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Ecological niche and species traits: key drivers of regional plant invader assemblages

Wilfried Thuiller · Núria Gassó · Joan Pino · Montserrat Vilà

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Abstract Linking species traits to niche properties is fundamental to understand the spatial structure of invasive species assemblages and the invasion process itself. Using information on 74 invasive species in Spain, the aims of this paper are to (1) test whether invasive plant species assemblages follow a nested pattern at the regional scale, (2) inspect the relationship between range size and niche properties (position and breadth) of invasive species to test whether the nested pattern is a product of species niche overlap; and finally (3) examine how species traits of invaders are related to their niche properties. We show that regional invasive plant species assemblages in Spain are organized in nested subsets. Invasive species with restricted range occur in areas invaded by widespread invaders. By relating nestedness metrics to species' niche properties from multivariate analyses, we found that these restricted invaders are less tolerant of broad climatic and landscape conditions than widespread invaders. Finally, regarding the association between niche properties and species traits, we found that species with large environmental niche breadth commonly exhibit non N-fixing strategy, short-life span, and clonal growth, while those with niche position in anthropogenic coastal areas were perennial and clonal species of unintentional and agricultural origin. Using an integrative approach linking the regional spatial structure of invasive plant assemblages, species niche properties and species traits, we were able to understand the potential causes of invasive species distribution in Spain. The approach developed in this research could be easily applied to other areas to disentangle the mechanisms driving invasive species distributions.

Keywords Alien plants · Clonal growth · Disturbance · Invasiveness · Inference-based model · Life-history traits · Nestedness · Niche position · Niche breadth · Range size

Introduction

Lessening the ecological and socio-economic impacts of invasive species requires a comprehensive understanding

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W. Thuiller (✉)
Laboratoire d'Ecologie Alpine, CNRS-UMR 5553,
Université Joseph Fourier, BP 53, 38041
Grenoble Cedex 9, France
e-mail: wilfried.thuiller@ujf-grenoble.fr

N. Gassó · J. Pino
CREAF (Centre for Ecological Research and Forestry
Applications), Universitat Autònoma de Barcelona,
08193 Bellaterra, Catalonia, Spain
e-mail: n.gasso@gmail.com

J. Pino
e-mail: Joan.Pino@uab.es

M. Vilà
Estación Biológica de Doñana-Centro Superior de
Investigaciones Científicas (EBD-CSIC), Avda. Américo
Vespucio s/n, Isla de la Cartuja, 41092 Sevilla, Spain
e-mail: montse.vila@ebd.csic.es

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of the factors driving invasions (Mack 1996; Pyšek et al. 2010). Invasion ecology has mainly focused on the factors that make either a species an invader (Hamilton et al. 2005; Rejmánek 1995) or a habitat prone to invasion (Pauchard et al. 2004; Pyšek 2004; Stohlgren et al. 2005). However, these two approaches have been kept separate until recently, when such species have begun to be considered as having a set of intrinsic and extrinsic traits that result invasiveness (i.e. potential to invade) in certain environmental conditions (Jiang et al. 2010; Sax and Brown 2000; Shea and Chesson 2002; Thuiller et al. 2010b). This integrated approach is fundamental to understanding the composition of invasive species assemblages, because both species properties and recipient habitat characteristics are known to determine the level of invasion in habitats and regions.

From a biogeographic perspective, one might wonder whether certain invaders have very general requirements explaining their large distributional ranges and overlaps, or whether they need specific environmental conditions. This question has seldom been explored. In a general context, a first step would be to investigate if species assemblages are nested at the regional scale. In other words, are species present in species-poor sites only subsets of the species from species-rich sites? In this case, assemblages with few species tend to be made up of the most frequently occurring species, while the least frequently occurring species are not restricted to specific sites but occur in species rich areas. This pattern has been mostly investigated for native animal communities (Wright et al. 1998), and whether such a nested pattern is also found in invasive plant species assemblages is unknown.

In the case of invasive plants, species distribution could be the outcome of a combination of factors such as minimum residence time (Ahern et al. 2010; Gassó et al. 2010; Phillips et al. 2010; Wilson et al. 2007), propagule pressure (Lockwood et al. 2005; Pyšek et al. 2010) and species ecological requirements as represented by their realized ecological niche (Thuiller et al. 2005; Vázquez 2006; Jiménez-Valverde et al. 2011). Although several studies have applied niche theory to invasion biology (Fitzpatrick and Weltzin 2005; Gallagher et al. 2010; Roura-Pascual et al. 2009), little effort has been made to establish a link between the physiological, morphological and reproductive attributes of species and their niche properties like niche position (e.g. average position on a given gradient) and niche breadth (e.g. standard deviation around the average position on a given gradient) (but see Kühn et al. 2006; Niinemets 2001; Thuiller et al. 2010a). The investigation of this topic will enlarge our understanding on the relationship between invader range size (i.e. the size of the distribution area) and species traits (Gassó et al. 2009; Lloret et al. 2005).

We argue here that the range size of an invader is related to its niche (Brown 1995; Gaston and Blackburn 2000). A broader niche, for instance, might enable the species to become more successful and to reach large range sizes (Vázquez 2006). Our hypothesis is that a nested pattern of species assemblages could be the result of a niche overlap among rare and widespread invasive species (Gaston and Blackburn 2000), and differences among niches might be, in turn, a consequence of differences between species traits (Albert et al. 2010; Thuiller et al. 2004; Vázquez 2006).

We examined the size of invader plant species' ranges across mainland Spain, their traits and the environmental characteristics of invaded areas in order to (1) test whether invasive plant species assemblages at the regional scale follow a nested pattern, (2) inspect the relationship between range size and niche position and breadth to test whether the nested pattern is a product of species niche overlap; and finally (3) examine if certain species traits are related to niche position or niche breadth, and therefore, are related to a species' potential of becoming widespread.

Methods

Study region

Spain is located in the SW of Europe and occupies 493,486 km^2. The region has a long history of plant species introductions, enough for many species to be distributed across a wide range of environmental conditions (Sanz-Elorza et al. 2004). Due to its geographic, topographic, climatic and geologic heterogeneity, Spain has a high landscape and habitat diversity (Ninyerola et al. 2000; Valladares et al.

2005), including arid, Mediterranean, temperate and alpine ecosystems, providing a broad environmental range for plant invasions (Gassó et al. 2009).

Data set

Invasive species and traits

Data on the distribution of invasive neophytes (i.e. established aliens introduced after 1500) were extracted from the Atlas of Invasive Plant Species in Spain (Sanz-Elorza et al. 2004). Invasive species are defined following Pyšek et al. (2004): alien species with self-sustainable populations without direct human intervention that produces offspring at considerable distances from the parent plants, and thus have the potential to spread over large areas. The Atlas contains presence records for over 100 species at a resolution of 10 km UTM (Universal Transverse Mercator) grid, but we restricted the analyses to 74 species found at least in 10 UTM grid cells in mainland Spain. This was made to avoid sporadic species with relatively unknown distributions and to make sure we had enough information related to environmental descriptors. Due to the potential heterogeneity of sampling effort across the country and the consequent difficulty of distinguishing between the absence of invasive species and missing data, the analyses were also limited to UTM cells with at least one invasive species recorded. In order to have comparable pixels with similar land surface, we also excluded coastal UTM cells with a land proportion lower than 60 %. The final number of UTM cells included in the analyses was 2401.

