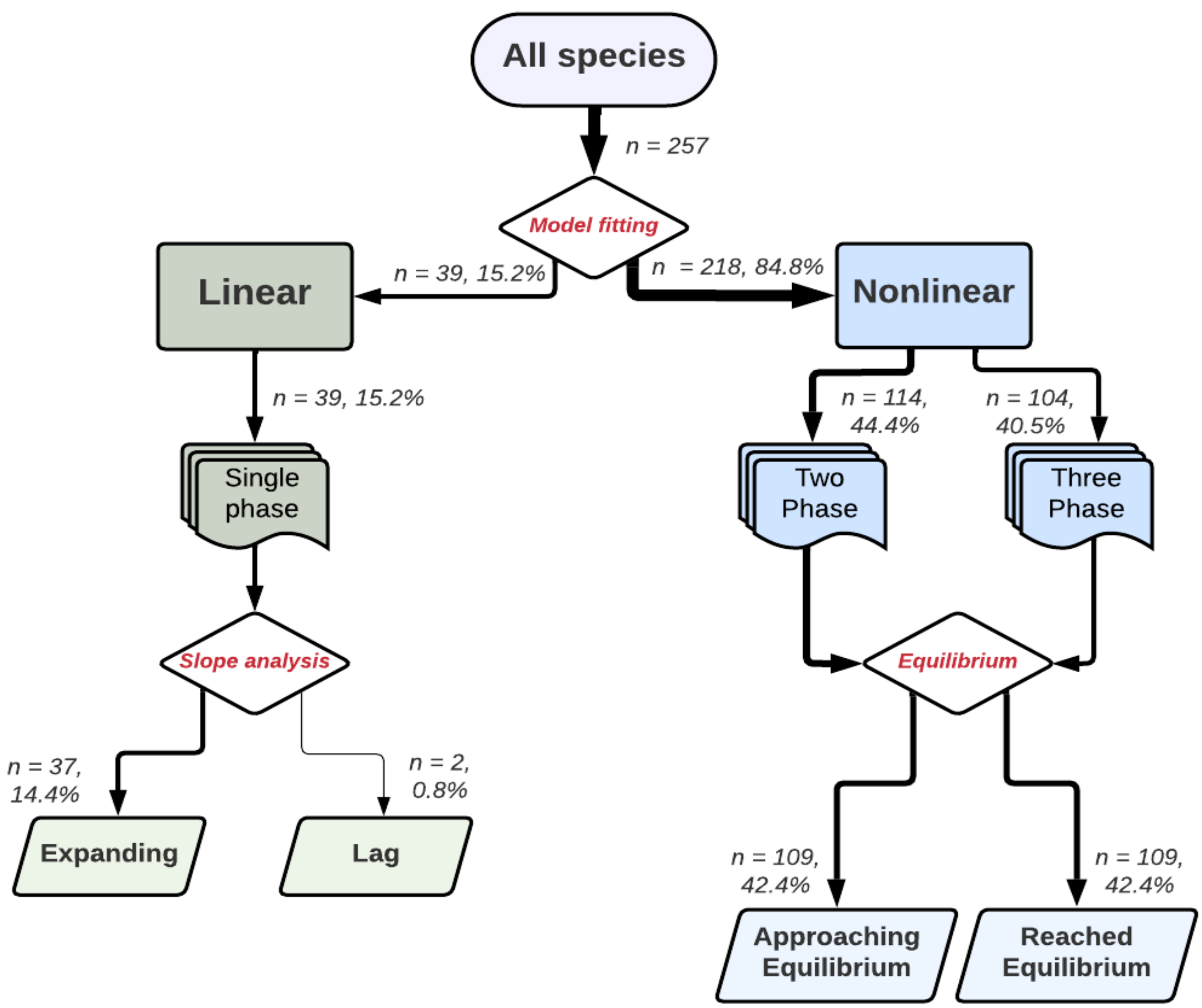


Figure 5. Expansion over time plotted for three different species, illustrating three patterns of expansion in introduced climate space. A is an example of a linear relationship, while B and C represent nonlinear relationships. *C. majus* (A) shows a single-phase pattern of expansion, indicated by a linear model best fit (red line). *L. vulgare* shows a two-phase pattern of expansion, indicated by an asymptotic model best fit (red line). *H. matronalis* (C) shows a three-phase pattern of expansion, indicated by a sigmoidal model best fit (red line). Refer to Fig. 2 for equations.

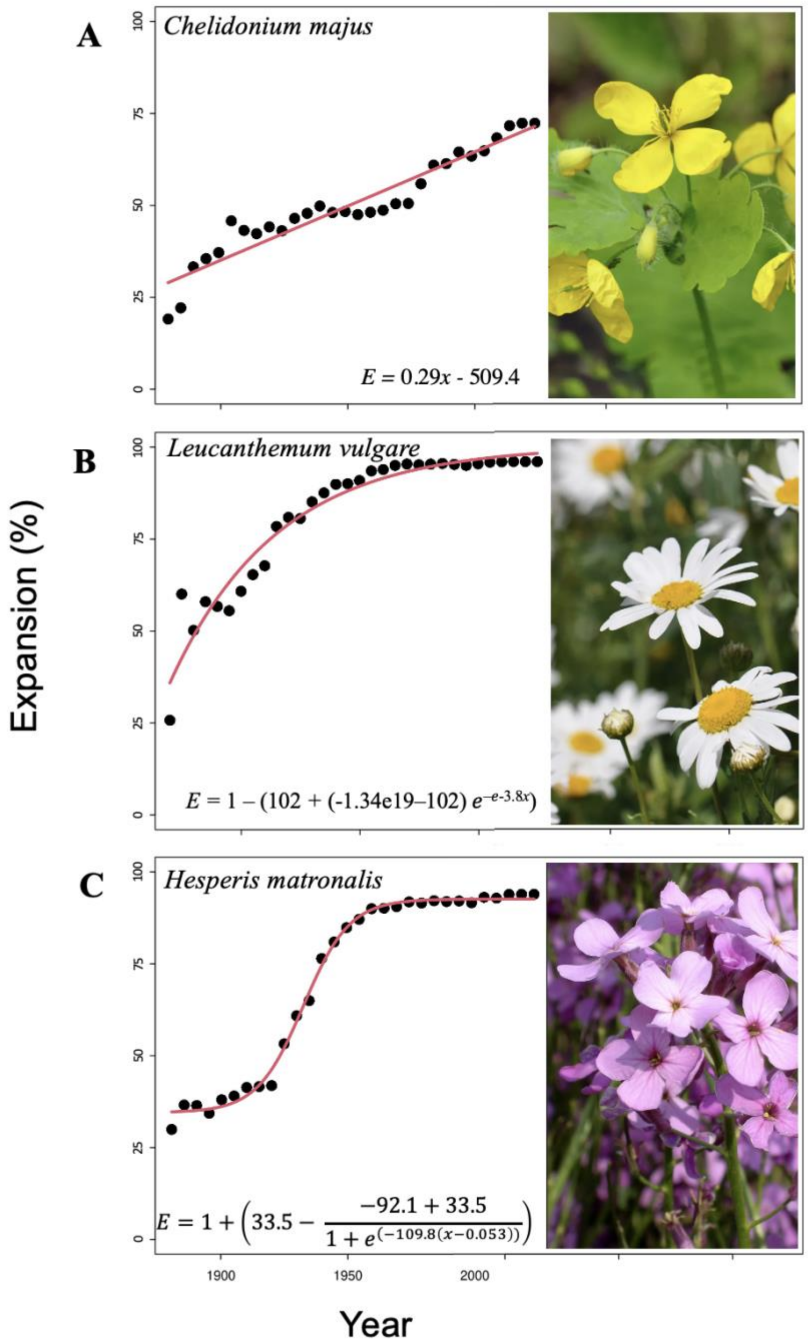


Figure 6. Histogram depicting the distribution of years to equilibrium across species at equilibrium (n=109). Median is represented by the blue dashed line (x=85), and mean is represented by the red dashed line (x=82).

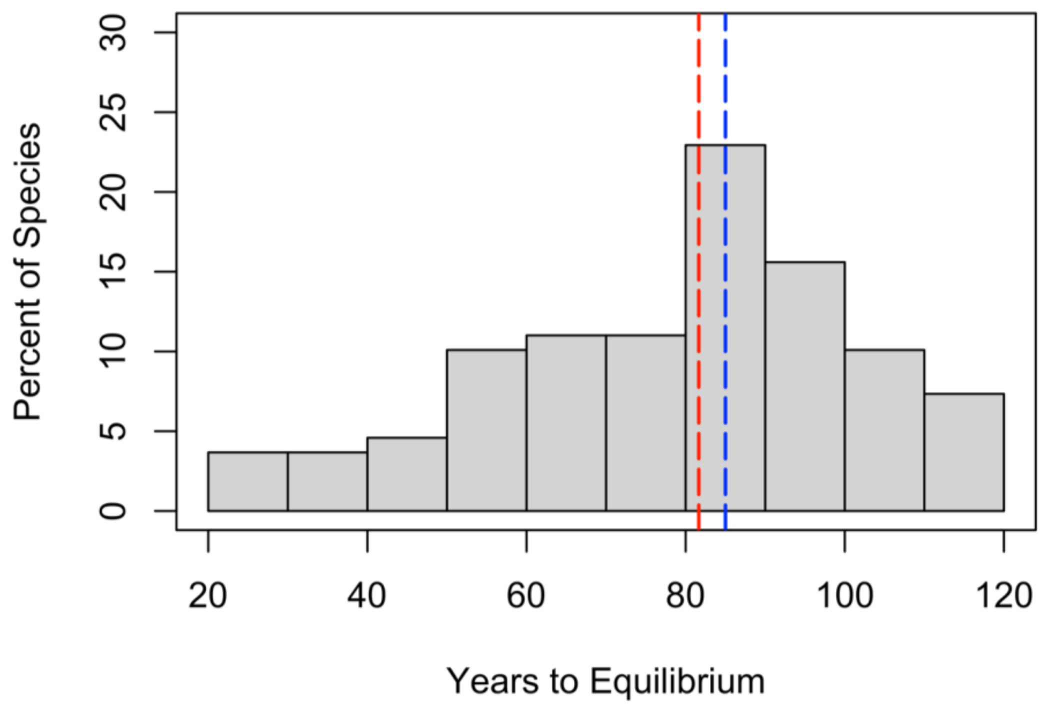
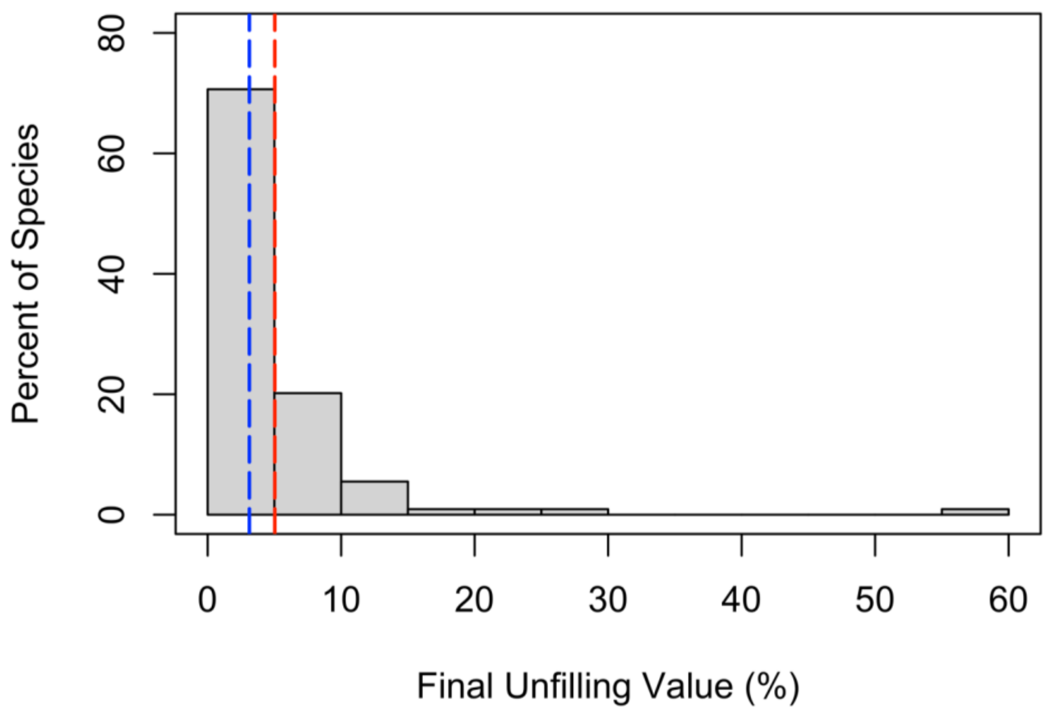


