

**Which traits determine the success of plant invaders?
A multivariate analysis of the flora of the United
Kingdom**



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Declarations:

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ABSTRACT

Invasive alien species (IAS) are a subset of naturalised species that can threaten native biodiversity, ecosystem processes and human health. Understanding the mechanisms of biological invasions remains a central goal, but few studies have considered the status of invaders and aspects of the invaded ecosystem in a single analysis.

The present study addresses this issue, with the aim of identifying whether specific functional traits determine successful plant invasions and how these traits interact with local environmental factors to determine spatial distribution patterns in the British Isles, taking into account of the potential for climate change to extend invaders' ranges. A multivariate approach involving RLQ analysis and a recently developed 'fourth-corner model' were used to quantify trait-environment relationships and to predict climate-change effects on species distributions. Four species subsets were analysed separately, based on their invasion status: natives (n=60), archaeophytes (n=66), neophytes (n=55), invasive (n=6), using trait data from the Ecoflora, present and projected climate data from the UK Climate Projections project, and distribution data from the National Biodiversity Network Atlas. Matrices of inferred trait-environment correlations were generated for each subset, and compared among subsets. The fourth-corner model was then used to predict the probability of site occupancy of the invasive species, under a medium emissions scenario, for the last decades of the 21st century.

Robust tendencies among native species, archaeophytes and neophytes were the association of high-pH and drought-tolerant species with warm summers, low-pH species with colder (or wetter) climates, and small-leaved species with cold winters and/or summers. IAS show the same association of leaf size with temperature, but also showed moisture-demanding and nitrophilous plants to be associated with warm summers and low-pH species with warm winters – reflecting these species' distinct habitat preferences. There were also indications that IAS are generalists, based on the fewer significant interactions overall compared to other species groups.

Potential consequences of climate change included projected increases in IAS site occupancy, particularly in Northern Ireland and western Scotland. *Symphoricarpos albus* and *Rhododendron ponticum* showed the largest increases, at 37% and 25% respectively. This suggests that the future British climate, with longer and warmer growing seasons, will increase habitat suitability for IAS in regions where at present they do not occupy.

KEY WORDS

archaeophytes, fourth-corner, functional traits, invasive alien plants, naturalised plants, neophytes, RLQ analysis

INTRODUCTION

What makes some species invasive whilst others remain naturalised or fail to establish when introduced to a new ecosystem? Researchers have been dealing with this question for decades, with the case for doing so ever more pressing since Seebens et al. (2017) revealed that worldwide, the rate of biological invasions shows no sign of abating.

Invasive alien species (IAS) represent a major component of global environmental change (Vilà et al. 2011). A further challenge is untangling the synergistic effects of other components of global change such as human-induced climate change, nitrogen deposition and land-use change (Drenovsky et al. 2012). Species, once constrained by biogeographic barriers, are now establishing self-sustaining populations outside their native ranges (Richardson and Pyšek, 2006). On a global scale, approximately 20-30% of species introductions cause socio-economic and ecological harm, with a smaller proportion of these regarded as highly invasive (Pimentel et al. 2001).

For an IAS to be classed as invasive, it must overcome a series of stages outlined by Richardson and Pyšek's (2006) "naturalized-invasion continuum", hereafter continuum. In brief, the continuum describes that a species must survive human-mediated transport from its native location to the new location to be classed as alien. Alien species that occasionally reproduce but fail to form self-propagating populations are described as casual aliens. Naturalised alien species are aliens that manage to establish self-propagating populations without human intervention. Invasive alien species are therefore a subset of naturalised alien species. They often reproduce in high numbers, and spread over large areas, and cause demonstrable socio-economic and ecological harms (Richardson and Pyšek, 2006).

The effects of IAS are wide-ranging: from causing a reduction in global biodiversity, with islands being particularly vulnerable (Reaser et al. 2007), changes to ecological processes such as nutrient cycling (Ehrenfeld, 2003). Issues with diseases and human health and wellbeing can also be attributed to IAS, with the spread of *Aedes albopictus*, a vector for arboviruses being a notable example (Pyšek and Richardson, 2010). Collectively, these result in considerable economic burdens on individuals and countries. The control and management of IAS incurs an annual loss of approximately 5% of the global economy (Pimentel et al. 2001). Ecologists and policy makers recognise the pressing need to minimise the ecological and socio-economic costs associated with IAS. It is therefore desirable to understand and predict the mechanisms for their arrival, establishment and spread. This strategy has been highlighted as a key goal in the EU 2020 Biodiversity Strategy (EC, 2011).

Modern invasion ecology is generally regarded as beginning with Charles Elton's (1958) influential book "*The ecology of invasions by animals and plants*". Since then, researchers have explored many approaches to explain the driving forces of invasion (Richardson and Pyšek, 2008). Prominent hypotheses include the *enemy release* hypothesis (Keane and Crawley, 2002), which suggests that successful invasions occur due to an absence of enemies in the new ecosystem. Lockwood et al. (2005) proposed that *propagule pressure* - the number and frequency of individuals released into a new area - aids establishment and increases the probability of invasion. The *novel weapons* hypothesis has also been postulated as a determinant of successful invasions, particularly with invasive plants (Callaway and Ridenour, 2004). These authors proposed that invasive species gain a competitive advantage in new ecosystems over their native counterparts through the possession of biochemical or allelopathic substances, which native species have not evolved to cope with. Other hypotheses have been suggested, and are reviewed by Catford et al. (2009) and Jeschke et al. (2012).

Whilst these various hypotheses have produced some important insights (e.g Thorpe et al. 2009) in general they lack sufficient empirical support, leading to limited applied relevance (Jeschke et al. 2012, Dick et al. 2013) and predictive capacity, especially in the context of environmental change (Dick et al. 2017). Increasingly, the study of functional traits has been explored to address these issues (Sakai et al. 2001). Functional traits are defined here as intrinsic measurable characteristics of an individual species pertaining to all aspects of plant life history (physiological, morphological, phenological), and can be understood as a proxy for individual species performance (Violle et al. 2007; Drenovsky et al. 2012). For plants, key traits include: maximum height, seed size, specific leaf area and peak flowering time (Gallagher et al. 2014).

Functional trait-based approaches have advanced from simple trait cataloguing and comparisons (Baker 1965) to complex frameworks resulting from meta-analyses (van Kleunen et al. 2010). IAS have been shown to have particular physiological traits pertaining to resource acquisition, such as taller maximum height, higher growth rates and larger leaf size (Gallagher et al. 2014). Other research has indicated reproductive allocation differences involving smaller seed mass (Schmidt and Drake, 2011) and distinctive flowering phenology (Godoy et al. 2008). But despite a large number of published studies, a comprehensive suite of 'invasive traits' remains elusive (van Kleunen et al. 2015). This situation can perhaps be explained by the context dependency of biological invasions, whereby the expression of traits is influenced by the environment, with residence time and

propagule pressure being additional confounding factors (Lockwood et al. 2005; Chytrý et al. 2008; Kimball et al. 2016).

Another caveat is invasion-stage dependency, which relates to the species' invasive status along the continuum (Moravcova et al. 2015). In other words, the relative importance of a species' trait is dependent on the stage of invasion. As a trait that aids colonisation, for example could be a hindrance to further establishment. A further problem with some studies is the failure to differentiate among categories of alien species (Theoharides and Dukes, 2007), e.g by analysing casual aliens together with naturalised aliens in a heterogeneous group. A way to address these context-dependencies is to consider the species and ecosystem interactions for species along all stages of the continuum (Kueffer et al. 2013).

The present study followed a comprehensive approach by comparing the traits of native plant species with established archaeophyte, neophyte and invasive species in the UK (Table 1). The aims were to investigate whether invasive plants possess unique functional traits that lead to their invasion success by considering the species and environment interactions using the powerful 'fourth-corner model', introduced by Brown et al. (2014). From this, the role of climatic factors in the expression of species traits based on their geographical distribution was inferred. The study also considers the potential effect of climate change on the invasive plant distributions. The fourth-corner approach has been used in a few recent ecological studies (e.g. Venn et al. (2016) and Mallen-Cooper et al. (2017)), but to date this study appears to be the first use the method to study plant invasions along the naturalized-invasion continuum and at a country level.

MATERIALS AND METHODS

Study Area

The UK (which includes the territories of England, Wales, Scotland and Northern Ireland) was the target region for the study. In total, the regions comprise an area of 242,495 km² (Jefferies, 2005), situated 49° to 61° N and 9° W to 2° E. The climate is temperate with influences from the North Atlantic westerly winds and continental Europe. The north-west of the UK is wetter and colder than the drier and warmer south-east (Met Office, 2017). Estimates vary, but there are ~3000 vascular plant species in the region (Table 1) (Preston et al. 2002). This excludes *Hieracium*, *Taraxcum*, *Rubus* and *Ranunculus* microspecies, which constitutes an additional 900 or so species.

Table 1 Number of vascular plant species in the British Isles taken from Preston et al. (2002).

Species status	Number of species
Native	1407
Archaeophytes	149
Neophytes	1155
Casuals	240
Total	2951

Definitions

Definitions of invasive species tend not to be-uniform, due the context dependency issue

(Richardson et al. 2000). In this study, the plant statuses are defined in Table 2.

Table 2 Key definitions in plant invasions used in this study for in a UK context. Casual aliens were excluded as not all trait data was available for this set of species.

