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Research Article

# An ecoregion-based approach to evaluate invasive plant species pools

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## Abstract

Invasive alien species are an important component of global change, threatening biodiversity, ecosystem functioning, economy, and human health. The number of alien species that attain the invasive status has experienced an exponential increase in recent years, leading some government agencies and stakeholders to allocate substantial resources to early detection, control, mitigation, and eradication programs. To develop effective nature conservation strategies, it is crucial to understand the invasive status of alien species and to identify priority species for management at spatial scales with a biogeographical basis. Despite significant progress in producing lists of alien species at the country level, a standard methodology for species assessment within ecological regions (i.e., regions with similar environmental or biogeographical characteristics) is still lacking. Here, we develop a systematic approach to determine invasion status and to prioritize invasive alien plant species within an ecoregion. We apply this approach in the Cantabrian Mixed Forests ecoregion, which encompasses biogeographically related areas from N Portugal, NW Spain, and SW France, and is strongly affected by plant invasions. By combining scientific evidence with expert opinion on the ecological characteristics of alien plants, we identified 175 invasive plant species in the study ecoregion, of which 37 cause massive environmental and/or socio-economic impacts. For each species, we provide comprehensive information and recommendations for scientists, land managers, policy makers, and other stakeholders under a biogeographical basis. This information includes species characteristics, invasion status/level, population trends, geographic locations and range size, local abundance, environmental and socio-economic impacts, and invaded habitats. We also accounted for administrative divisions within the ecoregion to facilitate the use of such evaluations in local-scale management and conservation plans. Our framework may be applied to any ecoregion worldwide, enhancing the assessment and management of invasive species pools within biogeographically meaningful regions.

**Key words:** Cantabrian Mixed Forest ecoregion, Iberian Peninsula, invaded habitats, invasive alien plant species, invasion level, invasion status, invasive alien plant species, invasive species impacts, management

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## Introduction

Invasive alien species are an important factor associated with global change, causing multiple ecological, economic, and social impacts around the world (Vilà et al. 2011; Shackleton et al. 2019; Diagne et al. 2021). In the IPBES Regional Assessments and Global Assessment Report, invasive alien species were identified as one of the main leading causes of biodiversity loss worldwide (IPBES 2019, 2023). The challenge of understanding, preventing, and early detection of biological invasions is a key priority for strategies and action plans adopted by countries and organizations to tackle key drivers of biodiversity loss and to promote more sustainable and integrated environmental management (e.g., the European Union's Biodiversity Strategy for 2030, the Post-2020 Framework of the Convention on Biological Diversity, and the United Nations 2030 Agenda for Sustainable Development). Understanding the invasion status of alien species established in a territory and identifying priority species for management is, therefore, pivotal to improve conservation efforts in natural and semi-natural habitats.

Despite significant progress in producing lists of invasive alien species for individual countries (Sanz-Elorza et al. 2004; Essl et al. 2011; Gederaas et al. 2012; Marchante et al. 2014; Pergl et al. 2016), a standard methodology for the assessment of invasive alien species within ecological regions is lacking in the literature. Ecological regions (ecoregions, hereafter) are ecologically homogeneous units that occur within a country or across several countries (see for example Ecoregions2017 ©Resolve). The geographic distribution of ecoregions is related to abiotic (e.g., climate and soil) and biotic (e.g., dominant vegetation) factors, and they are assumed to encompass areas with a similar biogeographic history and recurrent local ecosystems (Bailey 2004). The importance of ecoregions in environmental assessment and management has long been recognized (Omernik 2004), providing a holistic framework for integrating research and management actions in relatively large geographical areas (Loveland and Merchant 2004). Since ecoregions are effective units for biodiversity studies and nature conservation, they should also be preferred as study areas for evaluating invasive alien species. Managing invasive species at the ecoregion scale has the advantage of generating information and applying management actions throughout ecologically homogeneous areas, which are likely to be invaded by species with similar ecological characteristics, i.e. to share invasive species pools. The invasive behavior of a given species in part of an ecoregion may be a good predictor of its invasive potential throughout the ecoregion. This ecoregion-based approach may improve current efforts to manage invasive species within and across political divisions. Assessments at the jurisdictional scale are more feasible to implement, but may only consider part of an ecoregion, excluding information from nearby ecologically similar areas, which could be key for control efforts. Thus, developing a method to prioritize trans-boundary management based on a biogeographical basis is important to tackle biological invasions.

Species invasion within ecoregions is a seral process that involves overcoming biotic and abiotic filters at local and landscape scales (Theoharides and Dukes 2007; Catford et al. 2009). After surpassing major biogeographical barriers (e.g., mountain ranges and oceans), alien species (a.k.a. introduced, exotic, non-native) must survive and form self-sustained populations to continue the invasion process within an ecoregion (naturalization stage; Catford et al. 2009; Fig. 1). Then, the naturalized species must produce reproductive offspring (either by seeds or other

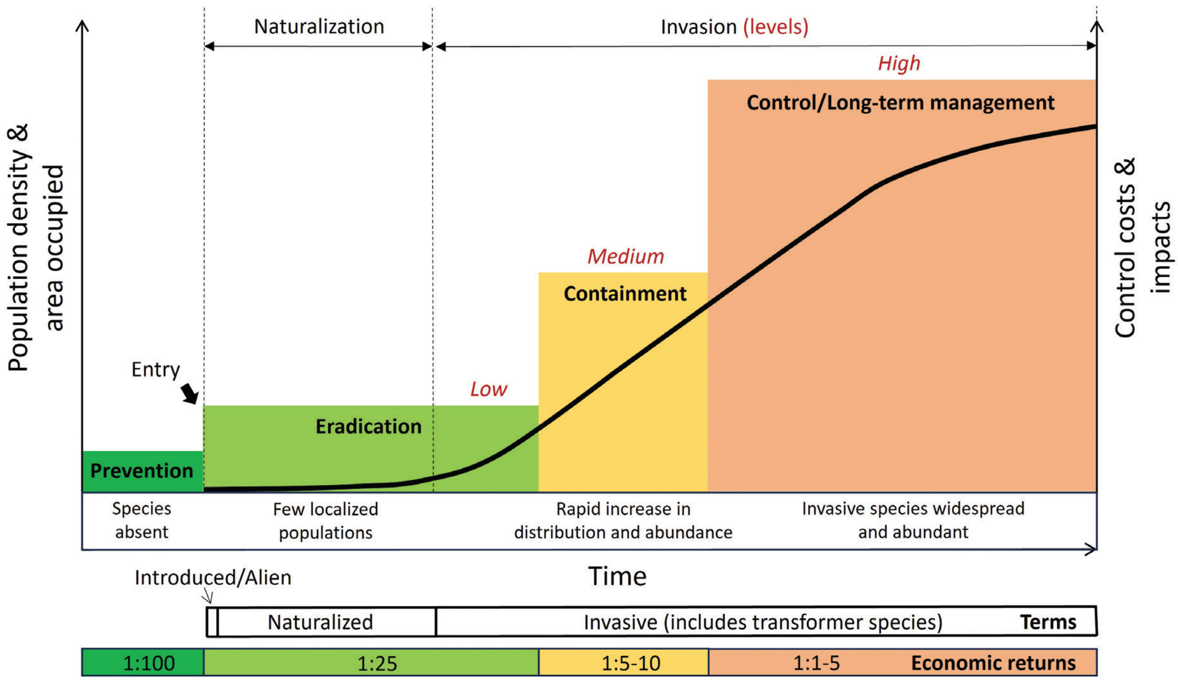


**Figure 1.** The generalized species invasion curve, adapted from Harvey and Mazzotti (2014) and Haubrock et al. (2022). Labels at the top refer to the stages of the invasion process (the invasion stage is divided into low, medium, and high level). Bold labels refer to management actions appropriate at each stage of invasion. White boxes below the graph indicate terms used to refer to alien species within each invasion stage. Economic return values listed at the bottom indicate the amount of money that is returned based on the money invested at each invasion stage, adapted from Victorian Government (2010) and Reid et al. (2021).

