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Research

Diaspore traits specialized to animal adhesion and sea current dispersal are positively associated with the naturalization of European plants across the world

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Understanding what drives non-native species naturalization (the establishment of a self-sustainable population outside its native range) is a central question in invasion science. Plant capacity for long-distance dispersal (LDD) is likely to influence the spread and naturalization of non-native species differently according to their introduction pathways. These pathways include intentional introductions (for economic use, e.g. for agriculture), unintentional introductions (e.g. seed contaminants), plant dispersal via human infrastructures (e.g. roads) and plant spread from an adjacent region where the species was previously introduced. We tested the relationship between sets of LDD traits (syndromes) of 10 308 European plant species and their global naturalization incidence (i.e. whether a species has become naturalized or not) and extent (i.e. the number of regions where a species has become naturalized) using the most comprehensive database of naturalized plants worldwide (GloNAF). Diaspore traits allowed the identification of four traditional LDD syndromes, namely those with specializations for dispersal by: wind (anemochorous), animal ingestion (endozoochorous), attached to animals (epizoochorous) and sea currents (thalassochorous). These evolutionary specializations have been historically interpreted by biologists even though actual dispersal is not always related to diaspore syndromes. We found that while epizoochorous and thalassochorous traits are positively associated with global plant naturalization incidence, anemochorous and endozoochorous traits show a negative relationship. Species' residence time outside their native range, their economic use and presence of epizoochorous traits (such as hooks, hairs and adhesive substances) are positively associated with global naturalization extent. Furthermore, we found that plant economic use reduces the influence of LDD syndromes on the naturalization incidence of intentionally introduced plants. While the success of non-native plants is influenced by a broad array of species- and context-specific factors, LDD syndromes play an important role in this context depending on the economic use of plants.

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Introduction

Long-distance dispersal (LDD) events reflect the transport of propagules across large distances by biotic or abiotic vectors (Higgins et al. 2003, Nathan 2005). While being rare, the importance of LDD for the distribution and spread of plants around the world has long been recognized (Ridley 1930, Carlquist 1966, Cain et al. 2000, Nathan 2006, Vargas et al. 2014, Arjona et al. 2018). In particular, LDD is paramount in the colonization of remote oceanic islands that receive all their biota from distant continents (Visher 1925, Nathan 2006, Gillespie et al. 2012, Vargas et al. 2014, Arjona et al. 2018). However, LDD is also critical for species range expansions because it facilitates species' tracking future climate change, and also the spread of non-native species (Shigesada and Kawasaki 2002, Hastings et al. 2005, Wilson et al. 2009, Corlett and Westcott 2013). Quantifying LDD by using field data is extremely difficult as the events of interest are rare, context dependent and unlikely to be observed in a quantitative way (Cain et al. 2000, Nathan et al. 2003). Thus, an alternative approach to estimate species capacity for LDD is to explore the role of morphological specializations of plant diaspores (i.e. typically seed and fruit traits) and to evaluate which syndromes (i.e. groups of traits associated with a particular dispersal mechanism) might be more successful. Because the action of some dispersal syndromes is limited to relatively short distances, noticeably those related to plant explosive mechanisms (autochory) and ant dispersal (myrmecochory) (Heleno and Vargas 2015), these can be distinguished from the syndromes potentilly promoting LDD. The former – so-called LDD syndromes (Carlquist 1967,

Vargas et al. 2012, Heleno and Vargas 2015) – facilitate plant dispersal by four main dispersal mechanisms, namely anemochory (wind dispersal), endozoochory (dispersal by animal ingestion), epizoochory (dispersal attached to animals) and thalassochory (dispersal by sea currents) (Heleno and Vargas 2015, Correia et al. 2018). Indeed, the historical hypothesis is that all life on islands has been significantly favored by LDD syndromes.

LDD syndromes may influence the spread of non-native species differently for species introduced via different pathways (Fig. 1). Species can be introduced to a new region either intentionally for economic purposes (e.g. for use in agriculture) or unintentionally by a human vector (for example, as seed contaminants). Alternatively, species spread in their new range can be further facilitated by human activities and infrastructures (e.g. tunnels, railroads) or by dispersal processes from an adjacent region where it was previously introduced (Hulme et al. 2008, CBD 2014, Harrower et al. 2018). For species that are intentionally introduced to other regions via human transport (mainly for economic use), the capacity for LDD dispersal may not be so relevant for new colonizations since humans have surpassed natural processes as drivers of species dispersal, and this action might not be so dependent on specific diaspore traits, or at least on those associated with natural dispersal (Mack and Lonsdale 2001). However, LDD syndromes might still play a role in the escape, spread and naturalization of intentionally introduced species, such as those used in agriculture (Carlquist 1966, Mack and Lonsdale 2001, Wilson et al. 2009, Dovrat et al. 2012). Therefore, diaspore specializations for LDD may play a role in the dispersal of non-native plants either intentionally
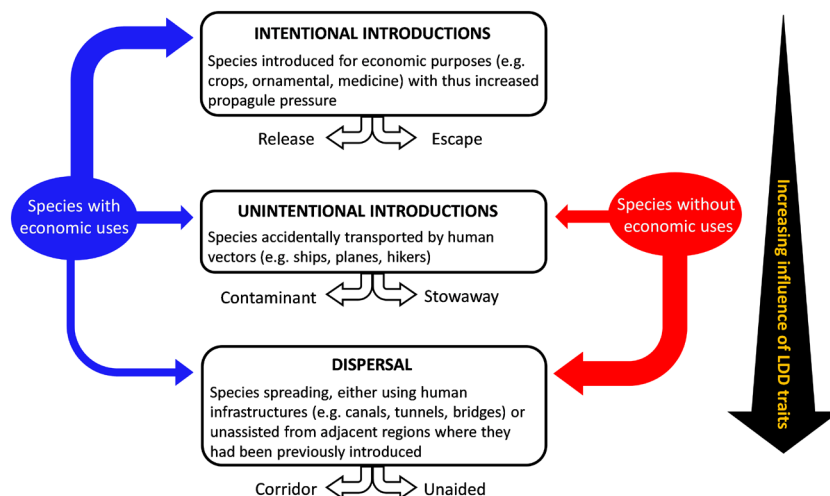