Term	Definition	Reference
Native plants	Species that occur in the British Isles without human assistance. This includes plants that recolonised within 10,000 years after the last ice age.	Crawley et al. 1996
Alien plants	Species that are found outside their biogeographical range due to intentional or accidental human mediated transport. <i>Synonyms non-native species, non-indigenous.</i>	Richardson et al. 2000
Casual alien plants	An alien species that may reproduce occasionally but does not form self-sustaining populations and can only persist in an area without repeated reintroduction for ~5 years.	Hill et al. 2005
Naturalised plants	An alien species that has established self-sustaining populations via means vegetative spread or seed reproduction.	Richardson et al. 2000
Invasive alien plants	A subset of naturalised alien species that often reproduce in high numbers and spread over large area, causing demonstrable economic and ecological harm.	Richardson & Pyšek, 2006
Archaeophytes	A naturalised alien species that has been present before 1500 AD.	Hill et al. 2005
Neophytes	A naturalised alien species that has been present since 1500 AD or was naturalised through reintroduction since 1500.	Hill et al. 2005

Plant traits

Functional trait data for British vascular native and alien species was obtained from the Ecoflora database (Fitter and Peat, 1994; Ecoflora, 2017). The database contains ecological traits on ~3300 species and subspecies from 184 families and 960 genera. Traits were selected *a priori*, based on empirical studies that implicated certain traits in invasion success (Table 3). MySQL (V5.6.34) queries

were used to interrogate the database and produce species-trait tables. The selection criterion was that the species had to contain data on all the seven selected traits. A case-wise deletion approach was taken here for species that did not meet the criterion, as the subsequent analysis required complete datasets. During the trait selection process, 22 traits were considered as important (Appendix 2), but only seven traits were made the final selection, as including more traits, would have further reduced the number of species in each subset, thereby reducing the strength of the analysis. The selected traits were designed to be comprehensive, representing the different life stages of plants, as well as a range of physiological, morphological and reproductive characteristics. In cases where there was more than one entry for quantitative traits, the data were aggregated and the

Table 3 Functional traits used for analysis. *Status was used to form the native, archaeophyte and neophyte subsets. **Abundance and population dynamics only used for the invasive species subset

Trait type	Trait	Biological significance for invasion	Trait attribute (abbrev)	Values	Source
Biogeographical	Status*	Where on the continuum the species lies	Native, Neophyte, Archaeophyte	Categorical	Richardson and Pyšek 2006 Hill et al. 2004
	Abundance**	Typically higher abundance in IAS	scattered, frequent, abundant	Ordinal	Richardson and Pyšek 2006
	Population dynamics**	Indicates rate of spread of IAS	declining, stable, increasing, fluctuating	Ordinal	Hastings et al. 2004
Morphological	Typical maximum height	Tendency to be greater in invasive species	values (cm) (typ_max_height)	Continuous	Gallagher et al. 2014
	Leaf Area	Tendency to be larger in IAS	<0.1, 0.1-1, 1-10, 10-100, 100-100, >1000 (cm ²) (LA)	Ordinal	Gallagher et al. 2014
Reproductive	Mean Seed Mass	Tendency to be smaller in IAS	values (mg) (av_seed_mass)	Continuous	Gallagher et al. 2014
Physiological	Ellenberg Indicators:	Tolerance to:			
	light	light conditions	Values 1-9 (1: deep shade, 9: full light) (E_light)	Ordinal	Hill et al. 2004

moisture	soil moisture	Values 1-12 (1: very dry soil, 12: submerged) (E_moisture)	Ordinal	Hill et al. 2004
pH	soil pH level	Values 1-9 (1: strongly acidic, 9: strongly alkaline) (E_pH)	Ordinal	Hill et al. 2004
nitrogen	soil nitrogen levels	Values 1-9 (1: infertile soil, 9: extremely rich soil) (E_nitrogen)	Ordinal	Hill et al. 2004

mean was calculated. A total of 700 species matched the criterion. From this dataset, subsets were created based on their status: native (n=60), archaeophyte (n=66), neophyte (n=55) and invasive (n=6). The native subset was reduced from 573 species to 60 through a random selection, as the subsequent statistical analysis could not cope with a larger species dataset.

Bioclimatic variables

It is well established, climate is a strong predictor for plant species distribution, as it governs all aspects of plant life history (Woodward, 1987; Sykes et al. 1996). Climate data were obtained from the UK Climate Projections (UKCP09) from the UK Met Office <http://ukclimateprojections.metoffice.gov.uk/>. Monthly mean values were extracted for precipitation (mm), air temperature (°C) and cloud cover (%) for 438 25 km² grid cells on the British National Grid (BNG). To investigate the effect of climate change on the distribution of invasive species, the three climate variables were obtained for the baseline reference period 1961-1990 and compared to the IPCC SRES A1B medium emission scenario for 2070-2099 period. This scenario was selected for the given period, as it constituted the most balanced (in terms of projected fossil and renewable energy use) and projected to the end of the century, which allowed for enough differences to ascertained between present and future climate.

To obtain more plant-relevant bioclimatic variables, the three meteorological climate variables were transformed in the Simple Process-Led Algorithms for Simulating Habitats (SPLASH) model (Davis et al. 2017). SPLASH contains a series of process-based models that use three foundational climate variable inputs: precipitation, temperature and fractional sunshine hours or cloud cover to calculate a series of indices, including a Moisture Index (ratio of annual precipitation to annual potential evapotranspiration) and an estimate of the Priestley-Taylor coefficient (α) (ratio of actual to potential evapotranspiration) as alternative measures of 'plant available' moisture. SPLASH includes accounting for the seasonal cycles of solar and net radiation and soil moisture in order to derive

these indices. The algorithms also allow for the effect of elevation (on solar radiation and evapotranspiration) although this effect is slight and was neglected here.

The SPLASH model and subsequent calculations were carried out in Python (V2.7). The model was run for two years, and only values for the second year were acquired, as in the first year, the model was still in a transient state. Annual values for moisture index (MI) for both baseline and future climate datasets were computed from SPLASH (Box 1). Both MI and α provided potential measures of plant-available moisture but MI was selected as the most appropriate measure, as Shuttleworth and Calder (1979) suggest caution with using α in study areas that receive high annual precipitation, such as the north-west of the UK, as α has an upper threshold of 1.26 – thus, this measure has little power to differentiate among very wet climates even though differences in rainfall continue to affect plant growing conditions after this maximum has been attained.

Using the two temperature datasets, growing degree days above 0°C (GDD₀) and mean temperature of the coldest month (MTCM) were calculated (Box 1).

Box 1 Equations for the bioclimatic variables calculated in the SPLASH models

Growing degree days above 0°C (GDD₀) in °C days:

$$GDD_0 = \Sigma \{(\text{for months where } T > 0^\circ\text{C}) \times (\text{days in month} \times T)\}$$

where T is the monthly mean temperature in °C. February was counted as having 28.25 days.

Mean temperature of the coldest month (MTCM) in °C:

$$MTCM = \bar{T} \text{ of month } T_{\min}$$

Where \bar{T} and T_{\min} are the mean and minimum temperature in °C respectively.

Moisture index (MI):

$$MI = \frac{P_a}{E_a^p}$$

where P_a is annual precipitation in mm a⁻¹ and E_a^p is annual potential evapotranspiration in mm a⁻¹ (Davis et al. 2017)

GDD represents the growing season length, which is linked to the winter chilling requirements for species, hence regulating the spring budburst phenology (Prentice et al. 1992). Interspecific variation exists with chilling thresholds, some tree species require temperatures <5°C (Prentice et al. 1996), but *Ribes* species need <0°C, so a minimum baseline of 0°C was selected to account for this variation (Jones et al. 2014). MTCM represents the cold tolerance of species, which is governed by their mechanistic responses to low temperatures (Woodward et al. 1990). It is also an important factor in limiting species distribution, particularly for woody species (Prentice et al. 1992).

Species presence

Presence data for the species in the subsets at 1 km² BNG resolution was obtained from the National Biodiversity Network Atlas (National Biodiversity Network Atlas, 2017). These data were then aggregated to 25 km² using the extract function in R raster package (V3.3.2) to match the resolution of the bioclimatic data (R Core Team 2017). The extract function used the centroid of each climate grid cell as a “sampling point” for the species distribution to re-project it at 25 km² resolution. This method produces some spatial uncertainty, as the nature of the BNG projection, a rotated latitude and longitude projection, with each grid cell not equidistant from its neighbour meant that spatially aligning the two datasets cannot be obtained with high accuracy. A species presence/absence matrix was then constructed for each of the subsets.

Data analysis

The relationship between the bioclimatic variables, species traits and their abundance was investigated by means of a RLQ/fourth-corner analysis. This integrated multivariate approach is an advance from a traditional species distribution model (SDM), which analyses species distribution based on their abundance (Brown et al. 2014). Incorporating species traits can help elucidate how and why species respond to a set of environmental variables, which is not answered in SDM, thereby solving the fourth-corner problem (Dray et al. 2014). The fourth-corner problem can be understood as an analysis of three matrices of environmental parameters (R), species occurrence as abundance or presence/absence (L) and species traits (Q), which forms the fourth-corner (D) – the trait-environment matrix. The resulting matrix D, allows the magnitude and direction of the trait-environment relationship to be interpreted from the fourth-corner coefficients (Brown et al. 2014).