Figure 7. Histogram depicting the distribution of most recent (year 2020) unfilling value across species at equilibrium (n=109). Median is represented by the blue dashed line (x=3.1), and mean is represented by the red dashed line (x=5).



Appendix

Table S1. Overview of all species included in the study, including family, species name, native range (see Table 1) and the total number of occurrence records in each native and introduced range. Record numbers are before thinning to one record per 10 km^2 pixel.

Family	Species Name	Native Range	Number of native range records	Number of introduced range records
Aceraceae	*Acer platanoides*	Eurasia	884	2810
Amaranthaceae	*Alternanthera philoxeroides*	South America	282	436
Anacardiaceae	*Schinus molle*	South America	501	527
	Pistacia chinensis	Asia	89	723
Apiaceae	*Anthriscus sylvestris*	Mediterranean	408	3840
	Daucus carota	Eurasia	1136	1099
	Pastinaca sativa	Eurasia	946	2416
	Torilis arvensis	Eurasia	997	2076
	Torilis japonica	Eurasia	123	2951
	Carum carvi	Mediterranean	524	3484
	Conium maculatum	Mediterranean	1564	2812
	Foeniculum vulgare	Mediterranean	747	1502
Aquifoliaceae	*Ilex aquifolium*	Mediterranean	205	1601
Araliaceae	*Kalopanax septemlobus*	Asia	29	812
Asteraceae	*Artemisia absinthium*	Mediterranean	523	2721
	Artemisia vulgaris	Eurasia	789	3780
	Carduus nutans	Mediterranean	829	2057
	Carduus pycnocephalus	Mediterranean	627	1526
	Anthemis cotula	Europe	1573	1904
	Arctium minus	Europe	1196	3689
	Carthamus creticus	Mediterranean	52	230
	Centaurea solstitialis	Mediterranean	662	885
	Carduus acanthoides	Eurasia	231	1216
	Chondrilla juncea	Mediterranean	296	1500

	Cichorium intybus	Mediterranean	1462	2811
	Centaurea benedicta	Eurasia	255	454
	Centaurea calcitrapa	Eurasia	177	964
	Centaurea nigrescens	Eurasia	112	427
	Centaurea cyanus	Europe	507	3894
	Centaurea montana	Europe	80	1062
	Centaurea nigra	Europe	445	1825
	Centaurea stoebe	Europe	1076	1826
	Cirsium vulgare	Eurasia	2222	2644
	Crepis tectorum	Eurasia	670	4979
	Cirsium arvense	Europe	2332	4202
	Lactuca saligna	Eurasia	415	759
	Lapsana communis	Eurasia	552	3842
	Glebionis coronaria	Europe	412	355
	Matricaria discoidea	Asia	2462	145
	Hypochaeris radicata	Europe	936	2661
	Onopordum acanthium	Eurasia	359	1162
	Pilosella officinarum	Eurasia	419	8420
	Leucanthemum vulgare	Europe	2304	5765
	Pilosella aurantiaca	Europe	1160	2438
	Pilosella caespitosa	Europe	972	1787
	Pilosella piloselloides	Europe	403	1693
	Pilosella x floribunda	Europe	276	2306
	Senecio sylvaticus	Eurasia	278	3027
	Tanacetum vulgare	Eurasia	938	3170
	Taraxacum erythrospermum	Eurasia	563	1099
	Taraxacum officinale	Eurasia	3316	2067
	Sonchus arvensis	Europe	1465	3440
	Tragopogon dubius	Eurasia	2099	1309
	Sphagneticola trilobata	South America	180	1202
	Tussilago farfara	Eurasia	844	3902
	Helminthotheca echioides	Mediterranean	577	1471
	Jacobaea vulgaris	Mediterranean	288	4425
	Lactuca serriola	Mediterranean	2525	3510
	Senecio vulgaris	Mediterranean	1860	5420
	Silybum marianum	Mediterranean	539	1075
	Sonchus asper	Mediterranean	2549	3589
	Sonchus oleraceus	Mediterranean	2743	4094
Berberidaceae	*Berberis vulgaris*	Eurasia	409	2592

	Berberis thunbergii	Asia	658	854
	Nandina domestica	Asia	126	558
Betulaceae	*Betula pendula*	Eurasia	577	5150
Boraginaceae	*Buglossoides arvensis*	Eurasia	884	4362
	Cynoglossum officinale	Eurasia	1073	2270
	Echium vulgare	Eurasia	890	4629
	Lappula squarrosa	Eurasia	982	2727
	Myosotis scorpioides	Eurasia	1112	4912
	Symphytum officinale	Eurasia	328	3668
Brassicaceae	*Arabidopsis thaliana*	Mediterranean	946	7768
	Brassica nigra	Mediterranean	1136	1099
	Brassica tournefortii	Mediterranean	1191	392
	Cakile maritima	Mediterranean	656	3887
	Descurainia sophia	Mediterranean	2343	3889
	Alliaria petiolata	Eurasia	1303	3591
	Barbarea vulgaris	Eurasia	2039	3936
	Berteroa incana	Eurasia	975	4213
	Capsella bursa-pastoris	Europe	4066	6480
	Cardamine impatiens	Europe	209	1902
	Draba verna	Eurasia	1163	6554
	Isatis tinctoria	Eurasia	292	2264
	Hirschfeldia incana	Mediterranean	1218	2167
	Lepidium draba	Eurasia	840	3228
	Hesperis matronalis	Europe	1226	2123
	Microthlaspi perfoliatum	Eurasia	248	677
	Lepidium campestre	Europe	1327	1083
	Rorippa sylvestris	Eurasia	785	3455
	Raphanus raphanistrum	Europe	1093	3558
	Thlaspi arvense	Eurasia	2232	3452
	Lepidium latifolium	Mediterranean	666	1520
	Nasturtium officinale	Mediterranean	3156	2304
	Rapistrum rugosum	Mediterranean	109	2549
	Sinapis arvensis	Mediterranean	1587	4610
	Sisymbrium irio	Mediterranean	1834	1606
Butomaceae	*Butomus umbellatus*	Eurasia	377	2060
Callitrichaceae	*Callitriche stagnalis*	Europe	215	3434
Campanulaceae	*Campanula rapunculoides*	Europe	583	3230
Caprifoliaceae	*Viburnum dilatatum*	Asia	71	2280

Caryophyllaceae	*Arenaria serpyllifolia*	Eurasia	1385	7376
	Agrostemma githago	Europe	371	3413
	Cerastium fontanum	Eurasia	1036	3696
	Cerastium glomeratum	Eurasia	2008	6473
	Dianthus armeria	Europe	1341	1621
	Myosoton aquaticum	Europe	465	2096
	Saponaria officinalis	Eurasia	1470	2992
	Silene flos-cuculi	Eurasia	298	4453
	Silene noctiflora	Eurasia	567	1966
	Stellaria media	Eurasia	2671	5507
	Silene vulgaris	Europe	1190	4947
	Silene latifolia	Mediterranean	1637	5447
	Spergula arvensis	Mediterranean	1046	5472
	Spergularia rubra	Mediterranean	1249	4637
Celastraceae	*Euonymus alatus*	Asia	473	3810
	Euonymus fortunei	Asia	215	1588
Chenopodiaceae	*Bassia hyssopifolia*	Eurasia	750	183
	Dysphania ambrosioides	South America	1572	1248
	Salsola tragus	Mediterranean	2260	532
Clusiaceae	*Hypericum perforatum*	Eurasia	2598	6552
Commelinaceae	*Commelina communis*	Asia	763	2357
	Murdannia keisak	Asia	106	650
	Tradescantia fluminensis	South America	54	423
Convolvulaceae	*Calystegia sepium*	Eurasia	2112	3511
Dipsacaceae	*Dipsacus fullonum*	Mediterranean	94	80
	Dipsacus laciniatus	Eurasia	192	158
Dryopteridaceae	*Cyrtomium falcatum*	Asia	130	3529
Elaeagnaceae	*Elaeagnus angustifolia*	Eurasia	860	635
	Elaeagnus pungens	Asia	77	760
	Elaeagnus umbellata	Asia	807	2845
Euphorbiaceae	*Euphorbia cyparissias*	Eurasia	766	3096
	Euphorbia esula	Eurasia	792	6484
	Phyllanthus urinaria	Asia	197	940
	Triadica sebifera	Asia	267	1058
	Vernicia fordii	Asia	66	619
Fabaceae	*Galega officinalis*	Mediterranean	66	587
	Genista monspessulana	Mediterranean	427	445
	Albizia julibrissin	Asia	449	960