Figure 1. Species with economic use (blue) and species without economic use (red) are introduced to new regions through different pathways. The width of blue and red arrows indicate the proposed likelihood of each species category going through a particular introduction pathway. Introduction pathways are based on Hulme et al. (2008) and CBD (2014). LDD = long-distance dispersal.

or unintentionally introduced. Evidence shows that invasive non-native plants (i.e. species that, once introduced outside their native range, establish self-reproducing populations and spread (Blackburn et al. 2011)), invest more resources in diaspore structures useful for dispersal, such as wings for wind dispersal or hooks for dispersal attached to animals (Murray and Phillips 2010) and thus have a greater dispersal ability than non-invasive plants (Zhou et al. 2021). There are abundant cases where it has been shown that seed dispersal plays a key role in facilitating plant invasions (Vavra et al. 2007, Dovrat et al. 2012, Monty et al. 2016, Linder et al. 2018, Martín-Vélez et al. 2021). While a recent study found no significant effect of LDD syndromes on plant invasiveness other than a negative effect of anemochorous traits, it was focused on European plant naturalizations exclusively in Europe (Fristoe et al. 2021). The question remains as to whether different patterns may be evident when considering the spread of these plants at a global scale.

In this study, we explore the role of LDD syndromes in promoting the naturalization of European plants across the world. To classify plants into LDD syndromes, we used the most comprehensive dataset for diaspore traits that have been described to favor LDD; this dataset was compiled by Heleno and Vargas (2015) and includes 10 308 species native to Europe (ca 95% of the known European flora). We matched these data with the most comprehensive distribution database of naturalized non-native plants worldwide (GloNAF – van Kleunen et al. (2019)). Since we hypothesized that LDD favors non-native plant invasions (Higgins et al. 1999, Cain et al. 2000, Shigesada and Kawasaki 2002, Hastings et al. 2005, Trakhtenbrot et al. 2005), we predicted that diaspore specializations that facilitate LDD (i.e. LDD syndromes) would favor the naturalization of non-native plants. We used two different metrics of naturalization success: naturalization incidence (i.e. whether a species has become naturalized or not in at least one GloNAF region outside its native range) and naturalization extent (i.e. the number of GloNAF regions where a species has become naturalized). Specifically, we tested the following research questions: 1) Do LDD syndromes affect plant naturalization success in terms of incidence and extent? 2) Are these effects, if any, consistent with the colonization of islands and mainland regions? 3) Are these effects, if any, consistent for plants with and without economic use? Regarding the second question, since island regions are generally more isolated than regions in continents (Carlquist 1967, Gillespie et al. 2012, Vargas et al. 2014), we expect that LDD syndromes will especially favor naturalization of plants in island regions. Regarding the third

question, we expect that the influence of LDD syndromes on naturalization success will be less important for plants with economic use, since these species might be targeted and dispersed by humans owing to traits other than those associated with natural diaspore dispersal processes.

Material and methods

Database

We used information on LDD syndromes from a comprehensive database of European Spermatophytes (Heleno and Vargas 2015), which includes 10 308 species from 137 families native to Europe. Here, each species was assigned LDD syndromes based on diaspore (typically seeds and fruits) morphology, including five classes (Table 1). Diaspores with wings or pappus (plumose hairs), which facilitate dispersal by wind, were considered anemochorous. Diaspores with fleshy and nutritive tissues, which favor animal ingestion, were considered endozoochorous. Diaspores with hooks or sticky substances, which promote the external adhesion to animals, were considered epizoochorous. Diaspores with corky tissues or air chambers, which favor floatability and protection in saltwater, were considered thalassochorous. Finally, diaspores with no specialized dispersal structures for LDD were considered unspecialized (Heleno and Vargas 2015). Since some plants show heterocarpy (production of different kinds of diaspores) and others show diaspore traits that facilitate LDD through more than one dispersal vector, we included both species with one and species with multiple LDD syndromes, following Heleno and Vargas (2015). In this way, we acknowledge the fact that some plants might take advantage of more than one LDD strategy. However, for comparison purposes we built a second LDD syndrome database where we considered only plants with a single LDD syndrome, discarding all plants with multiple LDD syndromes. Dispersal syndromes that favor short distance (local) dispersal, such as myrmecochory and autochory, were assigned to the unspecialized category because they are not relevant for LDD (Heleno and Vargas 2015).

We obtained distributional data of naturalized vascular plants from the GloNAF database ver. 1.2, which includes information of 13 939 taxa and 1029 regions, based on 210 data sources (van Kleunen et al. 2019). A region is defined here as the smallest geographic area for which a list of non-native plants is available (mostly countries, or distinct subnational regions such as federal states or islands), including

Table 1. Classification of plants into long-distance dispersal (LDD) syndromes according to diaspore traits, and their corresponding expected dispersal mechanism and vector. From Heleno and Vargas (2015).

