

# Simulating the effects of climate change on the distribution of an invasive plant, using a high resolution, local scale, mechanistic approach: challenges and insights

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## Abstract

The growing economic and ecological damage associated with biological invasions, which will likely be exacerbated by climate change, necessitates improved projections of invasive spread. Generally, potential changes in species distribution are investigated using climate envelope models; however, the reliability of such models has been questioned and they are not suitable for use at local scales. At this scale, mechanistic models are more appropriate. This paper discusses some key requirements for mechanistic models and utilises a newly developed model (PSS[gt]) that incorporates the influence of habitat type and related features (e.g., roads and rivers), as well as demographic processes and propagule dispersal dynamics, to model climate induced changes in the distribution of an invasive plant (*Gunnera tinctoria*) at a local scale. A new methodology is introduced, dynamic baseline benchmarking, which distinguishes climate-induced alterations in species distributions from other potential drivers of change. Using this approach, it was concluded that climate change, based on IPCC and C4i projections, has the potential to increase the spread-rate and intensity of *G. tinctoria* invasions. Increases in the number of individuals were primarily due to intensification of invasion in areas already invaded or in areas projected to be invaded in the dynamic baseline scenario. Temperature had the largest influence on changes in plant distributions. Water availability also had a large influence and introduced the most uncertainty in the projections. Additionally, due to the difficulties of parameterising models such as this, the process has been streamlined by utilising methods for estimating unknown variables and selecting only essential parameters.

**Keywords:** climate change, *Gunnera tinctoria*, individual-based mechanistic model, model parameterisation, plant invasions, propagule dispersal

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## Introduction

Biological invasions and climate change are considered two of the biggest threats to ecosystem functioning and biodiversity (Vitousek, 1994; Schröter *et al.*, 2005) but, despite the close association between them (Capinha *et al.*, 2012), they have generally been studied in isolation (Thuiller *et al.*, 2007; Walther *et al.*, 2009) until recently (Bourdôt *et al.*, 2012; Kriticos, 2012). Ecologists and conservation managers are increasingly relying on biological models for estimating how global change will affect biodiversity and ecosystem functioning (Loiselle *et al.*, 2003; Sanchez-Cordero *et al.*, 2005; Allouche *et al.*, 2006), with large scale, low resolution, climate envelope based modelling (CEM) approaches being the most widely used (Kearney & Porter, 2009; Huntely *et al.*, 2010; Merow *et al.*, 2011). Despite concerns about their reliability (Beale *et al.*, 2008; Duncan *et al.*, 2009), CEMs continue

to be used for estimating how species distribution might vary over the next century and have been used to highlight the potential for climate change and biological invasions to impact negatively on ecosystems (Sala *et al.*, 2000). However, the continued development and utilisation of these large-scale approaches, while useful for further highlighting broad trends, has limited practical value for those involved in management 'on the ground', since CEMs have a limited ability to accurately project species distributions at local or regional scales (Pearson & Dawson, 2003; Huntely *et al.*, 2010). Consequently, there is a need to develop models and methodologies for providing local scale, high-resolution information, focusing on specific areas where introduced species are known to have negative ecological and economic impacts and where they have the potential to cause further impacts in the future. This paper (i) discusses some key requirements for such models and utilises a newly developed model that incorporates these requirements to simulate climate induced changes in the distribution of an invasive plant (*Gunnera tinctoria*) at a local scale, (ii)

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introduces a new methodology for distinguishing specifically climate-induced alterations in species distributions from other potential drivers of change, and (iii) provides insights into streamlining the parameterisation of mechanistic models (MM).

The development of high-resolution local scale models for projecting the interacting effects of climate change and biological invasions presents many challenges. CEMs are of greatest use at a continental scale, where climate has the primary influence on species distribution (Gaston, 2003; Hansen *et al.*, 2006; Sommer *et al.*, 2010). However, as scale is reduced, other factors become increasingly important, such as habitat type and features, demographic processes, and propagule dispersal dynamics (Nielsen *et al.*, 2008; Huntely *et al.*, 2010). There is a growing consensus that at smaller scales mechanistic modelling approaches are more suitable, particularly when coupled with demographic sub-models and process-based propagule dispersal kernels (Helmuth *et al.*, 2005; Brook *et al.*, 2009; Franklin, 2010; Gallien *et al.*, 2010; Merow *et al.*, 2011); as yet, however, they have not been widely adopted. Hybrid approaches can also be used to span multiple scales (Gallien *et al.*, 2010).

At local scales, habitat type has been shown to be one of the critical determinants, if not the most critical determinant, of species distribution, particularly for invasive species (Williamson *et al.*, 2005; Chytrý *et al.*, 2009; Pyšek *et al.*, 2010). Therefore, at local scales, it is essential to incorporate habitat into the model framework and at sufficiently high resolution to account for habitat heterogeneity. The simplest approach is to classify habitats as suitable or unsuitable using a binary mask; however, multiple habitat dimensions should more realistically relate species' responses to different environments (Huntely *et al.*, 2010). The inclusion of habitat type directly addresses how different habitats will affect plant distribution and also indirectly addresses how species interactions affect this distribution, since specific habitat types will generally be associated with characteristic species sets in a given region (Bartish *et al.*, 2010). When multiple habitat dimensions are coupled with a model that can output abundance, as in the current paper, this allows for very detailed responses to be simulated.

Dispersal barriers and corridors are critical determinants of how species distribution can change through space and time (Johansson *et al.*, 1996; Fennell *et al.*, 2012). This is especially true when dealing with invasive species, whose spread is often associated with dispersal corridors (anthropogenic or natural) (Gelbard & Belnap, 2003; Williamson *et al.*, 2005). A dispersal kernel capable of simulating the spread dynamics of a species across heterogeneous habitats is, therefore,

required in order to simulate the dynamic factors that link potential and realised distributions (Franklin, 2010; Gallien *et al.*, 2010; Merow *et al.*, 2011).

In this study, we have used a newly developed model, Plant Spread Simulator [*G. tinctoria*] (PSS[gt]) (Fennell *et al.*, 2012) to make projections at a local scale on the spread potential (including the influence of climate change) of *G. tinctoria*, an invasive herbaceous plant (Gioria & Osborne, 2012). The PSS model is an individual-based, mechanistic, spatiotemporally explicit and discrete, stochastic computer simulation, constructed as a lattice of interconnected cells. Starting from a known point of origin in 1908, PSS has previously been used to reproduce the distribution of *G. tinctoria* in the study area with high accuracy (Fennell *et al.*, 2012). The area of the study is in County Mayo on the west coast of Ireland, where this species is becoming an increasing problem, often forming near mono-specific stands, reducing bio-diversity, altering land use, and negatively impacting on the visual appeal of invaded areas (Gioria & Osborne, 2012). There is also concern that climate change might facilitate its spread in this area (Gioria & Osborne, 2012). As both agriculture and tourism are important economic drivers in this region (Armstrong *et al.*, 2009), assessing the potential impacts of *G. tinctoria* invasions on the ecology of the area is particularly important, so that measures can be taken to reduce any economic or ecological impacts.

Five scenarios are evaluated, four different climate change scenarios (which incorporate changes in CO<sub>2</sub> concentration, temperature, and water availability), and a 'dynamic baseline benchmark' scenario where the drivers and constraints of past spread remain constant. An invasive species would likely continue to spread even if climatic conditions remain constant given that habitat in particular is an important driver; therefore, potential future distribution should be compared to projections that do not incorporate the impacts of climate change, a subtlety that is rarely considered. Accordingly, all climate change scenarios were compared to this dynamic baseline benchmark so that the exclusively climate-change-induced effects could be assessed. Since the model is spatiotemporally explicit, simulating distribution changes dynamically through time, variations away from this dynamic baseline can be examined and quantified at any time point and in any location.

One of the main factors preventing a more widespread adoption of MMs is the difficulty involved in gathering the data required for the parameterisation of, for example, demographic processes, dispersal dynamics, and species climate variable responses (Thuiller *et al.*, 2008). Since MMs are based on measurement of

the physiological responses of species to different biotic and abiotic variables, it is generally the case that for each model parameter (e.g., relationship between seed production and water availability), data is required on the known physiological response of a species to those parameters. In this paper, we address this issue in three ways. Firstly, only parameters directly related to the species demography have been included. Secondly, when calculating climate response curves, only changes in climate variable values within the relatively narrow range projected up to the end of the century were investigated, thus reducing data requirements and eliminating the need for complex response curves. Thirdly, when data was not available for a particular parameter, proxies were used, or the values were determined by parameter fitting.

