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LETTER

What it takes to invade grassland ecosystems: traits, introduction history and filtering processes

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Abstract

Whether the success of alien species can be explained by their functional or phylogenetic characteristics remains unresolved because of data limitations, scale issues and weak quantifications of success. Using permanent grasslands across France (50 000 vegetation plots, 2000 species, 130 aliens) and building on the Rabinowitz's classification to quantify spread, we showed that phylogenetic and functional similarities to natives were the most important correlates of invasion success compared to intrinsic functional characteristics and introduction history. Results contrasted between spatial scales and components of invasion success. Widespread and common aliens were similar to co-occurring natives at coarse scales (indicating environmental filtering), but dissimilar at finer scales (indicating local competition). In contrast, regionally widespread but locally rare aliens showed patterns of competitive exclusion already at coarse scale. Quantifying trait differences between aliens and natives and distinguishing the components of invasion success improved our ability to understand and potentially predict alien spread at multiple scales.

Keywords

Alien species, functional and phylogenetic similarity, invasibility, invasion success, invasiveness, Rabinowitz.

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INTRODUCTION

The repeated introduction of alien species is a major component of ongoing global changes and a major threat to global biodiversity (Walther *et al.* 2009; Vila 2013). Understanding and predicting which introduced species will spread, naturalise and finally become invasive requires two major steps: (1) characterising invasion success and (2) identifying its driving forces. Traditionally, invasion success was studied by focusing on either intrinsic biological characteristics conferring invasiveness or characteristics of the resident communities favouring invasion (invasibility; Richardson & Pyšek 2006). Additionally, historical factors, such as time since introduction or introduction pathways, also play a role (Wilson *et al.* 2007; Mahoney *et al.* 2015). Nevertheless, attempts to link the degree of success across species to intrinsic traits, community invasibility and introduction history in a combined way have been rare and have identified few generalities (e.g. Thuiller *et al.* 2006). One reason is that our ability to test the importance of complementary factors on invasion processes hinges on the development of integrative frameworks to better quantify and measure the invasion success of alien species (Colautti *et al.* 2014).

Studying the success of alien species requires detailed quantification of both their local performance and geographic spread. Most studies attempting to identify alien species of greatest concern have focused on frequencies of species occurrence. However, focusing only on occurrence data tends to over-estimate the success of species that occur in low abundances but are widespread, while under-estimating the success of species that dominate where present but are not widely distributed (Colautti *et al.* 2014). Here, we propose to account for different components of invasion success by applying for the first time the Rabinowitz's classification of rarity and abundance (Rabinowitz 1981; Fig. 1) to alien species. Combining frequency of occurrence with geographic range, local abundance and niche breadth gives a more comprehensive measure of invasion success in a given area. In this framework, aliens can be considered most successful when they are regionally widespread, locally abundant and have broad ecological preferences.

Pinpointing intrinsic functional traits associated with invasiveness to profile successful invaders has been a long-lasting quest in invasion ecology. For plants, a number of traits have been consistently found to facilitate invasion (Richardson & Pyšek 2006; Van Kleunen *et al.* 2010). Small seed sizes, prolific seed production and short juvenile periods regularly emerge as important determinants of invasiveness, as they correlate with long dispersal distances and high competitive potential at the juvenile stage (Richardson & Pyšek 2006).

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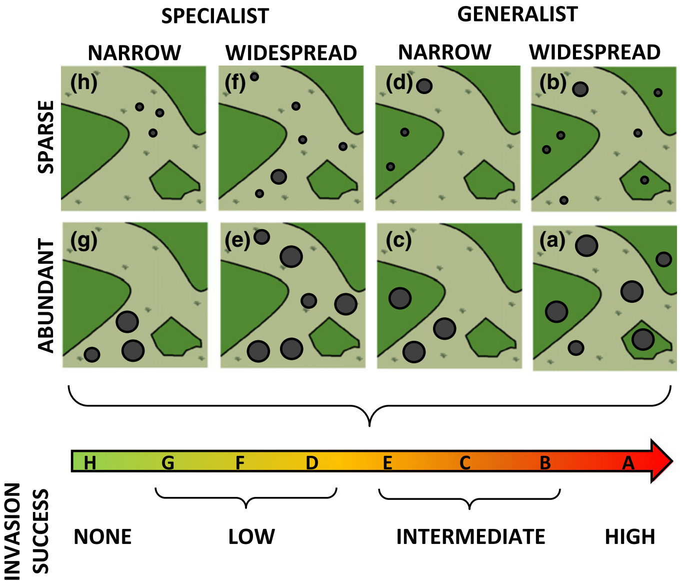


