



Full Length Article

Potential impact of four invasive alien plants on the provision of ecosystem services in Europe under present and future climatic scenarios

Giovanny Pérez^{a,b,1,*}, Montserrat Vilà^{c,d,2}, Belinda Gallardo^{e,f,3}

^a Complutense University of Madrid, C/ José Antonio Novais 12, 28040 Madrid, Spain

^b Autonomous University of Madrid, C/ Darwin 2, 28049 Madrid, Spain

^c Estación Biológica de Doñana (EBD), CSIC, C/Americo Vespucio, 26, 41092 Sevilla, Spain

^d University of Sevilla, Av. de la Reina Mercedes, 6, 41012 Sevilla, Spain

^e Instituto Pirenaico de Ecología (IPE), CSIC, Avda. Montañana 1005, 50059 Zaragoza, Spain

^f Biosecurity Initiative at St. Catharines (BioRISC), St. Catharine's College, CB2 1RL Cambridge, UK



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ABSTRACT

Invasive alien species (IAS) are one of the main threats to biodiversity conservation, with significant socio-economic and ecological impacts as they disrupt ecosystem services and compromise human well-being. Global change may exacerbate the impacts of IAS, since rising temperatures and human activities favour their introduction and range expansion. Therefore, anticipating the impacts of biological invasions is crucial to support decision-making for their management. In this work, the potential impacts of four invasive alien plant species: *Ailanthus altissima*, *Baccharis halimifolia*, *Impatiens glandulifera* and *Pueraria montana*, on the provision of three ecosystem services in Europe were evaluated under current and future climate change scenarios. Using a risk analysis protocol, we determined that the most affected services are food provisioning, soil erosion regulation and the maintenance of biological diversity. To evaluate future impacts, species distribution models were calibrated using bioclimatic, environmental and human impact variables. We found that most of continental Europe is suitable for the establishment of *A. altissima*, *B. halimifolia* and *I. glandulifera*, while the potential distribution of *P. montana* is more limited. Models anticipate a shift in the distribution range for the species towards the north and east of Europe under future scenarios. Bivariate analysis allowed the identification of trends for future impacts in ecosystem services by simultaneously visualising the potential distribution of invasive species and the provision of ecosystem services. Our models project an increase in critical and high impact areas on the analysed ecosystem services, with Western Europe and the British Isles as the most affected regions. In comparison, lower impacts are projected for the Mediterranean region, likely as a consequence of the northwards expansion of invaders. Measures need to be taken to mitigate the expansion and impact of invasive species as our work shows that it can jeopardise the provision of three key services in Europe.

1. Introduction

Invasive alien species (IAS) are one of the leading causes of biodiversity loss worldwide (IPBES, 2019). The Convention on Biological Diversity defines IAS as species whose introduction and/or spread outside their natural past or present distribution range threatens biological diversity (CBD, 2010). IAS can outcompete local species for

resources, predate on or transmit diseases to native species, reduce local species diversity and cause major ecosystem changes such as modifying primary productivity or nutrient cycling as they increase the size of their population and spread into new environments (Bellard et al., 2016; Charles and Dukes, 2007; Clavero and García-Berthou, 2005; Mollot et al., 2017; Vilà et al., 2011). Consequently, there is a growing concern about IAS threatening the conservation of native species and related

Abbreviations: IAS, Invasive Alien Species; IP, Invasive Plants; SDM, Species Distribution Models.

* Corresponding author at: Department of Ecology, Complutense University of Madrid, C/ José Antonio Novais 12, 28040 Madrid, Spain.

E-mail addresses: gioper01@ucm.es (G. Pérez), montse.vila@ebd.csic.es (M. Vilà), belinda@ipe.csic.es (B. Gallardo).

¹ ORCID: 0000-0002-5050-2020.

² ORCID: 0000-0003-3171-8261.

³ ORCID: 0000-0002-1552-8233.

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ecosystem services. Moreover, the global economic impact of IAS has been recently estimated at US\$26.8 billion annually, with costs increasing threefold per decade (Diagne et al., 2021); a figure considered largely underestimated by the scientific community, particularly for plants (Novoa et al., 2021). Economic costs of invasion mostly arise from damage to the agriculture, forestry, energy and health sectors, diminished delivery of ecosystem services, and cost of controlling and eradicating unwanted species (Vilà and Hulme, 2017a). Impacts on biodiversity and ecosystem services are set to increase under climate change, since rising temperatures will allow IAS to spread into regions where they could not previously survive and reproduce (Hulme, 2017; Seebens et al., 2015; Walther et al., 2009).

Current knowledge about the impacts of IAS on ecosystem services is strongly biased towards terrestrial habitats and services that have marketable values (e.g. provisioning), whereas nonmarketable services (e.g. regulating, cultural) are largely ignored (Vilà and Hulme, 2017b). IAS impacting provisioning services are usually pathogens, pests or predators that reduce crop or forestry production and consequently the quantity and quality of the products that can be obtained from ecosystems. Classic examples include historic invasive pests such as the fungus *Phytophthora infestans* involved in the Irish Potato Famine, or the phyloxera caused by *Daktulosphaira vitifoliae*, which devastated vineyards across Europe (Fried et al., 2017). IAS can also alter regulating ecosystem services. For example, plant invasions can change primary production and carbon sequestration, as has been observed in eastern China with *Spartina alterniflora* invasion, a plant that increases the soil and aboveground carbon pool, altering carbon exchange in salt marsh ecosystems (Zhou et al., 2015). Cultural ecosystem services can also be negatively impacted by IAS affecting public health or altering landscapes in their ornamental and inspiration/appreciation qualities; an example of this is the invasion of *Ulex europaeus* in Hawaii which has resulted in monotonous landscapes affecting the sense of place by local people (Dickie et al., 2014; Kueffer and Kull, 2017).

IAS impacts on ecosystem services can vary spatially, depending both on species abundance and service provision in a particular place. Under high abundance of invasive species, the loss of ecosystem services can reach the greatest magnitude in areas with high overall provision. However, the impact can also be important in areas where the provision of a service is rather poor because the presence of the invasive species can reduce the already scarce ecosystem delivery, thereby leading to a critical situation. Indeed, the success and therefore impacts of IAS are stronger either in areas of high native biodiversity (“the rich get richer” hypothesis, Stohlgren et al., 2006) or in degraded areas of low biodiversity (“empty niche” hypothesis, MacArthur, 1970). Yet, such duality of impacts at high vs. low service provisioning areas has been rarely approached in the literature.

Spatially-explicit analyses of the risk posed by invasive species on the provision of ecosystem services have been limited by the lack of field data to conduct quantifications. With the development of continental maps of ecosystem services provision and demand at the scale of Europe (e.g. the MAES project, Joint Research Centre, 2020), such risk assessment is now possible. Climate change is likely to intensify the pressure of IAS on ecosystem services through changes in the species abundance or dominance, changes in distribution range, and changes in *per capita* impact (Bradley et al., 2010). Therefore, spatial assessments of risk are fundamental to identify hot and cold spots of potential impact on the provision of ecosystem services and their likely changes under future climate change scenarios.

The main objective of this paper is to evaluate the potential impact of four invasive plants (IP) on the provision of ecosystem services in Europe under current and future climate change projections. To achieve this, the following specific objectives are proposed: (i) to evaluate the current impacts on ecosystem services of the four focus IP using a standard evaluation protocol; (ii) to project the potential expansion of the four case study IP under current and 2050–2070 climate change conditions; and (iii) to identify the areas of Europe where the expansion of the four

focus IP are most likely to affect the provision of ecosystem services, following their changes under climate change projections. Specifically, we focused on crop provision, net ecosystem productivity and soil erosion control as representative of the ecosystem services most affected by our focus plant species. We hypothesise that climate change will allow further expansion of the IP, particularly in altitude and towards the NE of Europe (as in Gallardo et al., 2017), which may affect the provision of ecosystem services in the Alpine, Continental and Atlantic biogeographical regions. This study provides novel evidence about the vulnerability of key provisioning and regulating services to the expansion of invasive species under climate change. Such investigation can be extrapolated to other species and services, allowing for a more holistic evaluation of the impacts of IAS that goes beyond biodiversity, and explores IAS consequences on nature’s contribution to people (Diaz et al., 2018).