Diaspore traits	LDD syndrome	Expected dispersal mechanism	Expected dispersal vector
Pappus (plumose hairs)	Anemochorous	Anemochory	Wind
Fleshy + nutritive tissues	Endozoochorous	Endozoochory	Animal ingestion
Hooks + resins	Epizoochorous	Epizoochory	Animal adhesion
Corky tissues + air chambers	Thalassochorous	Thalassochory	Sea currents
No specialization for LDD	Unspecialized	None related to LDD	None related to LDD

648 mainland regions and 381 island regions. Species names in the GloNAF database have been standardized according to The Plant List (<www.theplantlist.org>). For merging the database on LDD syndromes with the GloNAF database, we also standardized species names to The Plant List by using the *TPL* function from the 'taxonstand' package (Cayuela et al. 2012). We used two complementary proxies for naturalization success: naturalization incidence and naturalization extent (Razanajatovo et al. 2016). Naturalization incidence is a binary response variable (yes or no) that considers if a species has been recorded as naturalized outside its native range. For a given LDD syndrome the naturalization incidence is an indicator of the likelihood that a species with a particular LDD syndrome has naturalized outside its native range. From the 10 308 species in the LDD syndrome database, 2416 (23.44%) were recorded as naturalized in at least one region according to the GloNAF database. For these 2416 species we estimated the naturalization extent: the number of GloNAF regions where each species is reported to be naturalized. This metric is an indicator of the capability to spread across large regions for a species with a particular LDD syndrome.

A recent study (van Kleunen et al. 2020) has shown that economic use of plants increases their global naturalization success, likely because economic use of plants increases propagule pressure, particularly for intentional introductions (e.g. for horticulture). We propose that species with economic use and species without economic use are mostly under the influence of different introduction pathways (as defined by Hulme et al. (2008) and CBD (2014)) (Fig. 1). Species with economic use are mostly introduced intentionally, and are then either intentionally released in nature (e.g. for erosion control or landscaping) or escape cultivation (mainly through seed dispersal) (Hulme et al. 2008, Harrower et al. 2018). Species without any economic use can be introduced accidentally by human vectors such as a contaminant of a commodity (e.g. as seed contaminant) or attached to (or within) a transport vector (e.g. in ships' ballast water) (Hulme et al. 2008, Harrower et al. 2018). Alternatively, these species without economic use can disperse using human infrastructure that connects previously unconnected regions, or can colonize a region through unassisted dispersal from adjacent regions, where they were previously introduced (Hulme et al. 2008, Harrower et al. 2018). To test for the effect of the economic use of plants on naturalization incidence and extent, we used the dataset by van Kleunen et al. (2020) and assigned the 10 308 species from our LDD syndrome database, with which we estimated naturalization incidence and extent using GloNAF, into two groups – i.e. plants with and without economic use. We acknowledge that this is not a perfect proxy for introduction effort: some variation of introduction effort will not be explained by the economic use of plants. Further, the economic use of plants does not account for their accidental introductions by humans. In this regard, variations in propagule pressure (not explained by economic use) among species (Pyšek et al. 2015) for which we have no further data may also influence naturalization patterns.

To account for species' residence time outside their native range, a key driver that favors plant naturalization (Pyšek et al. 2015, Fristoe et al. 2021), we used data on the date of first record for each species. We expected that plant species with earlier first record dates would show higher naturalization extent because they had more residence time outside their native range. To estimate species' minimum residence time outside their native range we used a global database of first record dates for non-native species compiled by Seebens et al. (2017) and updated by Seebens et al. (2018). This database includes first record dates for 11 450 non-native vascular plants around the world. To test for the effect of the first record date on naturalization extent, we used the dataset by Seebens et al. (2017, 2018) and assigned the 2416 species from our LDD syndrome database, with which we estimated naturalization extent using GloNAF, their earliest first record date outside their native range. In other words, for each naturalized species we used its earliest record date anywhere in the world to account for its residence time outside its native range. We acknowledge that this approach has its limitations. First, data on first record are only available for a subset of regions around the world. Second, there may be a time lag between the introduction of a new species and its first record. Third, data on first record are only available for a subset of naturalized species around the world. Out of the 2416 naturalized species in our LDD syndrome database we obtained data on their first record for 1986 species (83.23%), so we restricted our dataset for analyses of naturalization extent to these 1986 species.

Statistical analyses

To test the relationship between plant naturalization incidence and extent, and LDD syndromes, we used phylogenetic regressions. We built a phylogenetic logistic regression to relate naturalization incidence (yes/no) for each species with its LDD syndromes by using the function *phyloglm* from the 'phylolm' package (Ho and Ane 2014). We fitted a phylogenetic linear model to relate the number of naturalized regions (log transformed to achieve normality) for each species with their LDD syndromes. Here, we used the function *phylolm* from the 'phylolm' package (Ho and Ane 2014). We wanted to compare naturalization incidence and extent among plants with specializations for LDD through different dispersal mechanisms. We included presence of diaspore specializations for anemochorous, endozoochorous, epizoochorous and thalassochorous dispersal as distinct LDD syndrome variables in each regression model. Note that species with multiple sets of specializations for LDD were assigned to multiple LDD syndromes (Table 1).

To assess if patterns of plant naturalization are affected by the economic use of plants, we included economic use as a binomial predictive variable (yes/no), together with its interaction with each LDD syndrome, in our models. To account for the effect of minimum species' residence time outside their native range, we included the year of first record for each species as a covariable in our models where naturalization

extent is the response variable. To standardize the year of first record, we rescaled it to a range from zero to one. We tested the independence of our predictive variables (through testing for multicollinearity, an indicator that the predictive variables are correlated) using the variance inflator factor (VIF: a measure of the amount of multicollinearity in a set of multiple regression variables) ('Car' package, *VIF* function) in R (Fox and Weisberg 2010); none of the LDD syndrome variables show significant multicollinearity (all VIF values below 2).

To evaluate if patterns of naturalization success differed between mainland and island regions, we repeated our analyses separately for each of these regions. Finally, to test if plants with multiple LDD syndromes made a difference in our results, we repeated the analyses with two LDD syndrome datasets: one including species with multiple LDD syndromes and one excluding them. While from a biological point of view we consider that including species with multiple LDD syndromes would be more accurate, from a statistical point of view considering only species with a single LDD syndrome would be a more conservative approach to test the role of the four LDD syndromes. This is because, for species with multiple LDD syndromes, it is particularly hard to discriminate which traits and mechanisms might be facilitating the naturalization. Therefore, comparing the results between both approaches becomes especially useful.