Figure 1 Conceptual visualisation of the Rabinowitz's framework. Shades of green indicate different environments, blue dots indicate a species' occurrence and the size of the dots indicates its local abundance. Depending on their geographical distribution (narrow vs. widespread), local abundance (abundant vs. sparse) and niche breadth (specialist vs. generalist) species can be divided into eight distinct classes (A through H in the figure). Only species in class A, geographically widespread, locally abundant and generalists, can be considered common. We follow the same rationale to argue that alien species that fulfil all of these characteristics have high invasion success. At the opposite extreme, aliens in class H are unsuccessful. In between, alien species common for only one criterion have low success, while species common for at least two criteria have intermediate success. From the three criteria, a continuous measure of invasion success can also be derived based on a dimension reduction analysis.

Fast relative growth rates are thought to favour highly invasive species in frequently disturbed or early successional ecosystems (Rejmanek & Richardson 1996; Dawson *et al.* 2011b; Ordonez & Olff 2013). Finally, studies highlighted that invasive plant species tend to be larger than non-invasive ones, probably in relation with the ability to capture light (Van Kleunen *et al.* 2010). Overall, the finding that successful alien plants share sets of functional characters is also supported by studies showing that certain phylogenetic lineages have higher proportions of invasive aliens than expected by chance (Lambdon 2008). Hence, it seems possible to screen successful alien plant species based on trait syndromes, such as the leaf–height–seed (LHS) spectrum (Westoby 1998), or based on their phylogenetic origins, which will capture biogeographic history and potential broad bioclimatic adaptations.

While traits conferring invasiveness can favour invasion, they do not guaranty its success. The abiotic and biotic characteristics of the recipient communities also determine invasion opportunities (invasibility, Thuiller *et al.* 2010). For instance, if environmental filtering is the main process determining alien species spread, the most successful aliens should share similar ecological adaptations to natives (Diez *et al.* 2008). If instead certain trait values confer greater competitive ability, the most successful aliens should be the ones that rank higher in the trait hierarchy (Kunstler *et al.* 2012; Gallien *et al.* 2014b). Conversely, if we assume more intense competition for resources between ecologically similar species, local communities are likely to be resistant to aliens that have very similar traits or are closely related to the resident natives (Darwin 1859; Elton 1958). Based on these assumptions, specific metrics of functional and phylogenetic similarity have been proposed in an attempt to infer the processes driving invasion (Thuiller *et al.* 2010; Gallien *et al.* 2014a). The application of these metrics has highlighted that invasion dynamics can broadly vary depending on the local ecosystem properties, the spatial scale and the amount of available resources (Diez *et al.* 2008; Carboni *et al.* 2013; Gallien *et al.* 2014b).

However, to date very few studies have explicitly investigated how multiple interacting drivers of invasion success vary among alien species (Pellock *et al.* 2013) and fewer still have considered different components of invasion success at the same time (Lemoine *et al.* 2015). If specific processes are important for regionally widespread, locally abundant and generalist alien species compared to less successful ones, identifying processes linked to invasion success seems of utmost importance. Ultimately, the identification of these crucial processes can help anticipating the most concerning invasions.

Here, we tackled the challenge of relating invasion success of alien species to intrinsic traits conferring invasiveness and to processes determining invasibility of native communities, while accounting for species' introduction history. First, we developed a framework for quantifying invasion success based on each alien species' invaded range area, local abundance and realised niche breadth in native communities. Second, we asked whether functional- and phylogenetic-based measures of community invasibility are good predictors of the degree of invasion success of aliens compared to their intrinsic traits and introduction history. While our initial aim was to pinpoint the processes determining invasion success, we also tested our framework in a predictive context. We did so in the context of temperate, C3-dominated permanent grassland communities, based on an extensive data set spanning the whole of France. Investigating invasion success is of high importance in these grasslands that are already severely threatened by urban development and the abandonment of traditional agricultural practices (Essl & Dirnböck 2008; Wesche *et al.* 2012).

