











## RESEARCH ARTICLE OPEN ACCESS

# From Purpose to Persistence: How Intentional Introductions by Humans Influence Ecological Niches of Non-Native Plants

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## ABSTRACT

**Aim:** The intentional or unintentional transport of non-native plants is key to overcoming geographic barriers. However, it remains unclear whether such introduction pathways associate with overcoming environmental barriers, which is key for successful invasion. Here, we test how intentionality of introduction associates with niche breadth and niche harshness.

**Location:** Europe.

**Time Period:** 1914–2020.

**Major Taxa Studied:** 220 plant species.

**Methods:** Across > 60,000 invaded vegetation plots, we tested whether intentionality of introduction (intentional, unintentional, or both) and characteristics of non-native plants (native climatic niche breadth, growth form, dispersal syndrome, height, residence time) were associated with their niche breadth, quantified through habitats, climate, and co-occurring flora. We tested how the intentionality of introduction was associated with environmental harshness (drought, salinity, oligotrophy, and elevation), while accounting for land-cover and habitat types.

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**Results:** Non-native plants introduced both intentionally and unintentionally had a broader habitat range, compared to non-native plants introduced only unintentionally. A broad climatic niche in the native range was associated with a broader invaded climatic niche, while a long residence time was associated with broader habitat and biotic niches. Intentional introduction was associated with the invasion of dry habitats and forests, whereas unintentional introduction was linked to the invasion of saline, high-elevation, and disturbed environments.

**Main Conclusions:** In addition to triggering invasions, the type of process responsible for introduction can partly explain how non-native plants overcome environmental barriers in the invaded range. The intentionality of introduction was associated with niche breadth only in terms of habitat range, while the association with niche harshness depended on the type of stress, which highlights the importance of integrative niche assessments. The relationship between intentionality of introduction and the invaded niche could relate to intentionality-specific differences in biological attributes (environmental tolerance, dispersal capacity, and preference for disturbance) and the introduction process (propagule pressure and residence time).

## 1 | Introduction

The current state of the Biosphere is unprecedented, as human activity has triggered a global wave of biological invasions (Roy et al. 2024). Indeed, a number of plant species equivalent to the native European flora have established self-sustaining populations outside their native ranges, thanks to human activity (van Kleunen et al. 2015; van Kleunen et al. 2019). In light of the pervasive impacts of invaders on biodiversity, ecosystem functioning, and human societies (Roy et al. 2024), it is crucial to gain a deeper understanding of invasion dynamics to develop effective conservation strategies (McGeoch et al. 2016).

The successful invasion by non-native plants requires overcoming geographical and environmental barriers: plants are first transported into a recipient area, where they vary in their ability to survive, reproduce, and disperse under a set of environmental conditions (Blackburn et al. 2011). A key factor in overcoming the geographical barrier is introduction pathways: processes that transport non-native plants, encompassing intentional and unintentional introductions (such as gardening and sowing of contaminated seed lots; Hulme et al. 2008; Harrower et al. 2018).

Introduction pathways can also be relevant for overcoming environmental barriers (Thuiller et al. 2006; Pyšek et al. 2011; Akatova and Akatov 2019; Riera, Pino, et al. 2024), because, although it is not a causal factor per se, plants with a common intentionality of introduction tend to share important characteristics that might shape their invasion dynamics (Novoa et al. 2020). Plants that share the intentionality of introduction tend to share biological attributes (Lambdon et al. 2008; Guo et al. 2019; Guo et al. 2022). For example, unintentionally introduced plants are more likely to be annual herbs and to have lighter seeds than intentionally introduced plants (von der Lippe and Kowarik 2012; Riera, Pino, et al. 2024). Moreover, intentionality of introduction also summarizes features of the introduction process that are difficult to measure, such as the human care and selection of suitable genotypes done by humans to ensure that intentionally introduced plants are successful (Donaldson et al. 2014; Pergl et al. 2017; Ni and Hulme 2021; Riera et al. 2021). Despite their potential usefulness, it remains poorly known whether the introduction intentionality (i.e., a coarse classification of introduction pathways) is associated with how non-native plants overcome environmental barriers. Given the potential of pathway-oriented management for preventing new introductions, a detailed understanding of

the role of intentionality of introduction is central to invasion ecology and effective management strategies (Hulme et al. 2008; McGeoch et al. 2016).

The link between intentionality of introduction and overcoming environmental barriers might be investigated by addressing two aspects of the plant's invaded realized niche (the set of invaded environmental conditions, Fristoe et al. 2021; Riera, Pino, et al. 2024). The first is niche breadth, which relates to the invasion under a wide range of environmental conditions (Catford et al. 2016; Fristoe et al. 2021; Palma et al. 2021; Riera, Pino, et al. 2024). Niche breadth is a rarely used metric for quantifying invasion success, which represents a relevant knowledge gap since invasion success is a multidimensional concept (mostly proxied through geographical spread or local abundance; Carboni et al. 2016; Catford et al. 2016; Fristoe et al. 2021). Previous works do not provide a consensus on whether intentionally or unintentionally introduced plants achieve wider niches (Pyšek et al. 2011; Thuiller et al. 2012; Banerjee et al. 2021; Rojas-Sandoval and Ackerman 2021; Riera, Pino, et al. 2024). In contrast, the relationship between niche breadth and a plant's pathway diversity (i.e., being introduced both intentionally and unintentionally, Pergl et al. 2017; Saul et al. 2017) remains untested and could yield further insights into how factors related to the introduction process explain invasion dynamics.

In addition to niche breadth, relevant insights can be obtained by studying niche harshness, which refers to the invasion of stressful environments in which abiotic conditions such as salinity or drought may jeopardize growth and reproduction (Alpert et al. 2000; Zefferman et al. 2015; Alexander et al. 2016). Harsh environments are usually resistant to invasion, and thus, it is important to understand whether the intentionality of introduction is associated with their vulnerability to invasion. Studies relating the intentionality of introduction to niche harshness have focused on elevation gradients, with contrasting results showing that high elevations are at greater risk of invasion from intentional or unintentional introductions (Thuiller et al. 2006; McDougall et al. 2011; Akatova and Akatov 2019; Chytrý et al. 2021; Riera, Pino, et al. 2024). To the best of our knowledge, other aspects of niche harshness, such as drought and salinity, have not been linked to the intentionality of introduction, which limits our understanding of factors explaining vulnerability to invasion in apparently resistant areas.

Here, we fill these gaps by testing hypotheses on how the intentionality of introduction is associated with the ability of non-native plants to overcome environmental barriers across Europe. First, we asked whether the intentionality of introduction was associated with the niche breadth of non-native plants, while accounting for key non-native plant characteristics (native climatic niche breadth, growth form, dispersal syndrome, height, residence time). We hypothesized that niche breadth would be greater among plants introduced both intentionally and unintentionally, with a long residence time in Europe, a wide niche in their native range, tall stature (i.e., the highest niche breadth among shrubs and trees), and seed dispersal mediated by animals. Second, we asked whether the intentionality of introduction was associated with the invasion of harsh environmental conditions by non-native plants (niche harshness). Thus, we modelled how environmental harshness filtered non-native plants according to the intentionality of their introduction. We hypothesize that harsh areas would be most at risk of invasion by intentionally introduced plants because they receive human care. Furthermore, we assessed the covariation between the intentionality of introduction and plant characteristics, which is helpful for understanding intentionality-specific macroecological patterns since the intentionality of introduction is not causal per se.

By studying the relationship between the intentionality of introduction and niche breadth we will advance our understanding of invasion success across its multiple dimensions, which is important for prioritizing management of species with the highest invasion potential (Carboni et al. 2016; Catford et al. 2016). Moreover, understanding the association between the intentionality of introduction and invasions in harsh areas is crucial, as these often harbour communities of high conservation value (Zefferman et al. 2015; Alexander et al. 2016).

## 2 | Materials and Methods

### 2.1 | Data

We extracted data for 1,237,259 vegetation plots from the European Vegetation Archive (EVA, accessed February 2021, Figure S1 and Table S1; Chytrý et al. 2016). Then, vegetation plots were classified into habitat types of the hierarchical habitat classification of the European Nature Information System (EUNIS; Chytrý et al. 2020). The classification was performed at three hierarchical levels: level three (166 types), level two (46 types), and level one (eight types). For example, a given vegetation plot could be classified as the habitat “Temperate *Salix* and *Populus* riparian forest” (level three), which is a type of “Broadleaved deciduous forests” (level two), which is itself a type of “Forests and other wooded land” (level one). The habitat classification was performed using a computer-based expert system based on attributes such as species composition and geographical position (Chytrý et al. 2020). We then reduced bias due to uneven sampling effort, by performing geographical resampling (Knollová et al. 2005): we overlaid a grid with cell size of 1.25' × 0.75' longitude × latitude (around 1.5 × 1.4 km) on the georeferenced plots and randomly kept a maximum of three plots for each combination of grid cell and habitat, using JUICE version 7.1 (Tichý 2002). We filtered the resulting 793,093 plots

by removing those classified as inland surface waters (thus increasing dataset's homogeneity) and those that could not be classified unambiguously to a unique habitat. Furthermore, we kept only the plots with at least one terrestrial neophyte, i.e., plants of extra-European origin introduced to our study area after 1500 AD (based on expert knowledge of the author team, and the Euro+Med database, <http://ww2.bgbm.org/EuroPlusMed/>). The final database included 220 non-native plants (and co-occurring flora) distributed across 75,957 plots in Europe (Figure S1), with the median area of 50 m<sup>2</sup> (range: 1–1000 m<sup>2</sup>) and the median year of collection of 1997 (range: 1914–2020). Of those plots, 81% ( $N=61,579$  plots) could be classified to the maximum level of detail in the hierarchy (level three), while the remaining 19% could only be classified to coarse habitat types (level one).