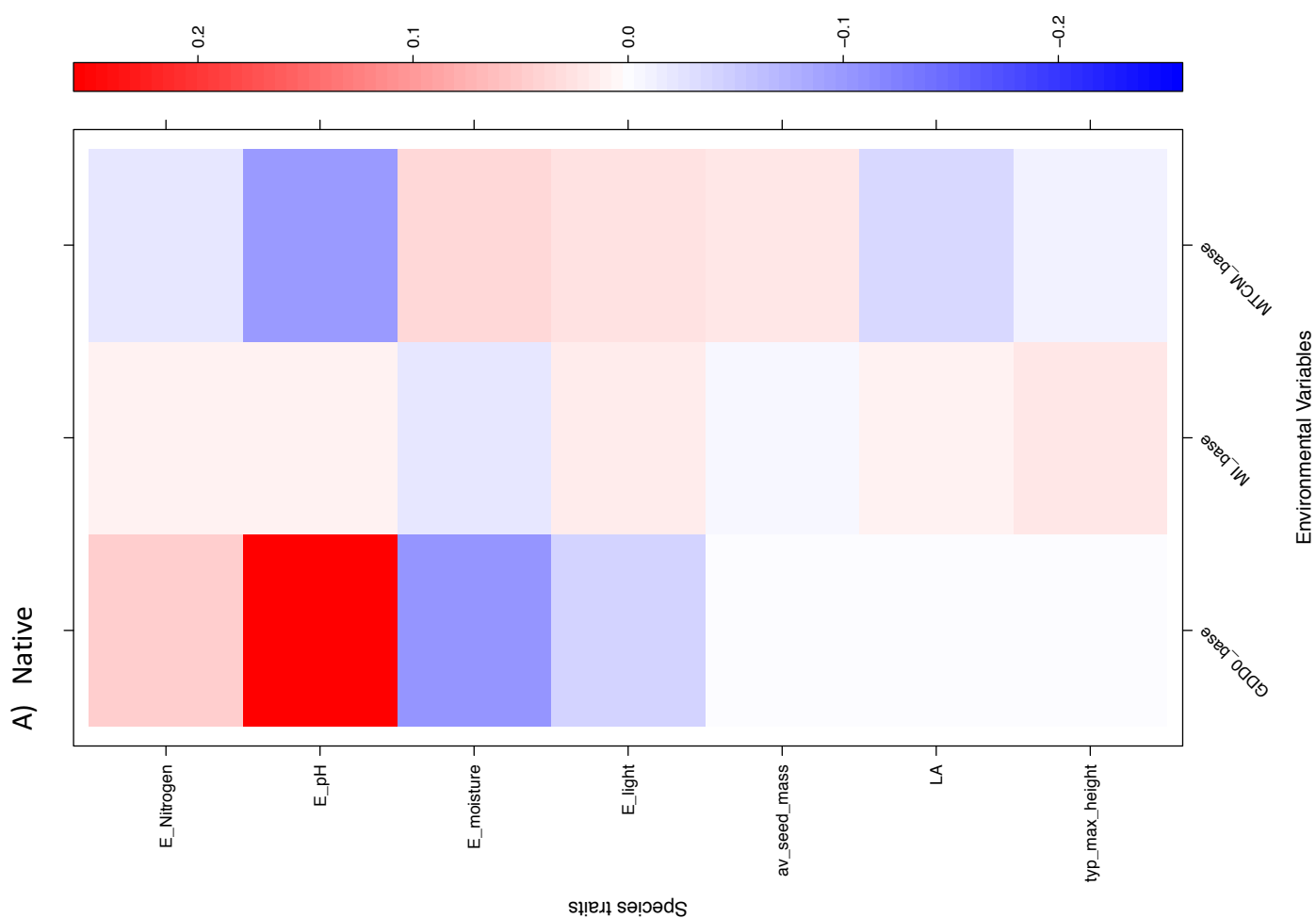
This analysis can be computed both in the ade4 and mvabund packages in R (Dray and Siberchicot, 2017; Wang et al. 2017). The latter package was chosen for this study, as the model can calculate predictions of new occurrence sites (L) based on new environmental parameters (R_1), whilst keeping L, Q and D matrices constant. In this study, R, L and Q corresponded to the bioclimatic variables, presence/absence records and seven traits respectively. The fourth-corner analysis was computed using the trait generalised linear model (traitGLM) separately for native (n=60), archaeophyte (n=66), neophyte (n=55) and invasive species (n=6) datasets. Least absolute shrinkage and selection operator (LASSO) penalty and log-log link binomial selection parameters were added to the model. The LASSO penalty reduces the model terms to zero if they do not contribute to the variation (Sitters et al. 2016) and is shown by Renner (2013) to enhance the model’s predictive performance. For binary abundance data, Wang et al. (2017) strongly suggest the use of a log-log link binomial family.

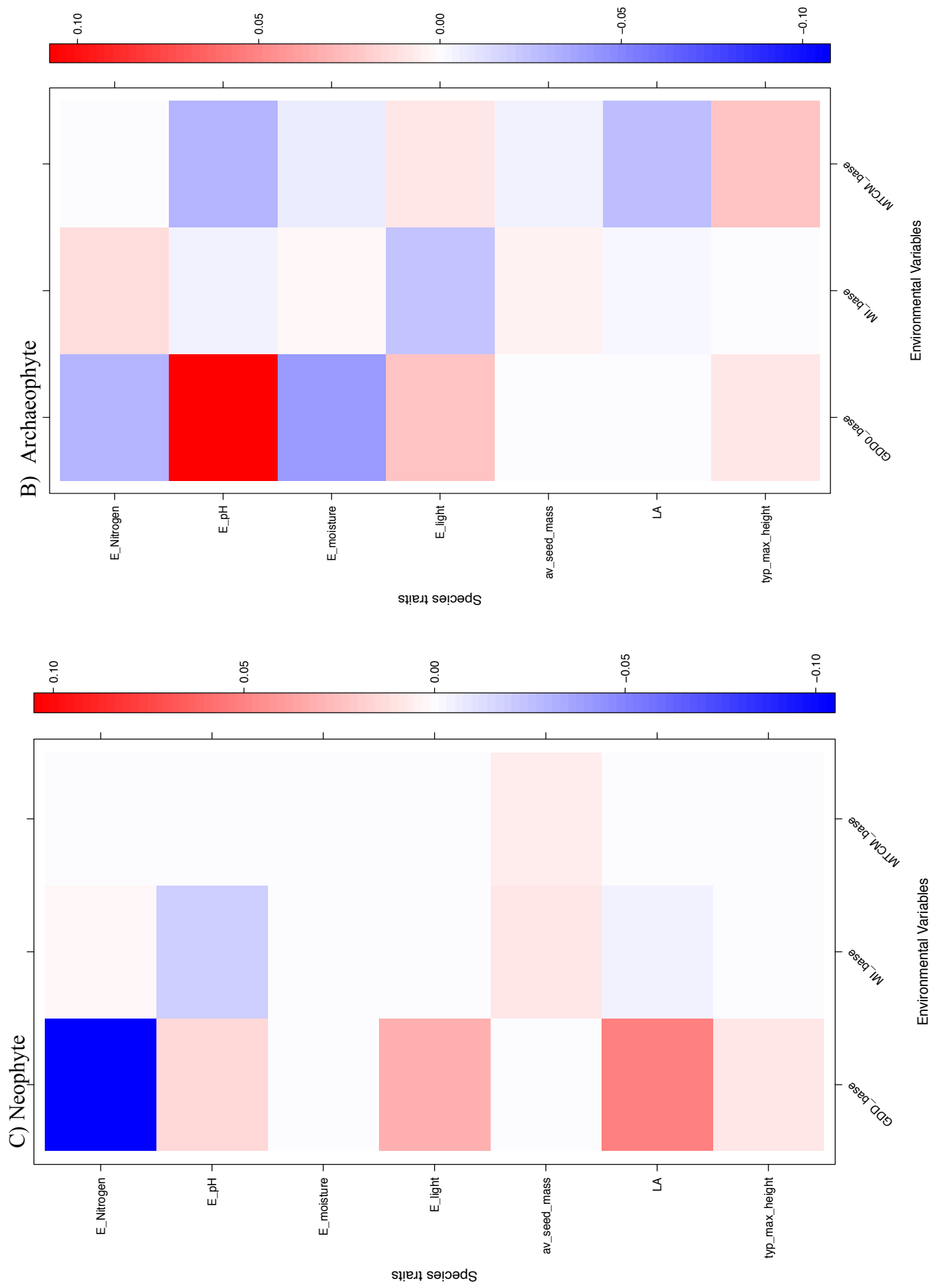
To establish whether a new climate scenario would cause a range shift of the highly invasive species, the predict traitGLM function was computed with future climate variables (R_1), whilst keeping the other matrices constant. This produced a series of probabilities of site occupancy for each of the 438 grid cells, which were then plotted using the raster and colorRamp package (R core team 2017).