METHODS

Study system, habitats and vegetation plots

Our study focuses on permanent grasslands (hereafter 'grasslands') defined as semi-natural herbaceous ecosystems supporting livestock farming systems. They are usually characterised by low external inputs (e.g. feed, fertiliser, energy). In France the area of grasslands is declining since the 1970s, but still covers *ca.* 10 million hectares (Violle *et al.* 2015).

We used a comprehensive database compiled as part of the DIVGRASS project (Violle *et al.* 2015) and reporting the composition of more than 50 000 vegetation plots throughout France, geo-referenced at a precision of around 5 km on average, for a total of 4280 species. The plant communities sampled consist of semi-natural grasslands (mesic, ruderal and trampled grasslands) created and maintained by mowing and grazing, and natural grasslands (mountain and dry calcareous grasslands) covering wide ecological gradients. The data consist of estimated relative cover of all species present within an area ranging from 25 to 100 m^2 (Appendix S1).

Each plot was assigned to one of the four broadly defined grassland habitats based on an analysis of modularity of the overall species-site network (Carstensen *et al.* 2013) and using the algorithm of Blondel *et al.* (2008). The four habitats were: (1) dry calcareous grasslands, (2) mountain grasslands, (3) mesic grasslands and (4) ruderal and trampled grasslands.

Alien species and introduction history

We focused on 160 herbaceous alien species defined as naturalised in France (Table S2) within the DAISIE database (www.europe-aliens.org), which provides an up-to-date inventory of species alien to European countries (Pyšek *et al.* 2009). Both neophytes (new alien species introduced > 1500) and few archaeophytes (old alien species, introduced < 1500) were listed in this database.

Species' introduction history (year of first record and main introduction pathway) in France was taken from DAISIE. If no record was available for France, we used the information from bordering countries as an approximation. We removed species with no information on introduction history leading to a final set of 127 alien naturalised species. To quantify minimum residence time, we determined the year of first record as the earliest year of all the records available for each alien species. Introduction pathways were based on the DAISIE hierarchical classification system (Table S1). We summarised this information by identifying the most common introduction pathway among 'Agriculture', 'Ornamental and horticulture', 'Unintentional through transport'' and 'Other'.

Phylogeny and traits

We reconstructed a molecular and dated genus-level phylogeny for the entire species pool based on DNA sequences available in GenBank (Roquet *et al.* 2013; Appendix S2). To calculate distance-based phylogenetic metrics (see below), we extracted the cophenetic distance between all species pairs from the phylogenetic tree.

We collated information on four functional traits: specific leaf area (SLA; the ratio of leaf area to dry mass), plant maximum height at maturity (Height), seed mass (SM) and growth form. These trait data were extracted from a number of databases and local data sets (see Appendix S3 and Violle *et al.* 2015, for details). LHS scheme captures variation in resource acquisition, establishment and competitive ability among species (Westoby 1998). SLA reflects species relative growth rate (faster growing species having higher SLA values), nutrient economy and water use efficiency. Seed mass reflects dispersal capability, seed production and longevity on the one hand, and species survival at the seedling stage on the other. Height captures species' ability to dominate the vegetation layer in a given habitat and to intercept light. Finally, we characterised growth form as either graminoid, forb or dwarf shrub. We kept only species for which we had information on at least two traits (2930 species from the initial 4280) and estimated the remaining missing values based on multivariate imputation by chained equations (van Buuren & Groothuis-Oudshoorn 2011; Appendix S3). To calculate distance-based functional metrics (see below), we compiled a pair-wise species dissimilarity matrix for all traits combined using the Gower distance (function 'daisy' in the 'cluster' package), as a multivariate measurement of functional dissimilarity.