For each species we calculated its range size as the number of occupied UTM cells (Gassó et al. 2010) and explored a list of intrinsic (i.e. seed size, clonal growth, longevity, life-form, dispersal and pollination syndromes, and nitrogen fixing capacity) and extrinsic traits (i.e. region of origin and pathway of introduction) that are commonly associated to invasiveness (Pyšek and Richardson 2007; Thuiller et al. 2006) (Table 1).

Residence time was estimated as the year of first bibliographic or herbarium record in Spain. All the above information was taken from Castroviejo et al. (1986–2000), Casasayas (1990), Bolós et al. (1993) and Sanz-Elorza et al. (2004). See Table 6 in Appendix for the trait values of all 74 species.

Table 1 Intrinsic and extrinsic species traits taken into account to explain invasive plant species niche position and breadth in Spain

	Category	Code
Intrinsic traits		
Seed size	Very large (>10 mm)	5
	Large (5–10 mm)	4
	Medium (2–5 mm)	3
	Small (1–2 mm)	2
	Very small (<1 mm)	1
N-fixing	Yes	Yes
	No	No
Clonal growth	Yes	Yes
	No	No
Longevity	Annual	Annual
	Biennial	Biennial
	Perennial	Perennial
Life-form	Chamaephyte	Ch
	Geophyte	Ge
	Hemicryptophyte	He
	Macrophanerophyte	Mc
	Mesophanerophyte	Ms
	Nanophanerophyte	Nn
	Therophyte	Th
	Vine	Vi
Dispersal syndrome	Anemochory	Wind
	Zoochory	Animal
	Hydrochory	Water
Pollination type	Anemophily	Wind
	Zoophily	Animal
Extrinsic traits		
Region of origin	America	AM
	South America	SM
	North America	NM
	Asia	A
	Europe	E
	Africa	SF
	Oceania	O
Pathway of introduction	Agriculture	A
	Gardening	G
	Silviculture	S
	Weed	W
	Unintentional	U

The different categories for each trait and the code used in Fig. 4 and Table 6 in Appendix are shown

Environmental data

Models for invader species' realized niches were based on information from a set of nineteen environmental predictors grouped under land cover, topographic and climatic variables (Table 2) gathered from different sources and averaged at 10 km UTM grid resolution. The proportion of main land cover categories (i.e. built-up areas, agricultural areas, forests, scrub and herbaceous vegetation, open spaces, wetlands and water bodies) were calculated from the CORINE Land Cover Map of Spain (http://www.fomento.es). Land cover diversity per UTM cell was estimated by calculating the Shannon index of the above-mentioned land cover categories (Shannon 1948).

Road length (m) and railway length (m) were calculated from maps obtained from the official server of the Spanish Ministry (http://www.cnig.es). We considered these human settlement variables as a measure of human footprint (Sanderson et al. 2002) and as surrogates for propagule pressure (Pyšek et al. 2002). Mean altitude (m) and altitude range (m) were calculated from the national Digital Elevations Model (DEM) at 100 m resolution (http://www.opengis.uab.es). Mean distance to the coastline (m) was calculated using MiraMon distance algorithms.

Finally, six climatic variables were calculated from the Digital Climatic Atlas of Spain (Ninyerola et al. 2005; http://opengis.uab.es/wms/iberia/index.htm), a grid set of 200 m × 200 m pixel size generated by modelling from the Spanish network of meteorological stations. We calculated the mean values per site of annual temperature (°C), minimum winter temperature (°C), temperature range (i.e. difference between maximum temperature in July and minimal temperature in January), annual rainfall (mm), summer rainfall (sum of the rainfall in June, July and August) and annual solar radiation (KJ m^{-2} day^{-1} μm^{-1}).

Nestedness in species assemblages

We used a nestedness index to estimate the degree of association among invasive species' occurrences in UTM cells. This procedure aimed at evaluating whether species composition in a given site was random (low nestedness) or species-poor sites were made up by the most frequent invaders from the regional pool (high nestedness). The minimum requirement for nestedness is that sites differ in their suitability, and species differ in their abilities to colonize and persist in them (Ryti and Gilpin 1987).

To validate the existence of a nested structure among species and sites, we estimated the nestedness index (N) as $N = (100 - T)/100$, where T is the so-called '*Temperature*' index, which measures the site-occurrence matrix disorder with values ranging from 0° to 100° (Atmar and Patterson 1993). Because we were interested in emphasizing ordered nestedness rather than disordered, we calculated the level of N, with values ranging from 0 (minimum N) to 1 (maximum N). N was calculated using the Nestedness Calculator Software (Atmar and Patterson 1993; Wright et al. 1998), which reorders the rows and columns of the matrix to minimize the unexpected occurrences, and pack the matrix into a state of maximal nestedness (i.e. sites in descending order of species richness and species in decreasing order of range extension). Then, T is calculated as the sum of squared deviations from the isocline of perfect nestedness of unexpected presences and absences, divided by the maximum value possible for the matrix, multiplied by 100. To assess the significance of T we compared the observed value of T with a benchmark of 500 random matrices provided by a null model in which each cell in the matrix has the same probability of being occupied (Gaston and Blackburn 2000). This is an efficient way to test if the observed nestedness differed from a random pattern (Wright et al. 1998).

Species' niche properties

To separate invader species niches based on species distribution and the environmental variables selected (Table 2), we used the outlying mean index analysis (OMI, hereafter), a method proposed by Dolédec et al. (2000) and implemented in the *ade4* library (Chessel et al. 2004) in R (R Development Core Team 2012). The OMI makes no assumption about the shape of curves of species response to the environment, and gives equal weight to species-rich and species-poor sites. This method determines niche position as the mean location of the species in the environmental space. Therefore, it measures the propensity of the species to select a marginal environment (as opposed to average or common environment where the mean position is close to 0). Niche breadth is calculated as the variability (SD) of the environment used by each species along the main axes calculated from the

Table 2 Environmental predictors and data sources used to model invasive plant species niche position and breadth in Spain

Variables	Data source
Landscape	
Percentage of built-up areas	CORINE Land Cover Map of Spain (http://www.fomento.es)
Percentage of agricultural areas	
Percentage of forests	
Percentage of scrub and herbaceous associations	
Percentage of open spaces	
Percentage of wetlands	
Percentage of water bodies	
Land cover diversity (Shannon index)	
Roads length (m)	Official server of the Spanish Ministry (http://www.cnig.es)
Railway length (m)	
Topography	
Mean altitude (m)	Digital Elevation Model (DEM) (http://www.opengis.uab.es)
Altitude range (maximum-minimum; m)	
Mean distance to the coastline (m)	
Climate	
Mean annual temperature (°C)	Digital Climatic Atlas of Spain (http://opengis.uab.es/wms/iberia/index.htm)
Temperature range (max July–min January; °C)	
Minimum winter temperature (°C)	
Annual rainfall (mm)	
Summer rainfall (mm)	
Mean annual radiation (KJ/m^2 day µm)	

environmental variables included in the OMI (Thuiller et al. 2004).