To test for the presence of a phylogenetic signal in plant naturalization incidence and extent we estimated Abouheif's Cmean (Abouheif 1999, Pavoine et al. 2008, Münkemüller et al. 2012) using the *abouheif.moran* function from the 'adephylo' package (Jombart and Dray 2010). For this purpose, and to account for any phylogenetic signal in our regression models, we built a phylogenetic tree including the 10 308 plants from the LDD syndrome database.

We used the supertree for vascular plants constructed by Zanne et al. (2014), updated and extended by Qian and Jin (2016), using the *S.PhyloMaker* function from the 'phytools' package in R (Revell 2012, Qian and Jin 2016). Further, to assess the proportion of variance in naturalization extent that is explained by phylogeny, we compared the coefficients of determination (R^2) of regression models with and without accounting for phylogeny (but identical in every other way). We tested for model assumptions (i.e. normality, homogeneity of variance and absence of high leverage data points) and these were valid in all cases. We log transformed the number of regions where species were naturalized to achieve normality, as recommended by Mundry (2014). We evaluated the homogeneity of variance for each model by visually inspecting model residuals (Quinn and Keough 2002). In addition, none of the species in our dataset showed a Cook's distance over 1, which indicates the absence of influential cases or high leverage points (i.e. data points with unusually high levels of a predictor variable, whose removal from the dataset cause a big change in the estimation of regression coefficients) (Cook and Weisberg 1982). All statistical analyses were performed using R ver. 4.1.1 (<www.r-project.org>).

Results

From the 10 308 species included in the LDD syndromes dataset (Heleno and Vargas 2015), 2416 (23.44%) were also found in GloNAF (van Kleunen et al. 2019), and 243 (2.36%) species were assigned to more than one LDD syndrome. Naturalization incidence and extent both show a wide variation among LDD syndromes. While considering both species with single LDD syndromes and species with
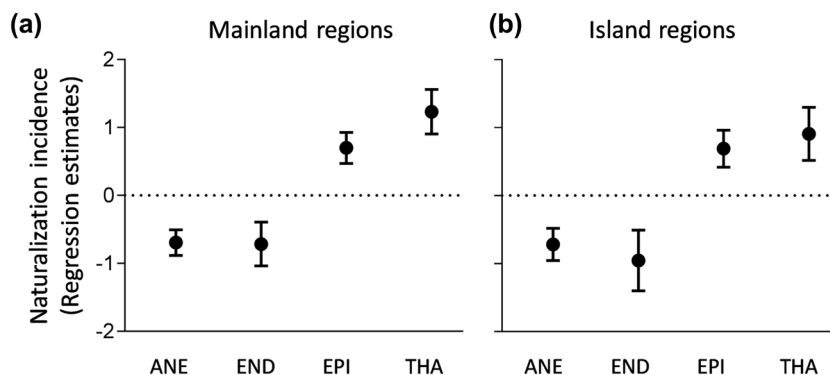

Figure 2. Diaspore specializations for epizoochorous and thalassochorous long-distance dispersal (LDD) are positively associated with plant naturalization incidence. Regression estimates (± 95% CI) from our phylogenetic logistic regressions including the presence (yes/no) of different LDD syndromes (ANE: anemochorous, END: endozoochorous, EPI: epizoochorous, THA: thalassochorous) and the economic use (yes/no) for each species as five separate predictive variables (in the same model), and the naturalization incidence as response variable including (a) only mainland regions and (b) only island regions. Both species with a single LDD syndrome and species with multiple LDD syndromes are included. Significant effects (p < 0.05) of predictive variables occur where the confidence interval does not overlap zero. Confidence intervals above zero indicate a positive effect of the LDD syndrome on plant naturalization incidence. Confidence intervals below zero indicate a negative effect of the LDD syndrome on plant naturalization incidence. Intervals that overlap with zero indicate no significant effect of the LDD syndrome on plant naturalization incidence. A total of 10 308 species were included in this regression, of which 2468 are anemochorous, 820 are endozoochorous, 722 are epizoochorous, 223 are thalassochorous and 1399 have an economic use. We use the same set of species for the regression on (a) mainland regions as for the regression on (b) island regions.

Table 2. Parameters of the phylogenetic logistic regression including long-distance dispersal (LDD) syndromes and economic use (yes/no) as predictive variables, and the naturalization incidence as response variable including only mainland regions, or only island regions. Significant effects (p < 0.05) are shown in bold. Both species with a single LDD syndrome and species with multiple LDD syndromes are included. A total of 10 308 species are included in this regression, of which 2468 are anemochorous, 820 are endozoochorous, 722 are epizoochorous, 223 are thalassochorous and 1399 have an economic use. We use the same set of species for the regression on mainland regions as for the regression on island regions.

Variable	Mainland regions				Island regions			
	Estimate	SE	z	p value	Estimate	SE	z	p value
(Intercept)	−1.90	0.05	−40.37	**< 0.001**	−2.40	0.06	−41.03	**< 0.001**
Anemochorous	−0.69	0.10	−7.17	**< 0.001**	−0.72	0.12	−5.93	**< 0.001**
Endozoochorous	−0.71	0.16	−4.34	**< 0.001**	−0.96	0.23	−4.19	**< 0.001**
Epizoochorous	0.70	0.12	6.02	**< 0.001**	0.69	0.14	5.00	**< 0.001**
Thalassochorous	1.23	0.17	7.39	**< 0.001**	0.91	0.20	4.57	**< 0.001**
Economic use	2.85	0.09	32.71	**< 0.001**	2.91	0.09	32.87	**< 0.001**
Anemochorous: economic use	0.36	0.18	2.05	**0.040**	0.38	0.18	2.08	**0.038**
Endozoochorous: economic use	0.47	0.24	1.94	0.052	0.65	0.28	2.29	**0.022**
Epizoochorous: economic use	−0.40	0.23	−1.79	0.073	−0.59	0.22	−2.73	**0.006**
Thalassochorous: economic use	−1.57	0.37	−4.30	**< 0.001**	−1.60	0.37	−4.36	**< 0.001**

multiple LDD syndromes, the average naturalization incidence ranges from 0.17 (± 0.01) for anemochorous species to 0.45 (± 0.03) for thalassochorous species (Supporting information). The average naturalization extent ranges from 25.89 (± 2.67) GloNAF regions for endozoochorous species to 61.63 (± 4.83) GloNAF regions for epizoochorous species.