Determining invasion success

We characterised invasion success based on the three components of the Rabinowitz's scheme (Fig. 1). First, to quantify regional distribution we calculated the species' frequency of occurrence, a measure that correlated strongly also with geographical spread (Fig. S1). Second, local abundance was taken from the average percentage cover of each alien species within the plots where it occurred. Third, niche breadth was calculated using a hyper-volume approach based on three bioclimatic variables and one productivity measure hypothesised to be important for the naturalisation and spread of alien species. Climatic variables were derived from the French meteorological model AURELHY (Bènichou & Le Breton 1987), based on interpolated measurements downscaled at 100 m resolution and summarising climatic information over the last 30 years (1971–2000). We focused on average annual precipitation, average daily minimum temperature in winter (December–February) and average daily maximum temperature in summer (June–August). We used the normalized difference vegetation index (NDVI), summed over the whole year as a proxy of gross primary productivity. Data were obtained from the moderate resolution imaging spectroradiometer (MODIS) for the years 2000–2014 and processed as described in Choler (2015). Based on these variables, we used multivariate kernel density estimation to construct a four-dimensional ecological hyper-volume for each alien species (Blonder *et al.* 2014). All variables were rescaled between 0 and 1 (by subtracting the minimum and dividing by the range) for comparability. Hyper-volumes were constructed using a Silverman bandwidth estimator and a 0% quantile threshold (Blonder *et al.* 2014). We then used the calculated volumes in ecological space as proxies of niche breadth for each alien species.

On the basis of these three components of invasion success (regional distribution, local abundance and niche breadth), we then used two complementary approaches to characterise alien success: (1) we separated them into eight classes (corresponding to the classical Rabinowitz classes – Fig. 1), and (2) we synthesised the three components into a synthetic continuous index of success. The first approach categorises aliens into invasion classes that might require specific management strategies, while the second ranks species in terms of their overall invasion success with the aim of identifying the features that can best explain it.

For the first (categorical) approach, we first split species into common vs. rare groups for each Rabinowitz's criterion independently (number of plots, local abundance and niche breadth), based on the sum of squares from species to group centres. Then the species were assigned to one of the eight Rabinowitz's classes based on the cross-tabulation of the groups obtained for the three criteria (Figs 1 and 2).

For the second (continuous) approach, we calculated a synthetic index representing the species scores on the first axis of the principal component analysis (PCA) performed on the three components of invasion success. This PCA axis explained roughly 60% of the variability in the data (Figure S1). It was most strongly linked to regional distribution, but it also captured niche breadth and local abundance. This 'invasion success' indicator (or PCA1) was then used as a response variable in subsequent analyses to identify the most important drivers of invasion success.

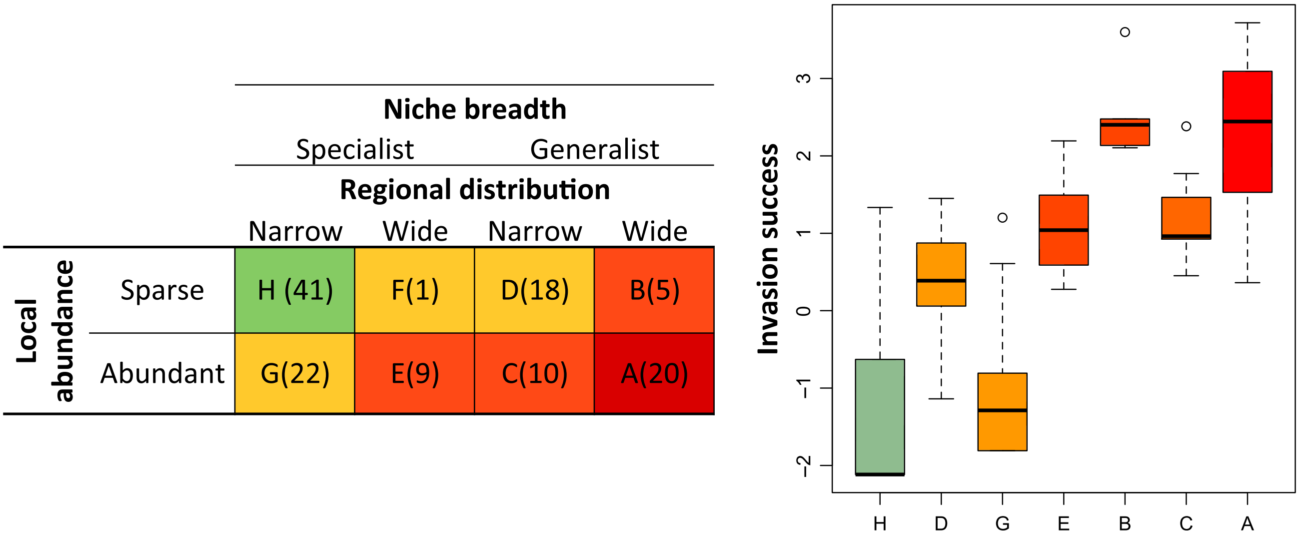
Phylogenetic and functional dissimilarity of alien species