## Materials and methods

### *Study species and location*

*Gunnera tinctoria* is a large herbaceous, polycarpic, perennial plant species, which can reach 2 m in height with leaves up to 2 m in diameter. It is a native of Chile and has become invasive in a number of countries worldwide including Ireland, the United Kingdom, the Azores, the USA and New Zealand. This species is considered to be one of the most invasive in Ireland (Armstrong *et al.*, 2009; Gioria & Osborne, 2012), and regulations have recently been put in place making it an offence to facilitate its spread. Its growing season is from March through November (Campbell & Osborne, 1993). Pollen is produced in large quantities in April (Armstrong, 2008). Leaf numbers increase until the end of April, and biomass increases from the start of the growing season through June (Campbell, 1995). Seed maturation and dispersal is generally in early autumn (Armstrong, 2008). It can spread vegetatively (via underground rhizomes and plant fragmentation) or by seeds (Armstrong *et al.*, 2009; Gioria & Osborne, 2009a,b). Long distance dispersal is through seed and rhizome fragments. It is believed that these are dispersed in a variety of ways, such as on the hooves of grazing animals, along roads on the tyres of farm machinery, or in transported topsoil (Gioria, 2007; Armstrong *et al.*, 2009). *Gunnera tinctoria* also spreads along the banks of rivers, streams and ditches, and propagules are believed to spread by water flow (Gioria, 2007; Armstrong *et al.*, 2009). A definitive account of the biology and ecology of *G. tinctoria* can be found in Gioria & Osborne (2012).

Globally, one of the areas where *G. tinctoria* has had the greatest ecological impact is on the west coast of Ireland (Fig. 1a), where it has been growing in the wild since at least 1908 (Preston *et al.*, 2002). *Gunnera tinctoria* has now colonized many areas on Achill Island, has formed large populations on the south-east of Clare Island and has spread along roads and waterways on the south of the island. It is well established in the northern and western parts of the Corraun peninsula and forms smaller populations on the mainland. *Gunnera tinctoria* is mostly found in former agricultural land, in areas associated

with human activity, and along neighbouring roads and rivers (Fig. 1b, c, d).

### *Model and validation*

The PSS model (Fennell *et al.*, 2012) simulates the influence of habitat type, habitat features (e.g., roads and rivers), propagule pressure, varying climatic conditions, age, and dispersal dynamics, on plant spread, establishment and survival.

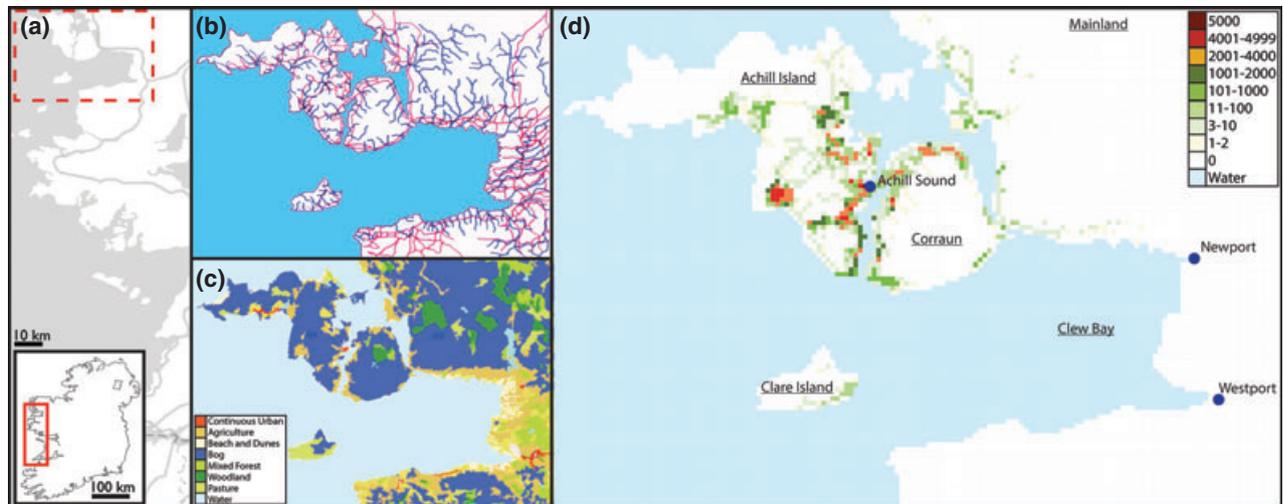
A mechanistic approach, which allows for the non-linear movement of propagules through heterogeneous environments (simulating the influence of dispersal barriers and corridors), is used to simulate dispersal from one cell to another. The method functions by assigning spread probabilities to each of eight nodes that connect all adjacent cells to each other. Cells connected by dispersal corridors are assigned higher spread probabilities. When a given propagule is selected to spread (based on a stochastic selection process), a number of cells within a maximum spread distance are selected randomly and each is assigned a spread potential value. These spread potential values are determined by calculating the product of all the cell connection probabilities linking one cell to another back to the cell of origin. For all potential destination cells, the path that results in the highest product of cell connection probabilities, out of all possible paths that do not turn back on themselves back to the cell of origin, is the potential path that the propagule will take through the cell lattice. From these potential paths, the path *taken* is determined using the tournament selection algorithm, as described in Fennell *et al.* (2012). The tournament selection algorithm preferentially selects higher probability destination cells, but does allow for occasional long distance low probability dispersal events.

Multiple climate variables can be included and the value of these climatic parameters can change dynamically from one time-step to another. Changes in climate variables occur uniformly across the entire cell lattice, as climate change data was not available at a high enough resolution to incorporate micro-climatic variation within this relatively small geographic area. The influence of these variables on the probability of asexual and sexual propagation, survivability, and establishment, is expressed as linear equations.

PSS was seeded at the probable point of origin in 1908 (based on historical records) and accurately reproduced the 2008 presence/absence of *G. tinctoria* in the study area (sensitivity = 0.733, specificity = 0.900, Cohen's kappa = 0.710, true skill statistic = 0.739, AUC = 0.891) (Fennell *et al.*, 2012). Kappa values of 0.7–0.75, in particular, are considered to indicate high accuracy (Jeschke & Strayer, 2008). Changes in spread rate through time also closely matched empirical records (sMAPE = 11.69). Abundances were also simulated accurately, based on validations using the Difference Level Test (DLT) (Fennell *et al.*, 2012).

### *Model parameterisation*

*Basic parameterisation.* The non-climate aspects of PSS[gt] were parameterised as described in Fennell *et al.* (2012), with

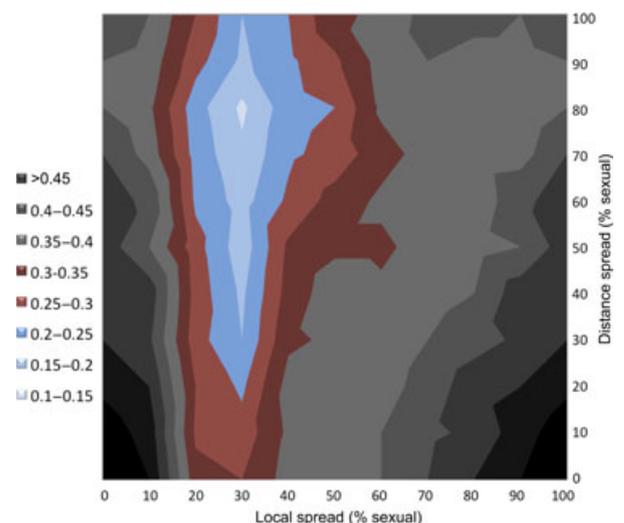


**Fig. 1** Composite map showing: (a) study location on the west coast of Ireland with the area used for the simulations highlighted by rectangular boxes in red; (b) locations of roads (red) and waterways (blue); (c) habitat types; (d) modelled distribution of *Gunnera tinctoria*, with the number of individuals at each location, based on a colour key located in the top right hand corner (maximum carrying capacity = 5000 individuals per cell). The side of each grid cell is equivalent to 0.3 km.