propagules), often in very large numbers, at considerable distances from the parent plants to be considered as invasive (Richardson et al. 2000; Pyšek et al. 2004). Such invaders can cause negative environmental, social, and/or economic effects within the ecoregion.

Once the alien species reaches the status of "invasive" within an ecoregion, its population density and range size progressively increase, at least until they fill a certain niche. Invasive species generally start with a small number of localized populations, whose eradication may be feasible, as represented in the widely accepted invasion curve (Harvey and Mazzotti 2014; Robertson et al. 2020; Haubrock et al. 2022; Fig. 1). However, invasive species are expected to rapidly increase in distribution and abundance throughout an ecoregion, because the specific environmental conditions of invaded areas (i.e., suitable areas) are spatially recurrent (Bailey 2004), thus, facilitating the invasion process. At this stage, the eradication of the species becomes unlikely, and managers should change their goals to limit further spread across the ecoregion with containment measures (Robertson et al. 2020). Finally, invasive species become widespread and abundant throughout the ecoregion, requiring long-term management aimed at population suppression and resource protection (Harvey and Mazzotti 2014; Haubrock et al. 2022). This control of invasive species should consider restoration measures, in an adaptative management approach (IPBES 2023). It is important to note that the invasion levels and management objectives described here (and depicted in Fig. 1) only apply to invasions in terrestrial and closed water systems, but not to marine and connected water systems (IPBES 2023).

Resources used for environmental management are often limited. The successful management of invasive species is often constrained by insufficient or inconsistent

funding and limited public awareness (Januchowski-Hartley et al. 2011). Thus, action plans generally consider which species should be targeted first, based on their distribution, local abundance, and environmental and socio-economic impacts on natural and semi-natural habitats (Pergl et al. 2016; Fristoe et al. 2021). Invasive species prioritization requires both quantitative data and expert knowledge based on scientific evidence that should be preferably related to a territory with similar environmental characteristics, considering both geographic and ecological features (i.e., an ecoregion).

In this study, we develop a systematic approach to determine the invasion patterns of the current invasive plant species and to identify priority species for management at the ecoregion level (Fig. 2). We applied this approach in the Cantabrian Mixed Forests, a European ecoregion severely affected by plant invasions. We combined published data with expert knowledge to 1) create a comprehensive list of the invasive alien plant species pool for the ecoregion, 2) provide information on invasion status/level (i.e., low, medium, and high levels of invasion), population

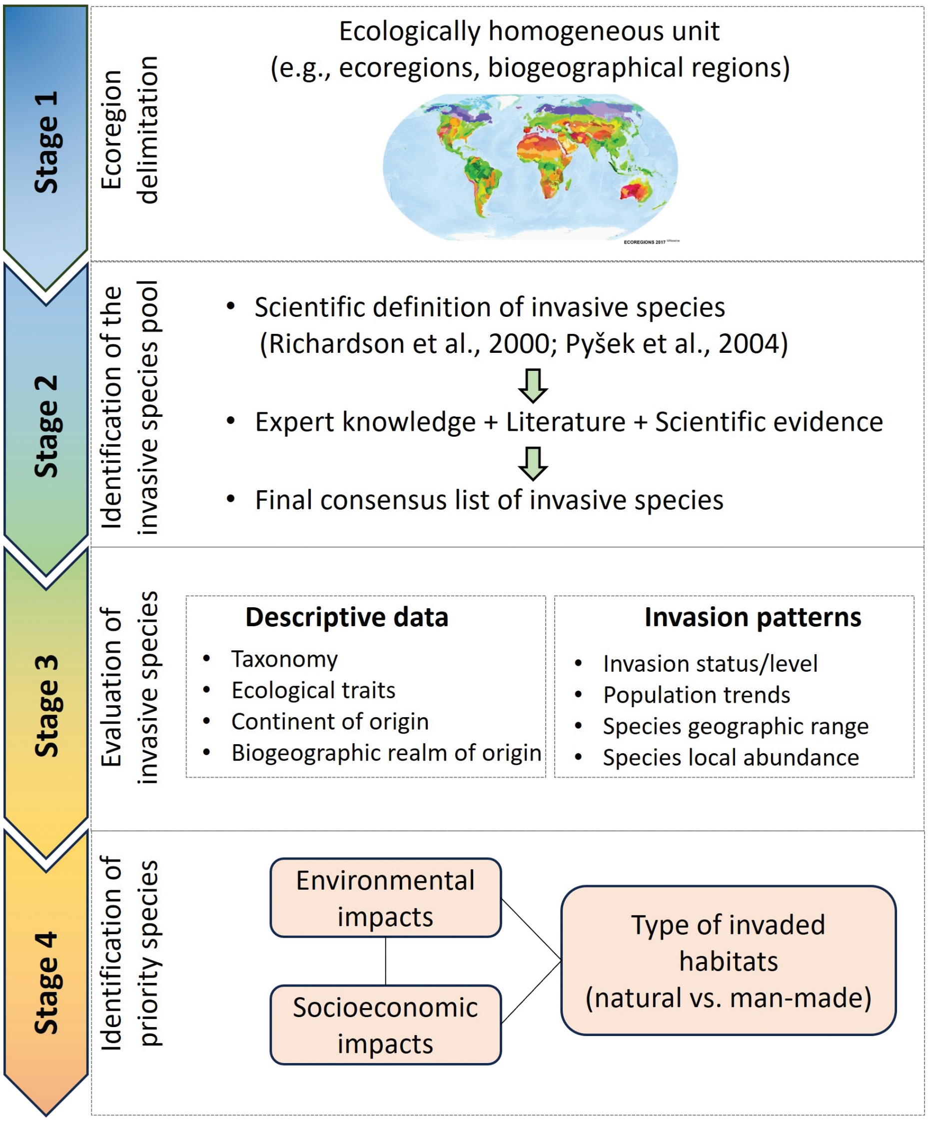


**Figure 2.** Proposed systematic approach to evaluate the invasive plant species pool of an ecoregion and to identify priority species for driving management actions.

trends, range size, and local abundance of each species, and 3) identify priority species based on their environmental and socio-economic impacts, and the type of invaded habitats.