Species' niche properties as a predictor of range size

The niche concept states a three dimensional relationship between niche position, niche breadth and species abundance or range size in an assemblage (Shugart and Patten 1972). We modelled range size (i.e. number of UTM where each species is present, log transformed) as a function of niche position and niche breadth on the two main gradients selected by the OMI.

Because species are linked by phylogeny (Harvey and Pagel 1991), using species as independent data points may inflate the degrees of freedom (Blomberg et al. 2003; Felsenstein 1985) and increase the Type-I error. We thus built a phylogenetic tree for our 74 species. The topology of the supertree was constructed with phylomatic (http://www.phylodiversity.net/phylomatic/phylomatic.html, Webb et al. 2008). Branch lengths were set by assigning an age to stem family nodes based on Wikström et al. (2001), and interpolating the remaining branch lengths of the other nodes using the branch length adjustment (bladj) algorithm in Phylocom (Webb et al. 2008).

To test how species range might be explained by niche properties and minimum residence time, we used generalized least squares models (GLS) controlling for the potential correlation between species associated with phylogenetic history. The variance explained by the GLS model was estimated by extracted the R^2 value from the regression between observed species range and predicted ones from the GLS model. We used the *gls* function within package nlme in R (R Development Core Team 2012).

Species traits explaining species niche properties

We related species' niche properties (position and breadth) on the two main niche axes to species traits with the same approach than above; i.e. generalized least squares model (GLS) controlled by phylogeny. To measure the actual power of each species trait over niche position and niche breadth, we used a multi-model inference approach (Burnham and Anderson 2002; Link and Barker 2006) on selecting all-subsets of the GLS using the AICc (Akaike information criterion, Akaike 1974) measure. The weight of evidence (w_{pi}) of each species trait as a predictor of niche position and niche breadth can be simply estimated as the sum of the model AIC weights over all models in which the selected predictor appeared (Brook and Bradshaw 2006; Carboni et al. 2010; Thuiller et al. 2007). The predictor with the highest w_{pi} (the closest to 1) gets the highest weight of evidence (i.e. has the highest relative importance) to explain the response variable. This approach based on a set of multiple models is far more robust than inferring variable importance based on a single stepwise selected model (Burnham and Anderson 2002; Link and Barker 2006). We used the *dredge* function within the package MuMIn in R to run this overall analysis.

Results

Nestedness in species assemblages

Site-occurrence matrix temperature was 4.85°, which gave a level of nestedness (N) of 0.952. After comparing this value with a benchmark of 500 random matrices, with an averaged T of 29.9° ± 0.24 (i.e. a mean nestedness of 0.70), we found that the probability of a random replicate being equally or more nested than our study matrix was less than 0.0001. There was thus a high level of nestedness in the site-occurrence matrix, indicating that the species present in sites with low invasive plant richness were a subset of species also occurring in richer sites.

Species niches properties

The first two axes of the OMI successfully explained 45 and 32 % respectively of the total variability when separating invasive species niches (Fig. 1). The first axis (anthropization hereafter) summarised a gradient of human transformation. This gradient opposed highly built-up areas in flat lands (i.e. dense coverage of roads and railways) to high altitude areas far from the coast and with a relatively low urban pressure. The second axis (climate-landscape hereafter) opposed forested to cropland areas. Forested areas were associated with cold and humid mountain ranges within relatively diverse landscapes, while croplands were concentrated in lowlands with warm and dry climatic conditions. Species niche positions of invasive species were widely distributed on the environmental ordination diagram (Fig. 1), mostly on the lowland areas with a high degree of anthropization.

The species with a higher level of specialization (i.e. niche position in marginal environments in the study area and narrow niche breadth) had, in general, a nested niche inside the niche of more generalist species (see Fig. 2 for an example).

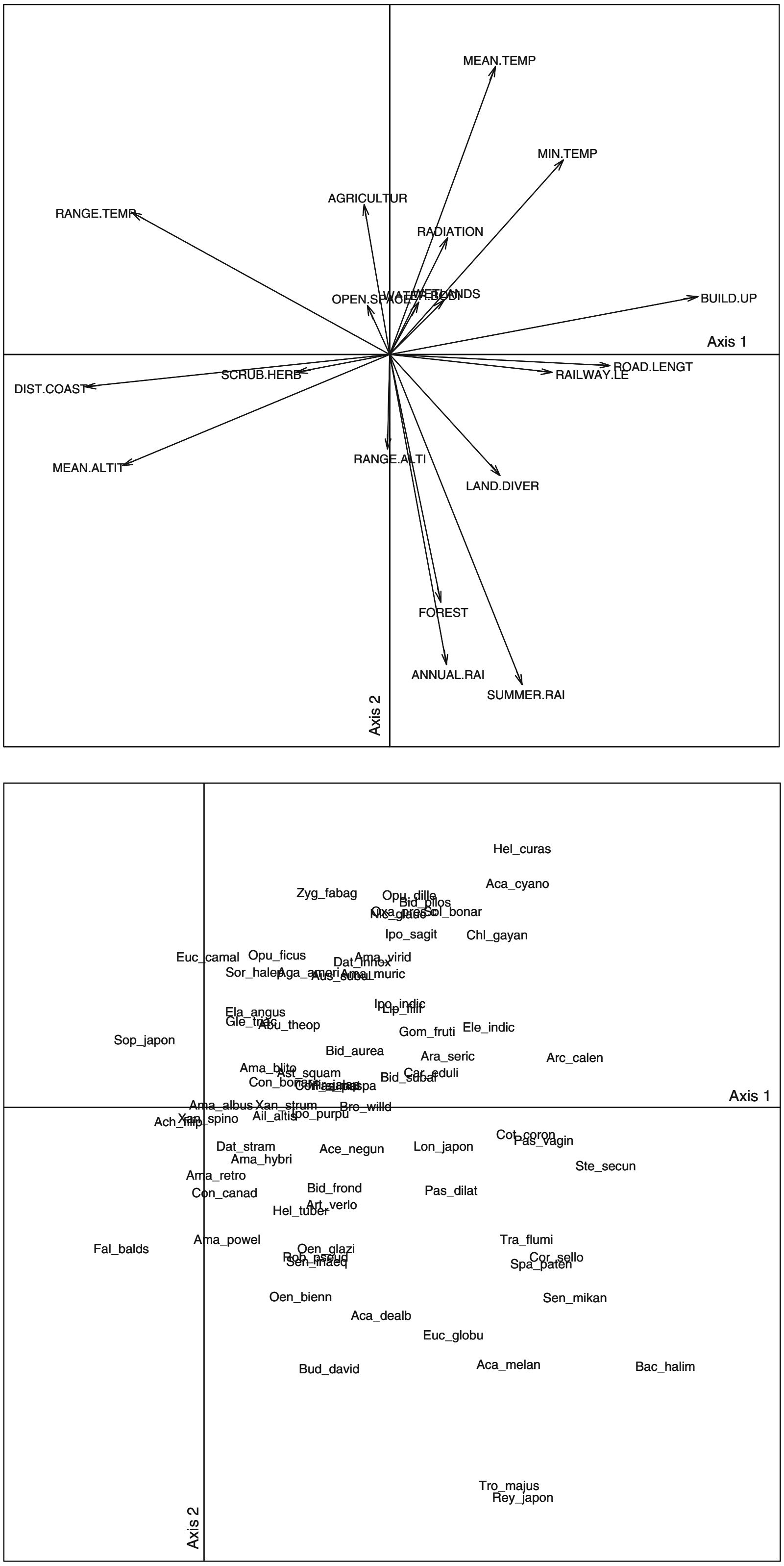
Species niche properties as a predictor of range size