the exception that local (within a cell) and distance (between cells) spread were both divided into two sub-categories, sexual and asexual spread. These parameters were sub-divided to allow more refined projections of the effects of climate, since data was available, in some cases, for the effect of climate parameters on both seed (sexual) and rhizome (asexual) production. A novel approach, that compares modelled population genetic distance data at different sexual : asexual ratios to an empirically determined analogue (for actual data see Fennell *et al.* (2010)), was used to estimate these variables. This was possible since individuals in the PSS model can be genetically explicit, with new individuals either being created asexually, producing identical genotypes, or by sexual crossing, producing new genotypes (Fennell *et al.*, 2012). PSS was seeded at the probable site of initial invasion with eleven different individuals that possessed the genetic identities (AFLP-based allelic data) of individuals from the putative founding population of *G. tinctoria* in this area (Fennell *et al.*, 2010). The ratio of sexual to asexual dispersal used in this study was fitted by sequentially varying these parameters until the average pairwise genetic distance ( $\phi$ iPTP) between populations within the simulation matched, as close as possible, those obtained empirically ( $\phi$ iPTP = 0.61 (Fennell *et al.*, 2010)). A population within the simulation was defined as all individuals in a particular cell. Simulations were run 10 times for each combination. Eleven individuals were randomly selected ten times from each run.  $\phi$ iPTP values were determined as in Fennell *et al.* (2010) for the 100 samples for each combination and average values were calculated. No set of simulation runs resulted in  $\phi$ iPTP values that were as high as those found empirically. This could be due to the fact that while the PSS model simulates three stochastic evolutionary processes (genetic drift, genetic bottlenecking and gene flow), other processes, such as adaptive evolutionary processes, could also be influencing results. A 30% probability for local sexual spread

and 80% probability for distance sexual spread generated genetic distances closest to those observed in the field ( $\phi$ iPTP [empirical] –  $\phi$ iPTP [simulated] = 0.14) (Fig. 2).

The general parameterisation included the probabilities of asexual and sexual local and distance spread, cell connection values, cell carrying capacity, establishment probabilities influenced by habitat type (agricultural land, bog land, etc.) and habitat features (roads, rivers, human habitation, etc.), age of sexual maturity, and age-dependent survivorship probabilities (see Fennell *et al.* (2012) for the specific values). The



**Fig. 2** Illustration showing variation away from the average pairwise genetic distance ( $\phi$ iPTP) for each percentage sexual distance spread and percentage sexual local spread combination. Lower values indicate greater similarity to empirical results.

same 47.4 × 32.4 km area as in Fennell *et al.* (2012) was used in the current study. This area was divided into 17 064 square-sided cells, where each side was equivalent to 0.3 km.

**Climate change scenarios.** Four different sets of climate change simulations were run (Table 1). Two different future carbon emission scenarios (CES1 and CES2) were simulated, based on worst and best case projections for carbon emissions, as outlined in the Special Report on Emission Scenarios (SRES) produced by the Intergovernmental Panel on Climate Change (IPCC) (Nakicenovic & Swart, 2000). The CES1 scenario represents a world of rapid economic growth, with global population peaking in mid-century but with cleaner technology developed. This scenario projects a rapid increase in atmospheric CO<sub>2</sub> concentrations, from current values (385 ppm) up to 915 ppm by the end of the century. The CES2 scenario represents the same population growth as CES1 but with greater use of clean energy. This scenario projects a gradual increase in atmospheric CO<sub>2</sub> concentrations, which start to level off in ca. 2060, peaking at 520 ppm in ca. 2080, before dropping to 515 ppm by the end of the century.

Both carbon emission scenarios were coupled with the average temperature increase projected by five different General Circulation Models (GCM (HadCM3, ECHam4, PCM, CGCM2, and CSIRO2)) (Woodward *et al.*, 2010). The average increase in temperature for Ireland by the end of the century, as projected by the 5 GCMs, was 3 °C for CES1 and 1.8 °C for CES2.

Each of the CO<sub>2</sub> concentration and temperature scenarios were sequentially combined with two different precipitation change scenarios (PCS1 and PCS2), which were based on projections made by the Community Climate Change Consortium for Ireland (C4i) (Dunne *et al.*, 2008). PCS1, based on the average projected change in precipitation for autumn and winter months in the study area, incorporates a 20% increase in precipitation by the end of the century. PCS2, based on the average projected change in precipitation for the spring and summer months, incorporates a 14% decrease in precipitation by the end of the century. These two precipitation scenarios were selected, since it is not clear whether autumn/winter or spring/summer rainfall has the greatest influence on the growth and spread of *G. tinctoria* (B. Osborne, unpublished data).

CES1 was coupled with PCS1 (Scenario A) and PCS2 (Scenario B), and CES2 was coupled with PCS1 (Scenario C) and PCS2 (Scenario D) (Table 1).

**Table 1** Current (baseline) climatic conditions in the study area and end of the century values for the different climate variables used in each scenario (extent of changes from current values are shown in brackets)

Scenario	CO <sub>2</sub> (PPM)	Soil Temp (°C)	Water (mm m <sup>-1</sup> )
Baseline	385	16.0	140
A and A*	915 (+137%)	19.0 (+3 °C)	168 (+20%)
B and B*	915 (+137%)	19.0 (+3 °C)	120 (-14%)
C and C*	515 (+38%)	17.8 (+1.8 °C)	168 (+20%)
D and D*	515 (+38%)	17.8 (+1.8 °C)	120 (-14%)

**Climate response parameterisation.** The effects of changes in various climatic variables were incorporated into simulations based on research carried out over the past three decades (Osborne, 1989; Campbell & Osborne, 1993; Hickey, 2002; Gioria, 2007; Hennessy, 2009; Gioria & Osborne, 2012; B. Osborne, unpublished data). Based on these studies, with some exceptions (outlined below), data was available for the effects of changes in CO<sub>2</sub> concentration, temperature, and water availability, on seed production, rhizome production, seedling germination, and survivorship. Specifically, observed climate-affected changes in seed production, rhizome production, seedling germination and survivorship were incorporated in the simulation parameters as equivalent changes in, respectively, the potential for sexual reproduction, asexual reproduction, establishment (probability that a propagule will establish after reaching a location) and survivorship (probability of surviving from one growing season to the next). When no data was available for a parameter, the required values were estimated from the literature or by the use of proxies. See Table 2 for a list of climate response parameters and their respective sources, i.e., empirical data (E), the literature (L), or proxies (P).

No data was available for the effect that CO<sub>2</sub> concentration changes have on establishment or seed production. While there is evidence that seed production can be increased at elevated CO<sub>2</sub> (Hennessy, 2009; Way *et al.*, 2010), germination rates do not appear to be significantly affected (St. Omar & Horvath, 1983; Way *et al.*, 2010). Data was available for the effect of CO<sub>2</sub> on total biomass production (Hennessy, 2009); this was used as a proxy for seed production since there is often a close link between the two (Samson & Werk, 1986; Schmid *et al.*, 1995). Data was also not available on the effects of changes in temperature on seed production, rhizome production, or survivorship. However, data was available on the effect of changes in temperature on *G. tinctoria*'s photosynthetic performance. As photosynthetic performance and biomass production are linked (Luo, 1979; Oren *et al.*, 1986), and since a strong relationship between biomass production and seed and rhizome production has been observed for *G. tinctoria* (Campbell & Osborne, 1993), temperature induced changes in photosynthetic performance were used as a proxy for changes in seed and rhizome production. Since increases in photosynthetic performance have also been linked to increased plant survivorship (Arntz *et al.*, 2000), temperature induced changes in photosynthetic performance were used as a proxy for changes in survivorship.