#### 2.1.1 | Assessment of Niche Breadth

To address our first question (how intentionality of introduction was associated with the niche breadth of non-native plants), we calculated five complementary metrics of niche breadth in the invaded range for each species: (i–iii) habitat range (at the three hierarchical levels of the EUNIS habitat classification system), (iv) biotic niche breadth, and (v) climatic niche breadth. Habitat range was a proxy of the breadth of vegetation types invaded by the species. We calculated it as the count of the different invaded habitats at three levels of the EUNIS hierarchy. The resulting variables were highly correlated with habitat range at level 1, so we focus on level 1 in the main text and show the results with levels 2 and 3 in Figures S2–S5 and Tables S2–S4. Biotic niche breadth was a proxy of the degree of habitat specialization, based on co-occurrences with native and non-native plants in the plots where the species was recorded (Zelený and Chytrý 2019). A habitat generalist would have high beta diversity among plots, since it co-occurs with a broad set of plants (the opposite is true for specialists). We calculated it by averaging Whittaker's multiplicative beta (Zelený and Chytrý 2019) across ten randomly drawn samples (ten plots per random sample, with replacement; ‘genspe’ package, Zelený 2015). Before calculation, we removed outliers (plots with a very different species composition, Botta-Dukát 2012). The resulting units were the mean number of invaded communities with no overlap in species composition. Climatic niche breadth was a proxy of the breadth of climatic conditions across plots invaded by the species. We calculated it as the geometric mean of the standard deviations of the first five axes of a Principal Component Analysis (PCA) of a set of bioclimatic variables with low correlation (following Palma et al. 2021, Supplementary Methods). We extracted bioclimatic variables from CHELSA (Karger et al. 2017) using ArcGIS 10.7.

For each non-native plant species, we gathered data on the intentionality of introduction and a series of potential drivers of niche breadth (Table 1): climatic niche breadth in the native range, dispersal syndrome, growth form and height, while also accounting for minimum residence time (Pyšek et al. 2011; Thuiller et al. 2012; Ainsworth and Drake 2020; Lazzaro et al. 2020; Banerjee et al. 2021; Fristoe et al. 2021; Giulio et al. 2021; Palma et al. 2021). Intentionality of introduction to Europe was based on the aggregation of published databases (national and sub-national scale; Klotz et al. 2002; Riera et al. 2021;

**TABLE 1** | Variables used to relate niche breadth to non-native plant characteristics in our statistical models, split by response and explanatory variables.

Variable	Description and summary
<i>Response variables: niche breadth</i>	
Habitat range	Count of invaded habitats, at three levels of the EUNIS habitat classification system. We presented results for level 1 (range = 1–8, median = 4, CV = 0.46) in the main text, while levels 2 (range = 1–24, median = 6, CV = 0.67) and 3 (range = 2–113, median = 10, CV = 0.97) yielded similar conclusions (see Data S1). Unit = habitat
Biotic niche breadth	Degree of habitat specialization (range = 2.24–7.93, median = 5.81, CV = 0.18). Unit = mean number of communities with no overlap in species composition
Climatic niche breadth	Breadth of invaded climatic conditions, in ordination space (range = 0–1.53, mean = 0.83, CV = 0.37). Unit = standard deviations
<i>Explanatory variables: non-native plant attributes</i>	
Intentionality of introduction	The mode of transport and introduction of a plant to a non-native range: ( $N = 3$ , both = 61, only intentional = 106, only unintentional = 53). Alternative coding yielded similar results (see Data S1): two categories (intentional = 167, unintentional = 114), and intentionality proportion (range = 0–1, median = 0.92, CV = 0.72, unitless)
Minimum residence time	Number of years since the first record outside of cultivation in our study area (range = 34–470, median = 160, CV = 0.55). Unit: years
Native climatic niche breadth	Breadth of climatic conditions inhabited in the native range, in ordination space (range = 0.134–1.829, median = 0.956, CV = 0.27). Unit = standard deviations
Height	Mean plant height reported in floras (range = 0.03–47.5, median = 0.82, CV = 2.02). Unit = meter
Dispersal syndrome	Main mechanism that disperses the seed away from the parental plant ( $N = 4$ : anemochorous = 46, endozoochorous = 40, epizoochorous = 17, unspecific = 117)
Growth form	Combination of longevity and growth habit ( $N = 3$ : annual herbaceous = 73, perennial herbaceous = 77, shrub/tree = 70)

Note: Values are provided with a dataset in which non-native plants introduced both intentionally and unintentionally were not duplicated ( $N = 220$  non-native plants). Abbreviations: CV, Coefficient of variation (standard deviation/mean); EUNIS, European Nature Information System.

Pyšek et al. 2022) and expert knowledge of the author team (custodians of databases covering multiple countries), complemented with a literature review (if no data were available in published databases). We gathered data from 14 sources (Table S5; full data in the online repository), which totalled eight low-overlapping sources after accounting for geographical overlap (sources were considered to have significant geographical overlap when they shared the country to which they contributed the highest amount of data; Table S5). Intentionality was scored using the Convention on Biological Diversity framework, with a focus on primary introduction pathways rather than secondary ones (Harrower et al. 2018). Examples of intentional introduction include many economically useful plants that are cultivated in forestry, planted as food source (crops), for ornamental (horticulture, gardening), medicinal, or gastronomical purposes, as forage for livestock, for erosion control, dune-fixing or wind-breaking. Examples of unintentional introduction include plants transported as contamination of seeds, soil, gravel, or wool, hitchhiking with construction or agricultural machines, cars, trucks or other transport vessels, or dispersed through ship ballast. The unaided spread of plants among European regions would be classified as an unintentional introduction, although we think that, given the large geographical area covered by many information sources, the impact of such unaided spread on our intentionality classification would be negligible. Gathering

intentionality information from a broad range of sources was necessary to account for the fact that non-native plants can be introduced in multiple non-exclusive ways (Harrower et al. 2018). We acknowledge that certainty in intentionality classification is not possible, given heterogeneous introduction histories across countries and the fact that the introduction events occurred decades or centuries ago (Essl et al. 2015). We coded the intentionality of introduction in three complementary ways: (i) three mutually exclusive categories (intentional, unintentional, both); (ii) intentionality proportion (sum of the number of assignments of intentional introduction weighted by the assignments of unintentional introduction and the overlapping of sources/total number of low-overlapping sources), (iii) two non-exclusive categories (intentional, unintentional; duplicating 61 non-native plants introduced both intentionally and unintentionally). Thus, we could account for diversity (i) and identity (ii, iii) of introduction pathways. For instance, *Erigeron canadensis* was assessed by thirteen different sources, but since many sources covered largely the same geographic area, the intentionality proportion of this species was calculated relative to seven low-overlapping sources. We weighted each assignment of “intentional introduction” by each information source based on: (i) the number of sources the focal source overlapped with, and/or (ii) whether the same source also assigned “unintentional introduction” in addition to the intentional one. In this example, *E. canadensis*

was assigned an intentional introduction by three sources, here called A, B and C: sources A and B partly overlapped with another source (weight: 1/3 each), source C also assigned an unintentional introduction and partly overlapped with another source (weights: 1/2 and 1/2). This species was coded in separate models as follows: (i) the “both” category, (ii) an intentionality proportion of:  $(1/3 + 1/3 + (1/2)/2)/7 = 0.131$ , and (iii) the “intentional” and “unintentional” category (the species was duplicated). Native climatic niche breadth was a proxy of the breadth of climatic conditions endured by non-native plants in their native range, following the same methodology used to calculate the climatic niche breadth in the invaded range. We obtained occurrence data in the native range by overlying occurrence coordinates on polygons delimiting the native range of each non-native plant (‘sf’ package, Pebesma 2018). We downloaded occurrence coordinates from the Global Biodiversity Information Facility (GBIF, Chamberlain et al. 2022; GBIF 2022), and filtered the occurrences following published guidelines (Supplementary Methods; Feng et al. 2019; Zizka et al. 2019). The native range was taken from the Plants of the World Online webpage (<http://www.plantsoftheworldonline.org/>), and the polygons delimiting such native range were level 2 regions of the Taxonomic Database Working Group (Brummitt 2001). Dispersal syndrome was set as the main mechanism dispersing seeds away from the parental plant: anemochorous, endozoochorous, epizoochorous, and unspecific. It was inferred from the external morphology of the diaspore unless stated in databases (Sanz-Elorza et al. 2004; Chytrý et al. 2021). Growth form included both longevity and growth habit: annual herbaceous, perennial herbaceous, shrub/tree, as reported in published databases (Sanz-Elorza et al. 2004; Chytrý et al. 2021). Height was the mean plant height reported in floras, in meters (Chytrý et al. 2021; Pignatti et al. 2017–2019). Minimum Residence Time (MRT) was calculated as the difference between 2020 and the earliest year of first record outside cultivation in any European region, which we obtained from published databases (Klotz et al. 2002; Chytrý et al. 2016; Seebens et al. 2018; Seebens 2020; Chytrý et al. 2021; Riera et al. 2021), complemented by a literature review when no data were available. We also calculated abundance (median and 95% quantile), to assess whether niche breadth depended on local abundance (Supplementary Methods).