2. Methods

The study area spans the entire European continent except Russia. In this work we selected four plants from the List of Invasive Alien Species of Union Concern (EU. European Union Regulation 1143/2014): *Ailanthus altissima* (Mill.) Swingle, *Baccharis halimifolia* L., *Impatiens glandulifera* Royle, and *Pueraria montana* (Willd.) Sanjappa & Pradeep. The selection criteria was the differentiation in biological traits, impacts and current invasive distribution (e.g. We selected a tree (*A. altissima*), a shrub (*B. halimifolia*), a vine (*P. montana*), and an annual herb (*I. glandulifera*)). Species in the List of Union Concern are recognised by all member states as a priority for management, according to a comprehensive risk assessment compiling the existing scientific evidence about their impacts on biodiversity and related ecosystem services (Genovesi et al., 2015). Our work can therefore support the prioritisation of management actions to achieve the goals set in the IAS Regulation “to prevent, minimise and mitigate the adverse effects of IAS on biodiversity and related ecosystem services”, as well as the EU Biodiversity Strategy for 2030.

The spatial evaluation of risks posed by IAS to ecosystem services followed four steps: 1) an evaluation of the potential impacts on the four focus IP on the provision of ecosystem services, 2) modelling the potential distribution of the focus IP under current and future conditions, 3) selection and reclassification of maps of the provision of representative ecosystem services in Europe, and 4) identifying areas in Europe where invasive species may compromise the provision of ecosystem services under current and future climate change projections.

2.1. Potential impacts of invasive plants on the provision of ecosystem services

The species impact on ecosystem services was evaluated using the Invasive Species Effects Assessment Tool - INSEAT protocol (Martinez-Cillero et al., 2019). This is the only risk analysis protocol that makes it possible to specifically assess the impacts of invasive species on 16 ecosystem services (Table 1), while the majority of existing protocols focus on impacts on biodiversity only, e.g. the EICAT protocol (IUCN, 2020). INSEAT uses a semi-quantitative scale with a range of +4 to -4 to assign scores according to a predetermined table of impact scoring that assesses both positive and negative effects (see Fig. 1 in Martinez-Cillero et al., 2019). For the protocol application, a literature review was conducted using the web search engines Google Scholar, Scopus and Web of Science, using a combination of keywords such as “ecosystem services”, “impacts”, “management”, “invasive species”, “well-being”, “economic”, “social-ecological” and the species’ scientific names. Also, we considered information from technical reports in the specialised databases CABI-Invasive Species Compendium and the IUCN Global Invasive Species Database (CABI, 2020; GISD, 2020).

Table 1

Ecosystem services evaluated in this study according to the INSEAT protocol. Adapted from Martínez-Cillero et al. (2019).

Code	Ecosystem services	Description
<i>Provisioning services</i>		
ES1	Crops or livestock	Provision of food
ES2	Harvested wild goods	Ornamental, medicinal resources, wild game
ES3	Trees, standing vegetation, peat	Material goods, fuels and construction
ES4	Water supply	Local water supply, drinking water
ES5	Wild species diversity	Genetic diversity for animal and plant breeding, biological diversity potential for benefits to people provisioning
<i>Regulating services</i>		
<i>Benefits obtained from regulation of ecosystem processes.</i>		
ES6	Purification	Detoxification and purification in soils, air and water.
ES7	Climate regulation	Local (e.g. temperature and precipitation) or global (e.g. carbon sequestration) regulation)
ES8	Hazard regulation	Moderation of extreme events as floods or storms
ES9	Pollination	Pollinator species maintenance or supply
ES10	Noise regulation	Attenuation or maintenance of sound levels
ES11	Erosion regulation	Erosion prevention and maintenance of soil fertility
<i>Cultural services</i>		
<i>Nonmaterial benefits obtained from ecosystems</i>		
ES12	Sense of place	Religious or spiritual meaning, sense of belonging
ES13	Inspiration or appreciation	Aesthetic appreciation and inspiration for culture, art, design
ES14	Recreation and tourism	Spaces for visiting, recreation, outdoor entertainment
ES15	Health	Mental and physical health, public health, disease regulation
ES16	Knowledge	Knowledge systems and educational values

2.2. Current and future potential range of invasive plants in Europe

Species distribution models (SDM) are an optimal tool to construct probability maps of areas vulnerable to the invasion of particular species and thus can be used for the detection and rapid response to biological invasions (Guisan et al., 2017; Srivastava et al., 2019). SDMs were used to determine the invasion probability of the four plant species under current and future climate change projections. A total of 150,307 global occurrence points were downloaded for all species (GBIF.org, 2020) which were then trimmed to 51,239 after a cleaning protocol (Zizka et al., 2019). This includes the removal of erroneous, duplicated, misleading or low-resolution coordinates, and the aggregation of occurrences to a 5 arc-minute resolution for each species to reduce the spatial autocorrelation of data (García-Roselló et al., 2015). Occurrence records used for calibration were 16,922 for *A. altissima*, 2,364 for *B. halimifolia*, 29,100 for *I. glandulifera* and 2,853 for *P. montana*. Global and European maps of the occurrence of the four species can be consulted in the [Supplementary Materials](#) (Fig. S1).

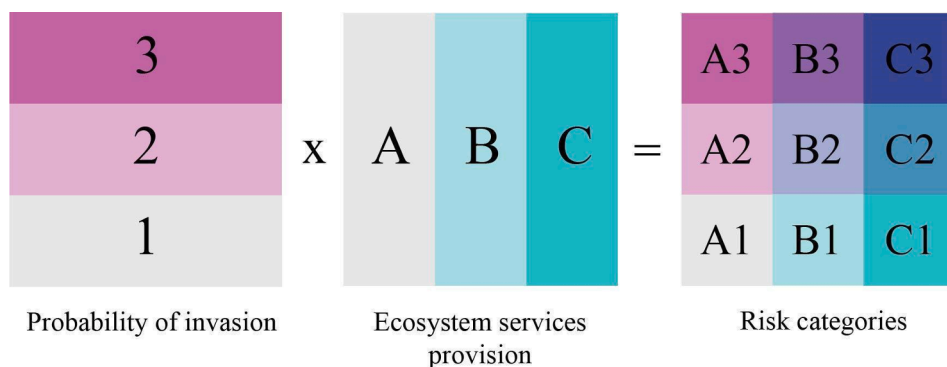


Fig. 1. Categories of the risk posed by invasive species to the provision of ecosystem services. Nine categories resulted from the combination of three levels of invasive species suitability scores (1, 2, and 3) and three levels of ecosystem services provision (A, B and C). This classification allowed evaluating spatially changes in the potential impacts of invasive species on the provision of ecosystem services. Most vulnerable areas correspond to risk categories A3 (critical impact) and C3 (hotspots).

Identifying the most appropriate variables for modelling is crucial to maximise the accuracy of distribution models and their transferability in space and time. In this study, we followed the selection protocol of Gallardo et al. (2017) that involved removing highly correlated (Pearson's $r > 0.7$) and multi-collinear variables (Variable inflation factor $VIF > 5$) while prioritising predictors that are ecologically meaningful to explain the large-scale distribution of the four study species (see Fig. S2 for a correlation matrix). Final variables considered included: maximum temperature of warmest month (bio5), minimum temperature of coldest month (bio6), precipitation of wettest month (bio13) and precipitation of driest month (bio14) from the WorldClim-Global Climate Data, (<https://worldclim.org/>, (Fick and Hijmans, 2017)), soil water pH at 0 – 5 cm depth (soil-pH) (Hengl et al., 2017), and the travel time to reach the nearest urban centre (accessibility) (Weiss et al., 2018). The chosen bioclimatic predictors represent extreme or limiting environmental conditions, which may constrain the establishment and spread of invaders, and are commonly used in distribution models (Gallardo et al., 2017). Accessibility was used as a proxy of anthropogenic impact to reflect the importance of human activity in the introduction and establishment of IAS, a variable that has demonstrated its value to improve the accuracy of distribution models for invasive species (Gallardo et al., 2015). All predictors were used at global coverage and 5 arc-minute resolution (approx. 5x5 km at the equator).