	Cytisus scoparius	Europe	530	2327
	Medicago sativa	Eurasia	2238	4245
	Melilotus officinalis	Eurasia	2410	3010
	Lotus corniculatus	Mediterranean	1422	10780
	Medicago lupulina	Mediterranean	3124	6597
	Sesbania punicea	South America	239	239
	Trifolium campestre	Eurasia	1136	5898
	Trifolium repens	Eurasia	2653	6272
	Trifolium aureum	Europe	921	3532
	Trifolium dubium	Europe	860	2915
	Vicia sativa	Europe	1793	9140
	Vicia cracca	Eurasia	1174	7183
	Vicia villosa	Eurasia	1945	4731
	Securigera varia	Mediterranean	316	1655
	Spartium junceum	Mediterranean	452	682
	Trifolium hirtum	Mediterranean	680	516
	Trifolium hybridum	Mediterranean	1508	3448
	Trifolium pratense	Mediterranean	2526	8074
	Quercus acutissima	Asia	64	1036
Geraniaceae	*Erodium cicutarium*	Mediterranean	1333	6935
	Geranium columbinum	Mediterranean	166	2717
	Geranium robertianum	Mediterranean	843	5092
	Geranium dissectum	Europe	868	2725
Grossulariaceae	*Ribes rubrum*	Eurasia	335	1772
Haloragaceae	*Myriophyllum spicatum*	Eurasia	1024	2831
Hydrocharitaceae	*Hydrilla verticillata*	Mediterranean	368	201
	Hydrocharis morsus-ranae	Mediterranean	139	1921
Iridaceae	*Iris pseudacorus*	Mediterranean	493	2792
Lamiaceae	*Ajuga reptans*	Mediterranean	241	2938
	Lamium amplexicaule	Mediterranean	1824	4370
	Marrubium vulgare	Mediterranean	2210	1673
	Nepeta cataria	Eurasia	1378	1521
	Galeopsis tetrahit	Eurasia	886	3816
	Glechoma hederacea	Eurasia	1634	4668
	Lamium maculatum	Eurasia	124	2102
	Leonurus cardiaca	Eurasia	1036	1586
	Galeopsis bifida	Europe	250	2106
	Melissa officinalis	Eurasia	321	927

	Mentha spicata	Eurasia	1104	1548
	Salvia aethiopis	Mediterranean	109	358
	Perilla frutescens	Asia	401	2074
Lauraceae	*Cinnamomum camphora*	Asia	175	1146
Liliaceae	*Allium vineale*	Europe	477	2133
	Asparagus officinalis	Europe	1156	1686
	Asphodelus fistulosus	Europe	492	229
	Convallaria majalis	Europe	259	3858
	Hemerocallis fulva	Asia	467	949
	Muscari botryoides	Europe	137	1271
Lythraceae	*Lythrum salicaria*	Mediterranean	2103	4436
	Lythrum hyssopifolia	Europe	938	599
Malvaceae	*Hibiscus trionum*	Europe	645	351
	Hibiscus syriacus	Asia	201	688
Menyanthaceae	*Nymphoides peltata*	Eurasia	111	697
Moraceae	*Ficus carica*	Mediterranean	324	609
	Broussonetia papyrifera	Asia	242	1709
Najadaceae	*Najas minor*	Eurasia	231	326
Oleaceae	*Olea europaea*	Mediterranean	268	1310
	Ligustrum vulgare	Eurasia	318	1992
Onagraceae	*Epilobium hirsutum*	Eurasia	306	3988
	Ludwigia peruviana	South America	185	795
Orchidaceae	*Epipactis helleborine*	Eurasia	985	4930
Papaveraceae	*Chelidonium majus*	Eurasia	635	3701
Plantaginaceae	*Plantago lanceolata*	Eurasia	2802	7739
	Plantago major	Eurasia	2944	6524
Polygonaceae	*Persicaria lapathifolia*	Eurasia	3473	7325
	Persicaria longiseta	Asia	798	3302
	Persicaria posumbu	Asia	132	2782
	Rumex acetosella	Eurasia	4097	6677
	Rumex crispus	Eurasia	3959	3689
	Rumex longifolius	Eurasia	150	1780
	Rumex obtusifolius	Eurasia	1333	4171
	Reynoutria japonica	Asia	966	2202
Pontederiaceae	*Eichhornia crassipes*	South America	453	788

Potamogetonaceae	*Potamogeton crispus*	Mediterranean	1010	2549
Primulaceae	*Lysimachia nummularia*	Eurasia	719	2249
	Lysimachia vulgaris	Eurasia	128	3512
Ranunculaceae	*Ficaria verna*	Mediterranean	196	3954
	Ranunculus repens	Mediterranean	1182	5090
	Ranunculus acris	Eurasia	1660	6072
	Ranunculus bulbosus	Europe	506	3346
Rhamnaceae	*Frangula alnus*	Mediterranean	683	4133
	Rhamnus cathartica	Mediterranean	894	2787
Rosaceae	*Prunus avium*	Mediterranean	425	1808
	Crataegus monogyna	Europe	523	6488
	Duchesnea indica	Asia	219	1303
	Potentilla recta	Eurasia	1489	2239
	Prunus mahaleb	Eurasia	255	1232
	Pyracantha coccinea	Eurasia	129	265
	Pyrus communis	Eurasia	348	2327
	Prunus padus	Europe	70	3848
	Pyrus calleryana	Asia	338	776
	Sorbus aucuparia	Eurasia	363	4557
	Spiraea japonica	Asia	177	2227
Rubiaceae	*Galium mollugo*	Mediterranean	635	3645
	Galium verum	Mediterranean	352	6283
Salicaceae	*Populus alba*	Mediterranean	644	1636
	Salix pentandra	Eurasia	166	4822
	Salix purpurea	Eurasia	300	2972
Sapindaceae	*Cardiospermum halicacabum*	South America	682	508
Scrophulariaceae	*Digitalis purpurea*	Europe	383	2314
	Linaria vulgaris	Eurasia	1766	5043
	Kickxia elatine	Europe	418	1163
	Paulownia tomentosa	Asia	201	288
	Veronica arvensis	Europe	1664	6123
	Veronica hederifolia	Eurasia	297	3902
	Verbascum blattaria	Mediterranean	1016	696
	Verbascum thapsus	Mediterranean	2058	3162
	Veronica beccabunga	Mediterranean	68	3497
Solanaceae	*Hyoscyamus niger*	Mediterranean	229	2941
	Solanum nigrum	Eurasia	902	4951
	Solanum viarum	South America	85	517

Trapaceae	*Trapa natans*	Mediterranean	125	420
Valerianaceae	*Centranthus ruber*	Europe	193	370
	Valeriana officinalis	Eurasia	272	4441
Verbenaceae	*Verbena bonariensis*	South America	146	444
	Vitex agnus-castus	Mediterranean	192	465
Violaceae	*Viola tricolor*	Eurasia	253	6022
Zygophyllaceae	*Tribulus terrestris*	Mediterranean	1766	1247
	Peganum harmala	Eurasia	150	729

Table S2. Full set of climate variables used in equilibrium analysis. All variables were derived from WorldClim version 2.1 for 1970-2000 (Fick, S.E. and R.J. Hijmans, 2017) at a resolution of 10 km^2.

Variable	Description
BIO1	Annual Mean Temperature
BIO2	Mean Diurnal Temperature Range (Mean of monthly (max temp - min temp))
BIO3	Isothermality (BIO2/BIO7) (×100)
BIO4	Temperature Seasonality (standard deviation ×100)
BIO5	Max Temperature of Warmest Month
BIO6	Min Temperature of Coldest Month
BIO7	Temperature Annual Range (BIO5-BIO6)
BIO8	Mean Temperature of Wettest Quarter
BIO9	Mean Temperature of Driest Quarter
BIO10	Mean Temperature of Warmest Quarter
BIO11	Mean Temperature of Coldest Quarter
BIO12	Annual Precipitation
BIO13	Precipitation of Wettest Month
BIO14	Precipitation of Driest Month
BIO15	Precipitation Seasonality (Coefficient of Variation)
BIO16	Precipitation of Wettest Quarter
BIO17	Precipitation of Driest Quarter
BIO18	Precipitation of Warmest Quarter
BIO19	Precipitation of Coldest Quarter

Table S3. Overview of results from the model comparison analysis. Each species (n=257) was fit to all three models and a ΔAIC score was calculated based on model fit**.** ΔAIC scores for each species and each model (asymptotic, sigmoidal, and linear) are presented here. Based on the model of best fit, each species was then assigned a 'pattern category' that best represents the patter of expansion: single-phase ('phase1'), two-phase ('phase2'), or three-phase ('phase3'). 'NA' indicates that the model did not fit the data.