We found evidence that phylogeny affects plant naturalization incidence, in both mainland regions (Abouheif's Cmean = 0.299, p = 0.001) and islands (Abouheif's Cmean = 0.271, p = 0.001), and also naturalization extent, in both mainland regions (Abouheif's Cmean = 0.177, p = 0.001) and islands (Abouheif's Cmean = 0.103, p = 0.001). Although total variance in naturalization extent explained by phylogeny alone is low (< 1%; Supporting information), we consider that the significant phylogenetic signal in our response variables justifies accounting for phylogeny in our models. After accounting for phylogeny, we found that epizoochorous and thassalochorous traits show a positive relationship with naturalization incidence, while anemochorous and endozoochorous traits show a negative
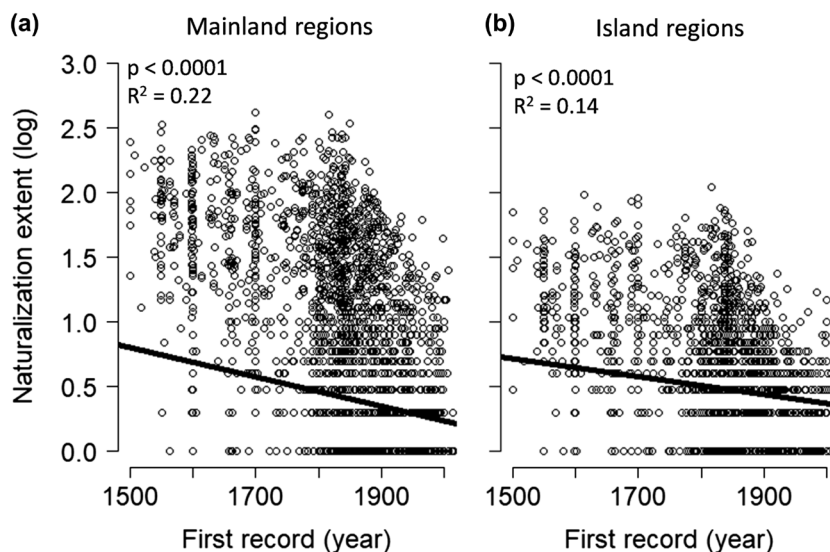

Figure 3. Species with earlier date of first record show higher naturalization extent. Phylogenetic linear regression among number of naturalized (a) mainland and (b) island regions (log transformed) and year of first record for each plant species. The estimates used in these plots come from our phylogenetic linear regressions including the presence (yes/no) of different long-distance dispersal (LDD) syndromes (ANE: anemochorous, END: endozoochorous, EPI: epizoochorous, THA: thalassochorous), the economic use (yes/no) and the year of first record for each species as six separate predictive variables (in the same model), and the naturalization extent as response variable including (a) only mainland regions and (b) only island regions. The informed R^2 corresponds to the full model, including all the mentioned predictive variables. A total of 1837 species are included in this regression for (a) mainland regions, of which 307 are anemochorous, 130 are endozoochorous, 235 are epizoochorous, 75 are thalassochorous and 954 have an economic use. A total of 1453 species are included in this regression for (b) island regions, of which 229 are anemochorous, 99 are endozoochorous, 190 are epizoochorous, 59 are thalassochorous and 837 have an economic use.

relationship, both in mainland regions and islands (Fig. 2). The economic use of plants shows a strong positive relationship with plant naturalization incidence (Table 2). Further, we found a significant interaction between the effect of economic use of plants and the effect of LDD syndromes on plant naturalization incidence. When considering naturalization in mainland regions, this interaction is significant for anemochorous and thalassochorous syndromes. In the case of naturalization in island regions, this interaction is significant for all four LDD syndromes (Table 2). For the LDD syndromes that show a positive relationship with naturalization incidence (epizoochorous and thalassochorous) the interaction with economic use shows a negative relationship with plant naturalization incidence. For the LDD syndromes that show a negative relationship with plant naturalization incidence (endozoochorous and anemochorous) the interaction with economic use shows a positive relationship with naturalization incidence. Therefore, in all cases where this interaction is significant, the economic use of plants weakens the relationship between LDD syndromes and plant naturalization incidence.

The date of first record shows a negative relationship with naturalization extent (i.e. species with earlier date of first record show higher naturalization extent) in both mainland and island regions (Fig. 3). The economic use of plants shows a strong positive relationship with naturalization extent (Table 3). After accounting for date of first record, and economic use of plants, we found that epizoochorous traits are associated with higher naturalization extent, while anemochorous, endozoochorous and thalassochorous traits show no effect, neither in mainland nor in island regions (Fig. 4). We found no significant interactions between the economic use of plants and their LDD syndromes. In all cases the date of first record and the economic use of plants show a stronger relationship with naturalization extent than LDD syndromes, suggesting that the former are more important drivers (Table 3).

When restricting our analyses to those species with a single LDD syndrome the direction of our results remains generally the same, and all the effect estimates are very similar, but the significance of some specific estimates change (Supporting information). The interaction between the effect of plant economic use and endozoochorous syndrome on naturalization incidence in mainland regions becomes significant. Further, the interaction between the effect of plant economic use and thalassochorous syndrome becomes non-significant in mainland regions. Additionally, the interaction between the effect of plant economic use and anemochorous syndrome becomes non-significant in island regions. Finally, the negative relationship between endozoochorous syndrome and plant naturalization extent becomes significant in mainland regions (Supporting information).