To account for uncertainty in future climatic conditions, we obtained four different climate projections. We used the Community Climate System Model, version 4 (CCSM4), and two different Representative Concentration Pathways (RCPs), that is, greenhouse gas concentration trajectories. For this study, we chose the 4.5 and 8.5 RCPs because they represent two different potential future conditions. Both RCP's were downloaded for the "medium-term" (representing average conditions predicted for 2041–2060, hereafter 2050) and the "long-term" periods (average for 2061–2080, hereafter 2070) from WorldClim-Global Climate Data. It should be noted that accessibility and soil-pH were considered to remain constant under future projections, since changes in these layers are not available for future conditions.

The entire modelling process was performed using the package BIOMOD2 v. 3.14.12 (Thuiller et al., 2014; Thuiller et al., 2009) in the R v.4.0.2 environment (R Core Team, 2020). Model calibration algorithms included two regression techniques: Generalized linear models (GLM) and Generalized additive models (GAM); and two machine learning techniques: Random Forest (RF) and Boosted regression trees (GBM). To calibrate the species niche, a random selection of 10,000 pseudo-absences was performed on a global scale, with a 0.5 prevalence, following the recommendations of Barbet-Massin et al., (2012). As there was no independent data to assess the predictive performance of the models, occurrence points were randomly split into test data (30%) and training data (70%). The calibration process was repeated 3 times per algorithm with different test/training partitions, for a total of 12 model replicates per species. For model evaluation, the True Skill Statistics (TSS) and the Area Under the Relative Operating Characteristic Curve

(AUC-ROC) were selected (Allouche et al., 2006; Lawson et al., 2014). Variables' importance was calculated using permutations (Thuiller et al., 2014). Finally, ensemble models were built using the TSS-weighted average of replicates, discarding those replicas with TSS < 0.7.

After calibration, models were projected onto Europe to obtain suitability maps under the five projections (one current and four future). Suitability is a measure of the match with the conditions of locations currently invaded by a species and ranges from 0 (completely dissimilar) to 100 (perfect match). We used the biogeographical regions defined by the European Environment Agency (<https://www.eea.europa.eu/>) as a reference to interpret spatial patterns of potential distribution (Fig. S3).

Finally, suitability scores were classified into three equal categories of risk: low risk (1: suitability values in the < 33.3% percentile), medium risk (2: suitability values between 33.4 and 66.6%) and high risk (3: suitability values in the > 66.7% percentile).

Species range change (SRC) under the four future projections was calculated using the function BIOMOD_RangeSize in Biomod2 package, according to Thuiller et al., (2014). This analysis strictly compares the range sizes between current and future states using each pixel status in the binary projections: positive values of SRC indicate an increase while negative values imply a reduction in climatic suitability.

2.3. Maps of the provision of ecosystem services in Europe

Maps of ecosystem services provision in continental Europe (except Russia) were obtained from the project MAES: Mapping and Assessment of Ecosystems and their Services (Maes et al., 2015), via the European Union's Joint Research Centre data repository (Joint Research Centre, 2020). From the available maps, we selected three proxies for the ecosystem services most commonly affected by our focus species, as identified through INSEAT (see step 2.1):

i) *Crop Provision*. The contribution of ecosystems to crop provision is calculated by Maes et al. (2020) by disentangling the yield generated by natural inputs (i.e. sunlight, wind, rainfall, evapotranspiration, soil) from what is generated by human inputs (i.e., planting, irrigation, chemical products). The map represents the percentage of the yield that can be attributed to the ecosystem contribution, and varies from 0, when yield is entirely derived from human inputs, to 1 when no human input is involved (Vallecillo et al., 2020). This map is used as a proxy of ES1 Crops or livestock (Table 1).

ii) *Net Ecosystem Productivity (NEP)*. This is an indicator based on spot measurements of the Normalized Difference Vegetation Index (NDVI) scaled between 0 and 1. Although the relationship between biodiversity and productivity is controversial, it has been shown that primary productivity is closely correlated to biological richness at large spatial scales (Fraser et al., 2015; Šímová and Storch, 2017). Lacking a more specific map of plant species richness in Europe, NEP was used as a proxy of ES 5 Wild species diversity (Table 1).

iii) *Soil erosion control*. This is an indicator that reflects the relationship between the capacity of ecosystems to avoid soil erosion and how much soil is retained by vegetation, scaled from 0 (no erosion control) to 1 (optimal erosion control). It was used as a proxy of ES 11 Erosion regulation (Table 1).

Ecosystem services values were reclassified into three equal categories: low service provision (A: values in the ≤ 33.3% percentile), medium service provision (B: between 33.4 and 66.6%) and high service provision (C: values in the ≥ 66.7% percentile).

2.4. Spatial analysis of risk based on bivariate choropleths

We categorised the risk associated with invasive species considering both the environmental suitability for the species, and the provision of ecosystem services. First, we assumed that invasive species are likely to be more harmful in areas under high environmental suitability, which may favour the abundance, cover or *per capita* impact of the invader. This assumption is based on the environmental matching hypothesis

(Ricciardi et al., 2013), which has been demonstrated for aquatic invasive species showing higher impact at water temperatures closer to their optima (Iacarella et al., 2015) and insect pests causing severe tree defoliation only under high climate suitability (Canelles et al., 2021). Furthermore, in a meta-analysis of 450 correlations between species abundance and environmental suitability calculated from SDMs, Weber et al. (2017) found a consistent positive relationship that was independent of spatial scale and SDM method. This means that under high suitability values, we may expect not only a higher probability of establishment but also a higher abundance or coverage, and consequently impact, of invasive species. Second, within areas under high suitability for a particular invasive species, we considered that impacts depend on the provision of ecosystem services. Thus, while the overall magnitude of the impact may be greatest in high-provisioning areas, impacts are also likely to become critical in low-provisioning regions. Indeed, low service provision has been shown to decrease the social-ecological resilience of natural ecosystems to disturbance pressures like that posed by invasive species (Collier, 2015).

We defined a total of nine risk categories (Fig. 1) by combining the probability of invasion (1, 2 and 3 categories) and the provision of ecosystem services (A, B and C categories). Each 5 arc-min pixel in the study area was assigned to a risk category, so that bivariate choropleth maps and analysis allowed detecting patterns in the spatial distribution of the two variables simultaneously, which would be challenging individually.

For the analysis, particular emphasis was put on the following categories:

- *Coldspots* (A1) represent sites where both species suitability and ecosystem service provision are low; consequently no major impacts are to be expected.
- *Critical impact* (A3) represent sites where ecosystem service provision is low and the probability of invasion is high; consequently, even a small impact (in terms of magnitude) of the invader on the functioning of ecosystems could lead to a critical provision of the service. For instance, in areas where natural ecosystems are unable to provide protection against soil erosion, the colonisation of plants increasing erodibility can have major effects on the state of the ecosystem.
- *Safe provision* (C1) represents sites showing high ecosystem provision and low probability of invasion, where no major problems associated with the invader are expected.
- *Hotspots* (C3) represent sites combining both high probability of invasion and high delivery of ecosystem services. Consequently, this is where we may expect the greatest reduction in the magnitude of the provision of ecosystem services. For example, for a species affecting food provision, we may expect the greatest decrease in crop yields in C3 sites.

This classification process was applied to each of the four species, three ecosystem services, and five present and future conditions, obtaining a total of 60 bivariate choropleth maps. Comparison between present and future allowed the identification of sites where the four invasive species can affect ecosystem services to a greater extent.