The generalized least square model of range size as a function of niche position and breadth while accounting for phylogenetic relationships explained almost half of the variation in range size ($R^2 = 0.43$, $p < 0.0001$) (Table 3). In this model, range size was negatively related to position and breadth on axis 1. The species with niche positions close to the average environmental conditions showing small to medium niche breadth, such as *Sorghum halepense*, *Robinia pseudoacacia* or *Amaranthus retroflexus*, were also the species with the largest range size (Fig. 3, Table 5 in Appendix). Those species do not need to have a large niche breadth to have large range size given they occupy the most widespread environmental conditions. Species with restricted distribution ranges were found in highly human-disturbed places with a relatively wide tolerance over the anthropization gradient (Fig. 3). In contrast, range size was positively related with niche breadth on axis 2: large range size species were, on average, more tolerant of broad climate and landscape conditions represented by axis 2 (Table 3). Interestingly, minimum residence time had no influence on species range in respect to niche properties (Table 3).

Species traits explaining species niche properties

Models accounting for both niche position and breadth on axis 1 explained slightly more variance than models for axis 2 on the OMI ordination (Table 4).

Fig. 1 Representation of the explicative variables and niche position of 74 invasive plant species in Spain in the first two axes of the OMI ordination analysis. The first axis denotes a gradient of anthropization. The second axis is a gradient of climatic and landscape gradient from mountainous forested areas to lowland croplands. See Table 2 for a complete description of variables and Table 5 in Appendix for species acronyms



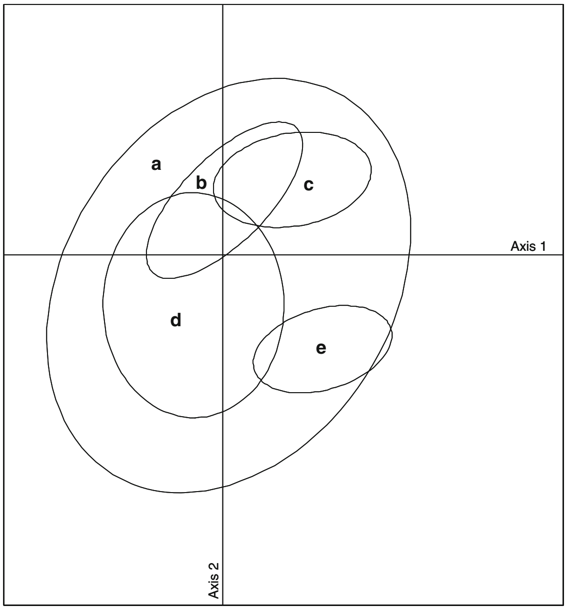


Fig. 2 Graphical representation of the niche of four invasive plant species with restricted distribution ranges: (*b*) *Eucalyptus camaldulensis*, range size = 75 UTM 10 km; (*c*) *Opuntia dillenii* 17 UTM; (*d*) *Fallopia baldschuanica*, 86 UTM and (*e*) *Acacia melanoxylon*, 71 UTM nested inside the niche of (*a*) *Conyza canadensis*, 505 UTM, a species with a wide distribution range. The first axis denotes a gradient of anthropization. The second axis is a gradient of climatic and landscape gradient from mountainous forested areas to lowland croplands. Niche position is the centre of each species ellipsoid and niche breath is the width of the ellipsoid as a function of the maximal deviation of site conditions from niche position

Table 3 Phylogenetic generalized linear models accounting for variation in the distribution range size of invasive plant species in Spain, as a function of their niche position and breadth on the main two axes of the OMI ordination and minimum residence time

	Value	SE	*t* value	*p* value
Intercept	5.66	0.47	11.95	<0.0001
Axis 1 position	−0.60	0.11	−5.68	<0.0001
Axis 1 breadth	−0.30	0.10	−3.12	<0.01
Axis 2 position	0.03	0.09	0.32	0.75
Axis 2 breadth	0.24	0.08	3.13	<0.01
Residence time	0.00	0.00	1.02	0.31

The model explained almost half of the variation in range size ($R^2 = 0.43$, $p < 0.0001$)

In general, species niche position over axis 1 representing a gradient of anthropization was mainly conditioned by longevity, N-fixing and clonal growth (Table 4). Perennial, N-fixing and clonal invasive species occur generally more in highly human-disturbed places close to the coast (Fig. 4).

Niche breadth over axis 1 was mainly related to pathway, N-fixing and longevity traits (Table 4). Species with wider niche breadth over the natural to human-disturbed gradient were predominantly introduced for gardening and agricultural purposes, are non N-fixing and biennial species. Reversely, small niche breadth species over axis 1 were predominantly species introduced for silviculture (Fig. 4).

Niche position over axis 2 representing a gradient from forested to cropland areas was mainly related to N-fixing species and longevity intrinsic traits and pathway of introduction (Table 4). Unintentionally introduced species, agricultural weeds, and crop plants were those present in the warmest, driest, agricultural areas. Species occurring in such habitats were perennial, non N-fixing species (Fig. 4).

Finally, species niche breadth over axis 2 was mainly affected by longevity, clonal growth and pathway of introduction (Table 4). Short-lived clonal species (i.e. annuals and biennials) introduced through agriculture (i.e. crops and weeds) had generally a wider tolerance to different climatic and landscape conditions than the other species (Fig. 4).

Discussion

Nested pattern and species niches

At the regional scale, invasive plant species assemblages in Spain are organized in nested subsets: species with restricted distribution ranges occur in sites with high invasive plant richness, whereas sites with few species are generally populated by widespread invaders. One of our initial hypotheses was that such a nested pattern could reflect species niche overlap. Here we show that range size is indeed related to niche position and breadth of invaders, suggesting a niche overlap among invasive plant species. However, there are several alternative explanations for this nested pattern. Nestedness might be generated by factors such as passive sampling effect, patch area and isolation, and habitat distribution (Wright et al. 1998), or may simply be an artefact of particular species' distributions (Gaston and Blackburn 2000). In our database, there could be a passive sampling effect