Different LDD syndromes show different patterns of naturalized plant distributions across the world (Fig. 5). While a relatively high number of species from all four LDD syndromes have naturalized in southern Africa and southern Oceania, anemochorous and thalassochorous naturalized plants seem to be distributed in high numbers across North America, and those with anemochorous and epizoochorous traits in northern Europe and southern South America.

Discussion

Our results show that species with diaspore specializations for epizoochorous and thalassochorous LDD are more likely to become naturalized outside their native range (naturalization incidence). We also show that epizoochorous traits are associated with the spread of non-native plants outside their native range (naturalization extent), although species residence time and economic use both play a more important role here. In contrast, species with diaspore specializations for anemochorous and endozoochorous dispersal are

Table 3. Parameters of the phylogenetic linear regression including long-distance dispersal (LDD) syndromes, economic use (yes/no) and year of first record (rescaled to a range from zero to one) as predictive variables, and number of naturalized mainland, or island regions (i.e. naturalization extent, log transformed) as response variable. Significant effects (p < 0.05) are shown in bold. The regression focused on mainland regions has an $R^2 = 0.22$, while the regression focused on island regions has an $R^2 = 0.14$. The informed R^2 correspond to the full models, including all the mentioned predictive variables. Both species with a single LDD syndrome and species with multiple LDD syndromes are included. A total of 1837 species are included in this regression for mainland regions, of which 307 are anemochorous, 130 are endozoochorous, 235 are epizoochorous, 75 are thalassochorous and 954 have an economic use. A total of 1453 species are included in this regression for island regions, of which 229 are anemochorous, 99 are endozoochorous, 190 are epizoochorous, 59 are thalassochorous and 837 have an economic use.

|	Mainland regions				Island regions			
Variable	Estimate	SE	t	p value	Estimate	SE	t	p value
(Intercept)	3.64	0.31	11.89	0.000	2.46	0.20	12.04	0.000
Anemochorous	−0.02	0.06	−0.27	0.789	0.05	0.06	0.92	0.356
Endozoochorous	−0.23	0.13	−1.76	0.079	−0.11	0.12	−0.92	0.359
Epizoochorous	0.15	0.06	2.41	**0.016**	0.12	0.06	2.15	**0.032**
Thalassochorous	0.04	0.09	0.47	0.638	−0.04	0.07	−0.47	0.637
Economic use	0.40	0.04	11.33	**< 0.001**	0.19	0.03	6.41	**< 0.001**
First record date	−3.42	0.23	−14.68	**< 0.001**	−2.09	0.19	−11.23	**< 0.001**
Anemochorous: economic use	−0.06	0.08	−0.72	0.471	−0.09	0.07	−1.27	0.204
Endozoochorous: economic use	0.21	0.13	1.55	0.120	0.08	0.13	0.62	0.537
Epizoochorous: economic use	−0.07	0.08	−0.86	0.389	−0.03	0.07	−0.45	0.653
Thalassochorous: economic use	−0.15	0.15	−1.02	0.308	0.02	0.13	0.14	0.885
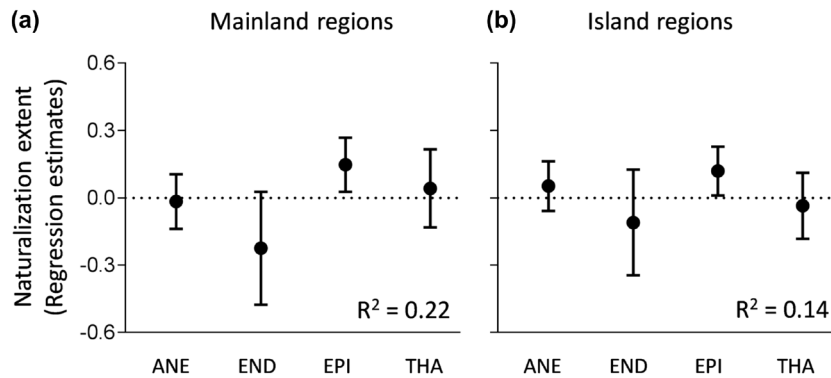
Figure 4. Diaspore specializations for epizoochorous long-distance dispersal (LDD) are positively related to plant naturalization extent. Regression estimates (± 95% CI) from our phylogenetic linear regressions including the presence (yes/no) of different LDD syndromes (ANE: anemochorous, END: endozoochorous, EPI: epizoochorous, THA: thalassochorous), the economic use (yes/no) and the year of first record for each species as six separate predictive variables (in the same model), and the naturalization extent as response variable including a) only mainland regions and b) only island regions. Both species with a single LDD syndrome and species with multiple LDD syndromes are included. Significant effects (p < 0.05) of predictive variables occur where the confidence interval does not overlap zero. Confidence intervals above zero indicate a positive effect of the LDD syndrome on plant naturalization extent. Confidence intervals below zero indicate a negative effect of the LDD syndrome on plant naturalization extent. Intervals that overlap with zero indicate no significant effect of the LDD syndrome on plant naturalization extent. The informed R^2 corresponds to the full model, including all the mentioned predictive variables. A total of 1837 species are included in this regression for (a) mainland regions, of which 307 are anemochorous, 130 are endozoochorous, 235 are epizoochorous, 75 are thalassochorous and 954 have an economic use. A total of 1453 species are included in this regression for (b) island regions, of which 229 are anemochorous, 99 are endozoochorous, 190 are epizoochorous, 59 are thalassochorous and 837 have an economic use.

less likely to naturalize outside their native ranges and neither of these, nor thalassochorous traits, consistently affect plant ability to spread over several regions. Hence, contrary to what was expected, not all LDD syndromes favor naturalization success, and some may even reduce it. These patterns remained the same when considering plant naturalization only in mainland regions or only in island regions. Therefore, some (but not all) LDD syndromes favored non-native plant naturalization not only on islands (as we expected) but also in mainland regions. Furthermore, we found that plant economic use downplays the role of LDD syndromes on their naturalization incidence.