### 2.1.2 | Assessment of Niche Harshness

To address the second question (how the intentionality of introduction was associated with niche harshness of non-native plants), we quantified the proportional importance of intentional introduction to the invasion of each plot by calculating the arithmetic mean of the intentionality proportion of all non-native plant species in each plot. For example, in a plot containing *Robinia pseudoacacia* (intentionality proportion = 1) and *Erigeron canadensis* (intentionality proportion = 0.131), intentional introduction would have a proportional importance of:  $(1 + 0.131)/2 = 0.566$ . A direct pairwise combination of environmental conditions invaded by non-native plant species introduced through each intentionality was not advisable because a single plot may be invaded by many non-native plants, each introduced through a different combination. Therefore, a pairwise comparison would include a substantial number of duplicates, reducing the quality of the test.

We gathered data for each plot on environmental harshness, approximated through drought, salinity, oligotrophy, elevation, and annual mean temperature (Table 2). We used this broad selection of variables to model the multiple types of environmental harshness, which is known to reduce the presence of non-native plants (Alpert et al. 2000; Zefferman et al. 2015; Alexander et al. 2016). Salinity, drought, and oligotrophy were binary variables indicating whether each type of stress occurred in the level three habitat types to which each plot was classified (based on expert knowledge; Table S6). Elevation was available for each plot from the EVA database (Chytrý et al. 2020), while annual mean temperature was taken from CHELSA (Karger et al. 2017). We also gathered data on potential confounding variables, including proxies for anthropogenic disturbance: urban land-cover, cropland land-cover, habitat type, annual precipitation, longitude, latitude, and country. Annual precipitation data were extracted from CHELSA (Karger et al. 2017). Urban and cropland land-cover (proportion of each class in a 500 m buffer, excluding the seas and oceans) were extracted from the CORINE dataset. Habitat type was the level one habitat of the EUNIS classification (eight types). Longitude, latitude, and the country where the plot was located were available in the EVA database (Chytrý et al. 2016). We extracted climatic and land-cover data with ArcGIS v10.7. We used only the subset of plots, 61,579 plots classified to EUNIS level three habitats, since the detailed identity of each invaded habitat was necessary to calculate metrics of harshness that consider local conditions (salinity, drought, and oligotrophy). An overview of the distribution of non-native plants across harsh conditions and habitats in Europe is provided in Table S7.

### 2.1.3 | Statistical Analyses

To address our first question, we tested the association of niche breadth with intentionality of introduction, plant characteristics (native climatic niche breadth, dispersal syndrome, growth form, height), and minimum residence; by fitting phylogenetic generalized least square models (PGLS, with Pagel’s lambda optimized through maximum likelihood, ‘phylolm’ package, Tung Ho and Ané 2014). We built a phylogenetic tree for all non-native plants in our dataset, using the ‘V.PhyloMaker’ package (Jin and Qian 2019), with default settings (nodes = build.nodes.1, scenarios = “S3”), and bounded absent genera to a closely related genus. We fitted a separate model for each of the five niche breadth metrics and each of the three categories of intentionality of introduction ( $N = 15$  models, Table S2). Since the three categorizations reached similar results, we report only the model with intentionality as three exclusive categories (intentional, unintentional, both) in the main text. The remaining models are summarized in Figures S2–S4 and Tables S2–S4. To improve model fit, we ln-transformed the three habitat range metrics. Our models were not biased by collinearity (all variance inflation factors (VIFs) in all full models < 5, Table S2). To assess the association among niche breadth metrics, we calculated a Pearson’s correlation matrix (Figure S5). To assess whether the results on niche breadth were robust to the modelling approach, we also fitted Generalized Linear Mixed Models (taxonomy as random intercepts; Supplementary Methods). These supplementary models yielded very similar results to the PGLS models, and

**TABLE 2** | Variables used to relate niche harshness to the intentionality of introduction in our statistical models, split by response variable, explanatory variables describing multiple aspects of niche harshness, explanatory variables describing potential confounders, and random effects.  $N = 61,579$  plots.

Variable	Description and summary
<i>Response variable</i>	
Mean intentionality proportion	Proportional importance of intentional introduction for the invasion of each plot (range = 0.00–1.00, median = 0.28, CV = 0.86): arithmetic mean of the intentionality proportion of all non-native plants in each plot. For example, a plot containing <i>Robinia pseudoacacia</i> (intentionality proportion = 1) and <i>Erigeron canadensis</i> (intentionality proportion = 0.131) would have a mean intentionality proportion = $(1 + 0.131)/2 = 0.566$ . Unit = unitless
<i>Explanatory variables: niche harshness</i>	
Elevation	Vertical distance between plot and sea level (range = –7–2720, median = 166, CV = 0.99). Unit = meter
Annual mean temperature	Yearly average of temperature (range = –1.7–19.7, median = 10, CV = 0.25). Unit = °C
Salinity	Stress caused by the presence of salt in the soil, or sea-spray, in the level 3 habitat type to which the plot was classified ( $N = 2$ : no = 60,842, yes = 737)
Drought	Stress caused by the scarcity of moisture in the soil (at least seasonally), in the level 3 habitat type to which the plot was classified ( $N = 2$ : no = 51,353, yes = 10,226)
Oligotrophy	Stress cause by the scarcity of nutrients, in the level 3 habitat type to which the plot was classified ( $N = 2$ : no = 53,592, yes = 7987)
<i>Explanatory variables: potential confounders</i>	
Urban land-cover	Proportion of urban land-cover in a 500 m buffer around the plot, excluding the sea or ocean (range = 0.00–1.00, median = 0, CV = 1.55). Unit = unitless
Cropland land-cover	Proportion of cropland land-cover in a 500 m buffer around the plot, excluding the sea or ocean (range = 0.00–1.00, median = 0.43, CV = 0.79). Unit = unitless
Habitat type	Type of habitat that the plot was classified to, at level 1 of the EUNIS habitat classification system ( $N = 8$ : coastal = 1635, forest = 18,076, grasslands = 11,030, heathlands, scrub and tundra = 2004, little soil, sparse vegetation = 153, littoral biogenic = 308, man-made = 25,387, wetlands = 2986)
Annual precipitation	Yearly sum of precipitation (range = 203–2730, median = 691, CV = 0.31). Unit = millimetre
Longitude	Coordinate specifying the east–west position of the plot (range = –10.26–30.46, median = 14.47, CV = 0.58). Unit = degree
Latitude	Coordinate specifying the north–south position of the plot (range = 34.93–68.35, median = 49.19, CV = 0.08). Unit = degree
<i>Random effect</i>	
Country	Country in which the plot was located ( $N = 37$ )

Abbreviations: CV, Coefficient of variation (standard deviation/mean); EUNIS, European Nature Information System.

are summarized in the [Supplementary Results](#), Figures [S6](#) and [S7](#), and Table [S8](#). To assess whether niche breadth estimates depended on local abundance, we refitted the PGLS models by adding two measures of local abundance (median abundance and 95% quantile), in separate models.

To address our second question, we tested the effect of environmental harshness on the proportional contribution of intentional introduction to the invasion of each plot, by fitting a generalized linear mixed model (GLMM, ‘glmmTMB’ package, Brooks et al. 2017). The GLMM had a binomial distribution (logit link), and country as random intercepts (to account for country-specific differences in trading history and in the recording of non-native plants in vegetation plots). We removed annual mean

temperature (VIF = 16) to reduce collinearity (all VIFs in the reduced model < 5). We obtained  $R^2_{\text{marginal}}$  and  $R^2_{\text{conditional}}$  values using the ‘MuMIn’ package (theoretical variances method, Bartoń 2022). Spatial autocorrelation was low in the model’s residuals (assessed following Padullés Cubino et al. 2021, Figure [S8](#)). We also considered a species-level approach, in which harshness was summarized at the species level, with the intentionality proportion of each species as the explanatory variable ([Supplementary Methods](#)). We fitted separate GLMMs (taxonomy as random intercepts): proportion of plots enduring particularly harsh conditions (drought, salinity, oligotrophy; binomial GLMMs), median and extreme values for relevant continuous variables (elevation, annual mean temperature, annual precipitation, cropland land-cover, urban-landcover; gaussian

GLMMs and PGLS). The results from these supplementary models did not yield new insights (Table S9 and Supplementary Results).

Prior to all analyses, we standardized all numerical explanatory variables to a mean of zero and unit variance (Schielzeth 2010). We then fitted quadratic terms, if they improved the AICc (Akaike Information Criterion corrected for small sample sizes) of a univariate model containing a linear term, and the 95% confidence interval of the quadratic term did not overlap zero. For all analyses, we used multimodel inference to obtain model-averaged coefficients (full-averaging, ‘MuMin’ package; Bartoń 2022). We ranked models using AICc and kept for inference the subset within six units of the top-ranked model. We approximated the relative importance of predictors through standardized general dominance: the proportional contribution of each predictor to the model’s total explained variation (dominance analysis, ‘domir’ package; Luchman 2024). We calculated explained variation with  $R^2_{\text{adjusted}}$  for the PGLS models of niche breadth, and with  $R^2_{\text{marginal}}$  for the GLMMs of niche harshness. For the models of niche harshness, we used estimated marginal means and trends to calculate effects at the proportion scale (Lenth 2023).