## Materials and methods

### Study ecoregion

The study was conducted in the Cantabrian Mixed Forests ecoregion (Fig. 3) as defined by the World Wide Fund for Nature (WWF), and described in the RESOLVE Ecoregions dataset (Ecoregions2017 ©Resolve; https://ecoregions.appspot.com/). We slightly re-defined the ecoregion limits to accommodate the latest biogeographical updates in the Iberian Peninsula and SW France (Fernández-Prieto et al. 2020). The extent of the ecoregion largely fits with the Atlantic-European Province in the Iberian Peninsula (Rivas Martínez et al. 2011) and the Natura 2000 Atlantic biogeographic region in the Iberian Peninsula (https://ec.europa.eu/environment/nature/natura2000/platform/faq/index_en.htm). The ecoregion includes territories in north-western Portugal, north-western Spain, and a small area in south-western France, representing c. 20% of the Iberian Peninsula (Fig. 3). Administratively, the study ecoregion comprises the Spanish autonomous regions of Asturias, the Basque Country, Cantabria, Galicia, and northern parts of Navarra and Castilla y León (including the provinces of Zamora, León, Palencia, and Burgos), as well as the Portuguese provinces of Aveiro, Braga, Bragança, Porto, Viana do Castelo, Vila Real, and Viseu, and the south-western part of the French Nouvelle-Aquitaine region.

Unlike most of the Iberian Peninsula, this ecoregion provides optimal conditions for warm-temperate and humid ecosystems, with precipitation patterns determined largely by the frequency of Atlantic fronts from the northwest. Such climatic variation, together with its varied topography, soil types, and land uses, fosters a high diversity of ecosystems, being one of the most important areas for terrestrial biodiversity, carbon, and water conservation of the Iberian Peninsula (Jung et al.

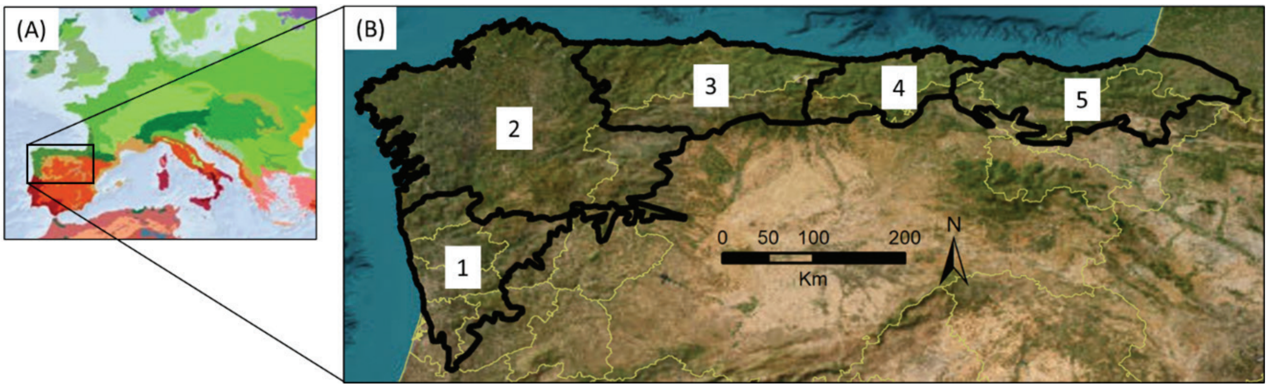


**Figure 3. A** ecoregions of western Europe, obtained from the RESOLVE Ecoregions dataset (Ecoregions2017 ©Resolve; https://ecoregions.appspot.com/). The black square includes the study ecoregion (in green), and part of other ecoregions **B** study ecoregion. Black lines delineate the study ecoregion and divide the different major areas within the ecoregion (see below), whereas yellow lines indicate Spanish autonomous regions and Portuguese provinces. Numbers correspond to major areas within the ecoregion: (1) north-western Portugal, (2) Galicia, western Zamora, and western León, (3) Asturias and northern León, (4) Cantabria, northern Palencia, and north-western Burgos, and (5) Basque Country, north-eastern Burgos, northern Navarra, and south-western French Nouvelle-Aquitaine.

2021). However, the studied ecoregion is also one of the most sensitive areas for biological invasions (Sanz-Elorza et al. 2004; Gassó et al. 2009; Aguiar and Ferreira 2013). In fact, the studied ecoregion is considered a current and future hotspot for plant invasions due to its benign climate and complex international trade connections, especially in the coastline (Gassó et al. 2012; Fernández de Castro et al. 2018). Current efforts to manage invasive species within the ecoregion are mostly conducted within political divisions (e.g., countries, administrative provinces, and regions mentioned above). A cross-boundary collaboration among political divisions (e.g., regions and countries) would likely enhance local and regional action plans aimed at preventing, early detection of, and control of biological invasions.

## Identification of the ecoregional invasive species pool

We first searched national and regional reports and databases to gather an initial list of plant species considered as invasive or potentially invasive in the study ecoregion (Sanz-Elorza et al. 2004; Fagúndez and Barrada 2007; González-Costales 2007; Campos and Herrera 2009; Marchante et al. 2021). We also gathered existing legal national lists of invasive species in use by the countries included in our ecoregion: Portugal (Decreto-Lei n.º 92/2019), Spain (Ley 42/2007, Real Decreto 630/2013, Real Decreto 216/2019, Orden TED/1126/2020, Orden TED/339/2023), and France (Inventaire national du patrimoine naturel; https://inpn.mnhn.fr). Then, we critically revised the initial list using a combination of local literature, expert knowledge, and evidence from both scientists and managers to create a complete and uniform (i.e., ensuring that the same definition of invasive was used) checklist of invasive plant species present in the ecoregion, here called the "ecoregional invasive plant species pool". We checked the World Flora Online (http://www.worldfloraonline.org/) and the Kew POWO (https://powo.science.kew.org/) databases to assign the proper taxonomy names and the synonyms for each invasive species.

Alien species are those whose presence in a given region is due to intentional or unintentional human involvement (Richardson et al. 2000; Pyšek et al. 2004). We considered an alien plant species as invasive when it produces reproductive offspring (either by seeds or other propagules) in areas distant from sites of planting/sowing, without direct intervention by humans, independent of their environmental, economic, and social impacts (sensu Richardson et al. 2000; Pyšek et al. 2004). This definition of invasive species is widely accepted among the scientific community, and separates species dispersal from their impacts (Catford et al. 2009). Those species that cause impacts are usually termed transformers (Richardson et al. 2000; Pyšek et al. 2004; Catford et al. 2009). However, legal definitions, and some authors, use the term invasive to refer to those established alien species that threaten or have adverse impacts on biodiversity and ecosystem services (IPBES 2023; Portuguese "Decreto-Lei n.º 92/2019"; Spanish "Ley 42/2007" and "Real Decreto 630/2013"). To have the most comprehensive list of invasive alien species, we included alien species already producing reproductive offspring in areas distant from sites of introduction in the study ecoregion and that have the potential to cause environmental alterations and socio-economic losses on the ecoregion (or are already causing them). However, we considered the impacts caused by each invasive species to identify priority species for management, as explained below.