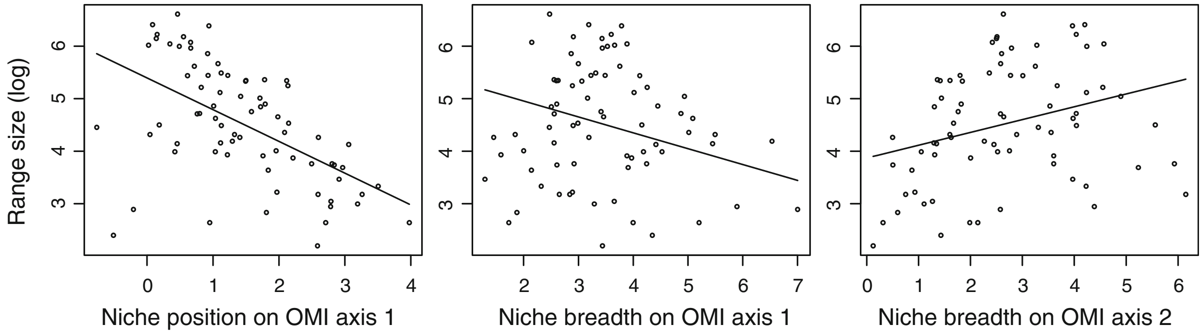


Fig. 3 Relationships between range size of invasive plant species in Spain and niche properties. Only the variables having a significant effect on range size are plotted (niche position on OMI axis 1, niche breadth on OMI axes 1 and 2). The first axis denotes a gradient of human-pressure. The second axis is a gradient of climatic and landscape gradient from mountainous forested areas to lowland croplands. The straight line corresponds to the estimated response of range size to niche properties by the GLS models

Table 4 Relative importance of the nine selected traits for explaining invasive plant species niche properties over axes 1 and 2 of the OMI ordination

Trait	Position axis 1	Breadth axis 1	Position axis 2	Breadth axis 2
N-fixing	**0.20**	**0.38**	**0.29**	0.31
Longevity	**0.26**	**0.23**	**0.28**	**0.61**
Dispersal syndrome	0.17	0.15	0.16	0.12
Pollination syndrome	0.18	0.16	0.22	0.25
Clonal growth	**0.20**	0.20	0.20	**0.32**
Seed size	0.00	0.02	0.06	0.04
Life-form	0.00	0.01	0.09	0.09
Origin	0.17	0.01	0.12	0.01
Pathway	0.05	**0.61**	**0.27**	**0.39**
R^2	0.20	0.27	0.13	0.23

The three traits with the highest relative importance on each niche property are shown in bold. The last row shows the variance explained by the models (all significant, $p < 0.0001$)

because the cartographic information of the Atlas of Invasive Plant Species in Spain (Sanz-Elorza et al. 2004) have been generated through 5 years of work compiling bibliographic and herbarium records. However, we minimized this effect by analysing only the cells with at least one invasive species and by selecting only species recorded at least in 10 UTM cells. Although we based the analysis in a grid cell of constant size (i.e. UTM 10 × 10 km), habitat isolation could also cause nestedness because only species with the highest colonization ability will be able to reach the most remote sites (Conroy et al. 1999; Kadmon 1995). Finally, the nested pattern of invasive species might also be determined by a similarly nested distribution of the habitat required for these species (Gaston and Blackburn 2000).

We show that all invasive species in Spain have their mean niche position from medium to highly anthropogenic sites, supporting the well-known association between invasion, human disturbance and human-mediated propagule pressure (Botham et al. 2009; Hobbs 1992). Other studies have also reported that the flora of urbanized areas and their surroundings is usually richer in alien species than natural areas (Carboni et al. 2010; Chocholouskova and Pyšek 2003; Seabloom et al. 2003). Thus, regionally rare species with restricted ranges are aggregated in highly anthropogenic areas, while widespread species have their niche positions closer to the average prevailing environmental conditions. Coastal areas in Spain have a mild climate and intense human pressures, concentrating tourism, trading and transport centres and, in turn, they accumulate most of the first records of alien species (Gassó et al. 2009).

The lack of association between range size and niche position on the climate-landscape gradient (2nd OMI axis) reinforces the idea that invasive species in Spain are not particularly constrained by environmental conditions. Nevertheless, range size was positively related to niche breadth along this gradient, which implies that broader niches in climate and landscape enable a species to become more widespread, as

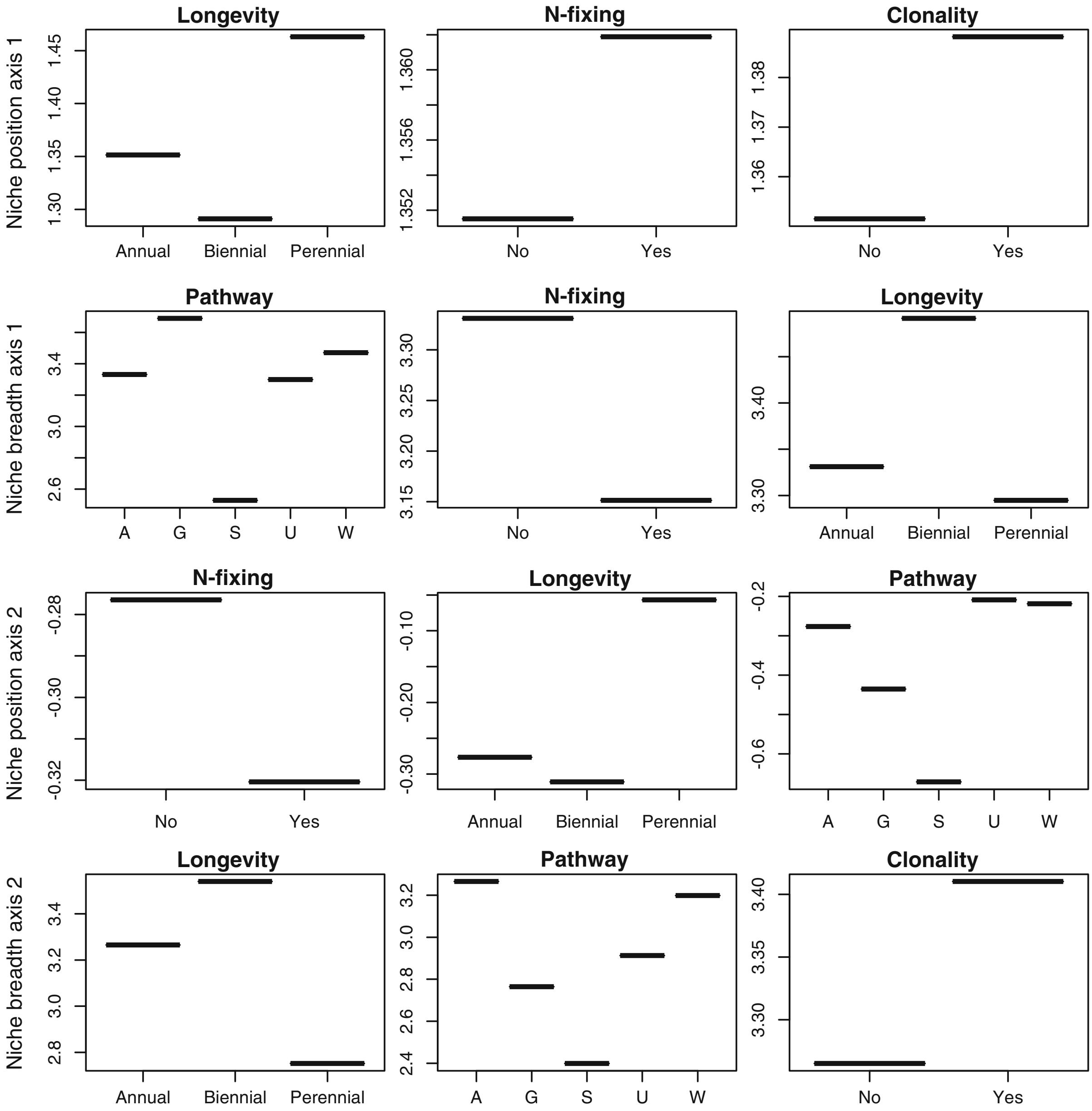


Fig. 4 Predicted mean niche value from the GLS models for invasive plant species traits. Only the three most important traits explaining niche properties are plotted (by order of importance from left to right). See Table 1 for trait code and Table 4 for trait importance (bold numbers)