3. Results

3.1. Potential impacts of invasive plants on the provision of ecosystem services

Using INSEAT, we identified the positive and negative impacts of the four IP on ecosystem services (Fig. 2, see Table S1 for a detailed description of impacts). In general, the services most negatively affected were: wild species diversity (ES5), erosion regulation (ES11), food provisioning in the form of crops or livestock (ES1) harvested wild goods (ES2) and tourism or recreation (ES14).

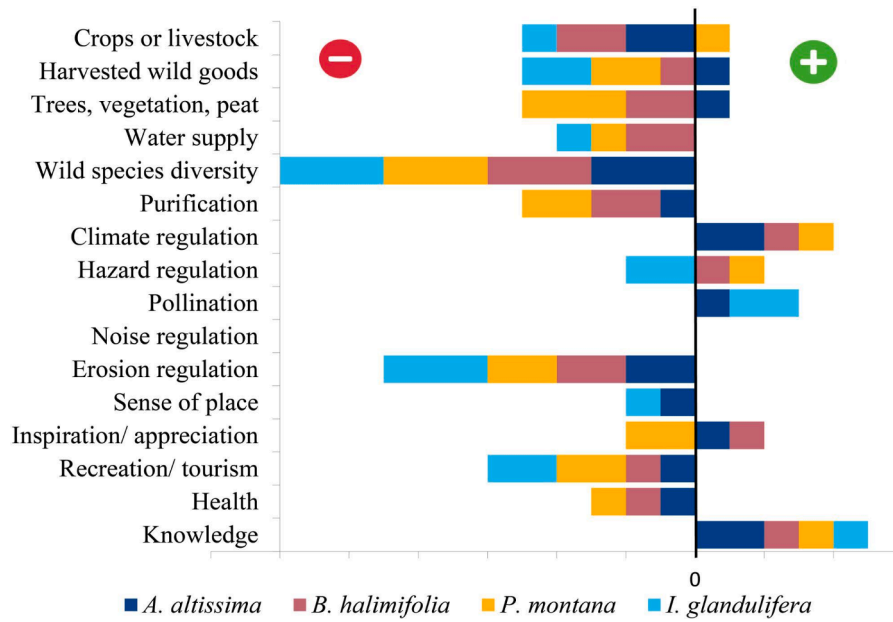


Fig. 2. Semi-quantitative evaluation of the impacts on ecosystem services of four IASSs. Impacts on each service are evaluated from -4 to $+4$ based on a literature search for each species (see more details in Table S1). Scores are shown accumulated for the four species to highlight the most frequently affected services across species.

3.2. Current and future potential spread of invasive plants in Europe

AUC-ROC (0.99 ± 0.01) evaluation statistics values across the four species and four different algorithms, which indicates a good agreement between observed data and models predictions. This is reflected in the

Species distribution models showed high TSS (0.92 ± 0.03) and

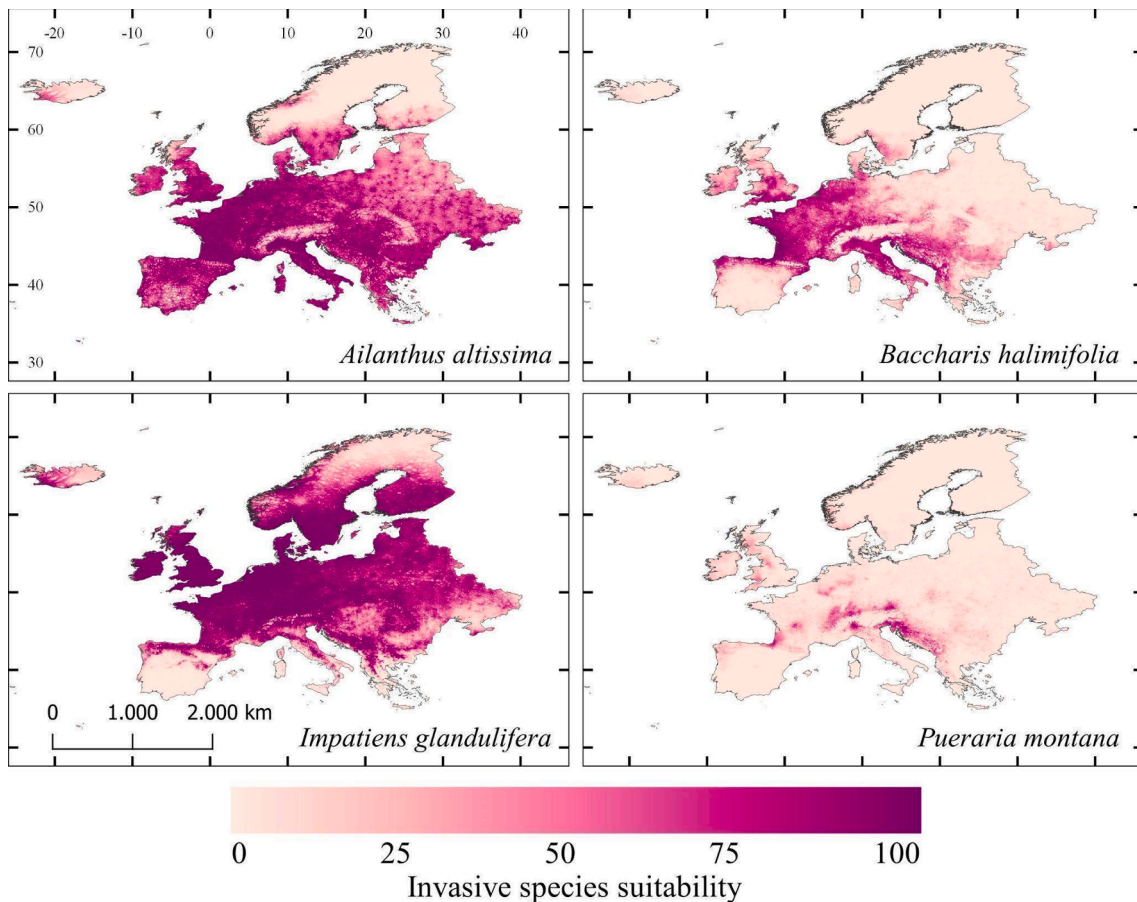


Fig. 3. Suitability of four IP in Europe under the current scenario, representing the potential for short-term expansion. Models are calibrated using climate, soil and anthropic conditions as predictors, and the current global occurrence of species.

robustness of the ensemble model for each species (TSS from 0.91 to 0.96; Table S2). Variable importance showed that accessibility (0.29 ± 0.01) and minimum temperature of the coldest month (0.30 ± 0.15) were the most important predictors. In contrast, precipitation of the wettest month (0.07 ± 0.07) and soil-pH (0.02 ± 0.02) were the least relevant. This was consistent across all of the modelling algorithms used (Table S3).

Models projection for the current scenario showed that there is a high probability of presence throughout most of the European continent for *A. altissima* and *I. glandulifera*, and slightly more limited in the case of *B. halimifolia*. In contrast, the potential distribution of *P. montana* is restricted to isolated patches in the Western part of the Atlantic and Continental biogeographic regions (Fig. 3). No future scenario predicts the occupation of the southern half of the Iberian Peninsula and the northern half of Scandinavia where climate conditions are more extreme (Figs. S4–S7). Also, a general decrease in species suitability in the Mediterranean region is predicted under all future projections, particularly for *A. altissima* (Fig. S4).

SRC maps and metrics anticipate the expansion for three of the evaluated species towards the northeast of Europe in the future (Figs. S8–S12). This situation is constant under the 2050 and 2070 projections for both RCP 4.5 and RCP 8.5 scenarios. In particular, *A. altissima* displays a mean SRC across the four projections of 17%; 50% in the case of *B. halimifolia*; and 169% for *P. montana*, which is expected to at least double its distribution (Fig. S13, Table S4). On the other hand, range reduction is expected for *I. glandulifera* under all future projections, displaying a mean SRC of –33% (Fig. S13, Table S4).