Furthermore, we quantified covariation among the intentionality of introduction, plant characteristics and minimum residence time, which is helpful to interpret intentionality-specific macroecological patterns (Guo et al. 2019; Guo et al. 2022). We quantified the covariation through linear models, Pearson’s correlation, and contingency tables, complemented with estimated marginal means and patterns and over- and under-representation to gain a deeper understanding of pairwise association between variables. We performed all analyses with R version 4.5.1 (R Core Team 2025). Data and code that reproduce our results are available in a stable repository (Riera, Chytrý, et al. 2024).

### 3 | Results

#### 3.1 | Relationship Between the Intentionality of Introduction and Niche Breadth

The intentionality of introduction was a significant correlate of habitat range (number of invaded habitats,  $R^2_{\text{adj}}$  of Phylogenetic Generalized Least Squares models, PGLS=0.25), one of our metrics of niche breadth for non-native plant species introduced to Europe (Figure 1; Figures S2–S5; Tables S2–S4). Non-native plants introduced to Europe both intentionally and unintentionally were present in one more habitat than plants introduced only unintentionally (e.g., contaminants of commodities or hitchhikers on vessels), but were similar to those introduced only intentionally (e.g., gardening or forestry). Intentionality of introduction was not significantly related to biotic niche breadth (number of invaded communities with no overlap in species composition;  $R^2_{\text{adj}}$ =0.06) nor climatic niche breadth (breadth of invaded climatic conditions;  $R^2_{\text{adj}}$ =0.13). Overall, the intentionality of introduction was the second or third most important correlate of niche breadth (relative contribution to  $R^2_{\text{adj}}$ : 16%–27%; absolute contribution to  $R^2_{\text{adj}}$ =0.02–0.07; Figure S3 and Table S4).

Non-native plants introduced a long time ago (i.e., with high minimum residence time) had greater habitat range and biotic niche breadth but similar climatic niche breadth than recent introductions (relative contribution to  $R^2_{\text{adj}}$ : 62%, 47% and 6%, absolute contribution to  $R^2_{\text{adj}}$ =0.16, 0.03, 0.01, respectively, Figure 1; Figures S2–S4; Tables S2–S4). Climatic niche breadth in the native range had a positive effect on climatic niche breadth in the invaded range but was not significantly related to biotic niche breadth and habitat range (relative contribution to  $R^2_{\text{adj}}$ : 67%, 43% and 4%, absolute contribution to  $R^2_{\text{adj}}$ =0.09, 0.03, 0.01, respectively). Dispersal syndrome, plant height, and growth form were of minor importance to niche breadth (each had a relative contribution to  $R^2_{\text{adj}}$ <10%, absolute contribution to  $R^2_{\text{adj}}$ =0.03–0.001, and non-significant effects). Local abundance was not key to understanding niche breadth (Supplementary Results, Figure S9; Table S10).

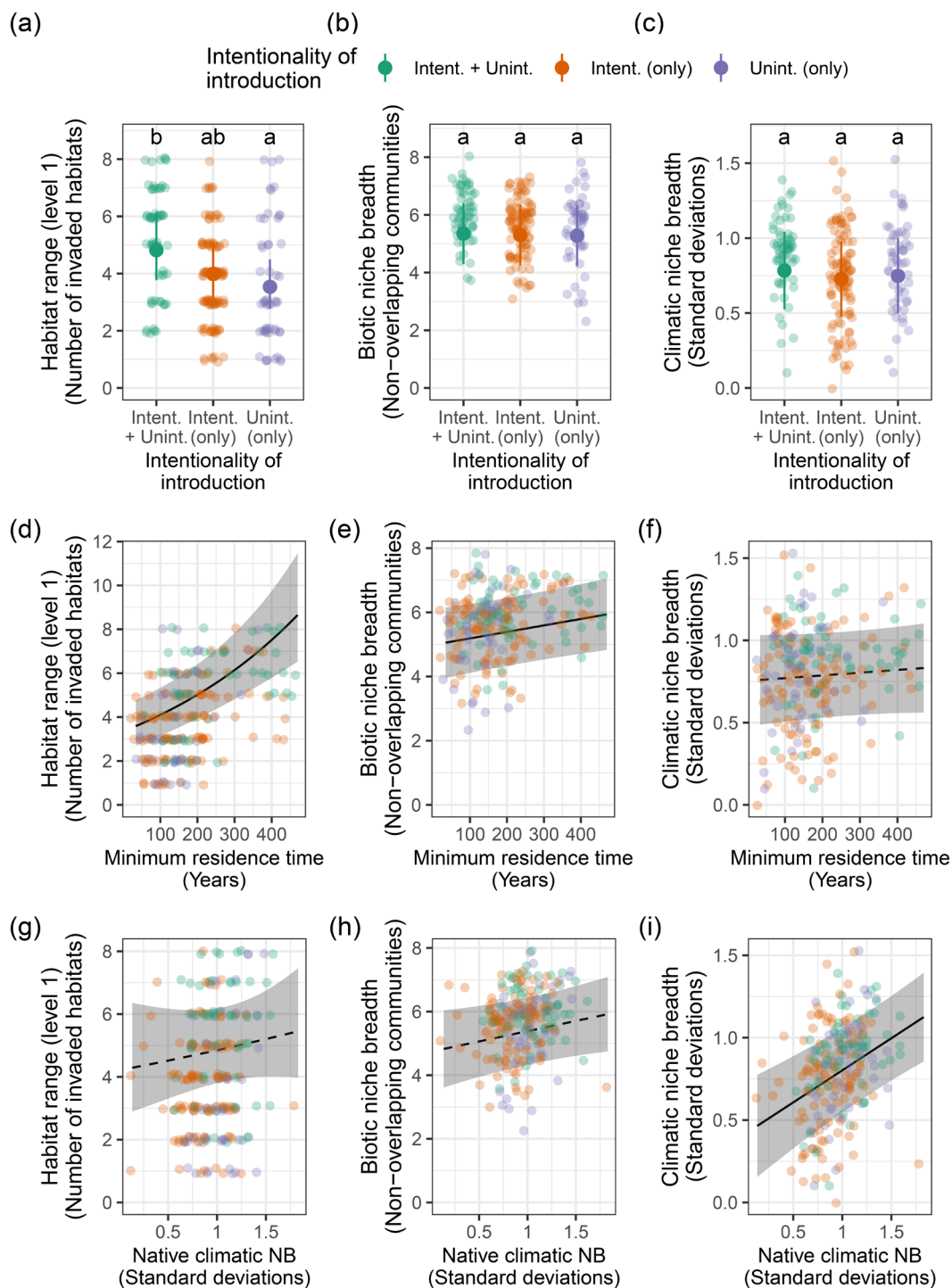
#### 3.2 | Relationship Between the Intentionality of Introduction and Niche Harshness

Intentionality of introduction was associated with niche harshness (Generalized Linear Mixed Model, GLMM, country as random intercepts,  $R^2_{\text{marginal}}$ =0.396,  $R^2_{\text{conditional}}$ =0.441; Figure 2). Dry conditions were associated with intentional introduction (i.e., greater proportional contribution of intentional introduction to invasion in dry vs. non-dry plots, model-averaged estimated marginal means  $\pm$  standard error:  $0.414 \pm 0.023$  vs.  $0.352 \pm 0.021$ ), while oligotrophy was non-significant. Saline conditions and increasing elevation were associated with reduced intentionality of introduction (non-saline vs. saline plots:  $0.486 \pm 0.022$  vs.  $0.280 \pm 0.026$ ; 100 m vs. 2500 m above sea level:  $0.376 \pm 0.029$  vs.  $0.201 \pm 0.069$ ). Niche harshness was a comparatively small part of the correlation between intentionality of introduction and the invaded environmental conditions (relative contribution to  $R^2_{\text{marginal}}$ <4%; absolute contribution to  $R^2_{\text{marginal}}$ =0.014; Figure S10; Tables S11 and S12).

Concerning potential confounders, habitat type was strongly correlated with intentionality-specific differences (relative contribution to  $R^2_{\text{marginal}}$ : 83%; absolute contribution to  $R^2_{\text{marginal}}$ =0.33); intentionality of introduction was lowest in man-made habitats and highest in forests (six-fold difference). Increasing cropland land-cover was associated with reduced intentionality of introduction (relative contribution to  $R^2_{\text{marginal}}$ : 5%; absolute contribution to  $R^2_{\text{marginal}}$ =0.02). Urban land-cover, annual precipitation, longitude and latitude were of minor importance to intentionality-specific differences in the invaded niche (each had a relative contribution to  $R^2_{\text{marginal}}$ <5% and an absolute contribution to  $R^2_{\text{marginal}}$ <0.02; see Supplementary Results and Supplementary Discussion).