RESULTS

Trait-environment relationship

The fourth-corner model enabled the trait-environment relationship to be determined for each of the species subsets along the naturalised-invasion continuum. Seven traits (typical maximum height, leaf area, seed mass and Ellenberg indicators: light, moisture, pH and nitrogen) and the three bioclimatic variables (growing degree days (GDD_0), moisture index (MI) and mean temperature of the coldest month (MTCM)) were analysed. The results of the fourth-corner analyses are presented in Figure 1A-D. For additional information on the significant fourth-corner coefficients, see Appendix 2





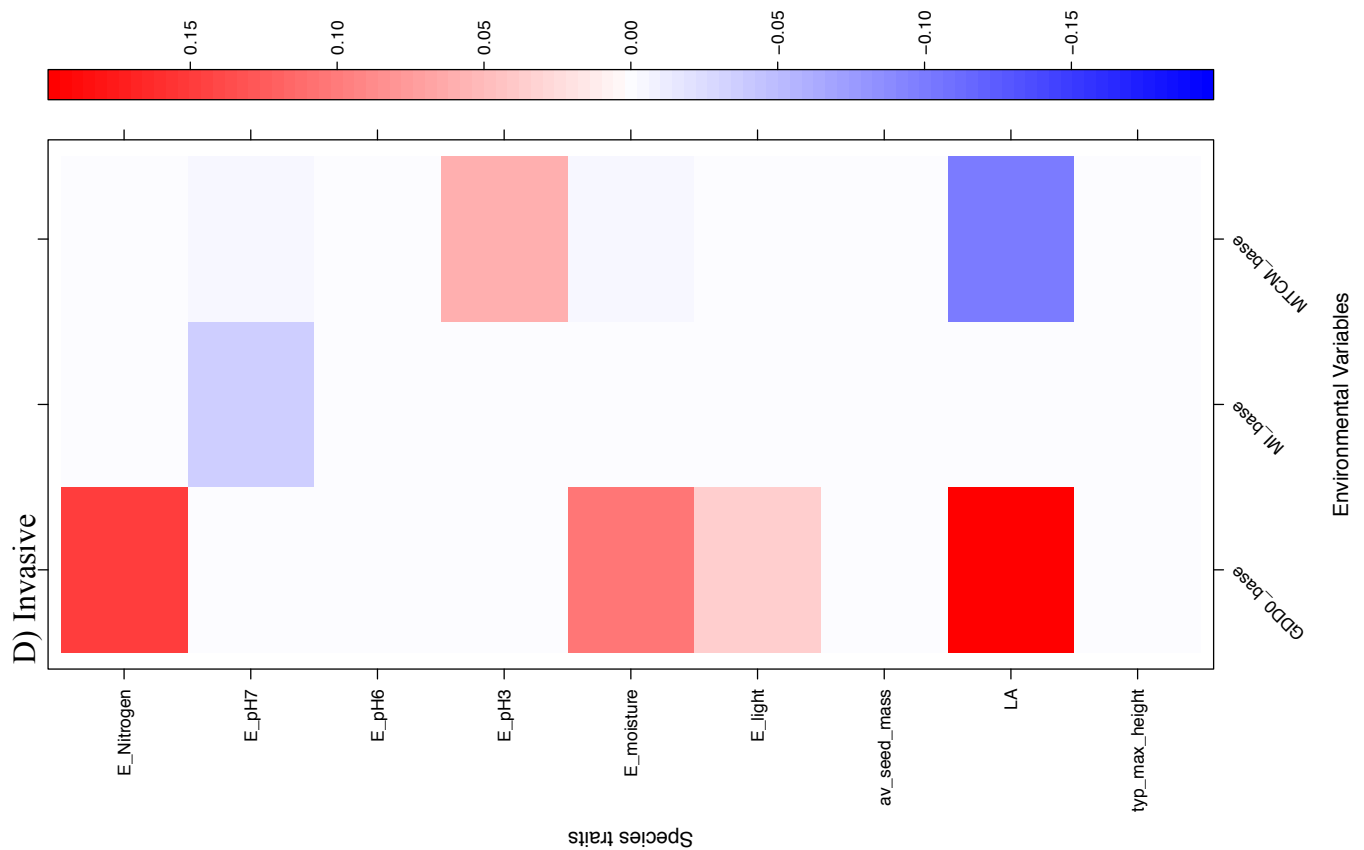


Figure 1 Results of the fourth-corner model with LASSO penalty for A) native (n=60), B) archaeophyte (n=66), C) neophyte (n=55) and D) invasive (n=6) species subsets. Red and blue squares indicate a positive and negative trait-environment relationship respectively. The brighter the squares the stronger the relationship. The scale indicates values of the fourth-corner coefficients. For meanings of species traits see Table 3. Note: for the invasive species subset, the Ellenberg indicator pH (E_pH) is displayed three times, due to the low variation in the values for the trait in the subset, causing the model to treat it as a factor.

For all four species subsets, GDD₀ formed the strongest associations with the species traits.

Additionally, typical maximum height and seed mass exhibited weak or no associations with any of the bioclimatic variables. The native and archaeophyte species produced a similar set of trait-environment associations. The two subsets showed a strong positive association between the Ellenberg pH indicator and GDD₀ (Figure 1A and B), indicating longer and warmer GDD increases the tolerance of species to alkaline soil conditions. Ellenberg pH and MTCM displayed a moderate negative relationship for both subsets.

Both subsets also showed a moderate negative association to GDD₀ to Ellenberg moisture signifying that species tolerance to dry soil conditions is reduced with longer and warmer GDD. A moderate negative relationship between Ellenberg pH and MTCM was also registered.

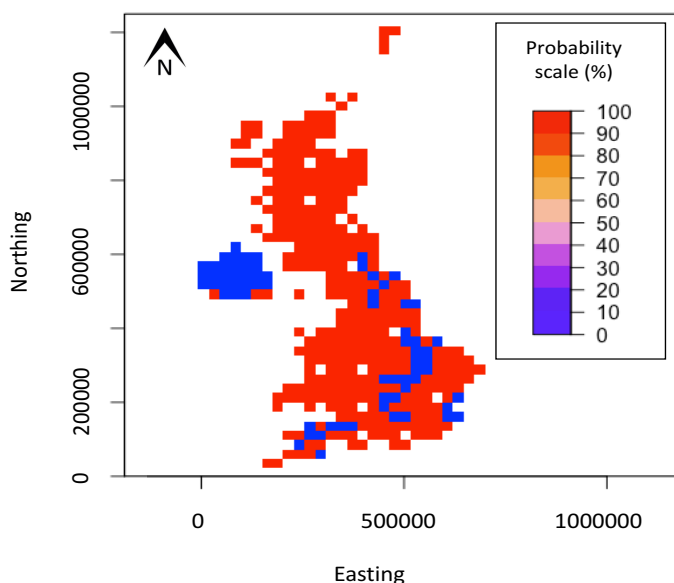
Neophyte species showed a strong negative association between GDD_0 and Ellenberg nitrogen (Figure 1C), indicating a strong preference for nutrient rich soils with cooler summers. Moderate positive associations with Ellenberg light and pH and leaf area were also displayed by this subset.

The trait-environment relationships within the invasive species subset differed considerably from the other three subsets (Figure 1D). There were fewer significant trait-environment interactions, with significant interactions being predominately positive. In contrast to the neophytes, the invasive species showed a strong positive association with Ellenberg nitrogen to GDD_0 . Leaf area displayed a strong positive and negative relationship with GDD_0 and MTCM respectively, indicating that species with smaller leaves are associated with colder temperatures. A moderate positive association for Ellenberg light and moisture were registered for GDD_0 , which was the only similarity with the neophyte subset in the case for the former trait.

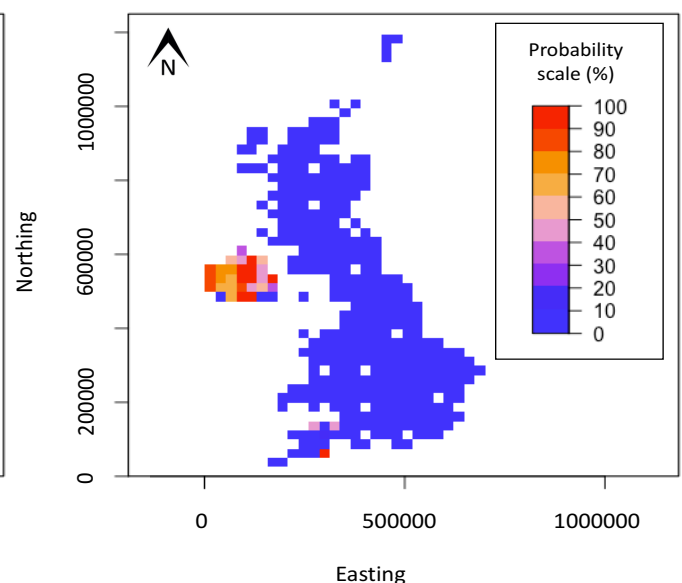
Invasive species distribution for baseline and future climate scenarios

All invasive species had projected increases in their range under climate change, compared to the baseline climate scenario (Figure 2A-L). *Symphoricarpos albus* was predicted to have the largest increase (37%) in projected occupancy of sites, followed by *Rhododendron ponticum* (25%). For *Acer pseudoplatanus*, *Fallopia japonica*, *Heracleum mantegazzianum* and *Impatiens glandulifera* projected range increases occurred in about 15% of sites. Appendix 3 displays the number probable site occupancy of each species.