To allow for potential variability in the effect of climate change on the simulation parameters, the empirically determined responses of *G. tinctoria* to climate variables were considered to be the maximum possible effect on plant performance; simulations were also run with the effects of the different climate variables reduced by 50%. This also helps buffer potential errors in the assumptions outlined above. In total, therefore, eight different sets of climate change simulations were run, the four scenarios mentioned above (scenarios A, B, C, and D), and those four scenarios with the effects of climate change reduced by 50% (scenarios A\*, B\*, C\*, and D\*) (Table 1). We believe that this should provide a good

**Table 2** Relationships between percentage changes in climatic variables ( $x$ ) and percentage changes in the probabilities of sexual reproduction, asexual reproduction, establishment and survivorship ( $y$ ), are expressed as linear equations. Only the relationships used in scenarios A, B, C, and D are given.  $R^2$  and  $p$  values could not be calculated for all parameters since the original raw data was not available for analysis (\*). Source column: E = empirical data and L = literature; P1 = CO<sub>2</sub> effect on total biomass used as proxy and P2 = temperature effect on photosynthesis used as a proxy. See Methods section for further details on proxy calculation

Climate variable	Parameter	Linear equation	$R^2$	$P$	Source
Water availability	Asexual propagation	$y = 0.0305x - 0.4381$	0.955	0.001	E <sup>†</sup>
	Sexual propagation	$y = 0.0014x + 0.0857$	0.626	0.062	E <sup>†</sup>
	Establishment	$y = 0.8333x - 66.667$	*	–	E <sup>‡</sup>
	Survivorship	$y = 0.4762x - 38.095$	*	–	E <sup>§</sup>
CO <sub>2</sub>	Asexual propagation	$y = 0.0121x + 0.7576$	*	–	E <sup>¶</sup>
	Sexual propagation	$y = 0.0212x + 26.576$	0.894	0.001	P1 <sup>¶</sup>
	Establishment	No effect			L <sup>**</sup> ,††
	Survivorship	No effect			E <sup>¶</sup>
Temperature	Asexual propagation	$y = 0.7x + 8.5$	0.909	0.001	P2 <sup>‡‡</sup>
	Sexual propagation	$y = 0.7x + 8.5$	0.909	0.001	P2 <sup>‡‡</sup>
	Establishment	$y = 20x - 300$	*	–	E <sup>‡</sup>
	Survivorship	$y = 0.7x + 8.5$	0.909	0.001	P2 <sup>‡‡</sup>

†Campbell & Osborne (1993).

‡Gioria (2007).

§Osborne (unpublished).

¶Hennessy (2009).

\*\*St. Omar & Horvath (1983).

††Way *et al.* (2010).

‡‡Osborne (1989).

spectrum of the potential climate change related effects on the spread of *G. tinctoria* up to the end of the century.

Relationships between percentage changes in climatic variables ( $x$ ) and percentage changes in the response variables ( $y$ ), are expressed as linear equations (Table 2). Projected changes in climatic variables over the next 100 years are within such a relatively narrow range that the incorporation of non-linear response curves was not necessary. If larger climate changes were being investigated, then the use of non-linear response parameters may be necessary. Whereas changes in temperature, water availability and CO<sub>2</sub> concentration might interact, resulting in positive or negative effects, the exact nature and impact of these interactions has not yet been investigated in detail. As a default, the effects of the three climate variables were considered to be additive.

### Analysis

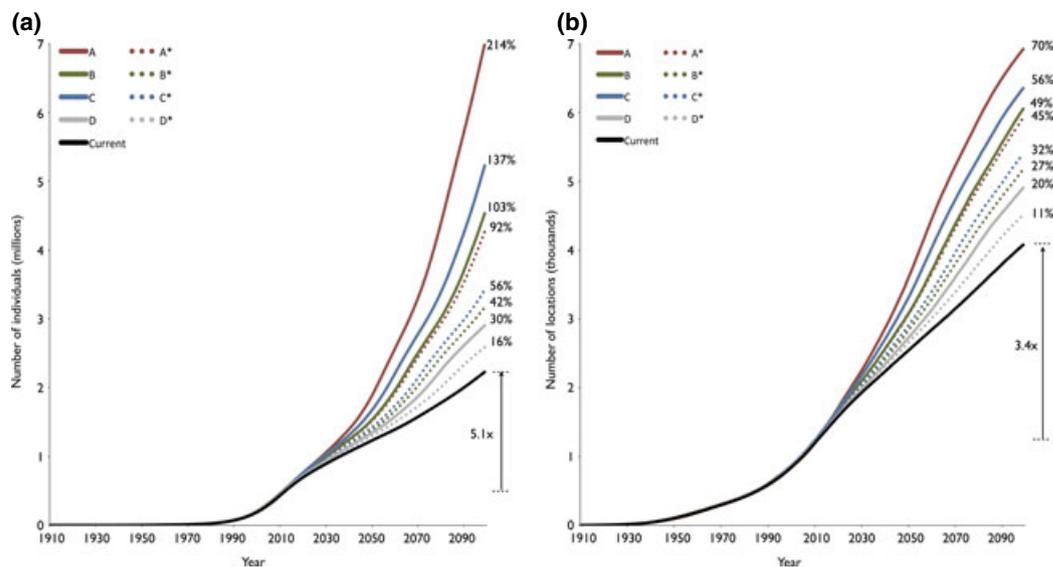
The model uses discrete time-steps, each of which corresponds to 1 year. Simulations were run up to 2100. Due to the stochastic nature of PSS, no two simulation runs would be the same. Consequently, for all parameter sets, simulations were run multiple times ( $n = 100$ ) and averages and relative standard deviations (RSD) were computed. Changes in CO<sub>2</sub> concentration, temperature, and water availability, were applied dynamically in yearly time-steps up to the end of this century. Changes in CO<sub>2</sub> and temperature were applied non-linearly based on IPCC predications. Changes in water availability were applied linearly (based on C4i

predictions), since non-linear curves were not available for the study location.

For all scenarios, the average total number of individuals and total number of cells populated by one or more individuals was calculated at each time-step. Increases in the number of individuals and locations invaded are shown in Fig. 3a and b.

The average number of individuals in each cell, for each climate change scenario, was compared to the average number of individuals in each cell in the scenario where current climate conditions remained constant (the dynamic baseline). The dynamic baseline scenario is the same as that modelled in Fennell *et al.* (2012) up to 2031 and has been extended beyond that to 2100 in this paper. Distribution maps of the baseline (Fig. 4a), and the scenarios that resulted in the largest (scenario A) and smallest (scenario D\*) increase above the baseline (Fig. 5a and b) are presented. Additional distribution maps are presented for scenarios A and D\*, showing the increase in number of individuals in each cell above the baseline (Fig. 5c and d), and showing the location of cells invaded above those projected in the baseline (Fig. 5e and f). To aid in the description of distributions, Table 3 defines population size categories.

In order to gauge the impact of each climate variable on the spread of *G. tinctoria* independently, simulations were run where all but one of the climate variables were kept at current levels. Each of the CO<sub>2</sub> concentration, water availability and temperature scenarios were activated sequentially and the results were compared to simulations where



**Fig. 3** Changes in the number of individuals (a) and the number of locations inhabited (b) over time, for all scenarios. The fold increase above 2008 is indicated by the vertical bars on the right hand side of the two panels, and the percentage increase above the dynamic baseline level for each climate change scenario is given by the numbers adjacent to each individual simulation denoted by the different lines.

current conditions remained constant until the end of the century (Fig. 6).

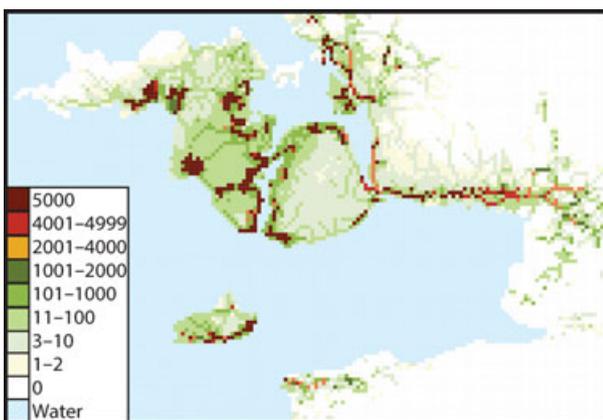
## Results

### *Total number of individuals and locations inhabited*

When climate variables were left constant at current values the projected number of individuals increased from current levels by a factor of ca. 5.1 (Fig. 3a) and the number of invaded cells increased by a factor of ca.

3.4 (Fig. 3b). This comprised 2 228 527 (RSD  $\pm$  4.8%) individuals inhabiting 4078 (RSD  $\pm$  3.7%) cells. These values represent the dynamic baseline with which the climate change scenarios were compared.