#### 3.3 | Relationship Among the Intentionality of Introduction and Other Non-Native Plant Characteristics

Plants introduced both intentionally and unintentionally were mostly annual and perennial herbs and arrived earlier than those introduced either only intentionally or only unintentionally. Plants introduced only unintentionally were mostly annual

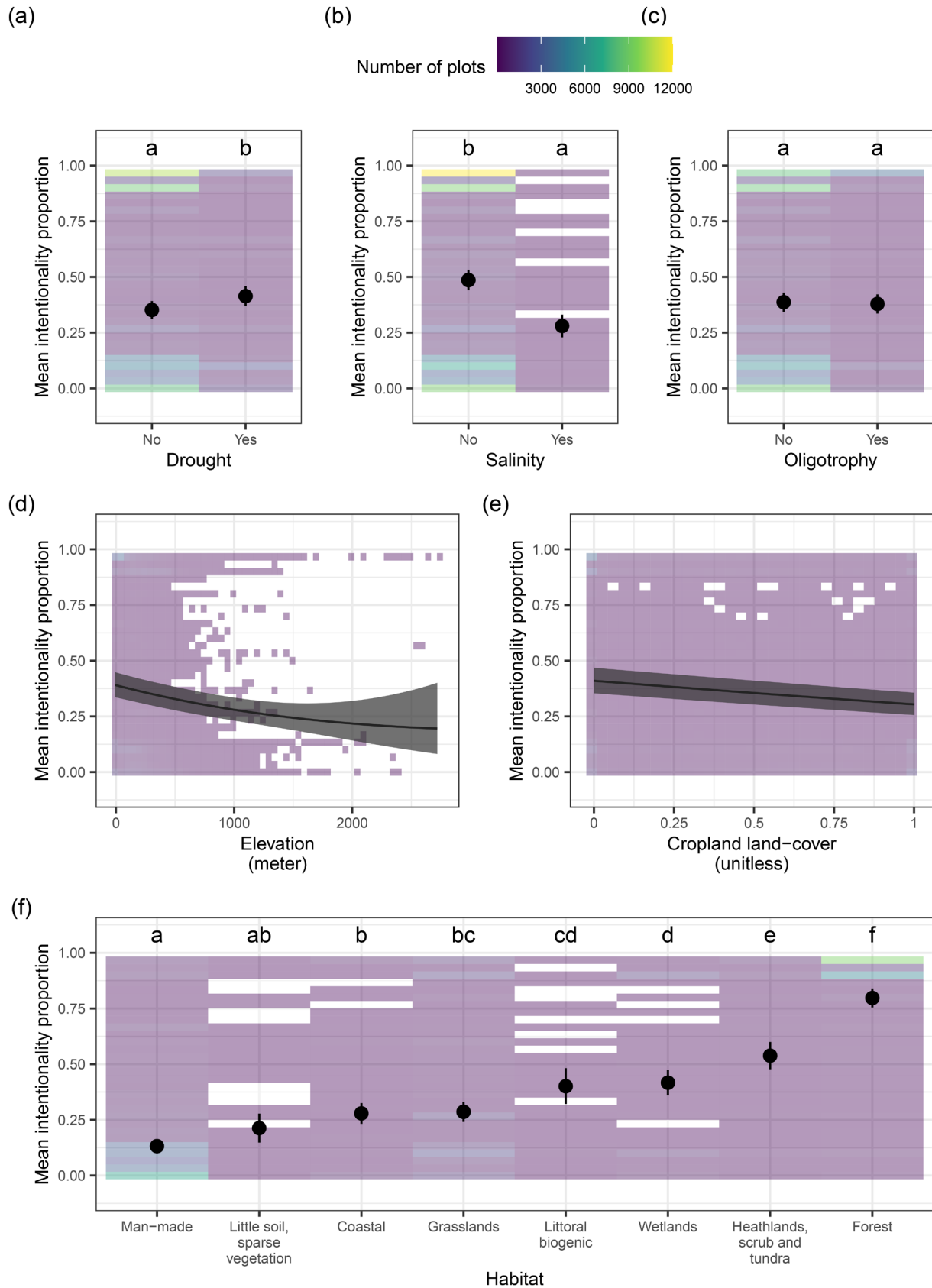


**FIGURE 1** | Effects of intentionality of introduction, minimum residence time, and native climatic niche breadth on niche breadth of non-native plants across Europe. Model-averaged predicted means (a–c) and trends (d–i), dashed lines indicate non-significant slopes, with 95% confidence intervals. Different letters in (a–c) indicate statistically significant pairwise differences (Tukey contrasts). Note that habitat range predictions were back-transformed from the log scale. Points represent non-native plant species, with random noise added for visualization.  $N=220$  for the habitat range and climatic niche breadth models (a, c, d, f, g, i),  $N=215$  for the biotic niche breadth (b, e, h). Alternative coding of intentionality of introduction as two categories (intentional, unintentional) or intentionality proportion yielded similar results (Figure S2). See Table S3 for the coefficients. Intent., intentional; NB, niche breadth, Unint., unintentional.

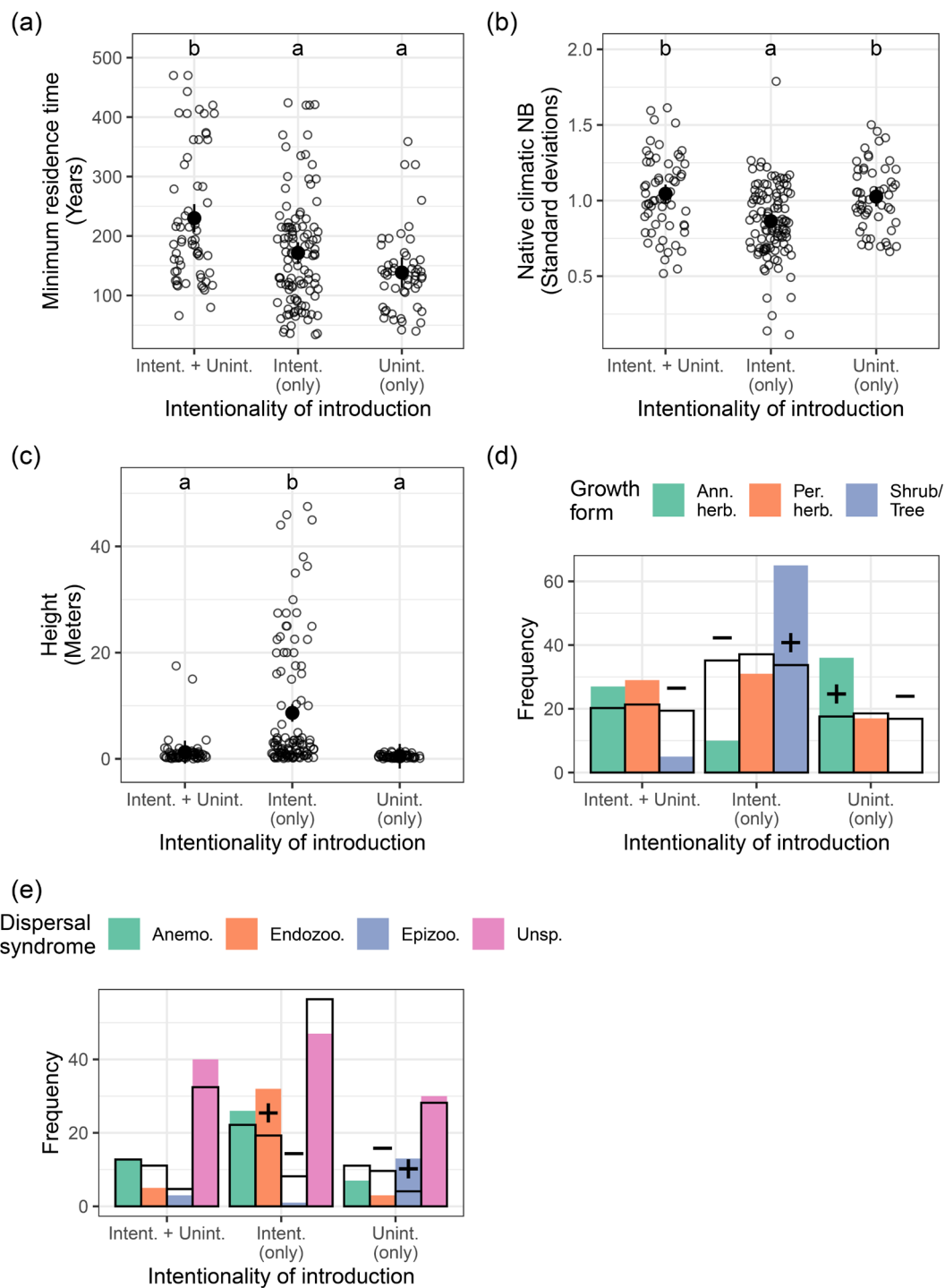
herbs (none were shrubs or trees) and included most of the epizoochorous plants. Plants introduced both intentionally and unintentionally, and those introduced only unintentionally, were shorter and had broader native climatic niches than plants introduced only intentionally (Figure 3; Figure S11; Table S13).

#### 4 | Discussion

Our study shows that the intentionality of introduction was associated with both niche breadth and niche harshness, although with small effect sizes. Therefore, we provide evidence that in addition



**FIGURE 2** | Effects of niche harshness and additional niche variables on mean intentionality proportion (how much intentional introduction contributed to the invader pool of a vegetation plot). Model-averaged estimated marginal means (a–c, f) and trends (d, e), with 95% confidence intervals. Different letters above the means indicate statistically significant pairwise differences (Tukey contrasts). Rectangular bins show the number of invaded plots ( $N = 61,579$  plots). See Figure S10 for coefficients and relative importance, and Tables S11 and S12 for exact values.