suggested by other studies (Brown 1995; Brown et al. 1995; Vázquez 2006). Interestingly, widespread species are not necessarily more tolerant to a wide range of anthropogenic conditions than restricted species, and their mean niche positions are located in sites with moderate human-dominated landscapes. This provides evidence that the intermediate disturbance hypothesis also holds for invader species richness (Hobbs and Huenneke 1992; McKinney 2002).

Species niches and traits

An overview of the relationship between species niches and traits revealed that some intrinsic (longevity, N-fixing capacity, clonal growth) and extrinsic (pathway) traits are related to niche position and niche breadth. Nitrogen-fixing capacity is commonly related to invasion success because of the competitive advantage that it represents in nitrogen poor soils (Pyšek and Richardson 2007; Thuiller et al. 2006). However, the ability to fix N is usually at the cost of being specialised to N poor soils (Fitter 1996). This trade-off explains why N-fixing species mostly occur in coastal areas with high human pressure, where N-rich habitats (i.e. croplands) are scarcer than inland, and exhibit relatively smaller niche breadth in comparison to non N-fixing species that can occur more or less everywhere.

Short-lived invasive species occurred in the most widespread environmental conditions and they showed the highest tolerance to climate-landscape variation. Short-lived species have been suggested to be better invaders than long-lived types (Cadotte and Lovett-Doust 2001; Pyšek et al. 1995; Pyšek and Richardson 2007) due to their yearly reproduction or their survival as dormant seeds in adverse conditions (Crawley 1997). In our dataset, clonal species are indeed found in many different types of ecosystems (i.e. coastal, human-disturbed, hot and dry places) and have large niche breadth on the second environmental gradients revealed by the OMI.

Extrinsic traits have recently been considered as predictors of invasion success (Pyšek and Richardson 2007; Thuiller et al. 2006). To our surprise, the pathway of introduction, a component directly associated to human activity is related to niche position on the climate-landscape gradient rather than to niche position on the anthropization gradient. Species both introduced by agriculture (i.e. crops and weeds) and unintentionally are mostly found in warm, dry agricultural areas; and exhibit larger niche breadth on the climate-landscape gradient than those introduced by other means.

Conclusions

We demonstrate here that linking niche position and breadth with nestedness of species distributions and invader range size can bring insightful lessons. Our analysis reveals that at the regional scale invasive species with restricted distribution do not have specific topo-climatic requirements, but rather occur in human disturbed areas also invaded by generalist and widespread invasive species. The invaders with a restricted distribution range are less tolerant of broad climate-landscape conditions than widespread invaders. With regard to widespread invaders, these are the species invading the average environmental conditions in Spain but not climatically extremes or heavily human-disturbed sites. Those invasion patterns are, in turn, modulated by with specific life-history traits such as longevity, N-fixing capability and clonal growth.

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Appendix 1

See Table 5.

Table 5 List of 74 plant invader species modelled

Family	Species	Species acronym	Range size (no. of UTM)	Axis 1 position	Axis 1 breadth	Axis 2 position	Axis 2 breadth
Malvaceae	*Abutilon theophrasti*	Abu_theop	111	0.76	2.56	0.73	2.58
Fabaceae	*Acacia cyanophylla*	Aca_cyano	21	2.79	3.65	1.85	1.27
Fabaceae	*Acacia dealbata*	Aca_dealb	210	1.50	2.63	−1.85	1.61
Fabaceae	*Acacia melanoxylon*	Aca_melan	71	2.60	1.45	−2.30	0.50

Table 5 continued

Family	Species	Species acronym	Range size (no. of UTM)	Axis 1 position	Axis 1 breadth	Axis 2 position	Axis 2 breadth
Aceraceae	*Acer negundo*	Ace_negun	66	1.29	6.54	−0.39	2.27
Asteraceae	*Achillea filipendulina*	Ach_filip	18	−0.21	7.00	−0.15	2.58
Agavaceae	*Agave americana*	Aga_ameri	231	0.93	3.23	1.15	1.80
Simaroubaceae	*Ailanthus altissima*	Ail_altis	230	0.61	4.12	−0.09	3.01
Amaranthaceae	*Amaranthus albus*	Ama_albus	467	0.14	3.43	0.02	2.50
Amaranthaceae	*Amaranthus blitoides*	Ama_blito	483	0.55	2.91	0.34	2.51
Amaranthaceae	*Amaranthus hybridus*	Ama_hybri	402	0.49	3.53	−0.46	4.24
Amaranthaceae	*Amaranthus muricatus*	Ama_muric	207	1.49	3.06	1.14	1.84
Amaranthaceae	*Amaranthus powellii*	Ama_powel	90	0.19	4.16	−1.16	5.56
Amaranthaceae	*A. retroflexus*	Ama_retro	608	0.08	3.19	−0.59	4.20
Amaranthaceae	*Amaranthus viridis*	Ama_virid	116	1.58	3.41	1.27	1.76
Asclepiadaceae	*Araujia sericifera*	Ara_seric	93	2.15	2.99	0.39	1.67
Asteraceae	*Arctotheca calendula*	Arc_calen	24	3.26	2.65	0.41	6.15
Asteraceae	*Artemisia verlotiorum*	Art_verlo	167	1.11	4.02	−0.87	4.24
Asteraceae	*Aster squamatus*	Ast_squam	350	0.92	2.87	0.29	2.60
Cactaceae	*Austrocylindropuntia subulata*	Aus_subul	51	1.22	1.59	1.12	1.31
Asteraceae	*Baccharis halimifolia*	Bac_halim	14	3.98	1.73	−2.32	0.32
Asteraceae	*Bidens aurea*	Bid_aurea	75	1.33	5.50	0.46	2.89
Asteraceae	*Bidens frondosa*	Bid_frond	89	1.13	2.90	−0.72	4.04
Asteraceae	*Bidens pilosa*	Bid_pilos	25	1.97	2.89	1.75	0.93
Asteraceae	*Bidens subalternans*	Bid_subal	134	1.79	2.60	0.22	1.82
Poaceae	*Bromus willdenowii*	Bro_willd	155	1.42	4.94	−0.01	4.90
Buddlejaceae	*Buddleja davidii*	Bud_david	102	1.04	5.09	−2.31	3.98
Aizoaceae	*Carpobrotus edulis*	Car_eduli	105	1.98	3.46	0.27	2.64
Poaceae	*Chloris gayana*	Chl_gayan	24	2.59	2.84	1.45	0.75
Asteraceae	*Conyza bonariensis*	Con_bonar	389	0.66	3.44	0.22	2.79
Asteraceae	*Conyza canadensis*	Con_canad	505	0.15	3.60	−0.75	4.04
Asteraceae	*Conyza sumatrensis*	Con_sumat	289	1.08	3.00	0.17	2.58
Poaceae	*Cortaderia selloana*	Cor_sello	62	3.06	4.42	−1.37	2.45
Asteraceae	*Cotula coronopifolia*	Cot_coron	43	2.81	2.92	−0.26	5.93
Solanaceae	*Datura innoxia*	Dat_innox	71	1.41	3.19	1.25	1.63
Solanaceae	*Datura stramonium*	Dat_stram	421	0.35	3.89	−0.34	4.57
Elaeagnaceae	*Elaeagnus angustifolia*	Ela_angus	63	0.46	5.45	0.82	1.35
Poaceae	*Eleusine indica*	Ele_indic	43	2.50	4.25	0.66	3.60
Myrtaceae	*Eucalyptus camaldulensis*	Euc_camal	75	0.05	1.85	1.32	1.60
Myrtaceae	*Eucalyptus globulus*	Euc_globu	209	2.12	2.60	−2.03	1.42
Polygonaceae	*Fallopia baldschuanica*	Fal_balds	86	−0.76	2.47	−1.23	3.31
Caesalpiniaceae	*Gleditsia triacanthos*	Gle_triac	54	0.42	4.53	0.76	1.05
Asclepiadaceae	*Gomphocarpus fruticosus*	Gom_fruti	55	1.96	2.00	0.63	2.75
Boraginaceae	*Heliotropium curassavicum*	Hel_curas	42	2.84	2.61	2.21	0.50
Asteraceae	*Helianthus tuberosus*	Hel_tuber	184	0.82	4.26	−0.92	4.55
Convolvulaceae	*Ipomoea indica*	Ipo_indic	150	1.71	3.17	0.86	1.44
Convolvulaceae	*Ipomoea purpurea*	Ipo_purpu	129	1.01	4.45	−0.08	3.53
Convolvulaceae	*Ipomoea sagittata*	Ipo_sagit	38	1.84	2.14	1.48	0.87