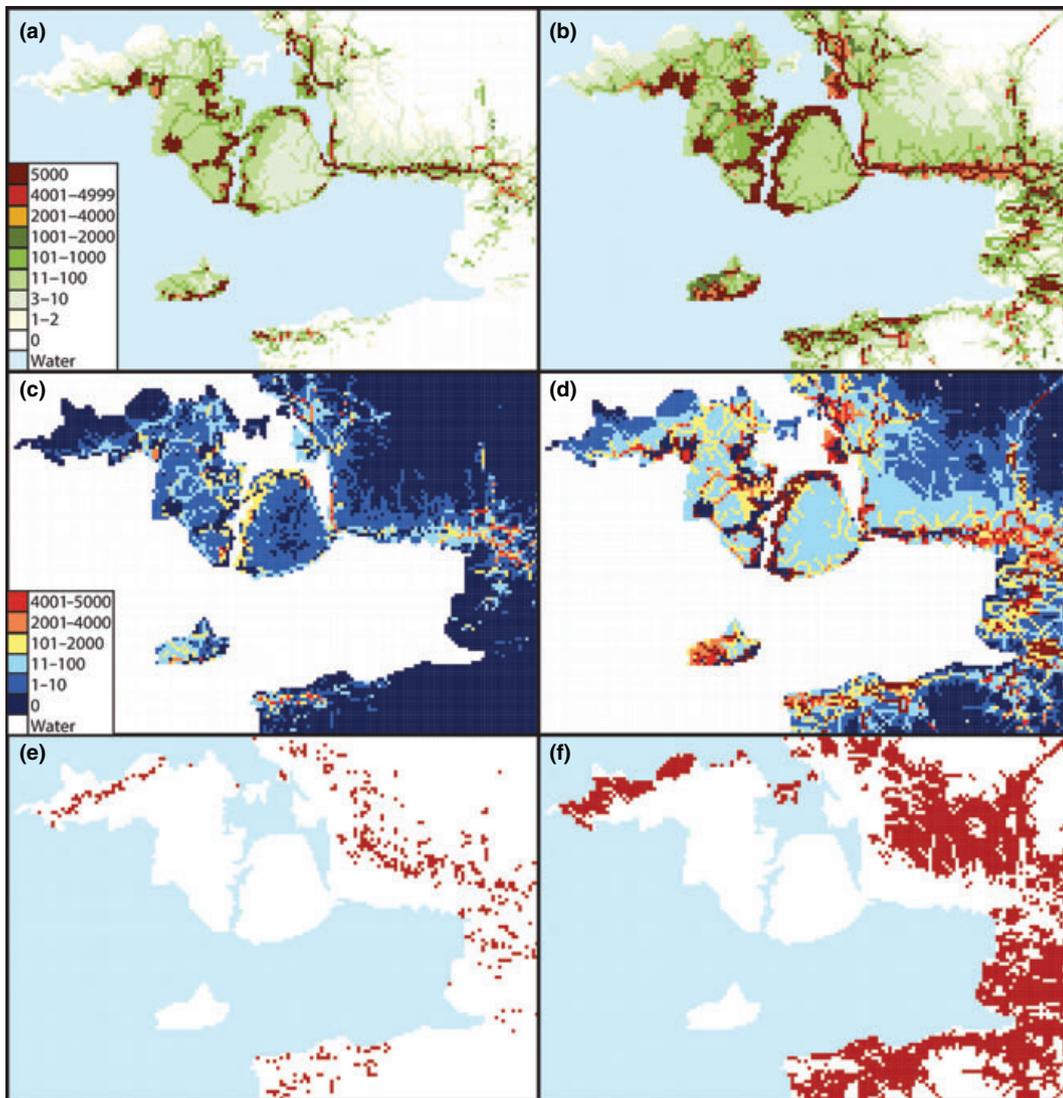
For all climate change scenarios, PSS projected an increase in the spread of *G. tinctoria* above the baseline, ranging from an increase of ca. 16% (2 588 329 (RSD = 2.9%) total individuals) and ca. 10% (4520 (RSD = 2.2%) total cells inhabited) in scenario D\*, to an increase of ca. 214% (6 995 234 (RSD  $\pm$  3.0%) total individuals) and ca. 70% (6922 (RSD  $\pm$  1.2%) cell total) in scenario A (Fig. 3). The average increase above the baseline was 86% (4 139 118 total individuals), and 39% (5658 total cells inhabited). A slight decrease in spread rates for all scenarios was observed from ca. 2010 to ca. 2040, at which point spread rates started to increase again.



**Fig. 4** Simulated distributions of *Gunnera tinctoria* in the study area by 2100 (dynamic baseline scenario); maximum carrying capacity = 5000 individuals per cell. The side of each grid cell is equivalent to 0.3 km.

### *Distribution*

When climate variables were left constant at current values until the end of the century (the dynamic baseline), the distribution of *G. tinctoria* was still projected to increase significantly (Fig. 4a) above the current distribution (Fig. 1d). On Achill Island, small to large populations were predicted in most agricultural land and areas associated with human activity. Scattered individuals or scattered clusters were predicted on most of the rest of the island, with the exception of the northwest. Small populations were predicted to form along some



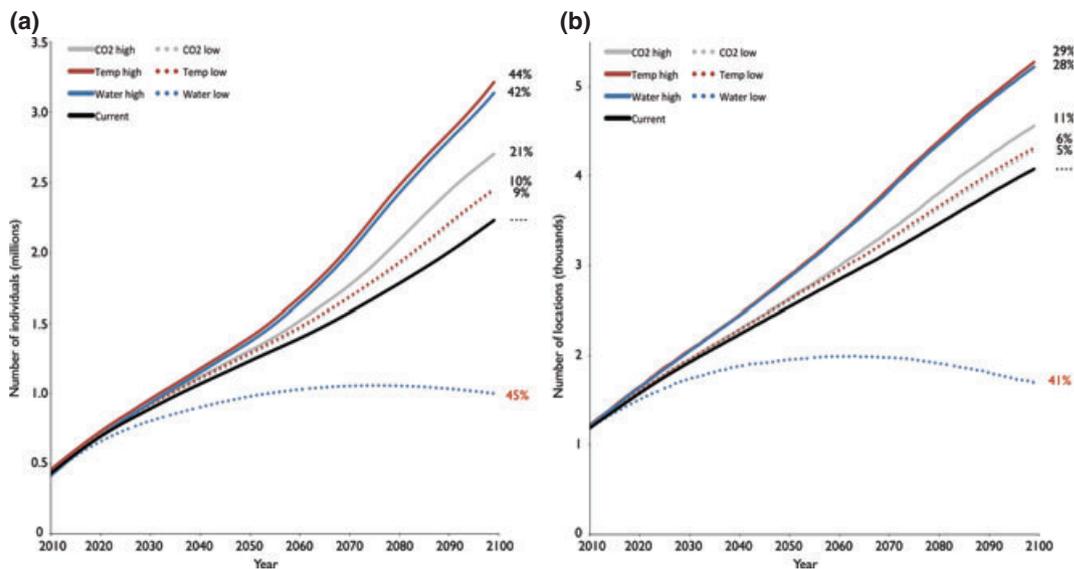
**Fig. 5** Simulated distributions of *Gunnera tinctoria* in the study area by 2100. Key in panel a, also refers to panel b (maximum carrying capacity = 5000 individuals per cell). The side of each grid cell is equivalent to 0.3 km. (a) Scenario D\*, number of individuals. (b) Scenario A, number of individuals. (c) Scenario D\*, increase in number of individuals compared to the dynamic baseline. (d) Scenario A, increase in number of individuals compared to the dynamic baseline. (e) Scenario D\*, location of cells invaded compared to the dynamic baseline (red shading). (f) Scenario A, location of cells invaded compared to the dynamic baseline (red shading).

inland roads and waterways. The populations on the north and west of the Corraun peninsula were predicted to increase in size from predominantly scattered clusters to populations ranging in size from small to large. The rest of the peninsula was predicted to have scattered individuals with scattered clusters forming along some roads and waterways. The invasion on Clare Island was predicted to increase substantially, with large populations forming in the south and south-east, with the rest of the island containing mostly scattered individuals and clusters. On the mainland, large populations were predicted in the northwest and small to large populations were predicted on the northern

coast of Clew Bay. Small to medium sized populations were predicted to form in the southwest and around Newport. Most of the more substantial invasions on the

**Table 3** Definition of cell population size categories used in distribution descriptions [based on Armstrong *et al.* (2009)]

Number of individuals	Population category
1–10	Scattered individuals
11–100	Scattered clusters
101–2000	Small populations
2001–4000	Medium populations
4000+	Large populations



**Fig. 6** Changes in the number of individuals (a) and number of locations inhabited (b) over time, for each climate change component. Percentage changes away from the dynamic baseline level for each climate change scenario component are given by the numbers on the right hand sides of the panels. The dotted grey line, which represents the low CO<sub>2</sub> scenario, is obscured in places by the dotted red line that refers to the low temperature scenario.

mainland were in agricultural and human-inhabited areas, with only scattered individuals and clusters in most other areas. This distribution (Fig. 4a) was considered the baseline with which the climate change scenarios were compared.