**FIGURE 3** | Patterns of covariation between the intentionality of introduction and the characteristics of non-native plants in our dataset. (a–c) Dots show non-native plant species (with random noise added for visualization), while different letters above means indicate statistically significant pairwise differences (Tukey contrasts). (d, e) The height of coloured bars shows observed frequencies. Based on a chi-squared test of independence, empty bars show expected frequencies, and plus and minus signs indicate significantly greater or less frequency than expected.  $N = 220$  non-native plants. Anemo., anemochorous; Ann. herb., annual herbaceous; Endozoo., endozoochorous; Epizoo., epizoochorous; Intent., intentional; NB, niche breadth; Per. herb., perennial herbaceous; Unint., unintentional; Unsp., unspecific.

to triggering invasions by overcoming geographical barriers, introduction pathways (at a very broad classification of intentional and/or unintentional) are also associated with the success of non-native plants in overcoming environmental barriers.

A combination of intentional and unintentional introduction was associated with a broader niche in the invaded range,

compared to only unintentional introduction, in line with our hypothesis. This advantage was weak, and existed only in terms of the number of invaded habitats, indicating the value of multidimensional frameworks that assess invasion success in complementary ways (Carboni et al. 2016; Catford et al. 2016; Fristoe et al. 2021; Giulio et al. 2021; Palma et al. 2021). We suggest that the advantage of combined intentional and unintentional

introduction (compared to only unintentional introduction) in invading habitats could relate to a diversification of propagule sources leading to high propagule pressure (i.e., a high number of seeds reaching target habitats; Pergl et al. 2017). This link between greater pathway diversity (i.e., combined intentional + unintentional introduction) and greater propagule pressure is consistent with the observation that being introduced through multiple pathways is associated with ecological impact and invasion success across non-native animals and plants (Pergl et al. 2017; Saul et al. 2017; Foxcroft et al. 2019; Zhao et al. 2023). High propagule pressure would reduce the chance of population extinction or loss of genetic variation (Uller and Leimu 2011). In turn, this would increase the likelihood of evolution of local adaptation (Oduor et al. 2016) and adaptive phenotypic plasticity (Richards et al. 2006), two mechanisms that could enable a plant to overcome many environmental barriers in the invaded range. Moreover, plants introduced both intentionally and unintentionally would start these adaptive processes at a greater diversity of spatial locations (Pergl et al. 2017), because the introduction epicentres of intentional and unintentional introductions often do not overlap (Riera et al. 2021), in line with our results on intentionality-specific niche differences in terms of habitat and land-cover (see below). Intentional introductions occur mostly in urban areas, due to the concentration of public and private gardens (Riera, Pino, et al. 2024). Unintentional introductions would also occur in urban areas (which are the final destination of contaminated commodities and ornamentals; Hulme et al. 2008; Ni and Hulme 2021) but also in croplands (sowing of contaminated seeds; Harrower et al. 2018), and trade and touristic infrastructures (harbours and airports where people and commodities carry hitchhiking seeds; Ni and Hulme 2021).

The advantage of plants with a combined intentional and unintentional introduction at invading more habitats than those introduced only unintentionally could also be related to covariation with minimum residence time (Pergl et al. 2017), in line with our hypotheses: plants introduced a longer time ago had greater habitat and biotic niche breadth (but similar climatic niche breadth). We found that plants introduced both intentionally and unintentionally tended to be introduced earlier than those introduced either intentionally or unintentionally. The increase in niche breadth over time (Pyšek et al. 2011; Ainsworth and Drake 2020; Lazzaro et al. 2020; Fristoe et al. 2021; Banerjee et al. 2021) could reflect that plants need time to disperse to different areas with different environmental conditions, and thereby occupy a broader niche (Ainsworth and Drake 2020; Banerjee et al. 2021). Furthermore, time is necessary for evolutionary processes that facilitate invasion of a wide breadth of conditions (Richards et al. 2006; Banerjee et al. 2021; but see Oduor et al. 2016).

In addition to covarying with minimum residence time, intentionality of introduction also covaried with native climatic niche breadth: non-native plants introduced both intentionally and unintentionally, and those introduced unintentionally tended to have broader niches in their native range compared to those introduced only intentionally. Such covariation did not translate into intentionality-specific differences in the breadth of the invaded climatic niche. The greater climatic niche breadth in the invaded range only had a positive effect on the breadth of the invaded climatic niche, suggesting the importance of

pre-adaptation to a wide range of climatic conditions (Guo et al. 2019). Moreover, the advantage of species with a broad native climatic niche could also be due to increased propagule pressure, as they are likely to be transported accidentally more often (because they may be more geographically widespread and locally abundant in their native ranges; Guo et al. 2019) and cultivated more frequently (because the broad tolerance is a desirable trait; Guo et al. 2019). Our findings on the effects of minimum residence time and native climatic niche breadth, on the breadth of the invaded niche, expand on already known roles of these variables on the invasion success of non-native plants and animals in terms of geographical spread or invasion status (Vázquez 2006; Dyer et al. 2016; Pyšek et al. 2020; Riera et al. 2021). In contrast, we found that dispersal syndrome, plant height, and growth form explained little of the variation in multiple dimensions of niche breadth, contrary to our hypothesis (Supplementary Discussion).

Besides the weak effects of pathway diversity (both intentional and unintentional introduction) on niche breadth, we found no effect of pathway identity on niche breadth, i.e., no difference between non-native plants introduced only intentionally or only unintentionally. Previous works linking niche breadth to intentionality of introduction have focused on smaller spatial scales and more detailed pathway classifications, and show contrasting results: no effect of intentionality of introduction on habitat range and climatic niche breadth (Riera, Pino, et al. 2024), greatest habitat range among ornamentals (Rojas-Sandoval and Ackerman 2021), broader invaded climatic niches with increasing number of uses (Banerjee et al. 2021), or that intentionality-specific differences in niche breadth may depend on which environmental variables defined the niche (Thuiller et al. 2012), or on the invasion status of non-native plants (Pyšek et al. 2011). Therefore, it is possible that in some contexts, unintentionally introduced plants may compensate the lack of human care and achieve similar niche breadth as intentionally introduced plants, for instance through greater pre-adaptation to climatic tolerance (wider native climatic niches compared to intentional introductions) or greater pre-adaptation to benefit from disturbance and urban mobility (greater incidence of ruderal strategy, lighter seeds and low stature, see below). Overall, the varying relationship between intentionality of introduction and niche breadth in the invaded range suggests that economic use is not necessarily linked to a successful invasion (Riera, Pino, et al. 2024). The relationship between the intentionality of introduction and invasion success was not clear-cut either in a study of the geographical spread across of non-native animals and plants (Riera et al. 2021), suggesting that considering pathway diversity in addition to pathway identity might yield complementary insights into the usefulness of pathways for understanding invasion success.

We showed that the intentionality of introduction was associated with the overcoming of harsh environmental barriers related to different types of stress: unintentional introduction was associated with both saline and high-elevation habitats, while intentional introduction was associated with the invasion of dry habitats. Previous results have linked the invasion of high-elevation habitats to both intentional (Thuiller et al. 2006; Chytrý et al. 2021; Riera, Pino, et al. 2024) and unintentional

introduction (McDougall et al. 2011; Akatova and Akatov 2019). Such contrasting patterns possibly reflect heterogeneity among mountain regions (Alexander et al. 2011; McDougall et al. 2011) and variation among global regions in the proportion of intentionally introduced plants (van Kleunen et al. 2020).

The intentionality-specific differences in overcoming harsh environmental conditions could be related to the effects of specific traits. Unintentionally introduced plants often have an annual growth form (Pyšek et al. 2011; Riera, Pino, et al. 2024; Riera et al. 2025) and ruderal strategy (Lambdon et al. 2008; Guo et al. 2022), which are traits associated with anthropogenic disturbance (Lambdon et al. 2008; Guo et al. 2022). A greater association of unintentionally introduced plants with anthropogenic disturbance is supported by our results on cropland land-cover and man-made habitats (Riera, Pino, et al. 2024) and might allow them to take advantage of reduced competition in saline and high-elevation habitats (Alpert et al. 2000; Zefferman et al. 2015; Alexander et al. 2016; Kalusová et al. 2023). Moreover, unintentionally introduced plants include more species with short stature (Riera, Pino, et al. 2024), epizoochorous dispersal, and light seeds (von der Lippe and Kowarik 2012), which are traits associated with human mobility (dispersal on clothing and vehicles; von der Lippe and Kowarik 2012; Ansong and Pickering 2014; Yang et al. 2021). A greater association with human mobility could increase the likelihood that unintentionally introduced plants will overcome the remoteness that characterizes many high-elevation sites (Alpert et al. 2000; Zefferman et al. 2015). Intentional introduction was only associated with overcoming harsh barriers in dry habitats, possibly because intentionally introduced plants are more likely to be pre-adapted stress-tolerators (Lambdon et al. 2008; Guo et al. 2022), such as succulents commonly used for xeriscaping (*Agave americana* and *Opuntia* spp.), which invade xeric habitats in the Mediterranean (Lambdon et al. 2008).