3.3. Spatial analysis of risk based on bivariate choropleths

3.3.1. General trends

We used bivariate choropleths to follow changes in the risk posed by IAS to the provision of three ecosystem services. Fig. 4 synthesises the area covered by each of the most important categories of risk under

current climate conditions. Under future projections, the spatial overlap between the four IP and areas delivering either low (A3) or high (C3) ecosystem services, are expected to increase for three of the evaluated species. The only exception is *I. glandulifera*, for which models project a reduction in its potential distribution under future conditions, which is translated into a decrease in areas potentially affected. It is also relevant to note that Safe areas (C1) decrease under future projections (Table S5, Figs. S14–S25). We provide below a detailed description of the potential impacts of IP on each of the three ecosystem services investigated.

3.3.2. Crop provision

Species showing the highest potential impact on the contribution of natural ecosystems to crop provision are *I. glandulifera* and *A. altissima*, followed by *B. halimifolia*. Hotspots (C3) are concentrated in the Atlantic and part of the Continental bioregions. Critical areas (A3) cover the rest of the Atlantic, Continental, Steppic and Pannonian regions (Fig. 5). The Mediterranean region is also largely classified as “critical” for *A. altissima*, and the Boreal region for *I. glandulifera* (Fig. 5). Under future projections, hotspots may increase by a minimum of 10% (*A. altissima*, 2070 RCP 8.5 scenario, Table S5) to a maximum of 218% (*P. montana*, 2070 RCP 4.5 scenario, Table S5). As an exception, the surface classified as hotspots may decrease between 21 and 59% for *I. glandulifera*.

3.3.3. Net ecosystem productivity

Patterns in the vulnerability of net ecosystem productivity to invasive species are similar to crop provision: vast areas of Europe are predicted to be hotspots for both *A. altissima* and *I. glandulifera* followed by *B. halimifolia*, particularly in the Continental and Atlantic bioregions (Fig. 6). Furthermore, hotspots are expected to increase up to 274% (*P. montana*, 2070 RCP 8.5 scenario, Table S5). However, hotspots decrease under all future projections for *I. glandulifera* (between 29 and 60%, Table S5).

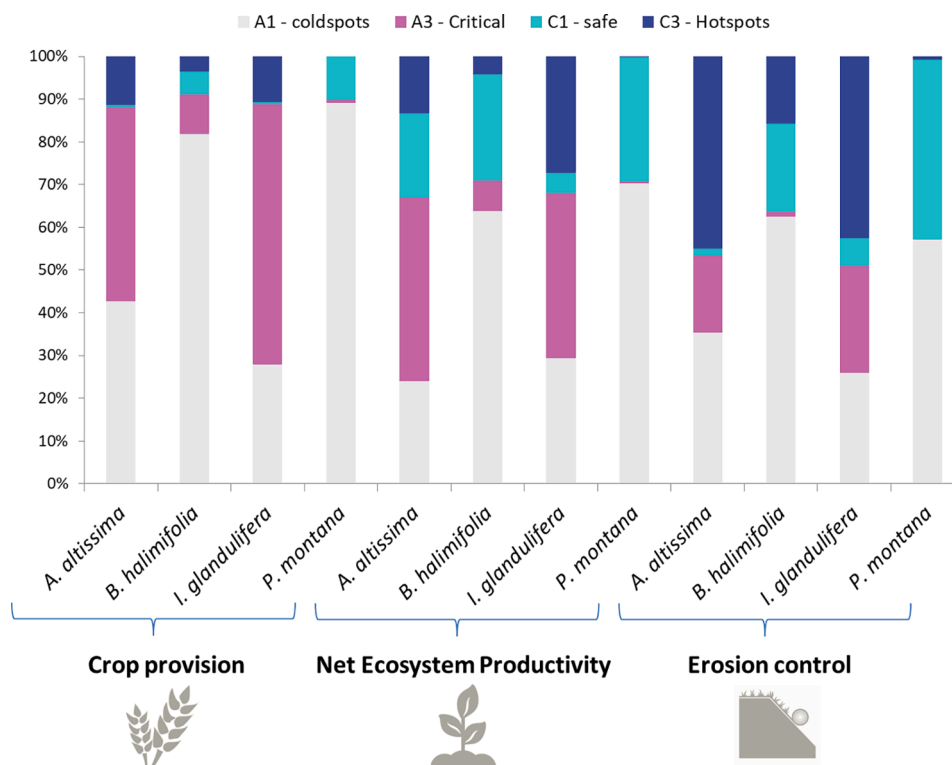


Fig. 4. Percentage of area in Europe classified into 4 risk categories combining the probability of invasion of four alien plants, and the provision of ecosystem services under current conditions. A3 represents sites where ecosystem service provision is low and the probability of invasion is high, C3 represents sites combining at the same time a high probability of invasion and delivery of ecosystem services.

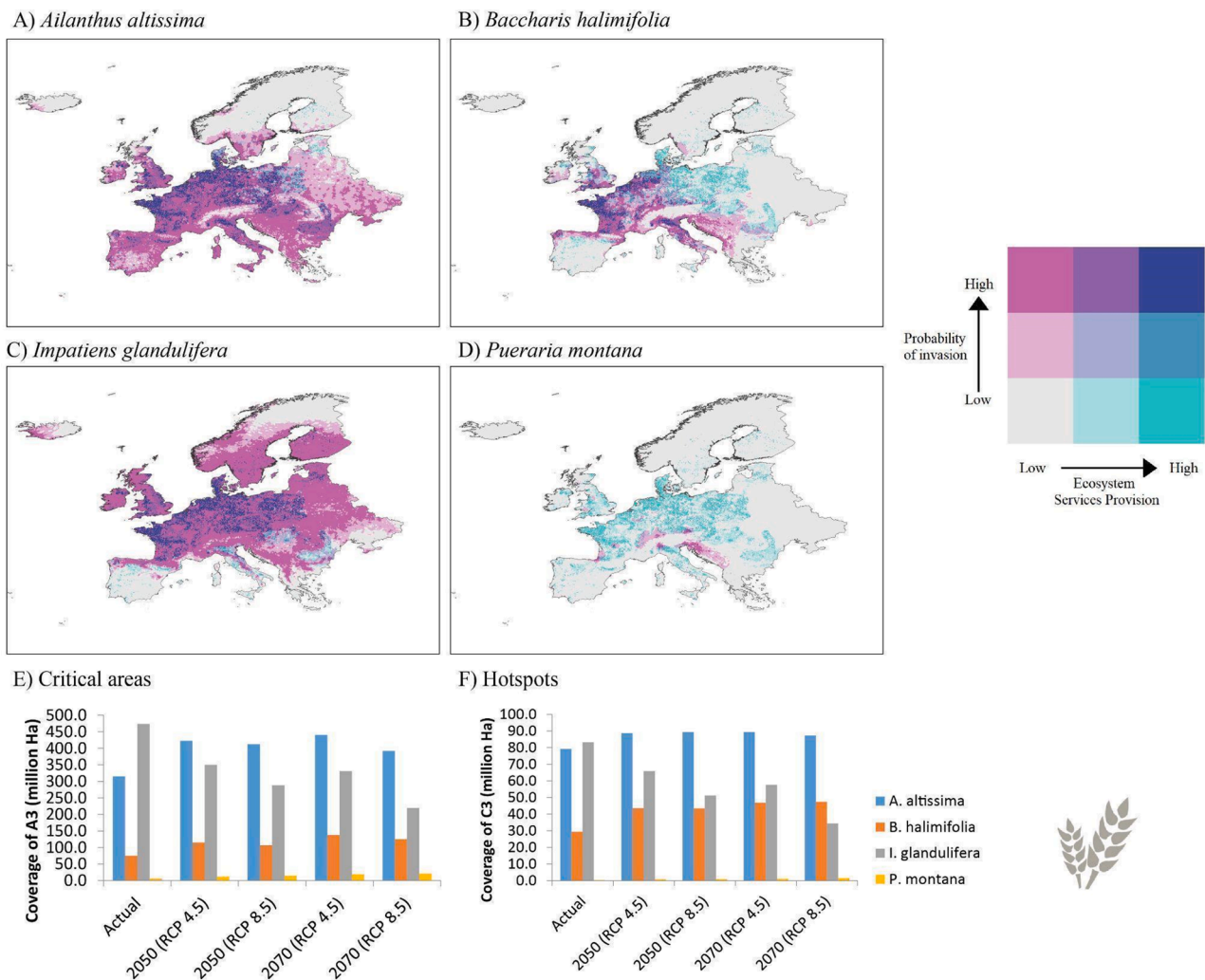


Fig. 5. Synthesis of the impacts of four IP on the ecosystem contribution to crop provision in Europe. A-D bivariate choropleths that combine information about the environmental suitability for each invasive species (darker pink = higher suitability and therefore potential impact) and the ecosystem provision (darker cyan = higher crop provision) under the current scenario. E-F: Potential temporal changes in the European area classified as critical areas (high invasion/ low provision of services) and hotspots (high invasion/ high provision of services).