Of the climate change scenarios used, Scenario D\* (Fig. 5a, c, e) resulted in a distribution closest to the baseline and Scenario A (Fig. 5b, d, f) resulted in the largest increase in the distribution of *G. tinctoria* above the baseline. Increases in the number of individuals were primarily due to intensification of invasion at sites already invaded in the baseline scenario; on average (all scenarios combined) ca. 94% of the increase in individuals above the baseline was due to intensification of invasion in these areas. The remaining ca. 6% increase in individuals was predicted in areas invaded beyond the baseline, which made up 28% of the total number of invaded cells.

#### Relative importance of different climate variables

The six climate scenario components (CO<sub>2</sub>: 915 ppm and 515 ppm; temperature: +3 °C and +1.8 °C; precipitation: +20% and -14%) were examined independently. The climate variable component that resulted in the largest increase in spread rates was the +3 °C scenario component (Fig. 5), which resulted in an increase in both the number of individuals and the number of invaded locations, above the baseline, of ca. 44% (SD = 3.9) and ca. 29% (SD = 2.4) respectively. The +20% precipitation scenario component resulted in a

similar outcome, with an increase in the number of individuals and invaded locations, above the baseline, of ca. 42% (SD = 3.0) and ca. 28% (SD = 2.4) respectively. Elevated CO<sub>2</sub> concentration had the smallest influence on spread rates, with the 915 ppm climate scenario component (an increase of 137% above current levels) resulting in only a ca. 21% (SD = 3.2) and ca. 12% (SD = 2.3) increase in individuals and invaded locations, respectively. The 515 ppm climate scenario components resulted in a ca. 9% (SD = 4.8) and ca. 5% (SD = 4.0) increase in individuals and invaded locations, respectively. The +1.8 °C climate scenario components resulted in a ca. 10% (SD = 4.0) and ca. 6% (SD = 3.5) increase in individuals and invaded locations, respectively. The -14% precipitation climate scenario component resulted in a decrease in the spread rate and a decrease in the number of populations by the end of the century, returning values of ca. 45% (SD = 1.3) and ca. 42% (SD = 1.2) of the baseline, for the numbers of individuals and invaded locations, respectively. For simplicity, only the maximum effects of each climate variable (not the halved values) are reported (Fig. 6), since the 50% responses provided no additional insight into the relative importance of each variable.

#### Discussion

If the drivers of, and constraints on, *G. tinctoria*'s past spread in the study area remain unchanged, its distribution is projected to increase substantially by

the end of the century. If left unmanaged, regardless of any climatic influences, *G. tinctoria* invasions still have the potential to cause negative ecological and economic impacts in this area. When climate change is factored in, *G. tinctoria* invasions are projected to be even more severe, potentially becoming a major issue in most agricultural areas, encroaching on habitats of local or regional significance, such as peatlands and waterways, as well as negatively impacting on the aesthetic qualities of large proportions of the landscape.

Most climate change impact studies compare future projections against a baseline, determined by current or recent values, and express the climate impacts as variations away from that static baseline (Bullock *et al.*, 2012). However, since an invasive species is likely to continue to spread even if climatic conditions remain constant, as indicated in this study, a dynamic approach should be used when calculating the baseline benchmark. By comparing future distributions that incorporate climate change to future distributions where the drivers and constraints of past spread remain constant, the exclusively climate change induced effects can be determined dynamically through time. The use of a process-based approach to simulating propagule dispersal, such as that used in PSS, makes this possible; correlative modelling approaches cannot address this subtlety. We are unaware of other studies that have used this dynamic baseline benchmarking approach to study invasive plant spread.

Projections made using correlative approaches are mostly based on shifting climate patterns and the effects that these shifts will have on species distributions (Heikkinen *et al.*, 2006; Hijmans & Graham, 2006). Consequently, they are only indicative of the *potential* new range of the species (Franklin, 2010; Gallien *et al.*, 2010). Propagules must travel through space and time in order for these potential distributions to be *realised*. This is highlighted in these results, as several areas (e.g., the very northeast of the study area), which are suitable for *G. tinctoria*, are not invaded in most scenarios due to the physical habitat barriers that constrain *G. tinctoria* spread. There are many other models that incorporate process-based propagule dispersal kernels, PRUNUS (Sebert-Cuvillier *et al.*, 2010) and WALD (Katul *et al.*, 2005) for example, and studies have been carried out on the potential effects of climate change on propagule distribution using mechanistic approaches (Bullock *et al.*, 2012; Renton *et al.*, 2012). However, we are not aware of studies that have simulated dispersal corridor effects over reasonably large (regional) scales by using a dispersal kernel that allows directed, non-linear movement of propagules through heterogeneous environments.

Based on this study, climate change has the potential to greatly facilitate the spread of *G. tinctoria* in this area by the end of the century. Projected increases above the dynamic baseline ranged from ca. 16% to ca. 214% for numbers of individuals and ca. 10% to ca. 70% for numbers of locations invaded, with an average increase of ca. 86% for numbers of individuals and ca. 39% for numbers of locations invaded. However, increases in the number of predicted individuals (ca. 94% on average) occurred primarily in areas that were already invaded in the baseline scenario. This indicates that, while climate change does have the potential to greatly increase the total area of *G. tinctoria* invasions, most climate change induced spread will be due to intensification of invasion in areas that would be invaded in any case.

The findings of this study are broadly in line with overall projections for Irish vegetation. Woodward *et al.* (2010), using general circulation models, indicated that climate change could increase the net primary productivity (NPP) of Irish vegetation by between ca. 15% and ca. 85%, and net biome production (NBP) by as much as ca. 200%, by the end of the century. Their study concluded that invasive plant species may be the primary driving force for this increase, due partly to expected increases in the ranges of invasive plant species over the next century. These results also support the claim that climate change might increase the invasive spread of *G. tinctoria* on the west coast of Ireland and facilitate its spread further inland (Gioria & Osborne, 2012).

The majority of research carried out to date on the effect of climate change on biological invasions has focused on warming effects (Walther *et al.*, 2009) and has used correlative modelling approaches (Guisan & Zimmermann, 2000). In this study, we examined the effects of CO<sub>2</sub>, temperature, and water availability, using a mechanistic approach. Whereas changes in temperature were seen to have the largest potential to increase spread rates, the potential for changes in water availability to increase spread rates was almost as large. Furthermore, since in this area climate change is projected to cause increases in precipitation during autumn/winter and decreases in precipitation during spring/summer, water availability introduced the most uncertainty into the projections. This uncertainty arose because it is not clear whether spring/summer or autumn/winter rainfall has the greater influence on the spread of *G. tinctoria*; this may also be true for other invasive plant species. Like many invasive plant species, *G. tinctoria* completes most of its growth cycle early in the growing season (Campbell, 1995; Osborne & Sprent, 2002; Gioria & Osborne, 2012), when water availability, due to winter rainfall and low evaporative

demand, would presumably be high (Osborne *et al.*, 2011). Seed maturation and dispersal is generally in early autumn, falling again into high rainfall periods. Depending on whether spring/summer or autumn/winter rainfall has the greater influence on spread, and considering the strong observed relationship between water availability and *G. tinctoria* biomass production ( $R^2 = 0.0.894$ ,  $P > 0.001$ ; Campbell, 1995), and the strong water-related ecology of this species (Osborne & Sprent, 2002; Gioria & Osborne, 2012), climate change influenced alterations in precipitation patterns could greatly aid, or greatly hinder, future invasive spread. Perhaps rather surprisingly, atmospheric CO<sub>2</sub> concentrations had the smallest influence on *G. tinctoria* spread; however, its influence was by no means insignificant, particularly if the worst-case scenario CO<sub>2</sub> levels are reached by the end of the century. At a minimum, both temperature and water availability should be included in predictive models incorporating climate change scenarios into projections of plant spread. Establishing what seasonal precipitation periods have the greatest influence on invasive plant growth should also be considered a priority. Additionally, determining the interactive and cumulative effects of different climate parameters would allow for more accurate projections when multiple variables are being simultaneously investigated.