We collected descriptive data on the ecoregional invasive species pool from online databases, such as World Flora Online (http://www.worldfloraonline.

org/), Kew POWO (https://powo.science.kew.org/), USDA Plants (https://plants.usda.gov/), and Ecoregions2017 ©Resolve; https://ecoregions.appspot.com/). Descriptive data included: (1) growth form (graminoid or grass-like flowering plant belonging to the families Poaceae, Cyperaceae, and Juncaceae), forb/herb, vine, shrub, or tree), (2) lifespan (annual, biennial, or perennial), (3) growing environment (terrestrial or aquatic), (4) continent of origin (Africa, Asia, Australia/Oceania, Europe, North America, or South America), and (5) WWF biogeographic realm of origin (Afrotropical, Indo-Malaya, Australasia, Nearctic, Neotropical, or Palearctic).

## Evaluation of invasive alien plant species

### Invasion status/level and population trends

We divided the ecoregion into five areas corresponding to administrative units to facilitate the assessment of the species by local experts (co-authors of this study) who classified the invasion status/level and population trends of each species within their main areas of expertise. In Spain, the administrative units largely followed the boundaries of Spanish autonomous regions, in some cases merging proximal areas from regions that were not fully included (e.g., several counties from Castilla y León that belong to the study ecoregion). We defined three categories of invasion status/level: low, medium, and high (Fig. 1). Invasion levels were defined based on the distribution and abundance of the invasive species, which are usually correlated at the landscape scale. These invasion levels may be linked to categories of the invasion curve (Harvey and Mazzotti 2014; Haubrock et al. 2022), which shows management actions appropriate at each stage of invasion. It is important to note, however, that the invasion curve concept was not originally intended to be used for invasion level categorization. Low invasion level included those species whose invasion was localized in a few sites (small number of localized populations; eradication possible; e.g., *Xanthium spinosum* L. and *Yucca gloriosa* L.). Medium invasion level referred to those instances where several sites have been invaded (increase in distribution and abundance; eradication unlikely; containment may be the most adequate measure; e.g., *Tropaeolum majus* L.). High invasion level referred to widespread and abundant invasive species such as *Cortaderia selloana* (Schult. & Schult.f.) Asch. & Graebn. and *Robinia pseudoacacia* L. (long-term management aimed at population suppression and resource protection).

Population trends indicated the direction of change in the number of individuals or populations for each invasive species. Local experts assessed these population trends using information from invaded areas and their surroundings. We defined four categories of population trends: positive, negative, neutral, and unknown. Positive trends included species whose populations increase by their own means (natural dispersal). There may be human intervention (e.g., planting in gardens, for erosion control, etc.), but the taxon produces new breeding populations far from the plantation area. Negative trends referred to those instances where populations decrease, either by natural means (e.g., decrement of habitat suitability due to climate change) or by human interventions (management). Neutral trends included those species that maintain their populations (neither increase nor decrease). We used the category "unknown" to refer to those species for which there was not available information on population trends.

### Species geographic range

We obtained occurrence data for the invasive species pool at 1-km resolution (or higher) from different databases, including global databases such as the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; downloaded on 1 June 2023) and iNaturalist (https://www.inaturalist.org/; downloaded on 31 May 2023). We excluded records registered before 1950 to include relatively recent occurrence data and to avoid extinct populations. Also, we removed unsuitable data sources from GBIF (i.e., unknown data sources and fossil and living specimens such as plants living in botanical gardens) and iNaturalist (i.e., unverified data, cultivated individuals, and records without photos). We also obtained data from regional and national administration reports (e.g., González-Costales 2007), projects (e.g., LIFE Fluvial, https://www.lifefluvial.eu/; and LIFE Stop Cortaderia, http://stopcortaderia.org/), personal data bases (e.g., Juan Antonio Campos doctoral thesis), and from the Cantabrian (https://www.chcantabrico.es/) and Miño-Sil (https://www.chminosil.es/) hydrographic administrations. This literature search allowed us to build the most comprehensive and up-to-date database of invasive plant occurrences for the ecoregion (available at Mendeley Data repository; DOI: 10.17632/4gtnr58j2b.1). Geographic range sizes for each species were then calculated as the number of occupied 1×1 km cells across the ecoregion and within each major area of the ecoregion. Geographic ranges should not be confused with the above-mentioned invasion status/level, the latter providing a better representation of the species invasion level since it is based on expert-knowledge, and there are many species with missing spatial data at 1-km resolution (or higher).

### Species local abundance

Local abundance referred to the average cover of the species in the plant communities where it occurs, as defined by the cover/abundance scale of Braun-Blanquet, the most common scale used in vegetation surveys in the study area. We included average cover, but it is important to note that a species can reach different abundances depending on the type of invaded habitat. High abundance included those species with >50% of estimated average cover, based on expert knowledge (“4” and “5” categories of the Braun-Blanquet scale). Medium abundance included species with an average cover of 5–50% (“2” and “3” categories of the Braun-Blanquet scale). Low abundance included species with <5% of average cover (“r”, “+”, and “1” categories of the Braun-Blanquet scale).

## Prioritization of invasive alien plant species for management

We identified priority species for management based on their environmental and socio-economic impacts, as well as the type of invaded habitats.

### Environmental impacts

Environmental impacts on natural and semi-natural habitats were assessed based on the unified classification of impacts by Blackburn et al. (2014). Environmental impacts were assigned based on expert judgment into three levels: 1) limited/minimal (unlikely to have caused deleterious impacts on the native biota or abiotic

environment), 2) moderate (causes declines in the population densities of native species, but no changes to the structure of communities or to the abiotic or biotic composition of ecosystems), and 3) massive (leads to the replacement and local extinction of native species, and produces changes in the structure of communities and the abiotic or biotic composition of ecosystems; Blackburn et al. 2014).

### Socio-economic impacts

Socio-economic impacts on natural, semi-natural, and anthropogenic habitats were classified based on expert judgment into three levels: limited/minimal, moderate, and massive, based on the magnitude of their impact on agriculture, infrastructure, landscape (visual), and human health (Pergl et al. 2016).

### Type of invaded habitats

We identified which habitats were invaded by each species, based on expert knowledge. We used the European EUNIS habitat classification (Chytrý et al. 2020) to differentiate broad habitat categories: coastal habitats (marshes, dunes, beaches, and cliffs), wetlands (peatlands, bogs, and water bodies), grasslands (lands dominated by grasses, forbs, mosses, or lichens), shrublands (heathlands, scrub, and tundra), forests (forests and wooded lands), vegetated man-made habitats (crops, gardens, roadsides, hedgerows, and plantations), and constructed/industrial habitats (human settlements, buildings, and industrial developments).

### Priority scores

Each invasive species was assigned a score for the above-described categories: environmental impacts, socio-economic impacts, and type of invaded habitats. Environmental and socio-economic scores (separately) corresponded to 0 (limited/minimal impact), 0.5 (moderate impact), and 1 (massive impact). The score for the type of invaded habitats corresponded to 0 (species invading only man-made habitats such as vegetated man-made habitats and constructed/industrial habitats) and 1 (species invading natural habitats such as coastal habitats, wetlands, grasslands, shrublands, or forests).