We calculated a set of functional and phylogenetic similarity metrics to native species (invasibility metrics, Thuiller *et al.* 2010) based on pair-wise co-occurrences at two scales (Appendix S4). We first identified the native species that most often co-occurred with each alien species by using the V-score as a measure of species co-occurrence (Lepš & Šmilauer 2003; modified to account for species abundances). V-scores were calculated at both the plot (local community) and the habitat scale (defined by the set of plots belonging to the same habitat). Then, for each alien species, we calculated (1) the (absolute) Mean Distance to the Most often Co-occurring Species (MDMCS), and (2) whether it had higher or lower values than the natives for each trait (i.e. its hierarchical position on each trait gradient, Kunstler *et al.* 2012). MDMCS was based on both phylogenetic and functional distances, whereas the hierarchical index was calculated for each trait independently (Height.hier, SLA.hier and SM.hier). Overall these metrics measure the relative invasibility of native grassland assemblages at multiple scales (Table 1, Appendix S4). In the framework of the hierarchical filtering model of invasion biology (Richardson & Pyšek 2006), the habitat-level analyses provide insights into environmental filtering, while plot-level analyses allow recovering signals of biotic filtering.

Disentangling the factors explaining invasion success in grasslands

Modelling species independently of each other may bias analyses if closely related species have similar success. We tested for a phylogenetic signal of our continuous indicator of invasion success (i.e. PCA1) on the phylogenetic tree of alien species using Blomberg's K statistic (Blomberg & Garland 2002) and found no significant signal (Appendix S5; Fig. 3; $K = 0.074$, PIC variance $P = 0.931$). Hence, we considered alien species as phylogenetically independent in further analyses of invasion success.

We used boosted regression trees (BRT) to model invasion success of alien species as a function of introduction history (pathway and residence time), functional traits related to invasiveness (SLA, height, seed mass and growth form) and community invasibility metrics (functional and phylogenetic MDMCS at habitat and plot scales and trait-hierarchy metrics). BRTs allow handling different types of predictor variables, can fit nonlinear relationships, are robust to outliers, automatically handle interaction effects between predictors and are able to extract robust estimations of variable importance (Elith *et al.* 2008). We estimated variable importance for explaining invasion success based on the reduction of squared error attributable to each variable, normalised to sum up to 100 (relative influence). We estimated the goodness of fit of the overall model by assessing the R-square of fitted values against observed values. Models were fitted in R (R



		Niche breadth			
		Specialist		Generalist	
		Regional distribution			
		Narrow	Wide	Narrow	Wide
Local abundance	Sparse	H (41)	F(1)	D(18)	B(5)
	Abundant	G(22)	E(9)	C(10)	A(20)

Figure 2 Panel on the left: Numbers of alien species in the eight Rabinowitz's classes. Red: common based on three criteria; dark orange: common for two criteria; light orange: common for one criterion; green: rare. Panel on the right: Concordance between the continuous invasion success measure (based on the first axis of a PCA) and the Rabinowitz's classes for the 127 alien species. The least widespread class is on the left of the graph (class H – small regional distribution, locally not abundant, small niche breadth) and the most successful aliens are on the right (class A – regionally widespread, locally abundant, large niche breadth).