If mechanistic modelling approaches are to become more widely used, those parameters most important to population spread dynamics must be identified. Whereas complex mechanistic models that simulate very fine level physiological responses are excellent tools for increasing our understanding of ecophysiological relationships (Lockwood *et al.*, 2007), in the context of projecting population growth and spread at regional scales, such fine details are probably unnecessary. The advantage of a minimalist approach is to reduce both data and processing requirements, consequently allowing for more rapid development of mechanistic models that can be used at larger scales, and also reducing the potential for over fitting (Araújo & Guisan, 2006). It was for this reason that only parameters directly related to demography and spread were included in PSS[gt]. The high accuracy of PSS[gt] (Fennell *et al.*, 2012) in reproducing the distribution of *G. tinctoria* indicates that this approach has potential. This pragmatic approach to MM parameterisation, focusing on population and spread dynamics, has been used previously for simulating plant population responses to climate change (Renton *et al.*, 2012). When parameterising climate responses, there is only a requirement to acquire data within the relatively narrow range of change projected over the next century. The acquisition of data on how different habitat types affect establishment should

be prioritised, as there is an ever-growing body of evidence that indicates that habitat type is critical in determining invasive plant distributions (Williamson *et al.*, 2005; Chytrý *et al.*, 2009; Pyšek *et al.*, 2010; Fennell *et al.*, 2012). Additionally, since specific habitat types will generally be associated with characteristic species sets in a given region (this would not hold true at large scales), using multiple habitat dimensions indirectly addresses how species interactions affect distribution. Species interactions are also believed to play an important role in shaping species spread (Travis *et al.*, 2005; Gallien *et al.*, 2010). The distribution of other species in the study area could also change over time; however, this research does not directly address these potential changes. Land-use will also likely change over time and could have the potential to influence invasive species distributions (Chytrý *et al.*, 2012; Murray *et al.*, 2012); however, no such measure was included in these projections.

To conclude, determining invasive species distribution shifts in response to climate change at large scales is important; however, it is at a regional scale that the impacts of these potential changes will be most significant and have to be managed. Assessing spread potential at smaller scales, and developing tools and techniques to help mitigate potential damage, therefore, is potentially more important. When dealing with smaller scales, habitat type, demographic processes, and propagule dispersal, become increasingly important for determining spread patterns; CEMs cannot incorporate all these factors. Consequently, model development should shift to mechanistic approaches that incorporate both dispersal kernels capable of simulating dispersal barriers and corridors and multiple habitat dimensions. A minimalist approach, which focuses on parameters directly linked to demographic processes, can result in accurate simulations, while simultaneously reducing model development time and allowing increased model scale. At a minimum, temperature and water availability should be incorporated. Furthermore, the dynamic baseline benchmark approach, described above, should provide more realistic projections on the actual effects of climate change on species distribution. Based on the approaches used, it was concluded that climate change has the potential to greatly facilitate the spread of *G. tinctoria* in the study area and immediate action should be taken to mitigate potential economic and ecological damage.