Final priority scores ranged from 0 to 3 and corresponded to the sum of individual scores assigned to environmental impacts, socio-economic impacts, and type of invaded habitats. We categorized the invasive species into three prioritization categories, based on their priority scores: low (0 to 1), medium (1.5 to 2), and high (2.5 to 3) priority species.

## Results

### Ecoregional invasive species pool

We identified a total of 175 invasive plant species from 49 families in the WWF Cantabrian Mixed Forests ecoregion (Table 1; Suppl. material 1), which corresponds to approximately 4–5% of the ecoregional flora. Species considered as invasive in previous regional lists, but which were excluded in our invasive species pool, are shown in Suppl. material 2, along with the reason for their exclusion (i.e., naturalized species, archaeophytes, or even native species). Over half of the

species (55%) identified as invasive are included in the legal national lists of the countries that are part of the study ecoregion (Suppl. material 1). Specifically, 49% of the species are legally classified as invasive in Portugal (86 species), 21% in Spain (36 species), and 17% in France (30 species). The most represented families are Asteraceae, Poaceae, and Amaranthaceae, with 38, 25, and 13 species, respectively, whereas the rest of the families have eight or less species (20 families only have one species). Among growth forms, forb/herb is the best represented category (107 species), followed by graminoids (28), trees (14), vines (14), and shrubs (12; Table 2). Most of the invasive species are perennial (106), while annual (38) and biennial species (3) are less represented. Moreover, there are 25 species that behave as perennial or annual, and three as annual or biennial. Lastly, most species (156) are terrestrial, 10 can live in both terrestrial and aquatic ecosystems, and 9 are exclusively aquatic.

Most of the invasive species are native to the American Neotropical (76) and Nearctic (66) WWF biogeographic realms, followed by the Palearctic (41), Afrotropical (28), Indo-Malaya (22), and Australasia (12) realms (Suppl. material 1). The native range of 68 species extends over two or more realms. Regarding continent of origin, we found that most of the invasive species are native to North America (73) and South America (65). A relatively high number of species came from Africa (38) and Asia (36), whereas the native range of 16 and 12 species corresponded to Europe and Australia/Oceania, respectively. We found 60 invasive species that are native to two or more continents. Our invasive species list also includes 11 species that are native to the Mediterranean region of the Iberian Peninsula, but alien (and invasive) in our study ecoregion due to human introduction (Table 1; Suppl. material 1). Moreover, there are three hybrids that originated either from naturalized parental species in the introduced area (*Oenothera* × *fallax* Renner) or from artificial crosses (*Oenothera glazioviana* Micheli and *Platanus* × *hispanica* Mill. ex Münchh.).

## Invasion status/level and population trends

Most species have low or medium invasion levels in each major area within the ecoregion (Suppl. material 1), occupying a few localized sites (low level; 35–58%) or several sites (medium level; 21–47%). Only 15–20% of species invading each major area have a high invasion level, with widespread populations (Table 2).

There are more invasive species with positive population trends (26–66%) than negative (0–10%) or neutral (0–4%) trends in each major area within the ecoregion (Suppl. material 1). However, there is a high number of invasive species with unknown population trends (26–74%).

## Geographic range size

We found a high variability in the number of occurrence points at 1-km resolution that each invasive species has throughout the ecoregion (Table 2; shapefiles available at Mendeley Data repository; DOI: 10.17632/4gtnr58j2b.1). Most species (70%) have fewer than 100 registered occurrence points, 15% have 100–300 points, and 10% have 300–500 points. Only 5% of the species have 500–1,000 occurrence points (*Acacia dealbata* Link, *Prunus laurocerasus* L., *Robinia pseudoacacia*, *Pitto-*

**Table 1.** List of invasive plant species for the WWF Cantabrian Mixed Forests ecoregion. Species are separated according to their priority scores: high (2.5 to 3), medium (1.5 to 2), and low (0 to 1).

| | | | |
|---|---|---|---|
| **High priority species** | | | |
| *Acacia dealbata* | *Carpobrotus edulis* | *Hakea decurrens*[1] | *Paspalum dilatatum* |
| *Acacia mearnsii* | *Cortaderia selloana* | *Lemna valdiviana* | *Pontederia crassipes* |
| *Amaranthus hybridus* | *Crocosmia × crocosmiiflora* | *Ludwigia grandiflora* | *Reynoutria japonica* |
| *Baccharis halimifolia* | *Delairea odorata* | *Ludwigia peploides* subsp. *montevidensis* | *Robinia pseudoacacia* |
| *Bidens aurea* | *Dittrichia viscosa** | *Myriophyllum heterophyllum* | *Sporobolus indicus* |
| *Buddleja davidii* | *Elodea canadensis* | *Oenothera glazioviana* | *Tradescantia fluminensis* |
| *Bupleurum fruticosum** | *Elodea densa* | *Oenothera × fallax* | *Carpobrotus acinaciformis* |
| **Medium priority species** | | | |
| *Acacia longifolia* | *Cotula coronopifolia* | *Jacobaea maritima** | *Pinus radiata* |
| *Acacia melanoxylon* | *Cyperus eragrostis* | *Lobularia maritima** | *Pittosporum tobira* |
| *Ailanthus altissima* | *Eleocharis bonariensis* | *Lonicera japonica* | *Pittosporum undulatum* |
| *Aloe maculata* | *Erigeron bonariensis* | *Matthiola incana** | *Prunus laurocerasus* |
| *Alternanthera philoxeroides* | *Erigeron canadensis* | *Muhlenbergia schreberi* | *Pterocarya stenoptera*[2] |
| *Amaranthus graecizans** | *Erigeron floribundus* | *Myriophyllum aquaticum* | *Reynoutria sachalinensis* |
| *Amaranthus powellii* | *Erigeron karvinskianus* | *Oenothera rosea* | *Reynoutria × bohemica* |
| *Amaranthus powellii* subsp. *bouchonii* | *Erigeron sumatrensis* | *Oenothera stricta* | *Sporobolus alterniflorus* |
| *Amaranthus retroflexus* | *Euphorbia polygonifolia* | *Opuntia elata* | *Sporobolus pumilus* |
| *Arctotheca calendula* | *Hakea salicifolia* | *Oxalis latifolia* | *Stenotaphrum secundatum* |
| *Artemisia verlotiorum* | *Hedychium gardnerianum* | *Oxalis pes-caprae* | *Symphyotrichum subulatum* var. *squamatum* |
| *Arundo donax* | *Helianthus tuberosus* | *Paraserianthes lophantha* | *Tropaeolum majus* |
| *Azolla filiculoides* | *Helianthus × laetiflorus* | *Paspalum distichum* | *Valeriana rubra** |
| *Bacopa monnieri* | *Helichrysum petiolare* | *Paspalum vaginatum* | *Xanthium strumarium* |
| *Bidens frondosa* | *Hydrocotyle bonariensis* | *Petasites pyrenaicus* | *Yucca gloriosa* |
| *Bromus catharticus* | *Ipomoea indica* | *Phytolacca americana* | *Zantedeschia aethiopica* |
| **Low priority species** | | | |
| *Acacia provincialis*[3] | *Cyrtomium falcatum* | *Helichrysum foetidum* | *Potentilla indica* |
| *Agave americana* | *Datura stramonium* | *Hydrangea macrophylla* | *Salpichroa origanifolia* |
| *Ageratina adenophora* | *Dichondra micrantha* | *Impatiens balfourii* | *Selaginella kraussiana* |
| *Amaranthus albus* | *Digitaria debilis** | *Ipomoea purpurea* | *Senecio angulatus* |
| *Amaranthus blitoides* | *Digitaria ischaemum** | *Juncus tenuis* | *Senecio inaequidens* |
| *Amaranthus blitum* subsp. *emarginatus* | *Disphyma crassifolium* | *Lepidium didymum* | *Senecio tamoides* |
| *Amaranthus cruentus* | *Dittrichia graveolens** | *Lepidium virginicum* | *Setaria parviflora* |
| *Amaranthus deflexus* | *Dysphania ambrosioides* | *Matricaria discoidea* | *Sicyos angulatus* |
| *Amaranthus hypochondriacus* | *Eleusine indica* | *Mesembryanthemum cordifolium* | *Sisyrinchium angustifolium* |
| *Ambrosia artemisiifolia* | *Eleusine tristachya* | *Oenothera biennis* | *Solanum chenopodioides* |
| *Anredera cordifolia* | *Eragrostis virescens* | *Oenothera drummondii* | *Solanum mauritianum* |
| *Araujia sericifera* | *Erigeron primulifolius* | *Oxalis corniculata* | *Soleirolia soleirolii* |
| *Austrocylindropuntia subulata* | *Eucalyptus globulus* | *Oxalis purpurea* | *Soliva sessilis* |
| *Baccharis spicata* | *Euphorbia maculata* | *Panicum capillare* | *Sonchus tenerrimus** |
| *Bidens pilosa* | *Euphorbia prostrata* | *Panicum dichotomiflorum* | *Sorghum halepense* |
| *Cenchrus clandestinus* | *Euphorbia serpens* | *Paspalum notatum* | *Verbena brasiliensis* |
| *Cenchrus longisetus* | *Fallopia baldschuanica* | *Persicaria capitata* | *Verbena incompta* |
| *Cenchrus setaceus* | *Galinsoga parviflora* | *Persicaria pensylvanica* | *Veronica persica* |
| *Commelina communis* | *Galinsoga quadriradiata* | *Phyllostachys aurea* | *Vinca major* |
| *Cotula australis* | *Gamochaeta coarctata* | *Phytolacca heterotepala* | *Xanthium spinosum* |
| *Cyclospermum leptophyllum* | *Gladiolus undulatus* | *Platanus × hispanica* | |