Species Name	**ΔAIC Score**			**Pattern Category**
	Asymptotic	*Sigmoidal*	*Linear*	
Ajuga reptans	0.00	1.34	15.11	phase2
Anthriscus sylvestris	1.05	0.00	3.32	phase2
Arabidopsis thaliana	12.89	0.00	42.10	phase3
Artemisia absinthium	0.00	NA	78.64	phase2
Brassica nigra	36.80	0.00	62.72	phase3
Brassica tournefortii	NA	6.74	0.00	phase1
Cakile maritima	NA	NA	0.00	phase1
Carduus nutans	47.10	0.00	64.25	phase3
Carduus pycnocephalus	NA	NA	0.00	phase1
Carthamus creticus	6.79	0.00	3.15	phase3
Carum carvi	0.00	NA	103.14	phase2
Centaurea solstitialis	NA	NA	0.00	phase1
Chondrilla juncea	NA	0.00	47.81	phase3
Cichorium intybus	6.57	0.00	76.43	phase3
Conium maculatum	6.89	0.00	72.53	phase3
Descurainia sophia	0.00	NA	67.15	phase2
Dipsacus fullonum	50.94	0.00	50.24	phase3
Erodium cicutarium	0.00	NA	57.66	phase2
Ficaria verna	NA	NA	0.00	phase1
Ficus carica	30.91	0.00	29.14	phase3
Foeniculum vulgare	0.00	NA	56.11	phase2
Frangula alnus	0.00	NA	50.77	phase2

Galega officinalis	NA	0.00	2.45	phase3
Galium mollugo	NA	0.00	9.82	phase3
Galium verum	52.63	0.00	56.26	phase3
Genista monspessulana	0.00	NA	8.10	phase2
Geranium columbinum	25.04	0.00	29.47	phase3
Geranium robertianum	5.41	0.00	31.70	phase3
Helminthotheca echioides	0.00	NA	29.72	phase2
Hirschfeldia incana	25.29	0.00	24.91	phase3
Hydrilla verticillata	0.00	NA	4.12	phase2
Hydrocharis morsus-ranae	NA	NA	0.00	phase1
Hyoscyamus niger	23.08	0.00	49.69	phase3
Ilex aquifolium	0.00	NA	31.16	phase2
Iris pseudacorus	0.00	NA	42.87	phase2
Jacobaea vulgaris	1.12	NA	0.00	phase1
Lactuca serriola	0.00	NA	89.57	phase2
Lamium amplexicaule	19.37	0.00	92.11	phase3
Lepidium latifolium	0.00	NA	18.56	phase2
Lotus corniculatus	50.86	0.00	61.73	phase3
Lythrum salicaria	19.73	0.00	23.21	phase3
Marrubium vulgare	0.00	NA	69.47	phase2
Medicago lupulina	0.00	0.72	92.04	phase2
Nasturtium officinale	0.00	NA	110.52	phase2
Olea europaea	0.00	NA	8.46	phase2
Populus alba	0.00	1.38	26.28	phase2
Potamogeton crispus	52.46	0.00	66.39	phase3
Prunus avium	NA	0.00	10.22	phase3
Ranunculus repens	12.70	0.00	90.71	phase3
Rapistrum rugosum	NA	NA	0.00	phase1
Rhamnus cathartica	13.96	0.00	46.40	phase3
Salsola tragus	0.00	NA	128.45	phase2
Salvia aethiopis	2.33	NA	0.00	phase1
Securigera varia	30.06	0.00	27.59	phase3
Senecio vulgaris	2.35	0.00	86.80	phase3
Silene latifolia	23.18	0.00	73.29	phase3

Silybum marianum	5.86	0.00	8.28	phase3
Sinapis arvensis	19.63	0.00	73.21	phase3
Sisymbrium irio	0.00	NA	39.78	phase2
Sonchus asper	0.00	NA	87.10	phase2
Sonchus oleraceus	0.00	NA	61.21	phase2
Spartium junceum	NA	0.11	0.00	phase1
Spergula arvensis	0.00	NA	45.73	phase2
Spergularia rubra	10.25	0.00	68.46	phase3
Trapa natans	NA	NA	0.00	phase1
Tribulus terrestris	0.00	NA	60.05	phase2
Trifolium hirtum	NA	0.00	12.79	phase3
Trifolium hybridum	0.00	NA	101.98	phase2
Trifolium pratense	1.54	0.00	91.39	phase2
Verbascum blattaria	0.00	NA	51.59	phase2
Verbascum thapsus	21.64	0.00	98.50	phase3
Veronica beccabunga	0.00	NA	2.77	phase2
Vitex agnus-castus	0.00	NA	33.90	phase2
Acer platanoides	0.00	NA	36.61	phase2
Alliaria petiolata	NA	0.00	20.15	phase3
Arenaria serpyllifolia	7.91	0.00	70.24	phase3
Artemisia vulgaris	0.00	NA	25.54	phase2
Barbarea vulgaris	0.00	NA	46.62	phase2
Berberis vulgaris	11.08	0.00	59.13	phase3
Berteroa incana	47.77	0.00	100.50	phase3
Betula pendula	NA	NA	0.00	phase1
Buglossoides arvensis	3.82	0.00	45.87	phase3
Butomus umbellatus	14.36	0.00	12.40	phase3
Calystegia sepium	0.00	NA	87.78	phase2
Carduus acanthoides	56.49	0.00	61.64	phase3
Centaurea benedicta	0.00	NA	11.17	phase2
Centaurea calcitrapa	0.00	NA	18.60	phase2
Centaurea nigrescens	NA	NA	0.00	phase1
Cerastium fontanum	0.00	NA	60.59	phase2
Cerastium glomeratum	42.93	0.00	106.85	phase3

Chelidonium majus	NA	NA	0.00	phase1
Cirsium vulgare	6.38	0.00	88.06	phase3
Crepis tectorum	12.74	0.00	33.06	phase3
Cynoglossum officinale	23.95	0.00	86.41	phase3
Daucus carota	27.70	0.00	52.83	phase3
Dipsacus laciniatus	NA	NA	0.00	phase1
Draba verna	13.73	0.00	69.74	phase3
Echium vulgare	18.04	0.00	72.09	phase3
Elaeagnus angustifolia	0.00	NA	24.75	phase2
Epilobium hirsutum	1.60	0.00	21.18	phase2
Epipactis helleborine	NA	3.70	0.00	phase1
Euphorbia cyparissias	0.00	NA	50.62	phase2
Euphorbia esula	49.36	0.00	88.49	phase3
Galeopsis tetrahit	20.12	0.00	47.49	phase3
Glechoma hederacea	0.00	NA	82.86	phase2
Hypericum perforatum	38.51	0.00	77.08	phase3
Isatis tinctoria	0.00	NA	17.84	phase2
Lactuca saligna	0.00	NA	31.88	phase2
Lamium maculatum	0.00	NA	3.42	phase2
Lappula squarrosa	0.00	NA	136.56	phase2
Lapsana communis	0.00	NA	29.86	phase2
Leonurus cardiaca	0.00	NA	47.63	phase2
Lepidium draba	0.00	NA	21.33	phase2
Ligustrum vulgare	NA	0.00	33.75	phase3
Linaria vulgaris	0.00	NA	67.45	phase2
Lysimachia nummularia	0.00	NA	33.51	phase2
Lysimachia vulgaris	NA	NA	0.00	phase1
Medicago sativa	0.00	NA	49.07	phase2
Melilotus officinalis	25.60	0.00	79.65	phase3
Melissa officinalis	2.42	0.00	24.03	phase3
Mentha spicata	0.00	NA	110.29	phase2
Microthlaspi perfoliatum	3.43	3.73	0.00	phase1
Myosotis scorpioides	0.00	1.93	65.41	phase2
Myriophyllum spicatum	10.21	0.00	8.44	phase3

Najas minor	NA	0.00	30.36	phase3
Nepeta cataria	0.00	NA	104.06	phase2
Nymphoides peltata	NA	0.00	10.07	phase3
Onopordum acanthium	56.93	0.00	55.09	phase3
Pastinaca sativa	1.01	0.00	58.70	phase2
Peganum harmala	0.00	NA	6.82	phase2
Persicaria lapathifolia	0.00	NA	58.64	phase2
Pilosella officinarum	17.02	0.00	25.86	phase3
Plantago lanceolata	0.00	NA	75.77	phase2
Plantago major	0.00	NA	93.17	phase2
Potentilla recta	0.00	NA	47.07	phase2
Prunus mahaleb	0.00	NA	24.44	phase2
Pyracantha coccinea	0.00	NA	3.11	phase2
Pyrus communis	7.40	0.00	9.83	phase3
Ranunculus acris	14.68	0.00	61.50	phase3
Ribes rubrum	0.00	NA	23.94	phase2
Rorippa sylvestris	13.11	0.00	24.29	phase3
Rumex acetosella	24.47	0.00	90.03	phase3
Rumex crispus	69.46	0.00	109.75	phase3
Rumex longifolius	18.40	0.00	17.27	phase3
Rumex obtusifolius	0.00	NA	44.54	phase2
Salix pentandra	NA	0.00	30.64	phase3
Salix purpurea	0.00	NA	33.10	phase2
Saponaria officinalis	0.00	NA	50.53	phase2
Senecio sylvaticus	0.00	NA	7.36	phase2
Silene flos-cuculi	10.23	0.00	7.41	phase3
Silene noctiflora	0.00	NA	77.17	phase2
Solanum nigrum	0.00	2.91	60.84	phase2
Sorbus aucuparia	0.00	2.90	42.24	phase2
Stellaria media	0.00	NA	86.84	phase2
Symphytum officinale	0.00	NA	27.27	phase2
Tanacetum vulgare	15.20	0.00	45.63	phase3
Taraxacum erythrospermum	16.31	0.00	45.98	phase3
Taraxacum officinale	0.00	NA	82.96	phase2

Thlaspi arvense	2.97	0.00	73.40	phase3
Torilis arvensis	0.00	NA	44.45	phase2
Torilis japonica	0.00	NA	9.98	phase2
Tragopogon dubius	0.00	NA	24.13	phase2
Trifolium campestre	0.00	2.32	27.00	phase2
Trifolium repens	39.02	0.00	85.75	phase3
Tussilago farfara	0.00	2.63	11.16	phase2
Valeriana officinalis	0.00	NA	16.45	phase2
Veronica hederifolia	NA	0.00	65.64	phase3
Vicia cracca	4.72	0.00	46.45	phase3
Vicia villosa	0.00	NA	56.78	phase2
Viola tricolor	NA	0.00	26.02	phase3
Agrostemma githago	0.00	NA	54.10	phase2
Allium vineale	30.09	0.00	33.61	phase3
Anthemis cotula	0.00	NA	101.46	phase2
Arctium minus	0.00	1.55	67.49	phase2
Asparagus officinalis	0.00	NA	40.43	phase2
Asphodelus fistulosus	NA	NA	0.00	phase1
Callitriche stagnalis	0.00	NA	15.06	phase2
Campanula rapunculoides	45.16	0.00	66.52	phase3
Capsella bursa-pastoris	0.80	0.00	43.78	phase2
Cardamine impatiens	0.00	NA	1.19	phase1
Centaurea cyanus	0.00	NA	55.33	phase2
Centaurea montana	0.00	NA	5.27	phase2
Centaurea nigra	2.46	0.00	35.12	phase3
Centaurea stoebe	0.00	NA	52.61	phase2
Centranthus ruber	NA	0.00	24.01	phase3
Cirsium arvense	0.00	0.89	93.13	phase2
Convallaria majalis	19.05	0.00	23.67	phase3
Crataegus monogyna	26.70	0.00	59.99	phase3
Cytisus scoparius	26.44	0.00	26.59	phase3
Dianthus armeria	32.51	0.00	64.12	phase3
Digitalis purpurea	0.00	NA	34.96	phase2
Galeopsis bifida	0.00	NA	10.01	phase2