3.3.4. Soil erosion control

As in previous services, hotspots and critical areas for soil erosion control were extensive in the Continental and Atlantic bioregions, particularly due to *A. altissima* and *I. glandulifera*, and to a lower extent *B. halimifolia* (Fig. 7). *A. altissima* shows high suitability in areas with poor erosion control of the Mediterranean bioregion, whereas *I. glandulifera* dominates in the Boreal region where natural ecosystems provide better erosion control. Under future conditions, hotspots increase between 34 to 58% (Table S5); with a decrease in hotspot extension for *I. glandulifera* (6 to 27% across projections, Table S5).

4. Discussion

This study offers the first comprehensive spatial analysis of the risk posed by invasive species on the provision of ecosystem services at a continental scale. We found both positive and negative impacts associated with four IP, the latter being related to harmful consequences for crop production, native biodiversity and erosion control. These impacts are particularly important in the Continental and Atlantic bioregions, showing a trend towards the north-east of Europe under future scenarios.

4.1. Potential impacts of invasive plants on the provision of ecosystem services

The INSEAT protocol is an effective tool for the rapid assessment of gains and losses in ecosystem services provision derived from the invasion of our four focus species. We found that the IP have mainly negative effects on ecosystem services, with soil retention, food provisioning and wild species diversity among the most affected. For instance *A. altissima*, *B. halimifolia* and *P. montana* alter soil nutrient cycling and retention by introducing large amounts of nitrogen and/or litter (Vilà et al., 2006; Castro-Díez et al., 2009; Hickman et al., 2010); while *I. glandulifera* do so by modifying the soil microorganisms community, indirectly affecting the local flora and causing terrestrial invertebrate species to decrease (Gaggini et al., 2018; Greenwood & Kuhn, 2014; Tanner et al., 2013; Ruckli et al., 2014). Furthermore, *A. altissima* and *I. glandulifera* produce allelopathic compounds that affect the germination of many other plants (Ullah, 2020; Bieberich et al., 2018; Sladonja et al., 2015; Peter, 2013); whereas *P. montana* is an aggressive competitor that affects forestry and agricultural systems by causing the death and fall of mature trees and preventing crop plants growth and germination (Forseth & Innis, 2004).

The four IP investigated in this study are included in the List of European Union Concern because of their demonstrated negative effects on

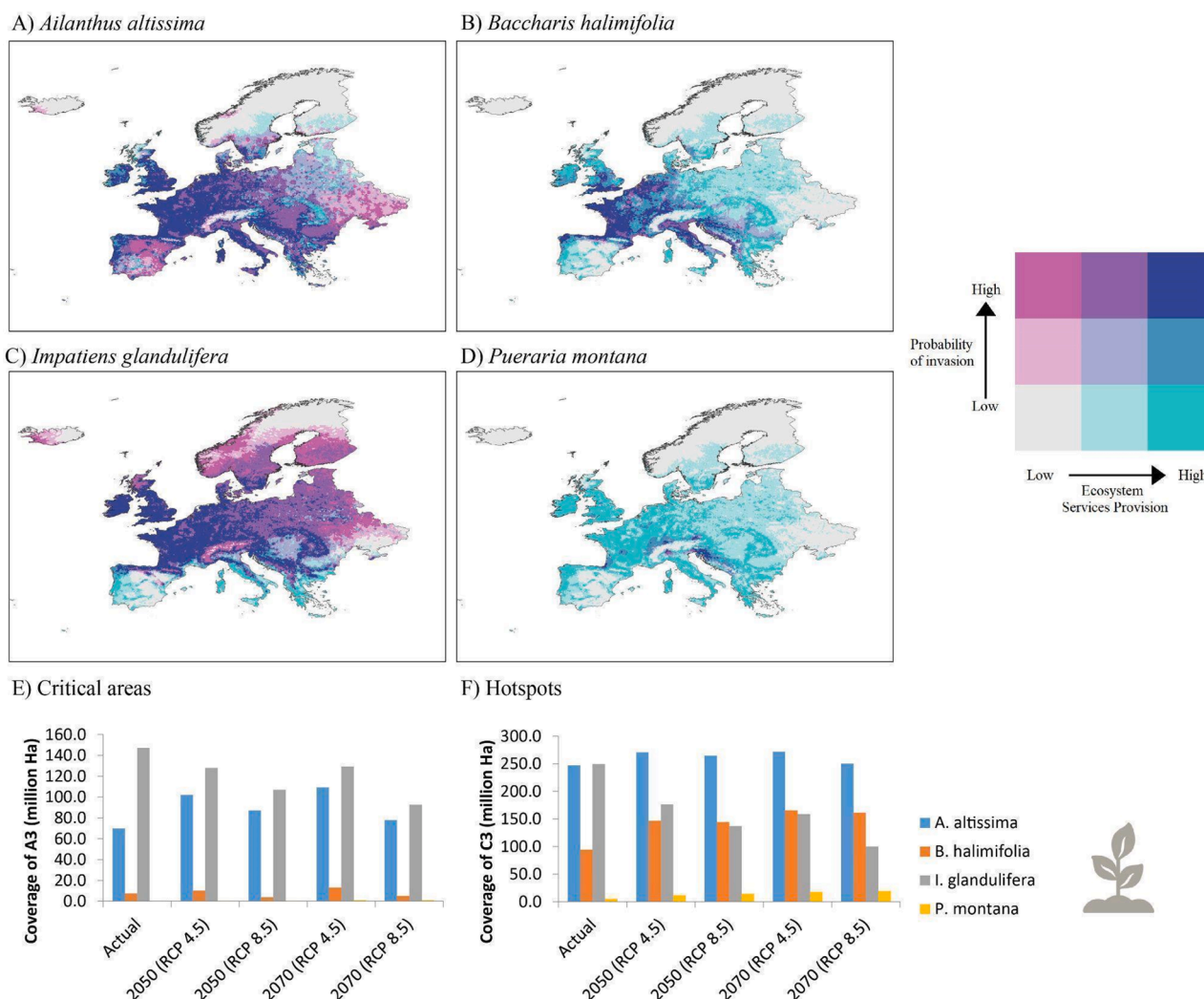


Fig. 6. Synthesis of the impacts of four IP on the ecosystem contribution to net ecosystem productivity in Europe. A-D bivariate choropleths that combine information about the environmental suitability for each invasive species (darker pink = higher suitability and therefore potential impact) and the ecosystem provision (darker cyan = higher crop provision) under the current scenario. E-F: Potential temporal changes in the European area classified as Critical areas (high invasion/ low provision of services) and hotspots (high invasion/ high provision of services).

biodiversity, particularly in natural habitats and protected areas with rich wild species diversity (e.g. Sladonja et al., 2015; Gutiérrez-López et al., 2014; Caño et al., 2014; Fried & Panetta, 2016; Hulme & Bremner, 2006; Kiełtyk and Delimat, 2019; Forseth & Innis, 2004). Other studies show little or negligible impacts of *I. glandulifera*, particularly in anthropic habitats with little conservation value (Sladonja et al., 2015). For instance, *I. glandulifera* does not seem to represent a threat to invaded riparian communities' plant diversity along six rivers in the Czech Republic (Hejda and Pyšek, 2006). Indeed, the impacts of invasive species are highly context-dependent and can be related to environmental conditions limiting the growth of the invader as well as the interaction of the invader with the recipient community (Ricciardi et al., 2013). Nevertheless, we should not underestimate the potential impacts of the four plants investigated here since some apparently benign alien species become invasive over time, with lag phases up to 30 years long, triggered by climate, environmental or human-use changes (sensu "sleeper species", Spear et al., 2021). Thus, following the precautionary principle, INSEAT as well as other evaluation protocols consider the maximum and not the average impact evidenced in the literature for invasive species.