The relationship among niche breadth, niche harshness and intentionality of introduction can be expanded to consider other taxonomic groups, and other geographical areas, which remain unexplored (to the best of our knowledge). This could reveal whether intentionality-specific patterns in the invaded niche are consistent across taxonomic groups with non-sessile lifestyles and contrasting physiology, or whether they are consistent across regions with contrasting histories. Admittedly, intentional introduction tends to dominate among vertebrates, while plants (and to a lesser extent, terrestrial invertebrates) are relatively unique in having high numbers of species introduced either intentionally or unintentionally (Pergl et al. 2017; Saul et al. 2017; Riera et al. 2021). Therefore, an assessment of the relationship between niche breadth or harshness, and intentionality of introduction might need to compare contrasting animal clades, each with a dominant type of introduction (i.e., introduction pathways). The assessment of the niche in the invaded range across animal groups remains poorly known (Pyšek et al. 2010; Liu et al. 2023), to the best of our knowledge. Some previous works have mapped regional variation in the proportion of animals (and plants) introduced through various introduction pathways, without modelling the underlying environmental correlates (Essl et al. 2015; Nunes et al. 2015; van Kleunen et al. 2020; Arianoutsou et al. 2021; Bueno et al. 2021). Another knowledge gap among animals relates to how the

multiple dimensions of niche breadth relate to other aspects of invasion success (such as local abundance and geographical spread), which has received more attention among plants (Carboni et al. 2016; Catford et al. 2016; Fristoe et al. 2021; Giulio et al. 2021; Palma et al. 2021).

## 5 | Conclusions

Our analyses reveal that the intentionality of introduction can partly explain the overcoming of environmental barriers by non-native plants in their invaded range. Being introduced both intentionally and unintentionally was weakly associated with a broader niche in the invaded range in terms of habitat range (compared to plants introduced only unintentionally), while we found larger effects for a long residence time and a broad niche in the native range. Unintentional introduction was associated with invasion of saline and alpine habitats, whereas intentional introduction was related to invasion of dry habitats. These results have the potential to guide management strategies focusing on introduction pathways, such as the reflection that although unintentional introductions are responsible for a minority of invasions (in terms of species number; Roy et al. 2024), they cannot be neglected as they pose an important invasion risk for harsh environments, such as alpine and saline habitats, which usually host communities of high conservation value. Non-native plants with characteristics related to invasion success (both intentional and unintentional introduction, broad native niches) could be given special attention in the development of screening procedures and biosecurity measures. The approach in this work could be expanded to assess the invasion dynamics and impacts of specific plant functional groups in specific environments, integrating pathways, traits, and ecosystem properties (i.e., invasion syndromes), which that could yield further useful insights for decision making and management (Novoa et al. 2020).

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data and code supporting the findings of this study are available on Zenodo: <https://doi.org/10.5281/zenodo.13343361>. Vegetation plots used in this paper are stored in the European Vegetation Archive, project reference number 115 (<https://euroveg.org/eva-database/projects>).

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Distribution of invaded vegetation plots across Europe, with data on habitat type ( $N=61,579$ ). Number of vegetation plots across regular rectangles, obtained with the 'ggplot2' package (Wickham, 2016), in particular: 'geom\_bin2d(bins=700)'. Country outlines were taken from 'map\_data("world")' 'ggplot2' package, (Wickham, 2016). **Figure S2:** Model-averaged coefficients of intentionality of introduction, plant attributes and minimum residence time on five metrics of niche breadth of non-native plants in Europe, across three codings of intentionality of introduction (a–c). A separate Phylogenetic Least Squares model (PGLS) was fitted to each metric of niche breadth. White filling indicates 95% confidence intervals that overlap 0. Habitat range was ln-transformed for analysis, numerical explanatory variables are scaled to mean = 0 and standard deviation = 1. The intercept is mean niche breadth of non-native plants for the mean value of numerical explanatory variables, and for the reference categories of: both intentional and unintentional (a) or exclusively intentional (b), dispersal anemochorous (a–c), growth form annual herbaceous (a–c). See Table S2 for sample size (range: 215–281). **Figure S3:** Relative importance of drivers of five metrics of niche breadth of non-native plants in Europe, across three codings of intentionality of introduction (a–c). A separate Phylogenetic Least Squares

model (PGLS) was fitted to each metric of niche breadth. Relative importance was calculated through dominance analysis, using the  $R^2_{adj}$  as metric of explained variation (the vertical axis shows standardized general dominance). Note that dispersal syndrome and growth form yielded negative values of relative importance in models of biotic niche breadth, and that their removal had little effect on the relative importance of other variables (two dots depict relative importance with and without them). See Table S2 for sample size (range: 215–281). **Figure S4:** Effect of key drivers on five metrics of niche breadth, using complementary intentionality of introduction codings: three categories (a–f), intentionality proportion (g–k), two categories (l–z). Model-averaged predicted means (a, b, l–p) and trends (c–k, o–z). Different letters above means indicate statistically significant pairwise differences (Tukey contrast), while dashed lines indicate non-significant slopes. Bars and bands are 95% confidence intervals. Dots show non-native plant species, with random noise added for visualization. Note that habitat range predictions were back-transformed from the log scale.  $N=220$  (a–f, h–k),  $N=215$  (g),  $N=281$  (l, q, v),  $N=276$  (m–p, r–u, x–z). Intent., intentional; NB, niche breadth; Unint., unintentional. **Figure S5:** Matrix of scatterplots (lower triangle) and Pearson's correlation (upper triangle) among the five metrics of niche breadth. The main diagonal shows a smoothed histogram. Each dot shows a non-native plant species, with random noise added for visualization.  $N=220$  for correlations not involving biotic niche breadth,  $N=215$  for correlations involving biotic niche breadth. **Figure S6:** Model-averaged coefficients of intentionality of introduction, plant attributes and minimum residence time on five metrics of niche breadth of non-native plants in Europe, across three codings of intentionality of introduction, in supplementary GLMMs (a–c). A separate GLMM was fitted to each metric of niche breadth. White filling indicates 95% confidence intervals that overlap 0. Coefficients for habitat range models are at the log-scale. Numerical explanatory variables are scaled to mean=0 and standard deviation=1. The intercept is mean niche breadth of non-native plants for the mean value of numerical explanatory variables, and for the reference categories of: both intentional and unintentional (a) or exclusively intentional (b), dispersal anemochorous (a–c), growth form annual herbaceous (a–c). See Table S8 for sample size (range: 215–281). **Figure S7:** Relative importance of drivers of five metrics of niche breadth of non-native plants in Europe, across three codings of intentionality of introduction, in supplementary GLMMs. (a–c) A separate GLMM was fitted to each metric of niche breadth, from which we calculated standardized general dominance (percentage contribution to explained variation, either  $R^2_{marginal}$  or a pseudo- $R^2$  for Conway-Maxwell-Poisson models). See Table S8 for sample size (range: 215–281). **Figure S8:** Autocorrelation in model's residuals ( $N=200$  randomly selected residuals). Correlogram of Moran's  $I$  (vertical axis) between residuals separated by a certain distance (horizontal axis, in degrees). **Figure S9:** (a, b) Model-averaged coefficients of intentionality of introduction, plant attributes and minimum residence time, and abundance (median and 95% quantile, respectively) on five metrics of niche breadth of non-native plants in Europe, across three codings of intentionality of introduction. A separate PGLS was fitted to each metric of niche breadth. White filling indicates 95% confidence intervals that overlap 0. Coefficients for habitat range models are at the log-scale. Numerical explanatory variables are scaled to mean=0 and standard deviation=1. The intercept is mean niche breadth of non-native plants for the mean value of numerical explanatory variables, and for the reference categories of: both intentional and unintentional (a) or exclusively intentional (b), dispersal anemochorous (a–c), growth form annual herbaceous (a–c). See Table S10 for sample size (range: 215–281). (c, d) Relative importance of drivers of five metrics of niche breadth of non-native plants in Europe, across three codings of intentionality of introduction. A separate PGLS was fitted to each metric of niche breadth, from which we calculated standardized general dominance (percentage contribution to  $R^2_{adj}$ ). See Table S10 for sample size (range: 215–281). **Figure S10:** Niche variables (describing the invaded niche) affect the proportional contribution of intentional introduction to invasion of plots by non-native plant species across Europe. Coefficients (a) and relative importance (b), obtained from a Generalized Linear Mixed Model (GLMM), with binomial errors. Note that numerical covariates are scaled to mean=0 and standard deviation=1 (scaling done