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## References

- Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology*, **43**, 1223–1232.
- Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, **33**, 1677–1688.
- Armstrong C (2008) Development of control measures and distribution mapping of *Gunnera tinctoria* on Achill Island, Co. Mayo, Ireland. Dissertation, University College, Dublin.
- Armstrong C, Osborne BA, Kelly J, Maguire CM (2009) Giant rhubarb (*Gunnera tinctoria*) invasive species action plan. Report prepared for NIEA and NPWS and published by Invasive Species Ireland, Dublin.
- Arntz AM, DeLucia EH, Jordan R (2000) From fluorescence to fitness: variation in photosynthetic rate affects fecundity and survivorship. *Ecology*, **81**, 2567–2576.
- Bartish IV, Hennekens S, Aidoud A, Hennion F, Prinzing A (2010) Species pools along contemporary environmental gradients represent different levels of diversification. *Journal of Biogeography*, **37**, 2317–2331.
- Beale CM, Lennon JJ, Gimona A (2008) Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences of USA*, **105**, 14908–14912.
- Bourdôt GW, Lamoureaux SL, Watt MS, Manning LK, Kriticos DJ (2012) The potential global distribution of the invasive weed *Nassella neesiana* under current and future climates. *Biological Invasions*, **14**, 1545–1556.
- Brook BW, Akçakaya HR, Keith DA, Mace GM, Pearson RG, Araújo MB (2009) Integrating bioclimate with population models to improve forecasts of species extinctions under climate change. *Biology Letters*, **5**, 723–725.
- Bullock JM, White SM, Prudhomme C, Tansey C, Perea R, Hooftman DAP (2012) Modelling spread of British wind-dispersed plants under future wind speeds in a changing climate. *Journal of Ecology*, **100**, 104–115.
- Campbell GJ (1995) Water supply, plant productivity and gas exchange responses of *Gunnera tinctoria* (Molina) Mirbel (Gunneraceae). Dissertation, University College, Dublin.
- Campbell GJ, Osborne BA (1993) Water regime and photosynthetic performance of *Gunnera tinctoria* (Molina) Mirbel. In: *Water Transport in Plants Under Climatic Stress* (eds Borghetti JG, Raschi A), pp. 247–255. Cambridge University Press, Cambridge.
- Capinha C, Anastácio P, Tenedório J (2012) Predicting the impact of climate change on the invasive decapods of the Iberian inland waters: an assessment of reliability. *Biological Invasions*, **14**, 1737–1751.
- Chytrý M, Pyšek P, Wild J, Pino J, Maskell LC, Vilà M (2009) European map of alien plant invasions, based on the quantitative assessment across habitats. *Diversity and Distributions*, **15**, 98–107.
- Chytrý M, Wild J, Pyšek P *et al.* (2012) Projecting trends in plant invasions in Europe under different scenarios of future land-use change. *Global Ecology and Biogeography*, **21**, 75–87.
- Duncan RP, Cassey P, Blackburn TM (2009) Do climate envelope models transfer? A manipulative test using dung beetle introductions *Proceedings of the Royal Society B*, **267**, 1449–1457.
- Dunne S, Hanafin J, Lynch P *et al.* (2008) Ireland in a warmer world: scientific predictions of the Irish climate in the twenty-first century. Report published by Community Climate Change Consortium for Ireland, Dublin.
- Fennell M, Gallagher T, Osborne BA (2010) Patterns of genetic variation in invasive populations of *Gunnera tinctoria*: an analysis at three spatial scales. *Biological Invasions*, **12**, 3973–3987.
- Fennell M, Murphy J, Armstrong C, Gallagher T, Osborne B (2012) Plant spread simulator: a model for simulating large-scale directed dispersal processes across heterogeneous environments. *Ecological Modelling*, **230**, 1–10.
- Franklin J (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321–330.
- Gallien L, Münkemüller T, Albert CH, Boulangeat I, Thuiller W (2010) Predicting potential distributions of invasive species: where to go from here? *Diversity and Distributions*, **16**, 331–342.
- Gaston KJ (2003) *The Structure and Dynamics of Geographic Ranges*. Oxford University Press, Oxford.
- Gelbard GL, Belnap J (2003) Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology*, **17**, 420–432.
- Gioria M (2007) The impact of three invasive species on soil seed bank communities. Dissertation, University College, Dublin.
- Gioria M, Osborne BA (2009a) The impact of *Gunnera tinctoria* (Molina) Mirbel invasions on soil seed bank communities. *Journal of Plant Ecology*, **2**, 153–167.
- Gioria M, Osborne BA (2009b) Similarities in the impact of three large invasive plant species on soil seed bank communities. *Biological Invasions*, **12**, 1671–1683.
- Gioria M, Osborne BA (2012) Biological Flora of the British Isles: *Gunnera tinctoria*. *Journal of Ecology*. in press.
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Hansen J, Sato M, Ruedy R, Lo K, Lea DW, Medina-Elizade M (2006) Global temperature change. *PNAS*, **103**, 14288–14293.
- Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) Methods and uncertainties in bioclimatic envelope modeling under climate change. *Progress in Physical Geography*, **30**, 751–777.
- Helmuth B, Kingsolver JG, Carrington E (2005) Biophysics, physiological ecology, and climate change: does mechanism matter? *Annual Review of Physiology*, **67**, 177–201.
- Hennessy J (2009) A comparative assessment of the effect of elevated carbon dioxide concentrations on *Gunnera tinctoria* and other plant species. Dissertation, University College, Dublin.
- Hickey E (2002) Changes in the community processes associated with the introduced and invasive species *Gunnera tinctoria* (Molina) Mirbel. Dissertation, University College, Dublin.
- Hijmans RJ, Graham CH (2006) The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, **12**, 2272–2281.
- Huntley B, Barnard P, Altweg R *et al.* (2010) Beyond bioclimatic envelopes: dynamic species' range and abundance modelling in the context of climatic change. *Ecography*, **33**, 621–626.
- Jeschke JM, Strayer DL (2008) Usefulness of bioclimatic models for studying climate change and invasive species. *Annals of the New York Academy of Sciences*, **1134**, 1–24.
- Johansson ME, Nilsson C, Nilsson E (1996) Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, **7**, 593–598.
- Katul GG, Porporato A, Nathan R *et al.* (2005) Mechanistic analytical models for long-distance seed dispersal by wind. *The American Naturalist*, **166**, 368–381.
- Kearney M, Porter W (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species ranges. *Ecology Letters*, **12**, 1–17.
- Kriticos DJ (2012) Regional climate-matching to estimate current and future sources of biosecurity threats. *Biological Invasions*, **14**, 1533–1544.
- Lockwood JL, Hoopes M, Marchetti M (2007) *Invasion Ecology*. Blackwell Publishing, Oxford.
- Loiselle BA, Howell CA, Graham CH, Goerck JM, Brooks T, Smith KG, Williams PH (2003) Avoiding pitfalls of using species distribution models in conservation planning. *Conservation Biology*, **17**, 1591–1600.
- Luo C (1979) Specific leaf weight (slw) as related to the yield and its components in rice. *Botanical Bulletin of Academia Sinica*, **20**, 145–157.
- Merow C, LaFleur N, Silander JA, Wilson AM, Rubega M (2011) Developing dynamic mechanistic species distribution models: predicting bird-mediated spread of invasive plants across Northeastern North America. *American Naturalist*, **178**, 30–43.
- Murray JV, Stokes KE, Van Klinken RD (2012) Predicting the potential distribution of a riparian invasive plant: the effects of changing climate, flood regimes and land-use patterns. *Global Change Biology*, **18**, 1738–1753.
- Nakicenovic N, Swart R (eds) (2000) *Special Report on Emissions Scenarios: A Special Report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.
- Nielsen C, Hartvig P, Kollmann J (2008) Predicting the distribution of the invasive alien *Heracleum mantegazzianum* at two different spatial scales. *Diversity and Distributions*, **14**, 307–317.
- Oren R, Schnlze D, Matyssek R, Zimmermann R (1986) Estimating photosynthetic rate and annual carbon gain in conifers from specific leaf weight and leaf biomass. *Oecologia*, **70**, 187–193.
- Osborne BA (1989) Effect of temperature on photosynthetic O<sub>2</sub> exchange and slow fluorescence characteristics of *Gunnera tinctoria* (Molina) Mirbel. *Photosynthetica*, **23**, 77–88.
- Osborne BA, Sprent JI (2002) Ecology of the *Nostoc-Gunnera* symbiosis. In: *Cyanobacteria in Symbiosis* (eds Rai AN, Bergman B, Rassmussen U), pp. 233–252. Kluwer Academic Publishers, Dordrecht.
- Osborne B, Fennell M, Murphy JE, Armstrong C (2011) The riddle of *Gunnera tinctoria* invasions: a particularly Irish enigma. In: *3rd International Symposium of Environmental Weeds and Invasive Plants* (eds Bohren C, Bertossa M, Schonenberger N, Rosinelli M, Conedera M), pp. 1–5. October 2–7. Monte Verita, Ascona, Switzerland. Available from <http://www.wsl.ch/epub/ewrs>. Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research WSL (accessed 17 December 2012)
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography*, **12**, 361–371.

- Preston CD, Pearman DA, Dines TD (eds) (2002) *New atlas of the British and Irish Flora: An Atlas of the Vascular Plants of Britain, Ireland, the Isle of Man and the Channel Islands*. Oxford University Press, Oxford.
- Pyšek P, Chytrý M, Jarošík V (2010) Habitats and land use as determinants of plant invasions in the temperate zone of Europe. In: *Bioinvasions and Globalization: Ecology, Economics, Management, and Policy* (eds Perrings C, Mooney H, Williamson M), pp. 66–79. Oxford University Press, Oxford.
- Renton M, Shackelford N, Standish AJ (2012) Habitat restoration will help some functional plant types persist under climate change in fragmented landscapes. *Global Change Biology*, **18**, 2057–2070.
- Sala OE, Chapin FS, Armesto JJ *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Samson DA, Werk KS (1986) Size-dependent effects in the analysis of reproductive effort in plants. *American Naturalist*, **127**, 667–680.
- Sanchez-Cordero V, Cirelli V, Mungai M, Sarkar S (2005) Place prioritization for biodiversity content using species ecological niche modelling. *Biodiversity Informatics*, **2**, 11–23.
- Schmid B, Bazzaz F, Weiner J (1995) Size dependency of sexual reproduction and of clonal growth in two perennial plants. *Canadian Journal of Botany*, **73**, 1831–1837.
- Schröter D, Cramer W, Leemans R *et al.* (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science*, **310**, 1333–1337.
- Sebert-Cuvillier E, Simonet M, Simon-Goyheneche V, Paccaut F, Goubet O, Decocq G (2010) *PRUNUS*: a spatially explicit demographic model to study plant invasions in stochastic, heterogeneous environments. *Biological Invasions*, **12**, 1183–1206.
- Sommer JH, Kreft H, Kier G, Jetz W, Mutke J, Barthlott W (2010) Projected impacts of climate change on regional capacities for global plant species richness. *Proceedings of the Royal Society B*, **277**, 2271–2280.
- St. Omar L, Horvath SM (1983) Elevated carbon dioxide concentrations and whole plant senescence. *Ecology*, **64**, 1311–1314.
- Thuiller W, Richardson DM, Midgley GF (2007) Will climate change promote alien plant invasions? In: *Biological Invasions* (ed. Nentwig W), pp. 197–211. Springer, Heidelberg.
- Thuiller W, Albert C, Araújo MB *et al.* (2008) Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 137–152.
- Travis JMJ, Brooker RW, Dytham C (2005) The interplay of positive and negative species interactions across an environmental gradient: insights from an individual-based simulation model. *Biology Letters*, **1**, 5–8.
- Vitousek PM (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1862–1876.
- Walther G-R, Roques A, Hulme P *et al.* (2009) Alien species in a warmer world: risks and opportunities. *Trends in Ecology and Evolution*, **24**, 686–693.
- Way DA, Ladeau SL, McCarthy HR, Clark JS, Oren R, Finzi AC, Jackson RB (2010) Greater seed production in elevated CO<sub>2</sub> is not accompanied by reduced seed quality in *Pinus taeda* L. *Global Change Biology*, **16**, 1046–1056.
- Williamson M, Pyšek P, Jarošík V, Prach K (2005) On the rates and patterns of spread of alien plants in the Czech Republic, Britain and Ireland. *Ecoscience*, **12**, 424–433.
- Woodward FI, Quaipe T, Lomas MR (2010) Changing climate and the Irish landscape. *Biology and Environment: Proceedings of the Royal Irish Academy*, **110B**, 1–16.