Geranium dissectum	0.00	NA	34.78	phase2
Glebionis coronaria	0.00	NA	21.74	phase2
Hesperis matronalis	79.84	0.00	90.53	phase3
Hibiscus trionum	0.00	NA	46.18	phase2
Hypochaeris radicata	0.00	NA	53.90	phase2
Kickxia elatine	41.25	0.00	46.46	phase3
Lepidium campestre	39.74	0.00	83.92	phase3
Leucanthemum vulgare	0.00	0.00	35.03	phase2
Lythrum hyssopifolia	0.00	NA	51.11	phase2
Muscari botryoides	10.72	0.00	8.04	phase3
Myosoton aquaticum	0.00	NA	59.65	phase2
Pilosella aurantiaca	0.00	NA	61.69	phase2
Pilosella caespitosa	2.53	0.00	27.10	phase3
Pilosella piloselloides	21.67	0.00	23.25	phase3
Pilosella x floribunda	24.24	0.00	29.53	phase3
Prunus padus	NA	0.00	28.44	phase3
Ranunculus bulbosus	0.60	NA	0.00	phase1
Raphanus raphanistrum	23.53	0.00	91.25	phase3
Silene vulgaris	7.19	0.00	64.06	phase3
Sonchus arvensis	0.00	NA	66.36	phase2
Trifolium aureum	0.00	NA	83.44	phase2
Trifolium dubium	0.00	NA	55.80	phase2
Veronica arvensis	2.44	0.00	50.82	phase3
Vicia sativa	0.00	NA	80.06	phase2
Albizia julibrissin	38.97	0.00	36.60	phase3
Bassia hyssopifolia	0.78	NA	0.00	phase1
Berberis thunbergii	0.00	1.04	8.89	phase2
Broussonetia papyrifera	NA	0.00	8.50	phase3
Cinnamomum camphora	21.68	0.00	18.98	phase3
Commelina communis	26.52	0.00	36.98	phase3
Cyrtomium falcatum	24.45	0.00	39.50	phase3
Duchesnea indica	NA	NA	0.00	phase1
Elaeagnus pungens	25.21	0.00	31.86	phase3
Elaeagnus umbellata	16.29	0.00	16.37	phase3

Euonymus alatus	2.23	4.90	0.00	phase1
Euonymus fortunei	0.00	NA	4.08	phase2
Hemerocallis fulva	30.23	0.00	30.65	phase3
Hibiscus syriacus	NA	0.00	23.63	phase3
Matricaria discoidea	0.00	NA	52.67	phase2
Murdannia keisak	0.00	NA	7.43	phase2
Nandina domestica	1.29	NA	0.00	phase1
Paulownia tomentosa	NA	0.00	12.73	phase3
Perilla frutescens	1.93	NA	0.00	phase1
Persicaria longiseta	0.85	NA	0.00	phase1
Persicaria posumbu	NA	0.00	38.47	phase3
Phyllanthus urinaria	0.00	NA	1.76	phase1
Pistacia chinensis	2.12	6.78	0.00	phase1
Pyrus calleryana	0.00	NA	2.55	phase2
Quercus acutissima	NA	0.00	1.01	phase1
Reynoutria japonica	NA	2.49	0.00	phase1
Spiraea japonica	NA	NA	0.00	phase1
Triadica sebifera	5.93	0.00	25.23	phase3
Vernicia fordii	0.00	NA	19.60	phase2
Viburnum dilatatum	NA	NA	0.00	phase1
Alternanthera philoxeroides	NA	4.05	0.00	phase1
Cardiospermum halicacabum	0.00	NA	31.73	phase2
Dysphania ambrosioides	11.93	0.00	41.11	phase3
Eichhornia crassipes	0.00	NA	6.34	phase2
Ludwigia peruviana	NA	0.00	10.74	phase3
Schinus molle	NA	NA	0.00	phase1
Sesbania punicea	NA	NA	0.00	phase1
Solanum viarum	8.85	NA	0.00	phase1
Sphagneticola trilobata	0.83	NA	0.00	phase1
Tradescantia fluminensis	NA	NA	0.00	phase1
Verbena bonariensis	0.00	NA	25.91	phase2

Table S4. Overall summary of results for species classification. Species with a linear pattern of expansion (n=39) were further categorized into two subcategories based on the rate of change of the fitted linear model: 'expanding' (i.e., rate of change >0±0.6%/year; n=37), or 'no change' (i.e., rate of change <0±0.6%/year; n=2). Species with a nonlinear pattern of expansion (n=218) were further categorized as 'reached equilibrium' if their expansion has stabilized in the last 30 years (n=109). The remaining nonlinear species (n=109) were categorized as 'approaching equilibrium', as slowing in expansion has slowed but not stabilized.

Linear		**Nonlinear**	
Expanding ***(n=37)***	**No change** ***(n=2)***	**Approaching equilibrium** ***(n=109)***	**Reached equilibrium** ***(n=109)***
Hydrocharis morsus-ranae	*Sesbania punicea*	*Acer platanoides*	*Agrostemma githago*
Brassica tournefortii	*Centaurea solstitialis*	*Ajuga reptans*	*Albizia julibrissin*
Phyllanthus urinaria		*Alliaria petiolata*	*Anthemis cotula*
Persicaria longiseta		*Allium vineale*	*Arctium minus*
Rapistrum rugosum		*Anthriscus sylvestris*	*Artemisia absinthium*
Dipsacus laciniatus		*Arabidopsis thaliana*	*Artemisia vulgaris*
Pistacia chinensis		*Arenaria serpyllifolia*	*Asparagus officinalis*
Quercus acutissima		*Berberis thunbergii*	*Barbarea vulgaris*
Spiraea japonica		*Berberis vulgaris*	*Berteroa incana*
Sphagneticola trilobata		*Broussonetia papyrifera*	*Brassica nigra*
Epipactis helleborine		*Buglossoides arvensis*	*Calystegia sepium*
Euonymus alatus		*Butomus umbellatus*	*Campanula rapunculoides*
Duchesnea indica		*Callitriche stagnalis*	*Capsella bursa-pastoris*

Centaurea nigrescens		*Cardiospermum halicacabum*	*Carduus acanthoides*
Lysimachia vulgaris		*Carduus nutans*	*Carthamus creticus*
Cardamine impatiens		*Centaurea calcitrapa*	*Carum carvi*
Solanum viarum		*Centaurea montana*	*Centaurea benedicta*
Reynoutria japonica		*Centaurea nigra*	*Centaurea cyanus*
Jacobaea vulgaris		*Centaurea stoebe*	*Cerastium glomeratum*
Ficaria verna		*Centranthus ruber*	*Chondrilla juncea*
Ranunculus bulbosus		*Cerastium fontanum*	*Cichorium intybus*
Tradescantia fluminensis		*Commelina communis*	*Cinnamomum camphora*
Microthlaspi perfoliatum		*Crepis tectorum*	*Cirsium arvense*
Viburnum dilatatum		*Cyrtomium falcatum*	*Cirsium vulgare*
Perilla frutescens		*Dysphania ambrosioides*	*Conium maculatum*
Trapa natans		*Echium vulgare*	*Convallaria majalis*
Carduus pycnocephalus		*Elaeagnus angustifolia*	*Crataegus monogyna*
Nandina domestica		*Elaeagnus umbellata*	*Cynoglossum officinale*
Chelidonium majus		*Epilobium hirsutum*	*Cytisus scoparius*
Cakile maritima		*Euonymus fortunei*	*Daucus carota*
Alternanthera philoxeroides		*Euphorbia esula*	*Descurainia sophia*
Schinus molle		*Frangula alnus*	*Dianthus armeria*
Asphodelus fistulosus		*Galega officinalis*	*Digitalis purpurea*
Bassia hyssopifolia		*Galeopsis tetrahit*	*Dipsacus fullonum*
Spartium junceum		*Galium mollugo*	*Draba verna*

Salvia aethiopis		*Galium verum*	*Eichhornia crassipes*
Betula pendula		*Genista monspessulana*	*Elaeagnus pungens*
		Geranium columbinum	*Erodium cicutarium*
		Geranium robertianum	*Euphorbia cyparissias*
		Helminthotheca echioides	*Ficus carica*
		Hemerocallis fulva	*Foeniculum vulgare*
		Hesperis matronalis	*Galeopsis bifida*
		Hirschfeldia incana	*Geranium dissectum*
		Hydrilla verticillata	*Glebionis coronaria*
		Hyoscyamus niger	*Glechoma hederacea*
		Hypericum perforatum	*Hibiscus syriacus*
		Hypochaeris radicata	*Hibiscus trionum*
		Ilex aquifolium	*Isatis tinctoria*
		Iris pseudacorus	*Lactuca saligna*
		Kickxia elatine	*Lactuca serriola*
		Lamium maculatum	*Lamium amplexicaule*
		Lapsana communis	*Lappula squarrosa*
		Lepidium latifolium	*Leonurus cardiaca*
		Ligustrum vulgare	*Lepidium campestre*
		Ludwigia peruviana	*Lepidium draba*
		Lysimachia nummularia	*Leucanthemum vulgare*
		Lythrum hyssopifolia	*Linaria vulgaris*
		Lythrum salicaria	*Lotus corniculatus*

		Medicago lupulina	*Marrubium vulgare*
		Melissa officinalis	*Matricaria discoidea*
		Murdannia keisak	*Medicago sativa*
		Muscari botryoides	*Melilotus officinalis*
		Myosotis scorpioides	*Mentha spicata*
		Najas minor	*Myosoton aquaticum*
		Nymphoides peltata	*Myriophyllum spicatum*
		Olea europaea	*Nasturtium officinale*
		Paulownia tomentosa	*Nepeta cataria*
		Peganum harmala	*Onopordum acanthium*
		Persicaria posumbu	*Pastinaca sativa*
		Pilosella aurantiaca	*Persicaria lapathifolia*
		Pilosella caespitosa	*Plantago lanceolata*
		Pilosella officinarum	*Plantago major*
		Pilosella piloselloides	*Populus alba*
		Pilosella x floribunda	*Potamogeton crispus*
		Prunus avium	*Potentilla recta*
		Pyracantha coccinea	*Prunus mahaleb*
		Pyrus calleryana	*Prunus padus*
		Ranunculus acris	*Pyrus communis*
		Rhamnus cathartica	*Ranunculus repens*
		Ribes rubrum	*Raphanus raphanistrum*
		Rorippa sylvestris	*Rumex acetosella*