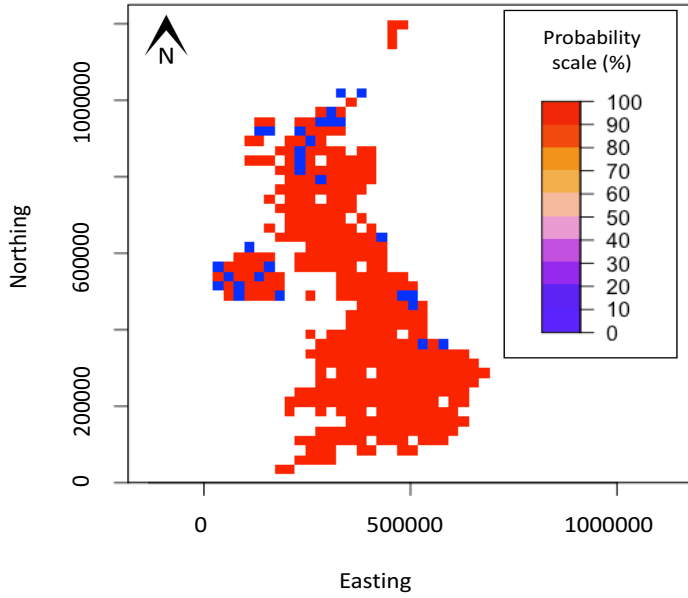
A) *Acer pseudoplatanus* (current)



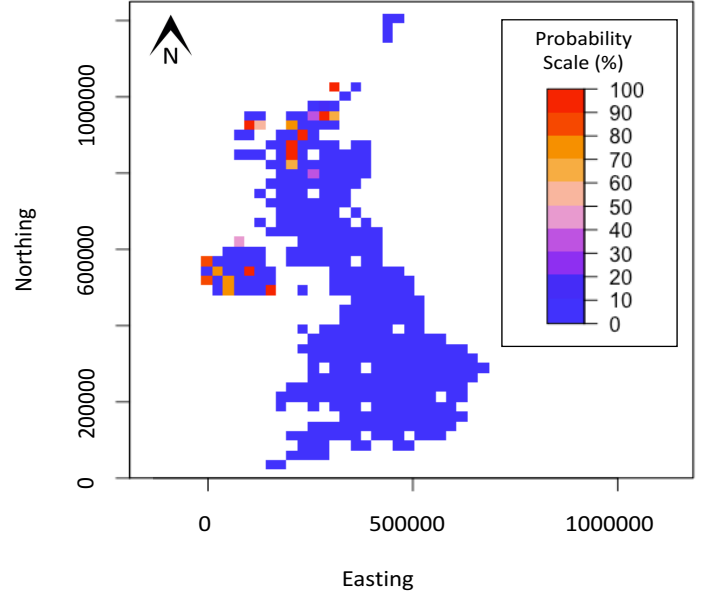
B) *Acer pseudoplatanus* (predicted)



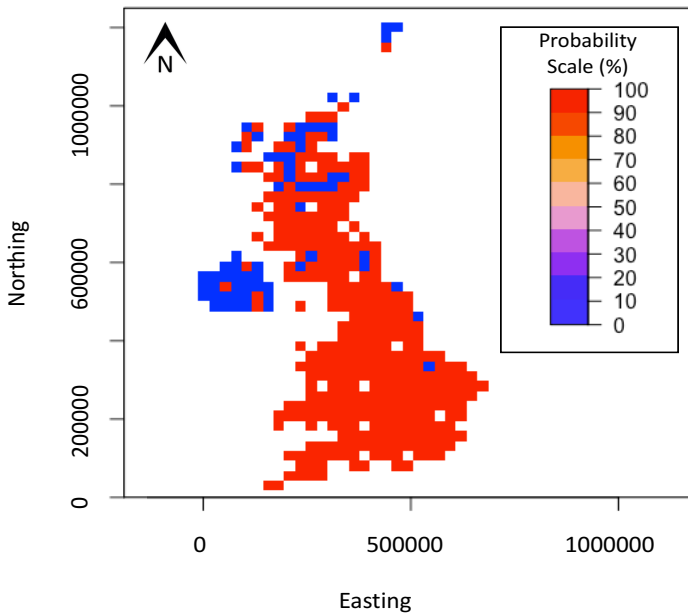
C) *Fallopia japonica* (current)



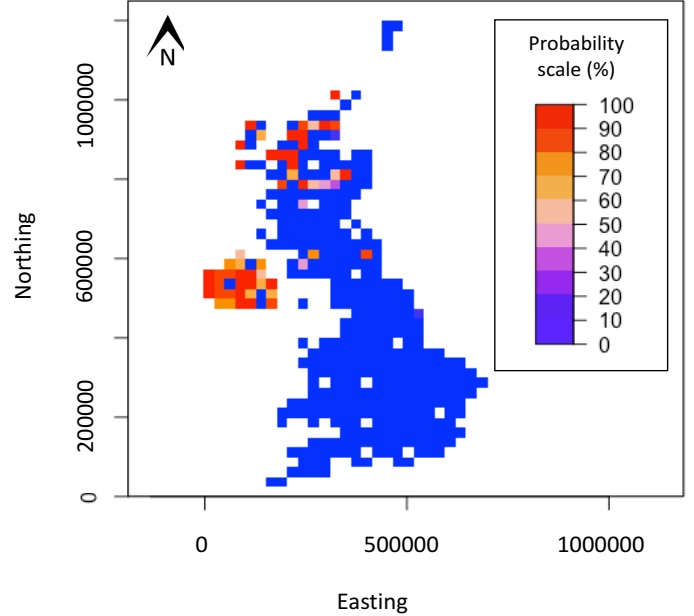
D) *Fallopia japonica* (predicted)



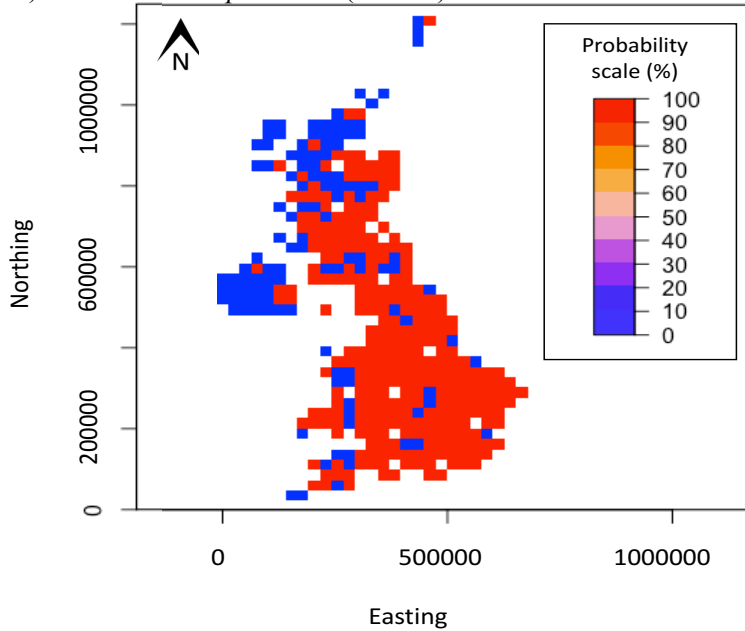
E) *Impatiens glandulifera* (current)



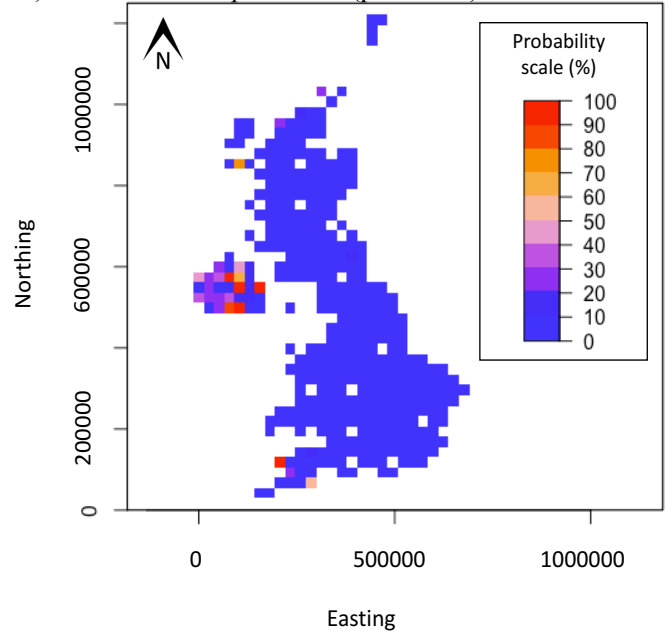
F) *Impatiens glandulifera* (predicted)



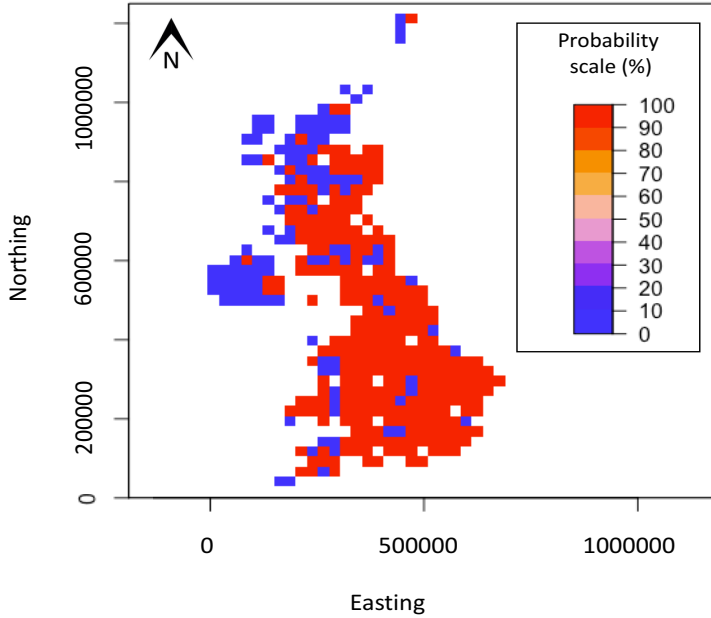
G) *Rhododendron ponticum* (current)