*Species native to the Mediterranean region of the Iberian Peninsula, but invasive in our study ecoregion. [1]Often misidentified as *Hakea sericea* (Barker 1996). [2]Often misidentified as *Pterocarya × rehderiana* (Muñoz-Garmendia et al. 2015) [3]Often misidentified as *Acacia retinodes* (Magona et al. 2018).

**Table 2.** Descriptive data (left) and invasion patterns (right) of the ecoregional invasive species pool.

| Variable | Categories | Nº species (N = 175) |
|---|---|---|
| Growth form | Forb/Herb | 107 |
| | Graminoid | 28 |
| | Shrub | 12 |
| | Tree | 14 |
| | Vine | 14 |
| Lifespan | Annual | 38 |
| | Biennial | 3 |
| | Perennial | 106 |
| | Annual/Biennial | 3 |
| | Annual/Perennial | 25 |
| Growing environment | Aquatic | 9 |
| | Terrestrial | 156 |
| | Terrestrial/Aquatic | 10 |
| Continent of origin | Africa | 38 |
| | Asia | 36 |
| | Australia | 12 |
| | Europe | 16 |
| | North America | 73 |
| | South America | 65 |
| Biogeographic realm of origin | Afrotropical | 28 |
| | Indo-Malaya | 22 |
| | Australasia | 12 |
| | Nearctic | 66 |
| | Neotropical | 76 |
| | Palearctic | 41 |
| Invasion status/level* | High | 19–24 |
| | Medium | 23–63 |
| | Low | 47–63 |
| Population trend* | Positive | 31–88 |
| | Negative | 0–11 |
| | Neutral | 0–6 |
| | Unknown | 35–94 |
| Geographic range size (1×1 km cells) | ~3,000 | 1 |
| | 500–1,000 | 8 |
| | 100–500 | 44 |
| | <100 | 122 |
| Local abundance | High | 60 |
| | Medium | 70 |
| | Low | 45 |
| Environmental impacts | Massive | 32 |
| | Moderate | 59 |
| | Limited | 84 |
| Socioeconomic impacts | Massive | 18 |
| | Moderate | 41 |
| | Limited | 116 |
| Type of invaded habitats | Coastal habitats | 58 |
| | Wetlands | 67 |
| | Grasslands | 13 |
| | Shrublands | 22 |
| | Forests | 30 |
| | Vegetated man-made | 128 |
| | Constructed, industrial | 40 |

*Invasion status/level and population trends were evaluated within administrative units of the ecoregion, to facilitate the assessment of the species by local experts and the application of such evaluations in local-scale management and conservation plans.

*sporum tobira* (Thunb.) W.T.Aiton, *Buddleja davidii* Franch., *Acacia melanoxylon* R.Br., *Zantedeschia aethiopica* (L.) Spreng., and *Cyperus eragrostis* Lam.). The most represented species is *Cortaderia selloana* with ~3,000 occurrence points.

### Species local abundance

We found that 34% of the invasive species often reach a high cover (>50%) in the invaded areas of the study ecoregion (Table 2; Suppl. material 1). Moreover, 40% of the species usually reach a cover of 5–50% (medium abundance), while only 26% of the species generally have a low local abundance (<5% of average cover).

### Environmental impacts

According to the data now available, almost half of the invasive species (48%) are reported to cause limited/minimal impacts on the native biota or abiotic environment of natural and semi-natural habitats, 34% are reported to cause moderate impacts (i.e., declines in the population densities of native species, but no changes to the structure of communities or to the abiotic or biotic composition of ecosystems), and only 18% are reported to cause massive impacts (i.e., lead to the replacement and local extinction of native species, and produce changes in the structure of communities and the abiotic or biotic composition of ecosystems; Table 2; Suppl. material 1).

### Socio-economic impacts

Most of the invasive species (66%) are reported to cause limited/minimal economic and social impacts on agriculture, infrastructure, landscape (visual), and human health, 24% are reported to cause moderate impacts, and only 10% are reported to cause massive impacts on the society and economy of the study ecoregion (Table 2; Suppl. material 1).

### Type of invaded habitats

Vegetated man-made habitats (including crops, gardens, roadsides, hedgerows, and plantations) are the most invaded habitats, harboring populations from 73% of the invasive species (Table 2; Suppl. material 1). Coastal and wetland habitats are also invaded by a relatively high proportion of species within the ecoregion (33 and 38% of species, respectively). Constructed/industrial habitats, forests, shrublands, and grasslands have a lower proportion of the invasive species (23, 17, 13, and 7%, respectively).

### Priority scores

We identified 28 invasive plant species with high priority scores, 64 species with medium priority scores, and 83 species with low priority scores (Table 1, Suppl. material 1), based on their environmental and socio-economic impacts, as well as the type of invaded habitats (natural vs. man-made).