		Rumex longifolius	*Rumex crispus*
		Rumex obtusifolius	*Salsola tragus*
		Salix pentandra	*Saponaria officinalis*
		Salix purpurea	*Senecio vulgaris*
		Securigera varia	*Silene noctiflora*
		Senecio sylvaticus	*Silene vulgaris*
		Silene flos-cuculi	*Sinapis arvensis*
		Silene latifolia	*Solanum nigrum*
		Silybum marianum	*Sonchus arvensis*
		Sisymbrium irio	*Sonchus asper*
		Sorbus aucuparia	*Sonchus oleraceus*
		Symphytum officinale	*Spergula arvensis*
		Tanacetum vulgare	*Spergularia rubra*
		Torilis japonica	*Stellaria media*
		Triadica sebifera	*Taraxacum erythrospermum*
		Tribulus terrestris	*Taraxacum officinale*
		Trifolium hirtum	*Thlaspi arvense*
		Trifolium hybridum	*Torilis arvensis*
		Tussilago farfara	*Tragopogon dubius*
		Valeriana officinalis	*Trifolium aureum*
		Verbascum blattaria	*Trifolium campestre*
		Verbena bonariensis	*Trifolium dubium*

		Vernicia fordii	*Trifolium pratense*
		Veronica arvensis	*Trifolium repens*
		Veronica beccabunga	*Verbascum thapsus*
		Veronica hederifolia	*Vicia sativa*
		Vicia cracca	*Vicia villosa*
		Viola tricolor	*Vitex agnus-castus*

Table S5. Overview of species determined to have reached equilibrium in North America (n=109). 'Year stabilized' was approximated as the first year of the first 30-year segment where the species' expansion pattern became stable (i.e., rate of change <0±0.6%/year). 'Time to equilibrium' was calculated as the difference in years between the end of the final time period (2020) and the year stabilized.

Species name	Year stabilized	Time to equilibrium (years)
Agrostemma githago	1925	65
Albizia julibrissin	1990	90
Anthemis cotula	1940	70
Arctium minus	1965	85
Artemisia absinthium	1990	100
Artemisia vulgaris	1975	95
Asparagus officinalis	1945	65
Barbarea vulgaris	1965	105
Berteroa incana	1955	55
Brassica nigra	1940	60
Calystegia sepium	1960	100
Campanula rapunculoides	1975	85
Capsella bursa-pastoris	1965	95
Carduus acanthoides	1980	90
Carthamus creticus	1990	30
Carum carvi	1990	110
Centaurea benedicta	1975	85
Centaurea cyanus	1960	80
Cerastium glomeratum	1950	90
Chondrilla juncea	1990	70
Cichorium intybus	1985	115
Cinnamomum camphora	1990	50
Cirsium arvense	1965	105
Cirsium vulgare	1960	90

Conium maculatum	1935	65
Convallaria majalis	1990	100
Crataegus monogyna	1990	110
Cynoglossum officinale	1955	95
Cytisus scoparius	1990	100
Daucus carota	1970	110
Descurainia sophia	1965	65
Dianthus armeria	1990	120
Digitalis purpurea	1990	90
Dipsacus fullonum	1960	60
Draba verna	1990	110
Eichhornia crassipes	1990	90
Elaeagnus pungens	1990	40
Erodium cicutarium	1985	105
Euphorbia cyparissias	1945	65
Ficus carica	1990	90
Foeniculum vulgare	1915	25
Galeopsis bifida	1960	30
Geranium dissectum	1980	90
Glebionis coronaria	1960	20
Glechoma hederacea	1970	100
Hibiscus syriacus	1990	90
Hibiscus trionum	1975	95
Isatis tinctoria	1990	50
Lactuca saligna	1990	50
Lactuca serriola	1950	60
Lamium amplexicaule	1990	110
Lappula squarrosa	1965	95
Leonurus cardiaca	1920	40
Lepidium campestre	1960	80
Lepidium draba	1990	90
Leucanthemum vulgare	1970	100
Linaria vulgaris	1985	115
Lotus corniculatus	1975	85

Marrubium vulgare	1915	45
Matricaria discoidea	1975	85
Medicago sativa	1960	80
Melilotus officinalis	1960	90
Mentha spicata	1925	65
Myosoton aquaticum	1965	55
Myriophyllum spicatum	1985	95
Nasturtium officinale	1910	40
Nepeta cataria	1950	80
Onopordum acanthium	1985	105
Pastinaca sativa	1960	80
Persicaria lapathifolia	1945	75
Plantago lanceolata	1960	80
Plantago major	1985	115
Populus alba	1975	85
Potamogeton crispus	1990	120
Potentilla recta	1990	90
Prunus mahaleb	1990	90
Prunus padus	1990	70
Pyrus communis	1990	90
Ranunculus repens	1985	115
Raphanus raphanistrum	1965	85
Rumex acetosella	1965	115
Rumex crispus	1925	65
Salsola tragus	1950	50
Saponaria officinalis	1960	80
Senecio vulgaris	1955	75
Silene noctiflora	1940	60
Silene vulgaris	1960	80
Sinapis arvensis	1940	60
Solanum nigrum	1945	65
Sonchus arvensis	1985	95
Sonchus asper	1965	95
Sonchus oleraceus	1920	40

Spergula arvensis	1960	80
Spergularia rubra	1985	105
Stellaria media	1960	80
Taraxacum erythrospermum	1960	60
Taraxacum officinale	1960	90
Thlaspi arvense	1960	90
Torilis arvensis	1990	70
Tragopogon dubius	1970	60
Trifolium aureum	1980	110
Trifolium campestre	1970	100
Trifolium dubium	1990	100
Trifolium pratense	1960	100
Trifolium repens	1980	120
Verbascum thapsus	1960	90
Vicia sativa	1960	90
Vicia villosa	1945	55
Vitex agnus-castus	1980	60

Table S6. Overview of ending expansion values for species at equilibrium (n=109). Expansion (%) was calculated as 100 – unfilling, and indicates the amount of native climate niche that is occupied in the introduced range.

Species name	Expansion at equilibrium (%)
Brassica nigra	100.0
Taraxacum erythrospermum	99.8
Nasturtium officinale	99.8
Dianthus armeria	99.7
Mentha spicata	99.6
Taraxacum officinale	99.6
Digitalis purpurea	99.5
Asparagus officinalis	99.4
Cytisus scoparius	99.4
Lepidium campestre	99.2
Senecio vulgaris	99.2
Trifolium campestre	99.2
Stellaria media	99.1
Plantago major	99.1
Carduus acanthoides	99.0
Vitex agnus-castus	99.0
Spergula arvensis	98.9
Spergularia rubra	98.8
Dipsacus fullonum	98.7
Leonurus cardiaca	98.7
Pastinaca sativa	98.7
Daucus carota	98.7
Populus alba	98.5
Cirsium vulgare	98.5
Rumex acetosella	98.5
Solanum nigrum	98.4

Medicago sativa	98.4
Vicia villosa	98.3
Sonchus asper	98.3
Marrubium vulgare	98.2
Trifolium aureum	98.2
Trifolium repens	98.2
Cichorium intybus	98.1
Trifolium dubium	98.1
Lactuca serriola	98.0
Persicaria lapathifolia	98.0
Nepeta cataria	98.0
Ranunculus repens	97.9
Conium maculatum	97.9
Geranium dissectum	97.8
Myriophyllum spicatum	97.8
Potamogeton crispus	97.7
Vicia sativa	97.6
Centaurea cyanus	97.5
Saponaria officinalis	97.4
Sonchus arvensis	97.4
Foeniculum vulgare	97.3
Galeopsis bifida	97.2
Cirsium arvense	97.1
Erodium cicutarium	97.1
Sonchus oleraceus	97.1
Leucanthemum vulgare	97.0
Matricaria discoidea	96.9
Tragopogon dubius	96.9
Cerastium glomeratum	96.9
Anthemis cotula	96.8
Torilis arvensis	96.6
Descurainia sophia	96.6
Raphanus raphanistrum	96.5
Campanula rapunculoides	96.4

Lamium amplexicaule	96.2
Salsola tragus	96.2
Draba verna	96.2
Silene noctiflora	96.2
Rumex crispus	96.2
Onopordum acanthium	96.1
Artemisia absinthium	96.1
Capsella bursa-pastoris	95.9
Sinapis arvensis	95.8
Ficus carica	95.7
Calystegia sepium	95.7
Potentilla recta	95.6
Lotus corniculatus	95.6
Hibiscus syriacus	95.5
Prunus mahaleb	95.4
Trifolium pratense	95.3
Thlaspi arvense	95.1
Euphorbia cyparissias	94.7
Myosoton aquaticum	94.6
Plantago lanceolata	94.4
Lappula squarrosa	94.0
Arctium minus	93.8
Verbascum thapsus	93.7
Crataegus monogyna	93.5
Berteroa incana	93.4
Glechoma hederacea	93.3
Hibiscus trionum	93.3
Carum carvi	93.1
Albizia julibrissin	93.1
Pyrus communis	93.0
Centaurea benedicta	92.0
Cynoglossum officinale	91.5
Silene vulgaris	91.4
Melilotus officinalis	91.1

Agrostemma githago	90.8
Lepidium draba	90.4
Linaria vulgaris	90.4
Chondrilla juncea	90.2
Artemisia vulgaris	90.0
Cinnamomum camphora	89.4
Isatis tinctoria	88.8
Elaeagnus pungens	87.5
Barbarea vulgaris	86.8
Lactuca saligna	86.6
Prunus padus	86.3
Convallaria majalis	80.2
Eichhornia crassipes	75.7
Carthamus creticus	73.2
Glebionis coronaria	40.2

Table S7. Overview of first year of the time series across all species (n=257). The pattern of expansion for each species depicts whether the trend in expansion was best predicted by a linear mode, or a nonlinear model (2-phase or 3-phase). The first time interval was defined as the first 5-year interval containing at least 5 occurrence records in the introduced range.