Table 5 continued

Family	Species	Species acronym	Range size (no. of UTM)	Axis 1 position	Axis 1 breadth	Axis 2 position	Axis 2 breadth
Verbenaceae	*Lippia filiformis*	Lip_filif	50	1.76	3.89	0.86	3.60
Caprifoliaceae	*Lonicera japonica*	Lon_japon	78	2.09	5.02	−0.38	3.55
Nyctaginaceae	*Mirabilis jalapa*	Mir_jalap	242	1.12	3.32	0.18	2.36
Solanaceae	*Nicotiana glauca*	Nic_glauc	127	1.72	2.50	1.64	1.30
Onagraceae	*Oenothera biennis*	Oen_bienn	112	0.80	4.87	−1.67	4.04
Onagraceae	*Oenothera glazioviana*	Oen_glazi	54	1.04	4.19	−1.26	2.52
Cactaceae	*Opuntia dillenii*	Opu_dille	17	1.81	1.88	1.81	0.60
Cactaceae	*Opuntia ficus-indica*	Opu_ficus	434	0.66	2.15	1.32	2.42
Oxalidaceae	*Oxalis pes-caprae*	Oxa_pes.c	213	1.78	2.55	1.67	1.36
Poaceae	*Paspalum dilatatum*	Pas_dilat	190	2.14	2.89	−0.77	3.67
Poaceae	*Paspalum paspalodes*	Pas_paspa	231	1.22	3.49	0.18	2.77
Poaceae	*Paspalum vaginatum*	Pas_vagin	40	2.97	3.91	−0.32	5.24
Polygonaceae	*Reynoutria japonica*	Rey_japon	14	2.71	4.00	−3.46	2.14
Fabaceae	*R. pseudoacacia*	Rob_pseud	594	0.94	3.79	−1.33	3.97
Asteraceae	*Senecio inaequidens*	Sen_inaeq	14	0.95	5.20	−1.37	1.99
Asteraceae	*Senecio mikanioides*	Sen_mikan	20	3.19	3.29	−1.73	1.11
Solanaceae	*Solanum bonariense*	Sol_bonar	48	2.21	3.97	1.66	2.00
Fabaceae	*Sophora japonica*	Sop_japon	11	−0.51	4.35	0.60	1.43
Poaceae	*S. halepense*	Sor_halep	743	0.46	2.47	1.19	2.63
Poaceae	*Spartina patens*	Spa_paten	32	2.91	1.29	−1.41	3.97
Poaceae	*Stenotaphrum secundatum*	Ste_secun	28	3.51	2.32	−0.59	4.23
Commelinaceae	*Tradescantia fluminensis*	Tra_flumi	19	2.78	5.90	−1.21	4.39
Tropaeolaceae	*Tropaeolum majus*	Tro_majus	9	2.58	3.44	−3.35	0.12
Asteraceae	*Xanthium spinosum*	Xan_spino	411	0.02	3.66	−0.09	3.28
Asteraceae	*Xanthium strumarium*	Xan_strum	275	0.72	3.76	0.01	3.25
Zygophyllaceae	*Zygophyllum fabago*	Zyg_fabag	64	1.12	2.55	1.83	1.29

Distribution range size was measured as the number of UTM 10 × 10 km where the species was observed, and niche position and breadth were extracted from the 2 main axes of the OMI ordination

Appendix 2

See Table 6.

Table 6 Extrinsic and intrinsic species traits for 74 plant invader species in Spain