before fitting quadratic terms). Coefficients are at the logit scale and model-averaged, those with a 95% confidence interval overlapping zero have white filling. The intercept is the mean intentionality proportion for a plot classified to the coastal habitat type, for the mean value of numerical covariates, and that does not endure drought, oligotrophy nor salinity. Relative importance was calculated through dominance analysis, using the marginal  $R^2$  as metric of explained variation (b shows standardized general dominance, and above the dots, numbers show general dominance, which are absolute values of marginal  $R^2$ ).  $N=61,579$  invaded plots. **Figure S11:** Patterns of covariation between intentionality of introduction and characteristics of non-native plants, with intentionality of introduction coded as: (a–e) two categories, and (f–j) intentionality proportion. (a–c, i, j) Different letters above means indicate statistically significant pairwise differences (Tukey contrast). (d, e) Height of coloured bars shows observed frequencies. Based on a chi-squared test of independence, empty bars show expected frequencies, and plus and minus signs indicate significant greater or less frequency than expected.  $N=282$  non-native plants (a–e), 220 non-native plants (f–j). Anemo., Anemochorous; Ann. herb., Annual herbaceous; Endozoo., Endozoochorous; Epizoo., Epizoochorous; Intent., Intentional; NB, Niche breadth; Per. herb., Perennial herbaceous; Unint., Unintentional; Unsp., Unspecific. **Table S1:** Number ( $N$ ) and percentage contribution of plots used in our final dataset ( $N=75,957$ ). Databases are sorted in decreasing order according to their percentage contribution. GIVD, Global Index of Vegetation-Plot Databases. **Table S2:** Overview of the full models of niche breadth (15 models). Sample size ( $N$ ) was higher when intentionality of introduction was coded as two non-exclusive categories due to duplicated species, and was lower for biotic niche breadth because five species had less than ten plots after removing outliers. The full models fitted the data (significant LRT), and had low collinearity (Lüdecke et al., 2021) ( $VIF < 5$ ) Intent., Intentional; lv., level of habitat classification; LRT, Likelihood Ratio Test; nb, niche breadth; p-V, p-Value; Unint., Unintentional; VIF, Variance Inflation Factor. **Table S3:** Model-averaged coefficients (95% confidence interval) of drivers of niche breadth across non-native plants across Europe. This table shows the results for 15 phylogenetic least square models: five metrics of niche breadth  $\times$  three ways to code intentionality of introduction. (a) three categories (Intentional vs. Unintentional vs. Both); (b) two categories (Intentional vs. Unintentional); and (c) intentionality proportion. See Table S2 for sample size (range: 215–281). **Table S4:** Relative importance of drivers of niche breadth for non-native plants in Europe. Values outside the parentheses are standardized general dominance (proportional contribution to the total  $R^2_{adj}$  of the PGLS model, which add up to 1, and are plotted in Figure S3), while values inside the parentheses are general dominance (absolute values of  $R^2_{adj}$ , which add up to the  $R^2_{adj}$  reported in Table S2) Note that dispersal syndrome and growth form yielded substantially negative values of relative importance in models of biotic niche breadth, so values from models without these variables are provided inside the brackets. Intent., Intentional; Unint., Unintentional. See Table S2 for sample size (range: 215–281). **Table S5:** Overview of the information sources on intentionality of introduction. Information sources were considered to have important geographical overlap when they shared the country to which they contributed the highest amount of data (they have the same letter in the “Overlap” column). Such overlapping sources were equally weighted when calculating the “intentionality proportion” variable (explanatory variable in the niche breadth models in the main text, and in the supplementary models of niche harshness). Countries within a given source are sorted from highest to lowest number of plots (“Geographic coverage” column). **Table S6:** Habitat harshness at level 3 of EUNIS hierarchical habitat classification. Based on expert knowledge, each habitat was classified into three, non-exclusive harshness categories: drought, salinity and oligotrophy ( $N=166$  invaded habitats with sufficient detail to be classified to level 3). EUNIS, European Nature Information System; MA, littoral biogenic (marine habitats); N, coastal habitats; Q, wetlands; R, grasslands; S, heathlands; scrub and tundra; T, forests; U, little soil; sparse vegetation; V, man-made. **Table S7:** Distribution of non-native plants across, (a) harsh environmental conditions, and (b) habitats. Table shows the number ( $N$ ) and percentage (%) of invaded plots per given harsh condition or

habitat. Species are sorted alphabetically, and those with the top ten highest number of invaded plots per harsh condition or habitat are in bold. Pint, intentionality proportion. **Table S8:** Overview of supplementary models of niche breadth (Generalized Linear Mixed Models). (a) Sample size ( $N$ ) was higher when intentionality of introduction was coded as two non-exclusive categories due to duplicated species, and was lower for biotic niche breadth because five species had less than ten plots after removing outliers. The full models fitted the data (significant LRT), and had low collinearity (Lüdecke et al. 2021) ( $VIF < 5$ ). categories, compois, Conway-Maxwell\_poisson; Fam, taxonomic family; Gen, taxonomic genus; Intent. Introd., Intentionality of introduction; Intent., Intentional; LRT, Likelihood Ratio Test; lv., level of habitat classification; nb, niche breadth;  $p$ -V,  $p$ -Value;  $R^2_{cond}$ , conditional  $R^2$ ;  $R^2_{mar}$ , marginal  $R^2$ ; Sp, species; Unint., Unintentional; VIF, Variance Inflation Factor. (b) Model-averaged coefficients (95% confidence interval) with intentionality of introduction coded as three categories (Intentional vs. Unintentional vs. Both). (c) Model-averaged coefficients (95% confidence interval) with intentionality of introduction coded as two categories (Intentional vs. Unintentional). (d) Model-averaged coefficients (95% confidence interval) with intentionality of introduction as intentionality proportion. (e) Relative importance of drivers of niche breadth for non-native plants in Europe. Values outside the parentheses are standardized general dominance (proportional contribution to the total  $R^2_{marginal}$  or pseudo- $R^2$  for Conway-Maxwell-Poisson, which add up to 1, and are plotted in Figure S7), while values inside the parentheses are general dominance (absolute values of  $R^2_{marginal}$  or pseudo- $R^2$  for Conway-Maxwell-Poisson models, which add up to the  $R^2_{marginal}$  or pseudo- $R^2$  reported in Table S8a). Intent., Intentional; Unint., Unintentional. **Table S9:** Overview of supplementary models of niche harshness (species level analysis). Models are sorted by average significance (in each pair of models) in a Likelihood Ratio Test, in which the null model only included the random components (note that it could not be calculated in two cases due to lack of convergence of the null model). F, taxonomic family; G, taxonomic genus; GLMM, Generalized Linear Mixed Model; Intent. prop., Intentionality proportion; Inter., Intercept; LRT, Likelihood Ratio Test; max., maximum; med., median; min., minimum; Pag. Lam., Pagel's lambda; PGLS, Phylogenetic Least Squares; qua., quadratic; Ra., random effects;  $R^2_{cond}$ , conditional  $R^2$ ;  $R^2_{mar}$ , marginal  $R^2$ ; S, species; temp., temperature. **Table S10:** Overview of supplementary models of niche breadth (PGLS) that include local abundance (median and 95% quantile). (a, b) Model overview, for median abundance and abundance at the 95% quantile (respectively). Sample size ( $N$ ) was higher when intentionality of introduction was coded as two non-exclusive categories due to duplicated species, and was lower for biotic niche breadth because five species had less than ten plots after removing outliers. The full models fitted the data (significant LRT), and had low collinearity (Lüdecke et al., 2021) ( $VIF < 5$ ). Intent., Intentional; LRT, Likelihood Ratio Test; lv., level of habitat classification;  $p$ -V,  $p$ -Value; Unint., Unintentional; VIF, Variance Inflation Factor. (c, d) Model-averaged coefficients (95% confidence interval) with intentionality of introduction coded as three categories (Intentional vs. Unintentional vs. Both); for median abundance and abundance at the 95% quantile (respectively). (e, f) Model-averaged coefficients (95% confidence interval) with intentionality of introduction coded as two categories (Intentional vs. Unintentional); for median abundance and abundance at the 95% quantile (respectively). (g, h) Model-averaged coefficients (95% confidence interval) with intentionality of introduction as intentionality proportion; for median abundance and abundance at the 95% quantile (respectively). (i, j) Relative importance of drivers of niche breadth for non-native plants in Europe. Values outside the parentheses are standardized general dominance (proportional contribution to the total  $R^2_{adj}$ , which add up to 1), while values inside the parentheses are general dominance (absolute values of  $R^2_{adj}$ , which add up to the  $R^2_{adj}$  reported in Table S10a). Intent., Intentional; Unint., Unintentional. **Table S11:** Environmental drivers of the mean intentionality proportion of invaded plots across Europe. Model-averaged coefficients and relative importance (standardized general dominance are relative contributions to marginal  $R^2$ , general dominance are absolute values of marginal  $R^2$ ) from Generalized Linear Mixed Models. CI, confidence interval. **Table S12:** Estimated marginal means and trends

(model-averaged), of the environmental drivers of the mean intentionality proportion of invaded plots across Europe. Different letters indicate significantly different means (Tukey contrast). CI, confidence interval; cld, compact letter display. **Table S13:** Pairwise covariation among intentionality of introduction, plant traits and minimum residence time, assessed for two datasets: (a) a dataset without duplicates (used for models coding intentionality as 3 categories [intentional, unintentional, both] and as intentionality proportion), (b) a dataset with duplicates (62 neophytes introduced through both intentionally and unintentionally are duplicated, used for models coding intentionality as 2 categories [intentional, unintentional]). Although intentionality proportion was not modelled using this duplicate dataset, we have included it to show covariation between alternative ways to code intentionality). In all cases, covariation between variables was assessed through calculation of effect size and a significance test: Pearson's correlation and  $t$ -test for continuous  $\times$  continuous, Cramér's V and Chi-square for categorical  $\times$  categorical, and  $R$ -squared and ANOVA (Analysis of variance) for continuous  $\times$  categorical. The tables rank covariation in absolute value, from greatest to lowest (all metrics of effect size had a theoretical range 0–1 in absolute value). Intent. Introd., intentionality of introduction; Int., intentional introduction; Unint., unintentional introduction.