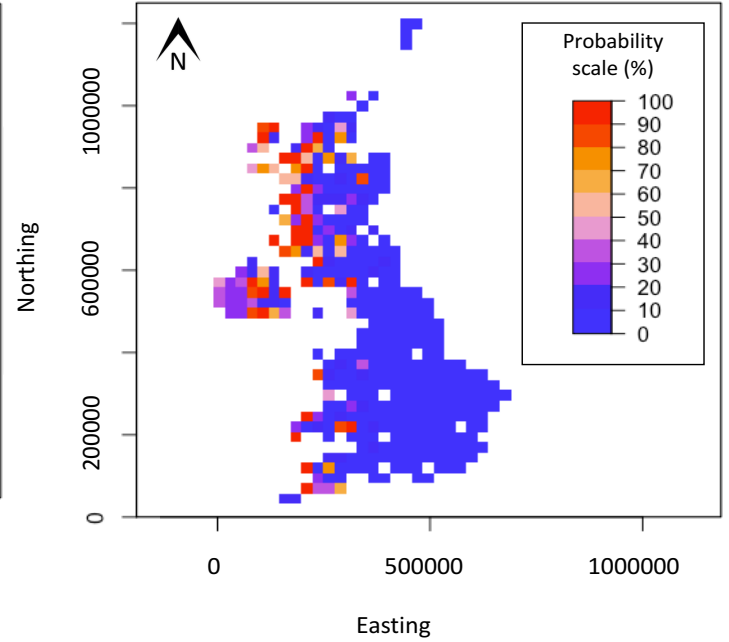
H) *Rhododendron ponticum* (predicted)



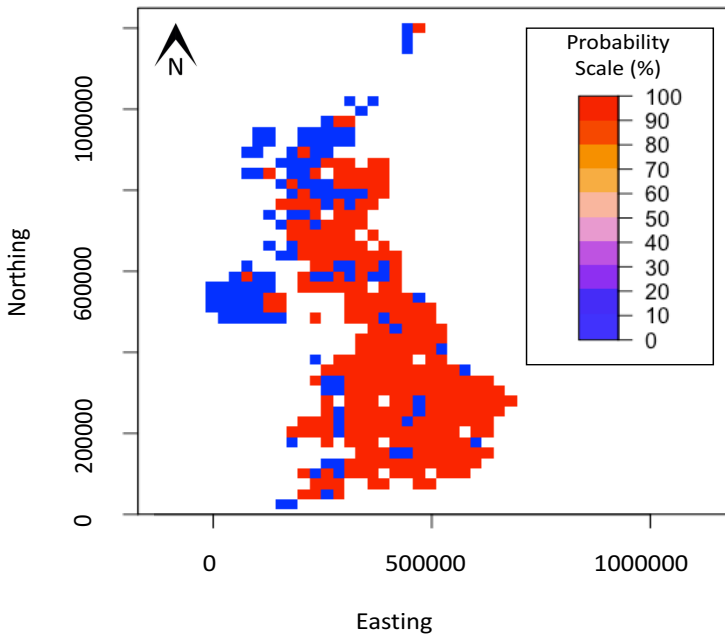
I) *Symphoricarpos albus* (current)



L) *Heracleum mantegazzianum* (predicted)



K) *Heracleum mantegazzianum* (current)



J) *Symphoricarpos albus* (predicted)

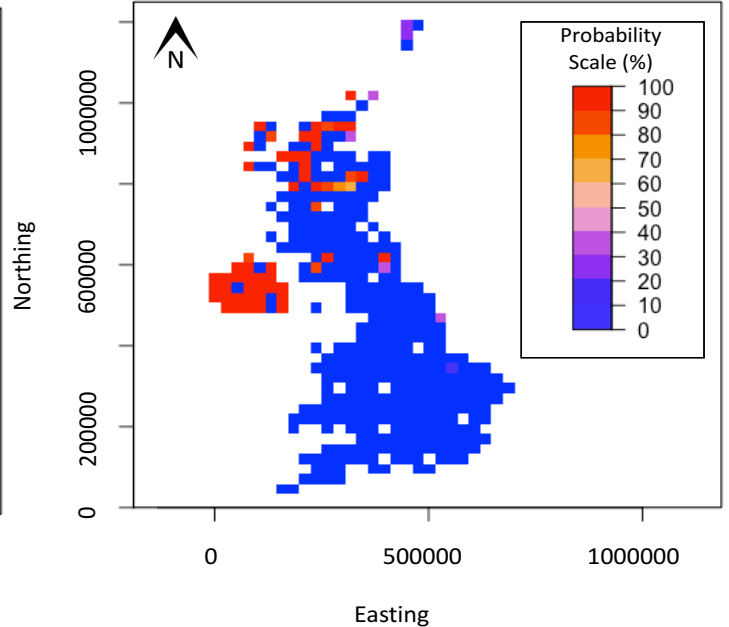


Figure 2 Distribution maps at 25 km² resolution on the British National Grid for six invasive species: *Acer pseudoplatanus* (A and B), *Fallopia japonica* (C and D) *Impatiens glandulifera* (E and F), *Rhododendron ponticum* (G and H), (I and J), *Symphoricarpos albus* (I and J) *Heracleum mantegazzianum* (K and L). Maps on the left show the current distribution of the species as presence (100% probability of occurrence) and absence (0% probability of occurrence) based on the NBN Atlas records (NBN Atlas, 2017). Maps on the right show projected increases (between 0-100%) in the species range based on the predict analysis in the fourth-corner model under a medium emission climate scenario for the 2070-2100 period. Note: white grid cells indicate where data was not available.

For all species, the region of Northern Ireland presented the highest projected increases, particularly for *H. mantegazzianum*, where all but 5 sites showed >90% chance of occurrence. This contrasted to *F. japonica* where only 8 sites saw moderate probability of occurrence. For *R. ponticum* and *S. albus*

the western part of Northern Ireland exhibited low projected site occupancy compared to the eastern part of the region. The Scottish region, indicated considerable projected gains for *F. japonica*, *I. glandulifera* and *H. mantegazzianum* at generally moderate to high probability of occurrence.

The species, *R. ponticum*, *A. pseudoplatanus* and *S. albus* had predicted increases in the southwest region at moderate or high probability level. This was more pronounced for *S. albus*, where most of the western side of the UK mainland exhibited considerable projected site occupancy.

DISCUSSION

This study was the first to use the fourth-corner model to compare traits of plant species along the naturalized-invasion continuum at a country level. Using this multivariate approach, it aimed to determine whether a suite of functional traits is associated with invasive species. The model allowed inferences of the trait-environment relationships for each of the species groups and for the invasive species, calculations of the probability of site occupancy in the UK under a future climate scenario. The results suggest differences in traits depending on the species status, particularly with the neophyte and invasive species and that bioclimatic variables relating to temperature formed the most significant relationships with traits.

Nitrogen-growing season interaction

Multiple studies (e.g. Lim et al. 2014; Stace and Crawley 2015) show that IAS are typically found in wetter and warmer nutrient-rich soils in disturbed areas in the UK. This agrees with the findings in this study, as IAS showed a preference for nitrogen-rich soils with warmer growing season. In Britain, nitrogen is the primary limiting soil nutrient, followed by phosphorous (Stace and Crawley 2015). Davis et al. (2000) suggest that the soil nutrient status is a factor in community susceptibility to invasion. Burke and Grime (1996) showed in their long-term field study that plots exposed to higher nutrient inputs had increased encroachment of IAS at the expense of native species. The authors hypothesised that the ecological differences between IAS and natives, where IAS are associated with faster relative growth rates, able to take advantage of eutrophic soils, over the slower growing native species evolved for oligotrophic conditions. With nitrogen deposition, especially from agriculture, a major component of global change (Sala et al. 2000), this could further benefit IAS at the expense of native species.

The inverse relationship was registered with neophytes. This contrasts with the Stace and Crawley (2015) UK study, where 85% of neophytes were found in soils of medium or high nutrient levels (Ellenberg values 4-9). This result could be explained by the small sample size (n=55) used in the

study, which represented 5% of the UK neophytes. In the neophyte subset, 44% of species registered Ellenberg scores of 5 or less, corresponding to medium-to-low nutrient status. This is likely to have biased the model.

Moisture-growing season interaction

The moisture-growing season interaction of natives and archaeophytes indicated a preference for drier soils, which contrasted to IAS, which had a higher affinity for wetter soils. These results concur with Chytrý et al.'s (2007) comparison of pan-European alien flora, where archaeophytes were found in drier and warmer habitats. In the UK, most archaeophytes are therophytic preferring drier cultivated habitats (Stace and Crawley 2015). This reflects their introductory history, where many archaeophytes (e.g. *Avena fatua*) were brought to the UK for cultivation from the drier southern Europe (Chytrý et al. 2008). The positive interaction displayed by IAS is likely to be driven by the high proportion of these species found in wet habitats (e.g. riparian areas). In the UK, these moist disturbed habitats represent the highest instances of plant invasion with *H. mantegazzianum*, *I. glandulifera* and *F. japonica* being the most abundant (Booy et al. 2015).

Generalist invasive alien species

Whilst the results indicated IAS preferences for nutrient-rich moist soils, there is additional evidence that they are generalists, demonstrated by the presence of fewer significant interactions. It has been noted by Higgins and Richardson (2014) that many IAS have broad edaphic tolerances, which is linked to the *fitness homeostasis* theory. The theory proposes that species that exhibit broad edaphic tolerances and efficient resource-use in their native range have higher potential for invasion when introduced to a new ecosystem. This was observed by Myśliwy (2014) who noted *I. glandulifera* had a "core" damp nutrient-rich habitat, but could tolerate a wide range of conditions in Poland. *I. glandulifera* and *F. japonica* originate from harsh, high altitude disturbed environments in the Himalayas and East Asia respectively (Booy et al. 2015). Their ability for efficient resource-use in their native range, confers a competitive advantage over natives in more ameliorable climates like the UK. Additionally, it highlights the importance that the affinity for certain edaphic conditions alone is not the most reliable measure of invasiveness and other factors need to be considered.