	Seed size	Longevity	Clonality	Dispersal	Pollination	N-fixing	Llifeform	Pathway	Origin	Origin code
Abutilon theophrasti	3	1	0	Animal	Animal	0	Therophyte	Agriculture	Europe	E
Acacia cyanophylla	4	3	1	Animal	Animal	1	Phanerophyte	Gardening	Oceania	O
Acacia dealbata	3	3	0	Animal	Animal	1	Phanerophyte	Gardening	Oceania	O
Acacia melanoxylon	3	3	1	Animal	Animal	1	Phanerophyte	Silviculture	Oceania	O
Acer negundo	5	3	0	Wind	Wind	0	Phanerophyte	Gardening	N America	NM
Achillea filipendulina	2	3	1	Wind	Animal	0	Geocryptophyte	Gardening	Europe	E
Agave americana	3	3	1	Animal	Animal	0	Chamaephyte	Gardening	N America	NM
Ailanthus altissima	5	3	1	Wind	Animal	0	Phanerophyte	Gardening	Asia	A
Amaranthus albus	2	1	0	Wind	Wind	0	Therophyte	Weed	N America	NM
Amaranthus blitoides	2	1	0	Wind	Wind	0	Therophyte	Weed	N America	NM
Amaranthus hybridus	2	1	0	Wind	Wind	0	Therophyte	Weed	America	AM
Amaranthus muricatus	2	3	0	Wind	Wind	0	Hemicryptophyte	Unintentionally	S America	SM
Amaranthus powellii	2	1	0	Wind	Wind	0	Therophyte	Weed	N America	NM
A. retroflexus	2	1	0	Wind	Wind	0	Therophyte	Weed	N America	NM
Amaranthus viridis	2	1	0	Wind	Wind	0	Therophyte	Weed	Africa	A
Araujia sericifera	4	3	1	Wind	Animal	1	Vine	Gardening	S America	SM
Arctotheca calendula	3	1	1	Wind	Animal	0	Therophyte	Unintentionally	Africa	AF
Artemisia verlotiorum	1	3	1	Wind	Wind	0	Geocryptophyte	Unintentionally	Asia	A
Aster squamatus	2	2	0	Wind	Animal	0	Therophyte	Unintentionally	America	AM
Austrocylindropuntia subulata	3	3	1	Animal	Animal	0	Phanerophyte	Gardening	S America	SM
Baccharis halimifolia	1	3	1	Wind	Wind	0	Phanerophyte	Gardening	N America	NM
Bidens aurea	2	3	1	Animal	Animal	0	Hemicryptophyte	Unintentionally	America	AM
Bidens frondosa	4	1	0	Animal	Animal	0	Therophyte	Unintentionally	N America	NM
Bidens pilosa	2	1	0	Animal	Animal	0	Therophyte	Unintentionally	America	AM
Bidens subalternans	2	1	0	Animal	Animal	0	Therophyte	Unintentionally	America	AM
Bromus willdenowii	3	2	0	Animal	Wind	0	Hemicryptophyte	Weed	S America	SM
Buddleja davidii	1	3	1	Wind	Animal	0	Phanerophyte	Gardening	Asia	A
Carpobrotus edulis	2	3	1	Animal	Animal	0	Chamaephyte	Gardening	Africa	AF
Chloris gayana	3	3	1	Wind	Wind	0	Hemicryptophyte	Gardening	Africa	AF
Conyza bonariensis	2	1	0	Wind	Animal	0	Therophyte	Unintentionally	America	AM
Conyza canadensis	1	1	0	Wind	Animal	0	Therophyte	Unintentionally	N America	NM

Table 6 continued

	Seed size	Longevity	Clonality	Dispersal	Pollination	N-fixing	Llifeform	Pathway	Origin	Origin code
Conyza sumatrensis	2	1	0	Wind	Animal	0	Therophyte	Unintentionally	S America	SM
Cortaderia selloana	3	3	0	Wind	Wind	0	Chamaephyte	Gardening	S America	SM
Cotula coronopifolia	2	1	0	Wind	Animal	0	Therophyte	Weed	Africa	AF
Datura innoxia	3	1	0	Animal	Animal	0	Therophyte	Unintentionally	S America	SM
Datura stramonium	3	1	0	Animal	Animal	0	Therophyte	Unintentionally	America	AM
Elaeagnus angustifolia	3	3	1	Animal	Animal	0	Phanerophyte	Gardening	Africa	AF
Eleusine indica	3	1	0	Wind	Wind	0	Therophyte	Weed	Asia	A
Eucalyptus camaldulensis	2	3	0	Wind	Animal	0	Phanerophyte	Silviculture	Oceania	O
Eucalyptus globulus	3	3	0	Wind	Animal	0	Phanerophyte	Silviculture	Oceania	O
Fallopia baldschuanica	1	3	1	Animal	Animal	0	Vine	Gardening	EAsia	A
Gleditsia triacanthos	4	3	1	Animal	Wind	1	Phanerophyte	Gardening	N America	NM
Gomphocarpus fruticosus	4	3	0	Wind	Animal	1	Phanerophyte	Gardening	Africa	AF
Heliotropium curassavicum	3	3	1	Wind	Animal	0	Geocryptophyte	Unintentionally	America	AM
Helianthus tuberosus	4	3	1	Animal	Animal	0	Geocryptophyte	Agriculture	N America	NM
Ipomoea indica	3	3	1	Animal	Animal	0	Vine	Gardening	America	AM
Ipomoea purpurea	4	1	1	Animal	Animal	0	Vine	Gardening	America	AM
Ipomoea sagittata	4	3	1	Animal	Animal	0	Vine	Unintentionally	America	AM
Lippia filiformis	1	3	1	Water	Animal	0	Chamaephyte	Gardening	S America	SM
Lonicera japonica	3	3	1	Animal	Animal	0	Vine	Gardening	Asia	A
Mirabilis jalapa	4	3	0	Wind	Animal	0	Hemicryptophyte	Gardening	America	AM
Nicotiana glauca	5	3	1	Wind	Animal	0	Phanerophyte	Gardening	S America	SM
Oenothera biennis	2	2	0	Animal	Animal	0	Hemicryptophyte	Gardening	N America	NM
Oenothera glazioviana	2	2	0	Animal	Animal	0	Hemicryptophyte	Gardening	Europe	E
Opuntia dillenii	3	3	1	Animal	Animal	0	Phanerophyte	Gardening	America	AM
Opuntia ficus-indica	3	3	1	Animal	Animal	0	Phanerophyte	Gardening	America	AM
Oxalis pes-caprae	1	3	1	Animal	Animal	0	Geocryptophyte	Weed	Africa	AF
Paspalum dilatatum	2	3	1	Wind	Wind	0	Hemicryptophyte	Weed	America	AM
Paspalum paspalodes	2	3	1	Animal	Wind	0	Hemicryptophyte	Unintentionally	America	AM
Paspalum vaginatum	2	3	1	Animal	Wind	0	Hemicryptophyte	Unintentionally	America	AM
Reynoutria japonica	3	3	1	Animal	Animal	0	Geocryptophyte	Gardening	Asia	A
R. pseudoacacia	3	3	1	Animal	Animal	1	Phanerophyte	Gardening	N America	NM

Table 6 continued

	Seed size	Longevity	Clonality	Dispersal	Pollination	N-fixing	Llifeform	Pathway	Origin	Origin code
Senecio inaequidens	3	1	1	Wind	Animal	0	Chamaephyte	Unintentionally	Africa	AF
Senecio mikanioides	2	3	0	Wind	Animal	0	Vine	Gardening	Africa	AF
Solanum bonariense	2	3	0	Animal	Animal	0	Phanerophyte	Gardening	S America	SM
Sophora japonica	5	3	1	Water	Animal	1	Phanerophyte	Gardening	EAsia	A
S. halepense	3	3	1	Wind	Wind	0	Geocryptophyte	Weed	Europe	E
Spartina patens	2	3	1	Animal	Wind	0	Geocryptophyte	Unintentionally	N America	NM
Stenotaphrum secundatum	1	3	1	Wind	Wind	0	Geocryptophyte	Gardening	America	AM
Tradescantia fluminensis	1	3	1	Animal	Animal	0	Geocryptophyte	Gardening	America	AM
Tropaeolum majus	4	1	0	Animal	Animal	0	Geocryptophyte	Gardening	S America	SM
Xanthium spinosum	3	1	0	Animal	Wind	0	Therophyte	Weed	S America	SM
Xanthium strumarium subsp strumarium	3	1	0	Animal	Wind	0	Therophyte	Unintentionally	America	AM
Zygophyllum fabago	3	3	0	Wind	Wind	0	Hemicryptophyte	Unintentionally	Europe	E

See Table 1 for a detailed description of categories

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