Species name	Pattern of expansion	First time interval
Acer platanoides	2-phase	1890
Agrostemma githago	2-phase	1860
Ajuga reptans	2-phase	1910
Albizia julibrissin	3-phase	1900
Alliaria petiolata	3-phase	1880
Allium vineale	3-phase	1890
Alternanthera philoxeroides	linear	1950
Anthemis cotula	2-phase	1870
Anthriscus sylvestris	2-phase	1920
Arabidopsis thaliana	3-phase	1880
Arctium minus	2-phase	1880
Arenaria serpyllifolia	3-phase	1860
Artemisia absinthium	2-phase	1890
Artemisia vulgaris	2-phase	1880
Asparagus officinalis	2-phase	1880
Asphodelus fistulosus	linear	1900
Barbarea vulgaris	2-phase	1860
Bassia hyssopifolia	linear	1930
Berberis thunbergii	2-phase	1920
Berberis vulgaris	3-phase	1870
Berteroa incana	3-phase	1900
Betula pendula	linear	1900
Brassica nigra	3-phase	1880
Brassica tournefortii	linear	1950
Broussonetia papyrifera	3-phase	1900
Buglossoides arvensis	3-phase	1850
Butomus umbellatus	3-phase	1930
Cakile maritima	linear	1940
Callitriche stagnalis	2-phase	1930

Calystegia sepium	2-phase	1860
Campanula rapunculoides	3-phase	1890
Capsella bursa-pastoris	2-phase	1870
Cardamine impatiens	linear	1970
Cardiospermum halicacabum	2-phase	1890
Carduus acanthoides	3-phase	1890
Carduus nutans	3-phase	1900
Carduus pycnocephalus	linear	1930
Carthamus creticus	3-phase	1960
Carum carvi	2-phase	1880
Centaurea benedicta	2-phase	1890
Centaurea calcitrapa	2-phase	1900
Centaurea cyanus	2-phase	1880
Centaurea montana	2-phase	1960
Centaurea nigra	3-phase	1900
Centaurea nigrescens	linear	1910
Centaurea solstitialis	linear	1910
Centaurea stoebe	2-phase	1910
Centranthus ruber	3-phase	1950
Cerastium fontanum	2-phase	1870
Cerastium glomeratum	3-phase	1860
Chelidonium majus	linear	1880
Chondrilla juncea	3-phase	1920
Cichorium intybus	3-phase	1870
Cinnamomum camphora	3-phase	1940
Cirsium arvense	2-phase	1860
Cirsium vulgare	3-phase	1870
Commelina communis	3-phase	1900
Conium maculatum	3-phase	1870
Convallaria majalis	3-phase	1890
Crataegus monogyna	3-phase	1880
Crepis tectorum	3-phase	1900
Cynoglossum officinale	3-phase	1860
Cyrtomium falcatum	3-phase	1900
Cytisus scoparius	3-phase	1890
Daucus carota	3-phase	1860
Descurainia sophia	2-phase	1900
Dianthus armeria	3-phase	1870
Digitalis purpurea	2-phase	1900
Dipsacus fullonum	3-phase	1900

Dipsacus laciniatus	linear	1970
Draba verna	3-phase	1880
Duchesnea indica	linear	1890
Dysphania ambrosioides	3-phase	1850
Echium vulgare	3-phase	1880
Eichhornia crassipes	2-phase	1900
Elaeagnus angustifolia	2-phase	1900
Elaeagnus pungens	3-phase	1950
Elaeagnus umbellata	3-phase	1910
Epilobium hirsutum	2-phase	1910
Epipactis helleborine	linear	1900
Erodium cicutarium	2-phase	1880
Euonymus alatus	linear	1910
Euonymus fortunei	2-phase	1940
Euphorbia cyparissias	2-phase	1880
Euphorbia esula	3-phase	1890
Ficaria verna	linear	1900
Ficus carica	3-phase	1900
Foeniculum vulgare	2-phase	1890
Frangula alnus	2-phase	1900
Galega officinalis	3-phase	1940
Galeopsis bifida	2-phase	1930
Galeopsis tetrahit	3-phase	1880
Galium mollugo	3-phase	1890
Galium verum	3-phase	1880
Genista monspessulana	2-phase	1940
Geranium columbinum	3-phase	1890
Geranium dissectum	2-phase	1890
Geranium robertianum	3-phase	1880
Glebionis coronaria	2-phase	1940
Glechoma hederacea	2-phase	1870
Helminthotheca echioides	2-phase	1910
Hemerocallis fulva	3-phase	1880
Hesperis matronalis	3-phase	1880
Hibiscus syriacus	3-phase	1900
Hibiscus trionum	2-phase	1880
Hirschfeldia incana	3-phase	1930
Hydrilla verticillata	2-phase	1970
Hydrocharis morsus-ranae	linear	1970
Hyoscyamus niger	3-phase	1880

Hypericum perforatum	3-phase	1860
Hypochaeris radicata	2-phase	1900
Ilex aquifolium	2-phase	1940
Iris pseudacorus	2-phase	1900
Isatis tinctoria	2-phase	1940
Jacobaea vulgaris	linear	1920
Kickxia elatine	3-phase	1880
Lactuca saligna	2-phase	1940
Lactuca serriola	2-phase	1890
Lamium amplexicaule	3-phase	1880
Lamium maculatum	2-phase	1890
Lappula squarrosa	2-phase	1870
Lapsana communis	2-phase	1890
Leonurus cardiaca	2-phase	1880
Lepidium campestre	3-phase	1880
Lepidium draba	2-phase	1900
Lepidium latifolium	2-phase	1940
Leucanthemum vulgare	2-phase	1870
Ligustrum vulgare	3-phase	1890
Linaria vulgaris	2-phase	1870
Lotus corniculatus	3-phase	1890
Ludwigia peruviana	3-phase	1910
Lysimachia nummularia	2-phase	1880
Lysimachia vulgaris	linear	1890
Lythrum hyssopifolia	2-phase	1880
Lythrum salicaria	3-phase	1870
Marrubium vulgare	2-phase	1870
Matricaria discoidea	2-phase	1890
Medicago lupulina	2-phase	1870
Medicago sativa	2-phase	1880
Melilotus officinalis	3-phase	1870
Melissa officinalis	3-phase	1870
Mentha spicata	2-phase	1860
Microthlaspi perfoliatum	linear	1940
Murdannia keisak	2-phase	1970
Muscari botryoides	3-phase	1890
Myosotis scorpioides	2-phase	1880
Myosoton aquaticum	2-phase	1910
Myriophyllum spicatum	3-phase	1890
Najas minor	3-phase	1960

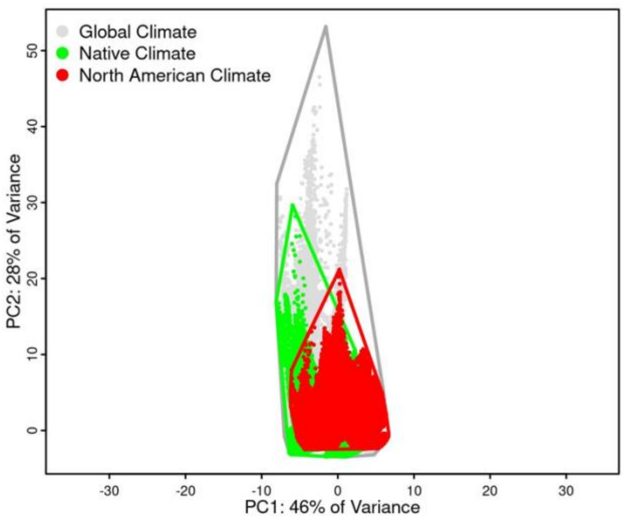
Nandina domestica	linear	1960
Nasturtium officinale	2-phase	1870
Nepeta cataria	2-phase	1870
Nymphoides peltata	3-phase	1910
Olea europaea	2-phase	1960
Onopordum acanthium	3-phase	1880
Pastinaca sativa	2-phase	1880
Paulownia tomentosa	3-phase	1900
Peganum harmala	2-phase	1950
Perilla frutescens	linear	1890
Persicaria lapathifolia	2-phase	1870
Persicaria longiseta	linear	1940
Persicaria posumbu	3-phase	1940
Phyllanthus urinaria	linear	1970
Pilosella aurantiaca	2-phase	1890
Pilosella caespitosa	3-phase	1910
Pilosella officinarum	3-phase	1900
Pilosella piloselloides	3-phase	1920
Pilosella x floribunda	3-phase	1920
Pistacia chinensis	linear	1950
Plantago lanceolata	2-phase	1880
Plantago major	2-phase	1870
Populus alba	2-phase	1890
Potamogeton crispus	3-phase	1870
Potentilla recta	2-phase	1900
Prunus avium	3-phase	1900
Prunus mahaleb	2-phase	1900
Prunus padus	3-phase	1920
Pyracantha coccinea	2-phase	1930
Pyrus calleryana	2-phase	1970
Pyrus communis	3-phase	1900
Quercus acutissima	linear	1970
Ranunculus acris	3-phase	1870
Ranunculus bulbosus	linear	1870
Ranunculus repens	3-phase	1870
Raphanus raphanistrum	3-phase	1880
Rapistrum rugosum	linear	1960
Reynoutria japonica	linear	1900
Rhamnus cathartica	3-phase	1890
Ribes rubrum	2-phase	1880

Rorippa sylvestris	3-phase	1880
Rumex acetosella	3-phase	1850
Rumex crispus	3-phase	1860
Rumex longifolius	3-phase	1900
Rumex obtusifolius	2-phase	1860
Salix pentandra	3-phase	1900
Salix purpurea	2-phase	1880
Salsola tragus	2-phase	1900
Salvia aethiopis	linear	1950
Saponaria officinalis	2-phase	1880
Schinus molle	linear	1910
Securigera varia	3-phase	1910
Senecio sylvaticus	2-phase	1910
Senecio vulgaris	3-phase	1880
Sesbania punicea	linear	1920
Silene flos-cuculi	3-phase	1900
Silene latifolia	3-phase	1880
Silene noctiflora	2-phase	1880
Silene vulgaris	3-phase	1880
Silybum marianum	3-phase	1900
Sinapis arvensis	3-phase	1880
Sisymbrium irio	2-phase	1920
Solanum nigrum	2-phase	1880
Solanum viarum	linear	1990
Sonchus arvensis	2-phase	1890
Sonchus asper	2-phase	1870
Sonchus oleraceus	2-phase	1880
Sorbus aucuparia	2-phase	1890
Spartium junceum	linear	1930
Spergula arvensis	2-phase	1880
Spergularia rubra	3-phase	1880
Sphagneticola trilobata	linear	1950
Spiraea japonica	linear	1910
Stellaria media	2-phase	1880
Symphytum officinale	2-phase	1880
Tanacetum vulgare	3-phase	1880
Taraxacum erythrospermum	3-phase	1900
Taraxacum officinale	2-phase	1870
Thlaspi arvense	3-phase	1870
Torilis arvensis	2-phase	1920