## Discussion

### Invasive species pool at the ecoregion level

This paper provides the first assessment of an invasive species pool at the ecoregion scale, with comprehensive information that can be used by scientists, educators, land managers, policy makers, and other stakeholders. We selected an ecoregion that is considered a hotspot of plant invasions due to its benign climate and complex international trade networks (Gassó et al. 2012; Fernández de Castro et al. 2018), but the same framework may be applied to any ecoregion of the world (excluding ecoregions (or their parts) that include marine and connected water systems (namely rivers), which present a different invasion process; IPBES 2023). Our invasive plant list included 175 alien species present in the WWF Cantabrian Mixed Forests ecoregion, all of them producing reproductive offspring in areas distant from sites of introduction, and with potential to cause environmental alterations and economic losses (or are already causing them). We are aware that this kind of reference lists cannot be definitive since the invasion process is dynamic and can be affected by many abiotic and biotic factors (Lockwood et al. 2013; Pergl et al. 2016; Hui and Richardson 2017). Furthermore, as it is based on expert knowledge, a list such as this may not be entirely consensual, as different experts may have different knowledge and perceptions of the territory and the species present within it. Thus, we will update the published list periodically in an open repository (Mendeley Data; initial list available at DOI: 10.17632/4gtnr58j2b.1), based on future feedback from researchers and managers, or when further discussions on the assessment of individual species or regional floras suggest additions or deletions to the proposed list.

Our ecoregional list of invasive plant species contains many species included in the legal national lists developed by the countries that are part of the study ecoregion (e.g., Portuguese “Decreto-Lei n.º 92/2019”, Spanish “Real Decreto 630/2013”, and French “Inventaire national du patrimoine naturel”). However, we also identified species with invasive behavior within the ecoregion that are not included in existing legal national lists, because such legal lists only include invasive species that cause environmental or economic impacts. Although most of the invasive species that are not included in national lists cause limited environmental and socio-economic impacts in the ecoregion, it is important to closely monitor them and to develop management plans to prevent potential impacts in the near future.

Our ecoregional assessment of invasive plant species may help managers and policymakers to develop action plans within and across political divisions. It is important to note that in Spain, which occupies most of the study ecoregion, the power over environmental matters is transferred to autonomous regions. Thus, management actions are generally developed at spatial extents lower than the ecoregion (i.e., our ecoregion encompasses several autonomous regions). For example, managers of a given jurisdictional area (e.g., Asturias) may use information on invasive species from nearby ecologically similar areas (e.g., Galicia) to predict invasion patterns and to improve management efforts. The ecoregional assessment may also facilitate collaborations among several jurisdictional areas to prevent, early detect, and control invasive species. Thus, ecoregional evaluations allow for the optimization of management plans across ecologically homogeneous areas. Given that legislation may not be sufficient to respond to the current threats of biological invasions (Pergl et al. 2016), ecoregional assessments should be prioritized for developing management plans within individual or administrative areas of a given ecoregion.

## Invasion status/level and population trends

Although we developed our framework in an ecoregion, i.e., a region with similar abiotic (e.g., climate and soil) and biotic (e.g., dominant vegetation) factors (Bailey 2004), we also accounted for administrative units within the ecoregion to assess invasion status/level and population trends. Thus, we provide information on invasion status/level and population trends for major areas that largely follow administrative boundaries within the ecoregion. We identified many species whose invasion was localized in a few sites or counties within the ecoregion (low invasion level; 35–58% of the species). Ideally, we would recommend the eradication of such species by implementing Early Detection and Rapid Response (EDRR) in administrative units of the ecoregion, which would be possible if management plans are developed shortly (Harvey and Mazzotti 2014; Robertson et al. 2020). However, in order to prevent further impacts, efforts must be focused on those species causing negative environmental and socioeconomic impacts, as we discuss in the Management priorities section below.

For the species already invading several sites (medium invasion level), eradication would be unlikely, but managers and policy makers can still contain the species and prevent further expansion across the study ecoregion (Robertson et al. 2020). However, 16–21% of species invading each major area have widespread and abundant populations (high invasion level), for which long-term management should be aimed at population suppression, resource protection, and habitats restoration (Harvey and Mazzotti 2014). We note, however, that in some situations (e.g., widespread low-impact species occupying highly disturbed areas with no conservation value), allocating a lot of resources associated with a low probability of success would not be the most optimal option, especially when it deviates resources from higher priority situations. In these cases, the "do-nothing" option should be considered, along with other measures such as burning and biological control.

Additionally, measures should be taken to prevent the introduction of species already present in some areas of the ecoregion but still absent in other(s). For example, prevention plans should be started in the western Spanish areas of the ecoregion to prevent the arrival of *Baccharis spicata* (Lam.) Baill., *Hakea decurrens* R.Br., and *Phytolacca heterotepala* H.Walter, which are already invading some areas of the Portuguese portion, and, if they enter, to early detect and quickly eradicate them. Moreover, our study indicates that we still lack information regarding population trends for many species, suggesting that field studies should focus on these species to investigate whether the invasive species is either experiencing rapid increase in distribution and abundance or, by contrast, undergoing population decrease by natural means (e.g., decline of habitat suitability due to climate change) or by human interventions (successful management).

## Species occurrence and local abundance

We have built the most comprehensive and up-to-date database of invasive plant species occurrences for the ecoregion, despite some limitations typically found in biodiversity observations (e.g., most records of occurrence are only of presence, and there is no information on the absence of the species in places where we have no records). Our database contains occurrence data at 1-km resolution (or higher) that can be used by scientists, managers, and policy makers to erad-

icate populations and control further spread of invasive plants. It is important to note that the number of occurrence points not always reflects only the distribution of the invasive species, but also the sampling biases of the data sources. In this sense, invasive species that are easier to spot (e.g., large terrestrial plants, plants with showy flowers or other distinctive feature), more accessible, or have more awareness activities or scientific projects targeting them (e.g., *Cortaderia selloana*, *Carpobrotus* spp. N.E.Br., or *Robinia pseudoacacia*) often have more occurrence points than invasive species that are less conspicuous or more difficult to spot. Besides occurrence data, we have compiled abundance data based on expert knowledge. Species that often reach high plant cover are more difficult to eradicate (34% of the identified invasive species, e.g., *Acacia dealbata*, *Bidens aurea* (Aiton) Sherff, *Buddleja davidii*, and *Crocosmia* × *crocosmiiflora* (Lemoine) N.E.Br.), because control efforts significantly increase once invasive plants form dense monospecific patches. However, most species often reach low or medium local abundance, which may facilitate management plans.