Positive impacts were also identified for each species, which could be explored for their incorporation into cost-benefit analyses of management. For example, *A. altissima* stands out as a species that can supply

wood, medicinal compounds and has an important ornamental value (Sladonja et al., 2015); *P. montana* provides forage and chemical compounds (Baptista et al., 2014; Cui et al., 2018); *I. glandulifera* shows promise in soil phytoremediation as hyper-accumulator of heavy metals (Coakley et al., 2019), and is highly attractive to pollinators, facilitating their establishment and spread (Cawoy et al., 2012; Thijs et al., 2011). The assessment of positive impacts should not be seen as an attempt to offset the negative impacts of IAS, but rather as an opportunity to provide additional information to scientists, administrators, and legislators (Eviner et al., 2012; Vimercati et al., 2020).

4.2. Potential current and future distribution of the invasive plants in Europe

All future projections showed a reduction in the species range in southern Europe and increase towards the northeast, with an overall potential increase in the invaded area (Figs. S8–S12). The suitability for invasion was highest across all current and future projections in the Atlantic and Continental bioregions, a common spatial pattern in the literature that has been attributed to a combination of high propagule pressure (e.g. intense human activity, history of trade, international connexions) and mild environmental conditions (Magliozzi et al., 2020; Gallardo et al., 2015; Chytrý et al., 2009). The only exception to this

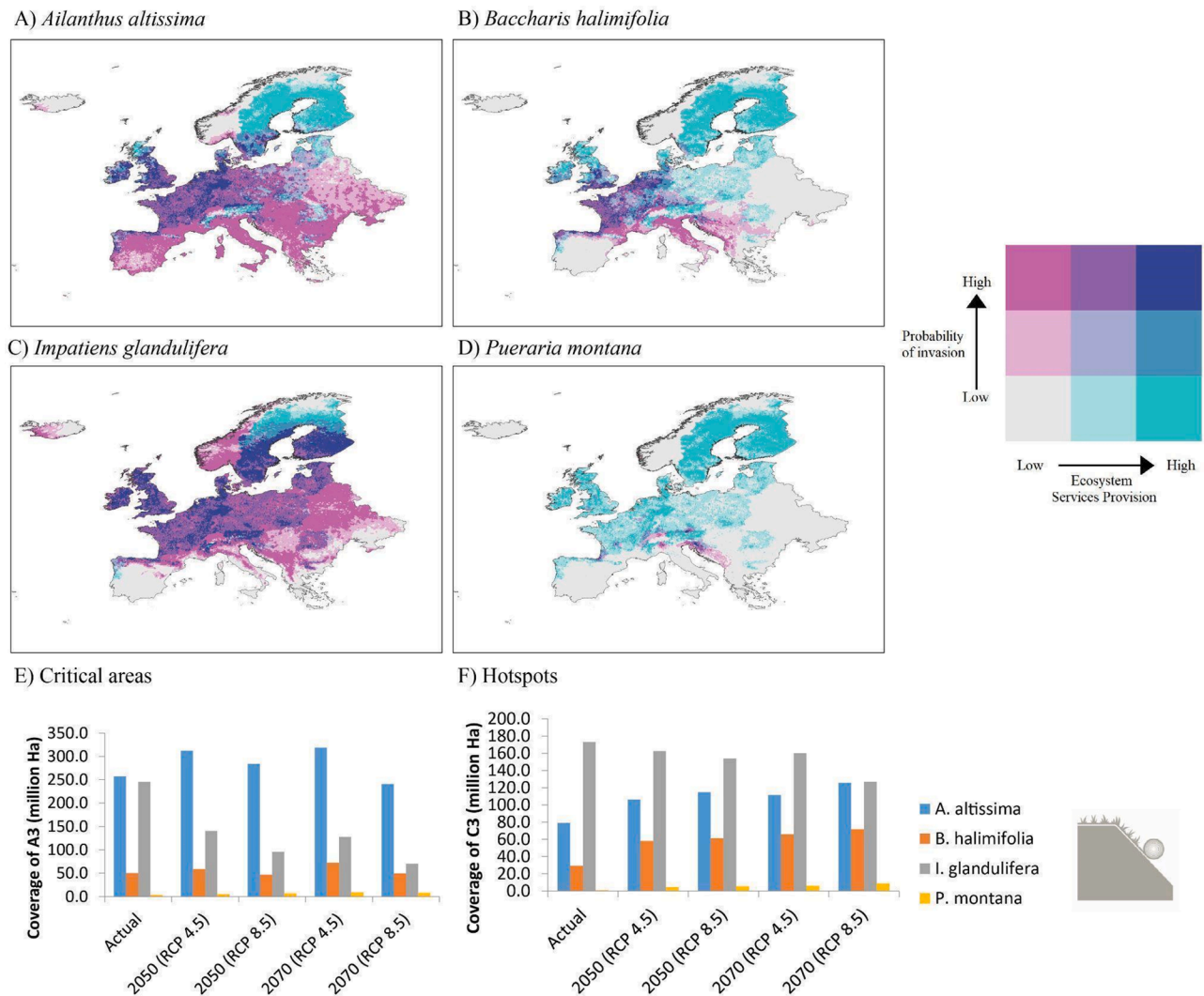


Fig. 7. Synthesis of the impacts of four IP on the ecosystem contribution to soil erosion control in Europe. A-D bivariate choropleths that combine information about the environmental suitability for each invasive species (darker pink = higher suitability and therefore potential impact) and the ecosystem provision (darker cyan = higher crop provision) under the current scenario. E-F: Potential temporal changes in the European area classified as critical areas (high invasion/ low provision of services) and hotspots (high invasion/ high provision of services).

general pattern is *I. glandulifera*, which shows a considerable reduction in its potential future range, particularly under the long-term RCP 8.5 scenario (Fig. S4). No other study has evaluated the potential distribution of the four IP on a continental scale, although there are several studies on a local and regional scale (Cabra-Rivas et al., 2015; Calleja et al., 2019; Motti et al., 2021). Our results are in agreement with laboratory experiments that showed how increased temperatures and drought stress negatively affect *I. glandulifera*: showing reduced number of flowers and leaves, shorter life-span, reduced photosynthetic output, nectar volume and pollen protein content (Descamps et al., 2021). SDMs may have underestimated the potential for this species to expand its northern distribution in Europe, where an increase in the length of the growing season could result in further spread northwards (Beerling, 1993), in turn increasing the magnitude of their impacts on ecosystem services.

P. montana deserves special attention because it shows the greatest distribution range increase potential, at least doubling (Fig. S13). The species shows a localised incipient distribution (Follak, 2011), however niche dynamics suggests that in Europe the species is at the initial stages of expansion and substantial expansion is expected (Montagnani et al., 2022). As the invasion progresses and the species fills its new realised niche, models tend to stretch the potential area under risk of invasion, a

process known as invasion ratcheting (Gallardo et al., 2013; González-Moreno et al., 2015). Precisely because the species is yet to show its full potential in the European continent, it is important to implement actions for its rapid management (Robertson et al., 2020). The early invasion status of this species is adequate for a successful eradication response (Anderson, 2005).