Torilis japonica	2-phase	1950
Tradescantia fluminensis	linear	1960
Tragopogon dubius	2-phase	1910
Trapa natans	linear	1910
Triadica sebifera	3-phase	1910
Tribulus terrestris	2-phase	1900
Trifolium aureum	2-phase	1870
Trifolium campestre	2-phase	1870
Trifolium dubium	2-phase	1890
Trifolium hirtum	3-phase	1960
Trifolium hybridum	2-phase	1880
Trifolium pratense	2-phase	1860
Trifolium repens	3-phase	1860
Tussilago farfara	2-phase	1880
Valeriana officinalis	2-phase	1900
Verbascum blattaria	2-phase	1870
Verbascum thapsus	3-phase	1870
Verbena bonariensis	2-phase	1940
Vernicia fordii	2-phase	1960
Veronica arvensis	3-phase	1850
Veronica beccabunga	2-phase	1940
Veronica hederifolia	3-phase	1890
Viburnum dilatatum	linear	1970
Vicia cracca	3-phase	1860
Vicia sativa	2-phase	1870
Vicia villosa	2-phase	1890
Viola tricolor	3-phase	1880
Vitex agnus-castus	2-phase	1920

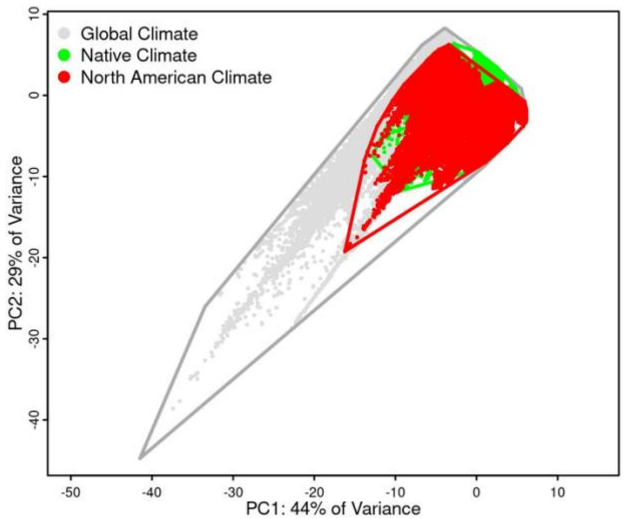
Figure S1. Principal component analysis (PCA) for each of the five native ranges included in this study (a-e). The panel shows the PCA plot for each range in climate space, with the red indicating the introduced (i.e., North American) climates, the green indicating the native range climates, and the grey indicating the global climates (climate combinations that exist outside of the native and introduced ranges). The right panel shows a summary table of the five highest contributing climate variables for each axis of the PCA, for each native range. Values closest to 1 indicate the highest contribution to the PCA. Sign indicates the direction of the relationship.

a) Mediterranean



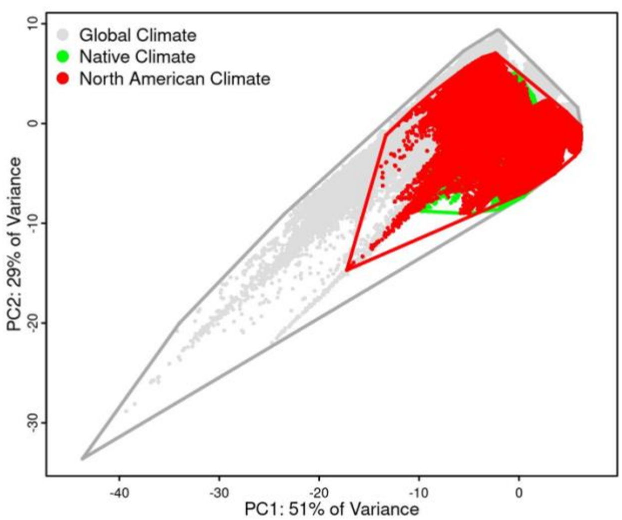
PC1	
Mean annual temp.	-0.985
Mean temp. of coldest quarter	-0.981
Min. temp. coldest month	-0.961
Isothermality	-0.931
Mean temp. of warmest quarter	-0.922
PC2	
Annual precipitation	0.961
Precipitation of driest quarter	0.814
Precipitation of wettest quarter	0.790
Precipitation of driest month	0.789
Precipitation of coldest quarter	0.766

b) Eurasia



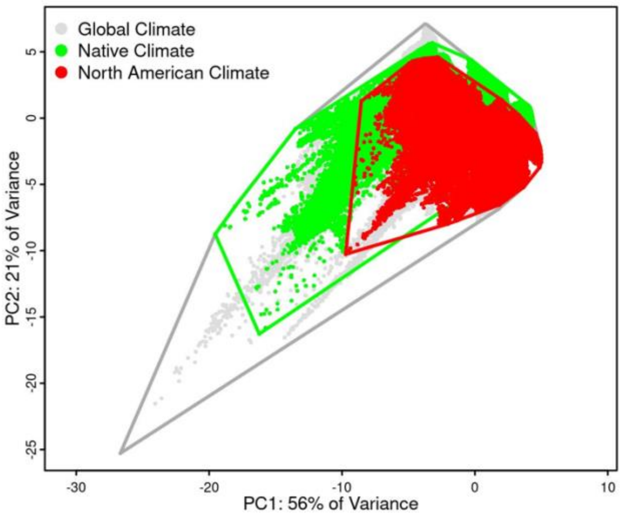
PC1	
Min. temp of coldest month	-0.924
Mean temp. of coldest quarter	-0.924
Mean annual temp.	-0.868
Mean temp. of driest quarter	-0.847
Temp. seasonality	0.827
PC2	
Precipitation of driest month	-0.726
Precipitation of driest quarter	-0.755
Mean diurnal temp. range	0.720
Annual precipitation	-0.698
Max. temp of warmest month	0.686

c) Europe



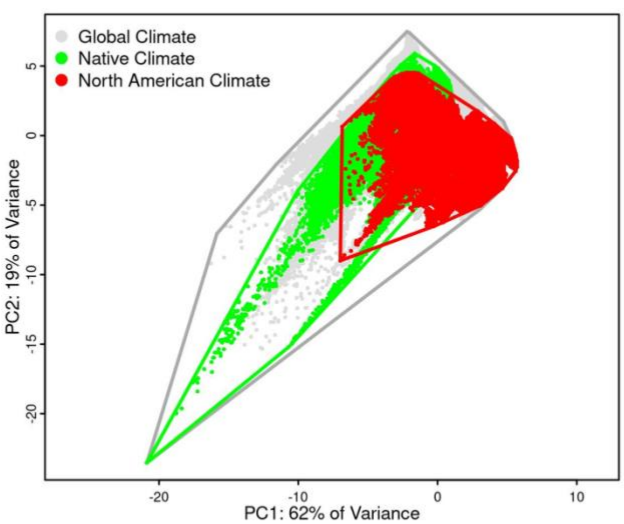
PC1	
Min. temp. coldest month	-0.901
Mean temp. of coldest quarter	-0.896
Precipitation of driest quarter	-0.876
Temp. seasonality	-0.850
Mean annual temp.	-0.822
PC2	
Max. temp of warmest month	0.761
Mean temp. of wettest quarter	0.745
Mean diurnal temp. range	0.745
Mean temp. of warmest quarter	0.716
Precipitation of driest month	-0.687

d) Asia



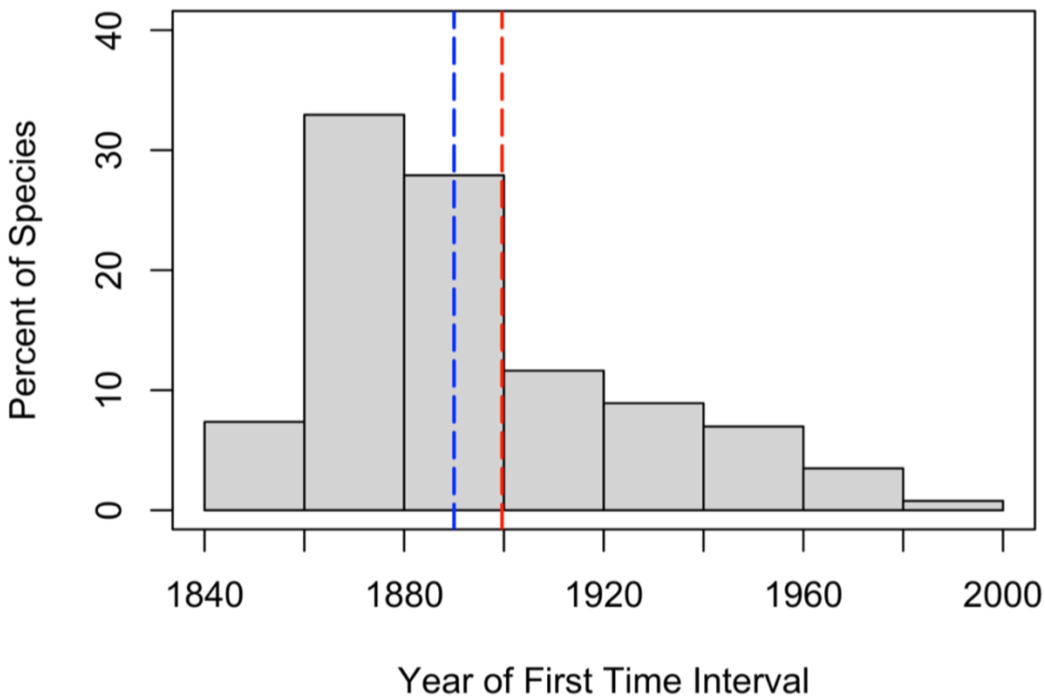
PC1	
Min. temp. of coldest month	-0.955
Mean temp. of coldest quarter	-0.950
Mean annual temp.	-0.922
Mean temp. of driest quarter	-0.890
Isothermality	-0.883
PC2	
Mean diurnal temp. range	0.754
Precipitation of driest month	-0.699
Precipitation of driest quarter	-0.688
Precipitation seasonality	0.674
Max. temp. of warmest month	0.618

e) South America



PC1	
Min. temp of coldest month	-0.966
Mean temp. of coldest quarter	-0.964
Mean annual temp.	-0.948
Mean temp. of driest quarter	-0.935
Isothermality	-0.927
PC2	
Precipitation of driest month	-0.756
Precipitation of driest quarter	-0.744
Mean diurnal temp. range	0.671
Precipitation seasonality	0.645
Precipitation of coldest quarter	-0.501

Figure S2. Histogram depicting the distribution of the year of the earliest time interval used in the expansion analysis, for each species (n=257). Each earliest time period was defined as the first 5-year time interval with at least five occurrences in the introduced range. Median year is represented by the blue dashed line (x=1890), and mean year is represented by the red dashed line (x=1900).



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