## Environmental and socio-economic impacts

We identified 37 invasive species with massive environmental and/or socio-economic impacts throughout the ecoregion (i.e., transformer species; sensu Richardson et al. 2000; Pyšek et al. 2004). Such species represent 21% of the invasive species present in the ecoregion and are reported to cause great impacts on community structure, ecosystem functioning, agriculture, infrastructure, landscape (visual), or human health. For example, *Reynoutria japonica* Houtt. and *Tradescantia fluminensis* Vell. form dense stands that reduce sunlight penetration and alter soil properties, suppressing native forest regeneration (Standish et al. 2001; Aguilera et al. 2010). *Baccharis halimifolia* L. converts the native herbaceous vegetation of coastal grasslands and estuarine communities into a landscape of monospecific woody stands, transforming the structure and function of littoral ecosystems (Fried et al. 2016; Lázaro-Lobo et al. 2022). Invasive emergent floating-leaved plants such as *Ludwigia grandiflora* (Michx.) Greuter & Burdet and *Ludwigia peploides* subsp. *montevidensis* (Spreng.) P.H.Raven and free-floating plants such as *Pontederia crassipes* Mart. and *Lemna valdiviana* Phil. form dense floating mats, which shade out submerged vegetation, decreasing the oxygen levels in the water column, and causing profound cascading impacts on insect assemblages and fish populations (Woodward and Quinn 2011; Lázaro-Lobo and Ervin 2021). Invasive submerged plants such as *Elodea densa* (Planch.) Casp. can outcompete other aquatic plant species and decrease species diversity (Yarrow et al. 2009). The invasive tree species *Acacia dealbata* and *Eucalyptus globulus* Labill. are fire promoters, increasing fire incidence, intensity, and spread rate, by producing and accumulating high-flammable biomass (Silva et al. 2009; Nunes et al. 2022). The pollen of *Ambrosia artemisiifolia* L. and *Cortaderia selloana* cause serious allergies and generate a second peak allergy season by blooming in late summer/fall, being a public health hazard (Nentwig et al. 2017; Rodríguez et al. 2021; Liendo et al. 2023). Lastly, control costs of invasive species can be massive. For example, containment actions on *Cortaderia selloana* populations in the autonomous region of Cantabria (northern Spain) were estimated to cost between €1,600,000–1,800,000 (LIFE Stop Cortaderia; http://stopcortaderia.org/).

## Type of invaded habitats

As expected, vegetated man-made habitats (including crops, gardens, roadsides, hedgerows, and plantations) were more prone to be invaded than areas that experience lower human interference. Such habitats are usually subjected to periodic disturbances that generate opportunities for alien plant colonization and establishment, also acting as dispersal corridors for invasive plants (Christen and Matlack 2006; Lázaro-Lobo et al. 2020). Gardens, agricultural lands, and tree plantations are the main source of invasive plant propagules, since most invasive plants are introduced for horticulture, agriculture, and forestry purposes (Richardson 1998; Reichard and White 2001). Also, many invasive plants are often planted or introduced in seed mixtures along linear infrastructures to provide ecosystem services such as erosion control and nutrient cycling (Lázaro-Lobo and Ervin 2019). However, several species can invade other habitat types that experience low human interference, depending on their individual ecological niches. Coastal and wetland habitats are especially vulnerable to plant invasions within the ecoregion, probably because such habitats have a high resource availability (especially wetlands), and experience periodic disturbances, which make them naturally susceptible to invasion (Campos et al. 2004, 2013; Giulio et al. 2020; Lázaro-Lobo and Ervin 2021). Additionally, wetland habitats are frequently invaded by species that reproduce vegetatively (e.g., *Alternanthera philoxeroides* (Mart.) Griseb., *Azolla filiculoides* Lam., *Elodea densa* (Planch.) Casp., *Myriophyllum heterophyllum* Michx., *and Pontederia crassipes*), which is one of the most important predictors of invasion success (Havel et al. 2015). Forests are generally less susceptible to invasion, especially undisturbed forested areas, as found by previous research (Tomasetto et al. 2013; Iannone et al. 2016).

## Management priorities

By evaluating the invasive plant species pool, we were able to identify 28 high-priority species for management at the ecoregional scale. Most such high-priority invaders (23 species) are included in legal national lists of invasive species in use by the countries that are part of the ecoregion. Some of the identified high-priority invaders already have widespread and abundant populations (i.e., high invasion level) throughout the ecoregion, such as *Acacia dealbata*, *Carpobrotus edulis* (L.) N.E.Br., *Cortaderia selloana*, *Robinia pseudoacacia*, and *Tradescantia fluminensis*. For those species, we propose the development of unified and cooperative control programs among the administrative units that comprise the ecoregion, aimed at population suppression, resource protection, and restoration of priority habitats. At the other extreme, some high-priority invaders have a small number of localized populations in one or a few administrative units, such as the aquatic species *Elodea canadensis* Michx., *Myriophyllum heterophyllum*, and *Ludwigia grandiflora*, and the terrestrial species *Amaranthus hybridus* L., *Bupleurum fruticosum* L., and *Oenothera* × *fallax*. For such invaders, we recommend the implementation of early detection and rapid response programs to eradicate the established populations (or contain them if eradication is not feasible).

It is important to note that our priority scores are based on the present situation and place great value on impacts; however, such scores will surely change in the future. For example, *Baccharis spicata* has a low priority score because nowadays it has minimal environmental impacts and invades only man-made habitats, but

it has the potential to rapidly increase its expansion throughout the ecoregion, increasing its impacts on natural habitats. Thus, priority scores will also be updated in subsequent versions of the dataset.

## Conclusions

This study demonstrates how the assessment of alien plant species at the ecological scale can be useful to identify priority species for management under a biogeographical basis. This information is key for optimizing resources used to control biological invasions (e.g., human effort, time, and funding), but also for evaluating long-term impacts of invasive species. We conclude that producing updated and revised catalogs of invasive species pools at the ecoregion scale is essential to evaluate biological invasions and to improve their management actions. Collecting ecoregional species pools will also be useful to prevent the local spread of invasive species from nearby areas with similar ecological and biogeographic characteristics.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

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### Author contributions

Conceptualization: BJA, ALL. Data curation: BJA, ALL, JAC, EFP, MIRB, HM, VGG, TEDG. Funding acquisition: BJA, ALL. Investigation: BJA, JAC, VGG, HM, EFP, ALL, MIRB, TEDG. Methodology: VGG, EFP, MIRB, JAC, ALL, TEDG, HM, BJA. Resources: MIRB, VGG, EFP, TEDG, JAC, BJA, HM. Supervision: BJA. Visualization: ALL. Writing – original draft: ALL. Writing – review and editing: TEDG, JAC, EFP, BJA, MIRB, HM, ALL, VGG.

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## Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### Invasive species list

Authors: Adrián Lázaro-Lobo, Juan Antonio Campos, Tomás Emilio Díaz González, Eduardo Fernández-Pascual, Víctor González-García, Hélia Marchante, María Inmaculada Romero Buján, Borja Jiménez-Alfaro

Data type: xlsx

Explanation note: Description of the invasive plant species identified in the WWF Cantabrian Mixed Forests ecoregion.



Link: https://doi.org/10.3897/neobiota.96.116105.suppl1

## Supplementary material 2

### Excluded species

Authors: Adrián Lázaro-Lobo, Juan Antonio Campos, Tomás Emilio Díaz González, Eduardo Fernández-Pascual, Víctor González-García, Hélia Marchante, María Inmaculada Romero Buján, Borja Jiménez-Alfaro

Data type: xlsx

Explanation note: Status of species excluded from our invasive species pool.



Link: https://doi.org/10.3897/neobiota.96.116105.suppl2