For plants with economic use, the presence of LDD traits seems to have less influence on naturalization success. In island regions, the role of all LDD syndromes is less important in the probability of naturalization of plants with economic use. In mainland regions, the same occurs for the role of anemochorous and thalassochorous traits in the probability of plant naturalization. These results strongly suggest that, for plants with economic use, anthropogenic propagule pressure has surpassed the role of natural dispersal processes (Mack and Lonsdale 2001), and has rendered the latter unimportant as drivers of plant naturalization (Chaloupka and Domm 1986, Pyšek et al. 2011).

Epizoochorous plants seem to have a higher potential for spreading than other plants, which might be due to their effectiveness in harnessing natural dispersal vectors (wild mammals, birds, etc.) (Fragoso et al. 2003, Aoyama et al. 2012, Rimac et al. 2018) or due to the importance of epizoochorous traits in the unintentional dispersal by anthropogenic vectors, such as attached to domesticated mammals

(Manzano and Malo 2006), attached to human clothes, shoes and equipment (Auffret and Cousins 2013, Ansong and Pickering 2014, Valkó et al. 2020) or as contaminants (Hulme et al. 2008, Riera et al. 2020). These introduction pathways may have contributed to high propagule pressure for such species, which could favor their naturalization success (Pyšek et al. 2015).

There are numerous cases of non-native plants that are dispersed over long distances through epizoochory (Vavra et al. 2007, Dovrat et al. 2012, Coughlan et al. 2015, Linder et al. 2018). For example, for the highly invasive *Bromus tectorum* (classified into the epizoochorous LDD syndrome), a significant proportion of its diaspores attach to animals and are dispersed over longer distances than through abiotic vectors (Monty et al. 2016), reaching distances of over 6 km (Tamme et al. 2014). Epizoochory has been shown to be the vector facilitating the dispersal for non-native plants into many different ecosystems, including grasslands (Castillo-Nelis and Wootton 2010), shrublands (Dovrat et al. 2012), mature forests (Castillo-Flores and Calvo-Irabién 2003), aquatic environments (Coughlan et al. 2015, 2017) and even by migratory birds (Costa et al. 2014). Human-mediated LDD of epizoochorous diaspores may have substantially increased dispersal opportunities for species accidentally transported (Kinlock et al. 2022). In particular, diaspore dispersal attached to tourists' clothes and shoes are known to pose a significant threat to conservation areas, transporting diaspores of many different species across the world (Mount and Pickering 2009, Pickering and Mount 2010, Ansong and Pickering 2014). Human facilitation of epizoochorous diaspore dispersal can also occur via cattle transport of diaspores
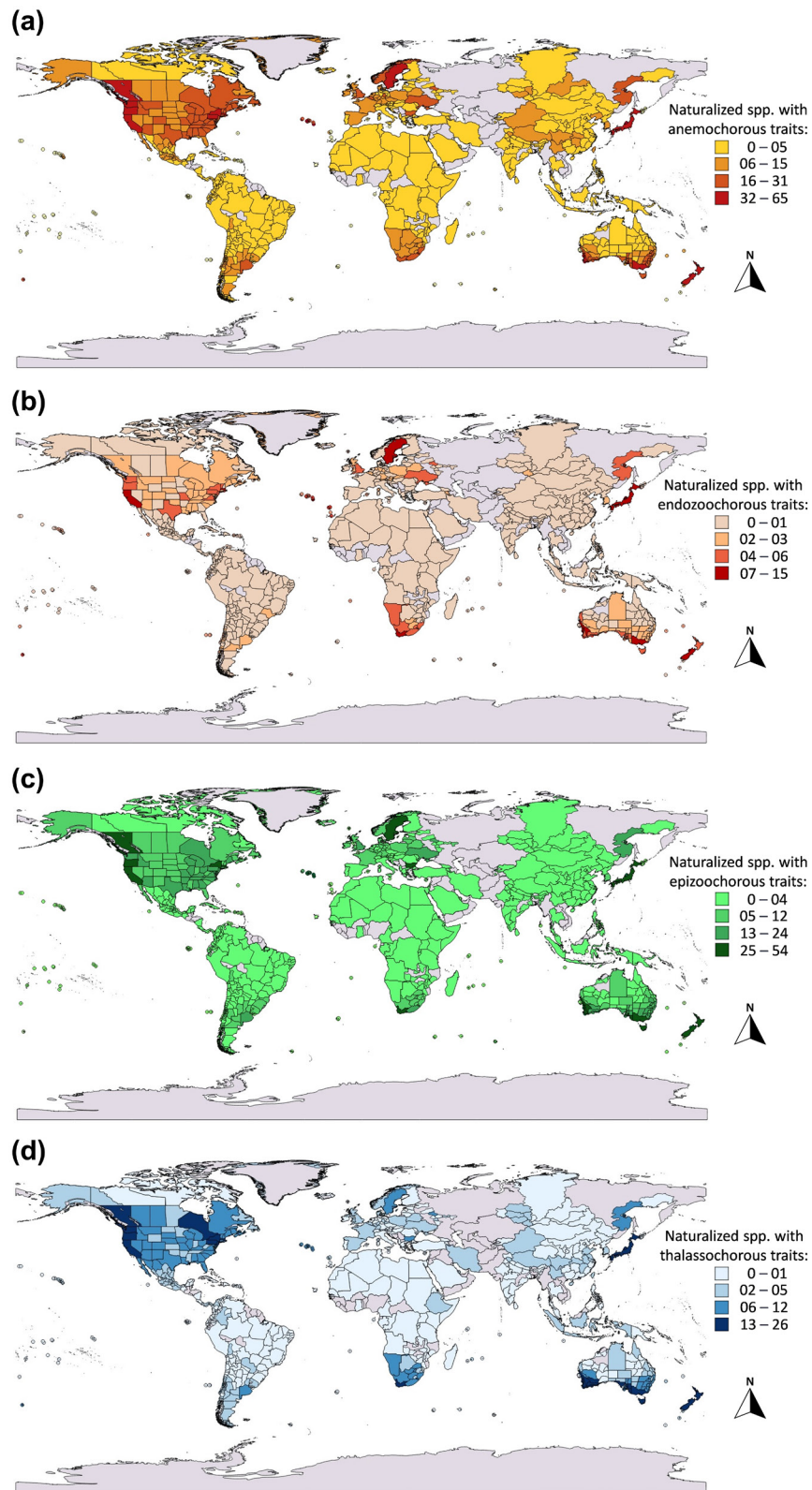
Figure 5. Different long-distance dispersal (LDD) syndromes show different patterns of naturalized plant distributions across the world. World map showing the number of naturalized species with (a) anemochorous, (b) endozoochorous, (c) epizoochorous and (d) thalazoochorous traits for each region included in this study. We coloured each region following a graded scale according to four intervals in the number of naturalized species obtained through the method of natural breaks. In the case of small islands we used coloured dots. Regions without data are grey. A region is defined here as the smallest geographic area for which a list of non-native plants is available (mostly countries, or distinct sub-national regions such as federal states or islands), including 648 mainland regions and 381 island regions.