Finally, it is worth noting that distribution models revealed little differences between the expected impacts under the 2050 and 2070 projections. This is a pattern common to other studies (e.g. Puchalka et al., 2021; Gallardo et al., 2017) that suggests that the effects of climate change on the invasion of plants (and consequently on ecosystem services) may unfold faster than expected, and thus management mitigation strategies need to be developed urgently.

4.3. Spatial analysis of the risk posed by invasive species to the provision of ecosystem services

IAS and climate change are likely to alter the provision of ecosystem services, but little is known about where and when both factors are more likely to interact (Charles and Dukes, 2007). Here we bridge this gap by providing the first comprehensive spatial analysis of the risk posed by four invasive species listed in the List of European Union Concern and

therefore a priority for management. We focused our analyses on three of the most frequently affected ecosystem services: crop provision, species diversity and erosion control, that we discuss below.

The ecosystem contribution to crop provision shows broad spatial variability, with larger values in Western and Eastern Europe that typically employ lower rates of irrigation and fertilisers (Vallecillo et al., 2019). This is precisely where our models anticipate the higher suitability for IP, thus the largest potential magnitude of impacts (Fig. 5). In contrast, low-provisioning values can be observed in areas with intensive crop production supported by extensive irrigation systems (Mediterranean region), which may be more strongly affected by other invasive species such as hydroids and molluscs that block irrigation structures and can affect the normal functioning of reservoirs and other hydraulic infrastructures (Gallardo et al., 2018; Rosa et al., 2011). Propagules of the four IP investigated can be easily transported by rivers and streams, spreading into agricultural ecosystems and affecting not only crop yield but also other related services. For example, the establishment of *B. halimifolia* in rivers and canals can cause feeding intoxication to livestock (Fried et al., 2016). Under future scenarios, the IP pressure measured as coverage of critical and hotspots areas on crop provisioning increases for all species except for *I. glandulifera*, which is expected to decrease slightly. This is important, because the report of the European Environmental Agency reveals no changes in the ecosystem contribution to crop provision but a substantial increase in demand (+7%) (Maes et al., 2020). Invasive species such as those analysed here can amplify the mismatch between the demand and provision of key ecosystem services in Europe.

Net ecosystem productivity may act as a surrogate for many ecosystem services given the crucial role of photosynthesis for many, if not all, ecosystem functions. Here we used net ecosystem productivity as a proxy to account for the impact of invasive species on local diversity. This impact can be elusive, since it does not occur on services directly used by people, namely, those with direct market valuation, but as a regulatory service that supports many others. There is an upward trend in net ecosystem productivity across Europe, registering +10% between 2000 and 2010, which is attributed to elevated atmospheric CO₂ concentrations, increased N deposition, longer growing seasons and afforestation (Maes et al., 2015). The change in the distribution range of invasive species in the future indicates higher probability of invasion in areas of low net ecosystem productivity and possibly low species richness (Fig. 6), which could alter local diversity and vegetation structure through various mechanisms such as allelopathic competition or rapid germination and growth (Hulme & Bremner, 2006; Vilà et al., 2006; Motard et al., 2011; Kieitky and Delimat, 2019). Impacts under future projections are located primarily in Eastern Europe and in the lower half of Scandinavia and the Alps. Hotspots of impacts on net primary productivity are expected to decrease for all four species under future projections. However, critical areas in Western Europe and the British isles are expected to increase for three of the four species (except for *I. glandulifera*), meaning that constant pressure of IP on low productivity areas is expected.

Soil erosion control is a key regulatory service that refers to the ability of ecosystems to retain soil and minimise natural or induced erosion. The capacity of ecosystems to avoid soil erosion has increased slightly between 2000 and 2010, at 0–1% (Maes et al., 2015). In this case, the impact of invasive species on erosion control may be most important in low provisioning (critical) areas, where even a slight reduction in the service provided by natural ecosystems can lead to important soil degradation and loss of vegetation cover. Climate change scenarios project a reduction of the pressure associated with IP in southern Europe, where the provision of erosion control is most critical (Fig. 7). We may highlight the potential impacts of *P. montana* in mountainous systems in the Alps region where soil erosion control is poor, and species spread is highly probable given our models results and current invasive distribution in the field.

4.4. Study limitations and research needs

The species investigated in this study are considered management priorities for the European Union, which does not necessarily mean they are among the worst invaders, let alone the most impacting upon ecosystem services. Other invasive species may present a more important threat to ecosystem services but unless we systematically evaluate a large number of species with the adequate tools (such as INSEAT), we lack evidence about the magnitude of potential impacts of invasive species on ecosystem services (Gallardo et al., 2019). We focused on impacts on three ecosystem services, however the four species pose a threat to additional services which require further evaluation, such as the regulation of the quality of air, water and soils, recreation and tourism. Likewise, there is an urgent need to understand inter-related global pressures on the provision of ecosystem services beyond climate change, including land-use change, overexploitation, and pollution.

Regarding predictors, we based our models on climatic variables that are often used to describe the large-scale niche of species and incorporated variables related to human transportation (Gallardo et al., 2015). Whereas accessibility partly accounts for land-use (Weiss et al., 2018) and can be used as a proxy of propagule pressure (Gallardo et al., 2017), land-use change often promotes the spread of opportunistic IP that are the first to colonise new open areas (Hobbs and Huenneke, 1992), and should be considered for future projections.

We must also note that models reflect suitability, that is, probabilities of invasion in the event of an introduction, and not absolute survival limits. A high suitability does not necessarily mean the species will establish, but simply that conditions are ideal. Environmentally suitable areas may never be occupied because of historical, dispersal or biotic limitations (Jiménez-Valverde et al., 2011). For the purpose of preventing species invasions it is nevertheless preferable to overestimate rather than to underestimate their potential distribution.

Because of the lack of future projections, we necessarily assumed that the provision of ecosystem services is maintained under future climate change. Certainly, after investigating trends over the last two decades (2000–2018), Maes et al., (2020) found rather small changes in the provision of ecosystem services in Europe (e.g. –1% in crop pollination, –0.1% in flood control per decade), but a considerable increase in the demand of ecosystem services (e.g. +7% in crop provision, +5% carbon sequestration, +3% flood control, +4% nature-based recreation), associated to increasing globalisation and consumption. Under such a scenario, invasive species constitute an additional pressure that may impair the flow of ecosystem services from natural ecosystems towards people. Future studies should consider the interplay between provision and demand of ecosystem services, both of which may vary spatially and be affected by invasive species differently.

Finally, the potential impacts of co-occurring invasive species beyond those investigated in this study deserve further attention, since the combined presence of multiple IAS may exacerbate their impacts (*sensu* invasional meltdown hypothesis, [Simberloff and Von Holle, 1999]) and could reach a point beyond which ecosystem functioning is severely or irreversibly compromised.

5. Conclusions

In this study we provide the first spatially-explicit evaluation of the potential impacts of IP at the continental scale, information that is fundamental to advance towards the development of future scenarios of invasion and guiding policy-making in Europe (Essl et al., 2019; Gallardo et al., 2019). Despite awareness of the susceptibility of ecosystems to biological invasions, impacts beyond biodiversity are still largely unknown, leaving threats to nature's contribution to society and good quality of life largely unquantified (Charles and Dukes, 2007). We conclude that the IP and climate change pose a threat to the provision of ecosystem services, particularly in the Atlantic and Continental

biogeographic regions. Further evidence is needed to quantify impacts and ensure that the provision of key ecosystem services – such as the provision of food and retention of soils – are protected independently from the underpinning biodiversity. Tools such as INSEAT in combination with species distribution models provide means to systematically evaluate the threat posed by multiple species in a comparable way, thereby allowing a more holistic assessment of the risks posed by IAS. This is important, since recent evaluations of the economic costs of invasion demonstrate that current investments in prevention and eradication could save trillions of dollars in diminished losses to human health, agriculture and forestry and in the preservation of natural systems and the services that they provide (Diagne et al., 2021). Bringing together ecology and economics to incorporate the impacts of IAS on ecosystem services into decision-making is key to restoring and maintaining the life-sustaining services that nature provides.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoser.2022.101459>.

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