Leaf area-temperature interaction

Both neophyte and IAS formed a significant positive correlation with leaf area and growing season. Leaf size provides insights into plant ecophysiological processes, including water balance, thermoregulation and light capture (Yates, 2010). In a global synthesis of the climatic role governing leaf size, Wright et al. (2017) found a latitudinal gradient with respect to leaf size. Larger leaves are associated with the warmer and wetter climate of the tropics. Large leaves have a greater leaf-to-air

transpiration gradient to maintain leaf temperature and avoid heat damage. Additionally, winter cold can result in frost damage, through lower rates of heat exchange, owing to the thicker boundary layer (Wright et al. 2017). It would be expected that the larger-leaved neophytes and IAS, predominately originating from East Asia (Chytrý et al. 2008), would be at a disadvantage in the UK. Many neophytes and IAS with low frost-tolerance are typically found in the warmer regions of the UK, where winter temperatures exceed 5 °C (Stace and Crawley 2015).

Native and archaeophytes species

Native and archaeophyte species produced a similar pattern for Ellenberg pH and moisture with GDD. This suggests the two species sets are similar in their abiotic preferences. These broad similarities concur with Pyšek et al.'s (2004) study of Czech alien flora. The researchers (2004) propose that the long residence time of archaeophytes, many from as early as the Late Bronze age (3400-2800 BCE) in the recipient ecosystem, have enabled them to adapt to the recipient climate. Interestingly, many British archaeophytes originate from warmer and drier climates in southern Europe and the Near East (Preston et al. 2004, Chytrý et al. 2008), and it would therefore be expected that archaeophytes would exhibit an opposing trend for moisture and GDD to native species. This was not observed in this study, which supports a strong case for archaeophytes adapting to a cooler and wetter British climate.

The moisture and high pH association for archaeophytes and to a lesser extent native species can be explained by the fact that in the UK, these conditions are associated with warmer calcareous grasslands or man-made habitats (Stace and Crawley, 2015). In the case of archaeophytes, the historical context of cultivation is a key explanation for this observed relationship.

Seed mass and maximum height

Both seed mass and typical maximum height were not detected as having significant interactions in the four species groups. Both these traits correlate (Thompson and Rabinowitz 1989), thus explaining why neither trait was significant. This finding disagrees with Crawley et al. (1996), who found these traits significant in alien species. However, their study did not differentiate between aliens. This highlights the importance of invasion stage-dependency in comparing alien trait studies.

Only temperature related bioclimatic variables GDD₀ and MTCM formed strong trait-environment associations, particularly for growing season. This suggests that for this study area, temperature was a stronger determinant for plant trait expression than MI. These findings corroborate with Moles et al.'s (2014) multi-species study of 21 plant traits across different biomes. Despite the authors use of a simpler measure of plant-available moisture (mean annual precipitation), a poor correlation with

plant traits was also registered. For regions where moisture is often limiting (e.g. Mediterranean ecosystems), MI might be a stronger predictor of species traits than the UK, where moisture availability is high.

Invasive species distributions

Most IAS showed concentrated distribution in the south and east of the UK, corresponding to the warmer climatic gradient. Their distribution also correlates with urban centres, as shown by the lack of species in the Scottish Highlands (Stace and Crawley 2015). Under the new climate change scenario all species showed projected increases. Whilst it is generally agreed that plant species with a more southerly distribution will move northwards in response to climate change (Hulme 2016), for IAS, part of this increase can be attributed to the species not already at equilibrium with the UK environment, as by definition neophytes are relatively 'new' arrivals to the UK. Hulme (2016) expresses caution with projecting future IAS distribution, as despite IAS demonstrating broad environmental tolerances, indicating a strong ecophysiological response to climate change, this might not result in range shifts. For example, longer growing seasons resulting in earlier flowering times might not translate to increased spread.

Whilst this study showed projected increases for all six IAS, the human dimension, an important factor in governing plant distribution was not included. This factor could constrain or facilitate species spread and future studies should integrate socio-economic factors (e.g. land use type and urban population density) to gain more representative distributional changes.

Limitations

This study has produced some important insights into the role of traits in plant invasions despite representing a small subset of the native and alien flora of the British Isles (~5%). The nature of using trait databases means that information is often incomplete (Taugourdeau et al. 2014). As the fourth-corner model can only compute with complete matrices, a case-wise deletion approach was used, which reduced the species list by ~80%. Moreover, some traits such as dispersal distance and relative growth rate would have been useful to include, although these are often difficult to measure out in the field (Drenovsky et al. 2012). To strengthen the existing Ecoflora database, additional work is needed in acquiring trait data, particularly for reproductive and phenological traits, such as chromosome number and flowering time, which have been shown to be significant in some studies (e.g. Pandit et al. 2011 and Godoy et al. 2008). With more robust and complete trait databases, future studies can analyse more species, thus gaining further insight into the role of a variety of traits in plant invasions.

Conclusions

This UK study on identifying traits in invasive plant species, was the first to use a powerful new multivariate analysis at a countrywide level. Key differences between plant species along the naturalised-invasion continuum were observed. Invasive species showed a tendency to have larger leaves and a preference for warm and damp growing conditions. This was also exhibited by neophyte species, albeit to a lesser degree. Native and archaeophyte species showed close trait alignment with a preference for cooler and drier growing conditions, reflecting the evolutionary adaptations due to the long residence time for the archaeophyte species. These observed trait differences between the species groups warrant further investigation, especially in the context of a changing climate, with future studies including more species and traits to see if the same patterns are observed. This will go some way in addressing a major concern in invasion ecology, that of measuring and predicting the spread of invasive alien species.

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APPENDIX

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APPENDIX 1 Species lists used in the fourth corner analysis

Table A1 Native species list

Native species	
<i>Aira praecox</i>	<i>Koeleria macrantha</i>
<i>Ajuga chamaepitys</i>	<i>Leymus arenarius</i>
<i>Ammophila arenaria</i>	<i>Limosella aquatica</i>
<i>Arabis hirsuta</i>	<i>Lotus corniculatus</i>
<i>Arrhenatherum elatius</i>	<i>Malva arborea</i>
<i>Atriplex laciniata</i>	<i>Menyanthes trifoliata</i>
<i>Brachypodium sylvaticum</i>	<i>Mibora minima</i>
<i>Buxus sempervirens</i>	<i>Ononis repens</i>
<i>Calluna vulgaris</i>	<i>Orchis militaris</i>
<i>Caltha palustris</i>	<i>Paris quadrifolia</i>
<i>Carex binervis</i>	<i>Pedicularis palustris</i>
<i>Carex caryophyllea</i>	<i>Persicaria hydropiper</i>
<i>Cerastium arvense</i>	<i>Persicaria lapathifolia</i>
<i>Cynoglossum officinale</i>	<i>Petasites hybridus</i>
<i>Dactylis glomerata</i>	<i>Phragmites australis</i>
<i>Elymus caninus</i>	<i>Pimpinella major</i>
<i>Erica cinerea</i>	<i>Potentilla argentea</i>
<i>Erica vagans</i>	<i>Quercus petraea</i>
<i>Eriophorum vaginatum</i>	<i>Ranunculus acris</i>
<i>Fraxinus excelsior</i>	<i>Rubus idaeus</i>
<i>Galium saxatile</i>	<i>Rumex obtusifolius</i>
<i>Gentianella anglica</i>	<i>Sedum villosum</i>
<i>Geranium pusillum</i>	<i>Senecio vulgaris</i>
<i>Glyceria fluitans</i>	<i>Sesleria caerulea</i>
<i>Helianthemum nummularium</i>	<i>Teesdalia nudicaulis</i>
<i>Heracleum sphondylium</i>	<i>Thymus serpyllum</i>
<i>Hydrocotyle vulgaris</i>	<i>Vicia hirsuta</i>
<i>Hypericum maculatum</i>	<i>Vicia tetrasperma</i>
<i>Inula conyzae</i>	<i>Viola lutea</i>
<i>Iris foetidissima</i>	
<i>Juncus squarrosus</i>	