attached to their fur over long distances, connecting isolated areas (Couvreur et al. 2004, Manzano and Malo 2006).

Thalassochorous traits appear to be favorable for naturalization. For plants that are not frequently transported by humans, traits that are related to dispersal through sea currents appear to increase colonization probability (Vargas et al. 2014, Gallego-Fernández et al. 2021). An alternative mechanism is via accidental transport by ships in ballast water (Hulme et al. 2008, Boltovskoy et al. 2011), where thalossochorous diaspores may survive because of their tolerance to salinity. Some examples of thalassochorus non-native plants include *Spartina* spp. (Daehler and Strong 1996, Grosholz et al. 2009, Borges et al. 2021), *Salsola soda* (Schwindt et al. 2018, Marbán and Zalba 2019) and *Tamarix* spp. (Gaskin and Schaal 2002, Birken and Cooper 2006, Ladenburger et al. 2006).

Surprisingly, not all LDD syndromes are positively related to plant naturalization. In fact, both endozoochorous and anemochorous dispersal are negatively related with naturalization incidence. Considering endozoochorous traits, non-native plants can easily integrate into native dispersal networks because frugivorous vertebrates are often highly generalist (Farwig and Berens 2012, Heleno et al. 2013, Traveset and Richardson 2014). One possibility is that non-native plants may show limited naturalization because there is great competition with native plants for the available animal dispersers (Debussche and Isenmann 1990). Another possible explanation is that habitat fragmentation hinders frugivorous diaspore dispersal in areas highly disturbed by humans (Rodríguez-Cabal et al. 2007, Cazetta and Fahrig 2022). The positive effect of epizoochorous traits and the negative effect of endozoochorous traits suggests that there is a limitation on the diaspore dispersal services provided by frugivorous species (i.e. those that intentionally ingest fruits) but no limitation in the unintentional dispersal by animals in general, including humans. It has been shown that defaunation, chiefly of large animals, can severely truncate diaspore dispersal services (Vidal et al. 2013, Dirzo et al. 2014, Pérez-Méndez et al. 2016, Emer et al. 2018); however, this significant disadvantage of fleshy fruited species to naturalize and expand their distribution range might signal an as yet underappreciated diaspore dispersal crisis.

In the case of anemochorous plants, although there are abundant cases of non-native species within this LDD syndrome, their naturalization success could be related to factors other than dispersal syndrome. For example, if we consider the *Pinus* genus, whose species have anemochorous diaspores (some widely naturalized) (Essl et al. 2010), their invasiveness has been explained by different aspects, such as a high introduction effort (Essl et al. 2010, McGregor et al. 2012), high climate matching (Essl et al. 2011, McGregor et al. 2012), high and continuous seed output (Richardson et al. 1990, Rejmánek and Richardson 1996) or their mutualistic symbiosis with ectomycorrhizal fungi (Moyano et al. 2020, 2021). Further, while most *Pinus* species are anemochorous (with very few exceptions), only a few species are invasive (Grotkopp et al. 2004). It could also be that some species

classified as anemochorous have anemochorous traits that are only relevant at relatively short distances (such as wings in *Pinus* spp.), and are still relatively ill-equipped to facilitate dispersal over large biogeographic barriers (e.g. across the sea). Further research will be needed to understand why endozoochorous and anemochorous traits might reduce plant naturalization success (Correia et al. 2018).

In this study, we show that only some LDD syndromes, namely epizoochorous and thalassochorous syndromes, significantly enhance the naturalization of European plants outside their native ranges. This effect is not only relevant for plant naturalization on islands, but also in mainland regions. Further, we found evidence that plant economic use downplays the influence of LDD traits on the naturalization incidence of intentionally introduced plants. While the success of non-native plants is influenced by a broad array of species- and context-specific factors, LDD syndromes play an important role in this context that varies with the economic use of plants.

Author contributions

Jaime Moyano: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Writing – original draft (lead); Writing – review and editing (lead). **Franz Essl**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ruben Heleno**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Pablo Vargas**: Conceptualization (supporting); Data curation (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Martin A. Nuñez**: Conceptualization (equal); Investigation (supporting); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (supporting). **Mariano A. Rodriguez-Cabal**: Conceptualization (equal); Formal

analysis (equal); Investigation (supporting); Methodology (supporting); Writing – original draft (equal); Writing – review and editing (equal).

Transparent peer review

Data availability statement

Supporting information

The Supporting information associated with this article is available with the online version.

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