Table A2 Archaeophyte species list

Archaeophyte species	
<i>Aegopodium podagraria</i>	<i>Linaria repens</i>
<i>Agrostemma githago</i>	<i>Lithospermum arvense</i>
<i>Agrostis gigantea</i>	<i>Malva neglecta</i>
<i>Agrostis stolonifera</i>	<i>Malva sylvestris</i>
<i>Alopecurus myosuroides</i>	<i>Mercurialis annua</i>
<i>Anchusa arvensis</i>	<i>Myosotis arvensis</i>
<i>Anisantha sterilis</i>	<i>Nepeta cataria</i>
<i>Apera spica venti</i>	<i>Papaver rhoeas</i>
<i>Arctium lappa</i>	<i>Reseda luteola</i>
<i>Artemisia absinthium</i>	<i>Salix alba</i>
<i>Artemisia vulgaris</i>	<i>Salix fragilis</i>
<i>Avena fatua</i>	<i>Salix triandra</i>
<i>Ballota nigra</i>	<i>Sambucus ebulus</i>
<i>Briza minor</i>	<i>Saponaria officinalis</i>
<i>Bromus secalinus</i>	<i>Silene gallica</i>
<i>Capsella bursa-pastoris</i>	<i>Silene latifolia</i>
<i>Castanea sativa</i>	<i>Silene noctiflora</i>
<i>Chaenorhinum minus</i>	<i>Sinapis arvensis</i>
<i>Chenopodium bonus-henricus</i>	<i>Smyrniolum olusatrum</i>
<i>Chenopodium glaucum</i>	<i>Tripleurospermum inodorum</i>
<i>Chenopodium hybridum</i>	<i>Urtica urens</i>
<i>Chenopodium polyspermum</i>	<i>Valerianella dentata</i>
<i>Echium plantagineum</i>	<i>Verbena officinalis</i>
<i>Euphorbia exigua</i>	<i>Veronica agrestis</i>
<i>Euphorbia helioscopia</i>	<i>Veronica hederifolia</i>
<i>Euphorbia peplus</i>	<i>Vulpia myuros</i>
<i>Fallopia convolvulus</i>	
<i>Filago pyramidata</i>	
<i>Galeopsis angustifolia</i>	
<i>Galeopsis speciosa</i>	
<i>Glebionis segetum</i>	
<i>Hordeum murinum</i>	
<i>Hyoscyamus niger</i>	
<i>Kickxia elatine</i>	
<i>Kickxia spuria</i>	
<i>Lamium album</i>	
<i>Lamium amplexicaule</i>	
<i>Lamium purpureum</i>	
<i>Legousia hybrida</i>	
<i>Lepidium ruderae</i>	

Table A3 Neophyte species list

Neophyte species	
<i>Acer platanoides</i>	<i>Prunus laurocerasus</i>
<i>Acorus calamus</i>	<i>Pseudofumaria lutea</i>
<i>Allium carinatum</i>	<i>Rhinanthus angustifolius</i>
<i>Allium triquetrum</i>	<i>Ribes uva crispa</i>
<i>Antirrhinum majus</i>	<i>Robinia pseudoacacia</i>
<i>Apera interrupta</i>	<i>Sambucus racemosa</i>
<i>Aster novae angliae</i>	<i>Sanguisorba minor</i>
<i>Campanula rapunculoides</i>	<i>Senecio squalidus</i>
<i>Claytonia perfoliata</i>	<i>Senecio viscosus</i>
<i>Claytonia sibirica</i>	<i>Sinapis alba</i>
<i>Cotoneaster horizontalis</i>	<i>Sorbus intermedia</i>
<i>Datura stramonium</i>	<i>Teucrium botrys</i>
<i>Digitaria ischaemum</i>	<i>Trifolium hybridum</i>
<i>Diploxys muralis</i>	<i>Veronica persica</i>
<i>Epilobium ciliatum</i>	<i>Veronica polita</i>
<i>Euphorbia cyparissias</i>	
<i>Galinsoga quadriradiata</i>	
<i>Geranium phaeum</i>	
<i>Hypericum calycinum</i>	
<i>Impatiens capensis</i>	
<i>Impatiens parviflora</i>	
<i>Leucosium vernum</i>	
<i>Linaria purpurea</i>	
<i>Lobularia maritima</i>	
<i>Lolium multiflorum</i>	
<i>Lonicera xylosteum</i>	
<i>Lupinus polyphyllus</i>	
<i>Lycium barbarum</i>	
<i>Mahonia aquifolium</i>	
<i>Matricaria discoidea</i>	
<i>Melampyrum arvense</i>	
<i>Melilotus albus</i>	
<i>Melilotus officinalis</i>	
<i>Mimulus guttatus</i>	
<i>Myrrhis odorata</i>	
<i>Oenothera biennis</i>	
<i>Oxalis corniculata</i>	
<i>Oxalis stricta</i>	
<i>Poa palustris</i>	
<i>Populus alba</i>	

Table A4 Invasive species list**Invasive species**

Acer pseudoplatanus
Fallopia japonica
Heracleum mantegazzianum
Impatiens glandulifera
Rhododendron ponticum
Symphoricarpos albus

APPENDIX 2 Traits considered for analysis**Table A5 Traits considered for analysis. * indicates traits used in the final analysis.**

Trait type	Trait name
biogeographical	Status*
	Typical abundance where naturally occurring*
	Dynamics*
	Northern limit GB
	January mean temp
morphological	July mean temp
	Typical Max height*
	Leaf area*
	Leaf longevity (type)
physiological	Leaf longevity (months)
	Ellenberg Indicator: Light*
	Ellenberg moisture*
	Ellenberg: pH*
reproductive	Ellenberg Indicator: Nitrogen*
	Ellenberg Indicator: Salt
	Vegetative reproduction/persistence: 1. method (e.g. rhizomes, tubers, stolons)
phenological	Vegetative reproduction/persistence: 2. pattern (e.g. ramets, diffuse ramets, patch forming)
	Seed mass*
	Flowering time: 1. earliest month
genetic	Flowering time: 2. latest month
	Flowering time: 3. peak month
	Chromosome number(s): 1. number

APPENDIX 3 Fourth-corner co-efficients

Table A6 Significant fourth-corner coefficients for native species subset (n=60). Positive and negative coefficients indicate a positive and negative relationship respectively between the trait and bioclimatic variables. GDD_{0_base} = growing degree days >0 °C, MI_{base} = moisture index and MTCM_{base} = Mean temperature of the coldest month.

Functional traits	Code	Bioclimatic variables		
		GDD _{0_base}	MI _{base}	MTCM _{base}
Typical maximum height	typ_max_height		0.019605955	-0.01146580
Leaf area	LA		0.009622196	-0.03575185
Average seed mass	av_seed_mass		-0.007408164	0.01897569
Ellenberg light	E_light	-0.03948984	0.017788166	0.02444710
Ellenberg moisture	E_moisture	-0.10371213	-0.021186391	0.03481359
Ellenberg pH	E_pH	0.25781365	0.012658498	-0.09837996
Ellenberg nitrogen	E_Nitrogen	0.04916674	0.012198013	-0.02178432

Table A7 Significant fourth-corner coefficients for archaeophyte species subset (n=66). Positive and negative coefficients indicate a positive and negative relationship respectively between the trait and bioclimatic variables. GDD_{0_base} = growing degree days >0 °C, MI_{base} = moisture index and MTCM_{base} = Mean temperature of the coldest month.

Functional traits	Code	Bioclimatic variables		
		GDD _{0_base}	MI _{base}	MTCM _{base}
Typical maximum height	typ_max_height	0.008241282		0.024537141
Leaf area	LA		-0.002326705	-0.025655609
Average seed mass	av_seed_mass		0.004806479	-0.004431314
Ellenberg light	E_light	0.023972268	-0.024219270	0.008515961
Ellenberg moisture	E_moisture	-0.040973060	0.001478711	-0.007360286
Ellenberg pH	E_pH	0.107683914	-0.004482103	-0.030323183
Ellenberg nitrogen	E_Nitrogen	-0.030166371	0.013984229	

Table A8 Significant fourth-corner coefficients for neophyte species subset (n=55). Positive and negative coefficients indicate a positive and negative relationship respectively between the trait and bioclimatic variables. GDD_{0_base} = growing degree days >0 °C, MI_{base} = moisture index and MTCM_{base} = Mean temperature of the coldest month.

Functional traits	Code	Baseline bioclimatic variables		
		GDD _{0_base}	MI _{base}	MTCM _{base}
Typical maximum height	typ_max_height	0.007881557	0.0009080917	
Leaf area	LA	0.051434085	-0.0035678904	
Average seed mass	av_seed_mass		0.0085983342	0.006622121
Ellenberg light	E_light	0.031620245		
Ellenberg moisture	E_moisture			
Ellenberg pH	E_pH	0.014150258	-0.0191768772	
Ellenberg nitrogen	E_Nitrogen	-0.105103420	0.0011463117	

Table A9 Significant fourth-corner coefficients for invasive species subset (n=6). Positive and negative coefficients indicate a positive and negative relationship respectively between the trait and bioclimatic variables. GDD_{0_base} = growing degree days >0 °C, MI_{base} = moisture index and MTCM_{base} = Mean temperature of the coldest month. * due to low variation in the Ellenberg pH values in the subset, the trait was treated as a factor instead of numeric

Functional traits	Code	Baseline bioclimatic variables		
		GDD _{0_base}	MI _{base}	MTCM _{base}
Typical maximum height	typ_max_height			
Leaf area	LA	0.19842979		-0.098756941
Average seed mass	av_seed_mass			
Ellenberg light	E_light	0.03584183		
Ellenberg moisture	E_moisture	0.10510772		-0.003579915
Ellenberg pH	E_pH3*			0.061386163
	E_pH6*			
	E_pH7*		-0.03622526	-0.002563114
Ellenberg nitrogen	E_Nitrogen	0.14971432		

APPENDIX 4 Projected distributions for invasive species

Table A10 Calculation table with number of sites (grid squares) with a projected increase in occupancy for six invasive species

Species	Number of sites			
	Projected increase	Total	Difference	% Difference
<i>Acer pseudoplatanus</i>	67	438	371	15.3
<i>Fallopia japonica</i>	67	438	371	15.3
<i>Heracleum mantegazzianum</i>	66	438	372	15.1
<i>Impatiens glandulifera</i>	70	438	368	16.0
<i>Rhododendron ponticum</i>	109	438	329	24.9
<i>Symphoricarpos albus</i>	162	438	276	37.0

APPENDIX 5 Script link

This link provides details of the scripts used in the analysis in MySQL, Python and R.

<https://www.dropbox.com/sh/iaepg15mkxgf7a6/AAAK93LHa9Zkq-Bfc01GBbDPa?dl=0>