Table 1 Summary of distance-based invasibility metrics used in this study, identifying the type of distance (functional vs. phylogenetic), the spatial scale of reference and the underlying assumptions. The hierarchical indices are reported only for the plot scale for brevity

Index	Distance	Scale	Description	Assumptions
MDMCS.Hab	Functional	Habitat	Mean functional distance to the most often co-occurring species within habitats	The overall similarity of species niches is well captured by a subset of measured traits; Environmental filtering is most captured by similarity to the native species with which the invader comes most often into contact at the habitat level
MDMCS.Hab	Phylogenetic	Habitat	Mean phylogenetic distance to the most often co-occurring species within habitats	The overall similarity of species niches is best captured by their phylogenetic relatedness; Environmental filtering is most captured by similarity to the native species with which the invader comes most often into contact at the habitat level
MDMCS.Plot	Functional	Plot	Mean functional distance to the most often co-occurring species within plots	The overall similarity of species niches is well captured by a subset of measured traits; Biotic resistance is driven by the native species with which the invader comes most often into contact within plots
MDMCS.Plot	Phylogenetic	Plot	Mean phylogenetic distance to the most often co-occurring species within plots	The overall similarity of species niches is best captured by their phylogenetic relatedness; Biotic resistance is driven by the native species with which the invader comes most often into contact within plots
Height.hier	Height	Plot	Mean height difference to the most often co-occurring species within plots	Competitive ability can be represented on a trait hierarchy of height (e.g. light interception); Biotic resistance is driven by the native species with which the invader comes most often into contact within plots
SM.hier	Seed Mass	Plot	Mean seed mass difference to the most often co-occurring species within plots	Competitive ability can be represented on a trait hierarchy of seed mass (e.g. colonisation); Biotic resistance is driven by the native species with which the invader comes most often into contact within plots
SLA.hier	SLA	Plot	Mean SLA difference to the most often co-occurring species within plots	Competitive ability can be represented on a trait hierarchy of seed mass (e.g. growth rate); Biotic resistance is driven by the native species with which the invader comes most often into contact within plots

Development Core Team 2014), using the ‘dismo’ package (Elith *et al*. 2008).

Finally, to test whether our approach for understanding invasion success was also able to predict which species from a given pool might become successful, we conducted a set of cross-validations through (1) repeated split sampling and (2) jackknifing, using several goodness-of-prediction statistics to assess performance (Appendix S6 for details).

RESULTS

Invasion success of alien plant species in French grasslands

On the basis of our three components of invasion success, we classified alien species into the eight abundance classes of the Rabinowitz’s framework (Fig. 2, Table S2). In particular, alien species were considered to be rare when (1) they occurred in less than 13 plots, (2) covered in average less than 2.5% of total cover in the plots where they occurred, and (3) occupied an ecological hyper-volume of < 0.008 SD^4.

Most alien species in French grasslands were rare, with almost one third of species being in the rarest category (narrow geographic range, sparse abundance and small niche breadth). Forty-four aliens were classified as abundant for at least two criteria (e.g. *Ambrosia artemisiifolia*) and 20 alien species fell into the most successful alien species category (class A, see Table S2 for the list of species).

The synthetic index of invasion success gave very consistent results with the categorical classification of invasion success (Fig. 2, right panel). The rarest alien species had the lowest values of the invasion success indicator, species that were common for only one criterion had low-to-medium values, while species common for at least two criteria had medium-to-high success indicator values. This result supports the dimension reduction approach through PCA as a mean of synthesising the Rabinowitz’s multi-dimensional scheme into a one-dimensional continuous success indicator.

Disentangling the factors explaining invasion success

Community invasibility metrics were collectively more important for explaining the invasion success of alien species than either intrinsic trait values or introduction history (Fig. 4). In particular, the dissimilarity to species co-occurring in the same habitat type was by far the most important predictor of success both from a functional and phylogenetic perspective. Specifically, the most successful alien species were phylogenetically close and functionally similar to the native species co-occurring in the same habitat (Fig. 5a and b), but dissimilar to those co-occurring in the same plots (Fig. 5e). Minimum residence time, a classical feature for explaining invasion success, was also important, but only in third place. Furthermore, having higher or lower seed mass compared to the natives co-occurring within plots (SM.hier.plot) was also

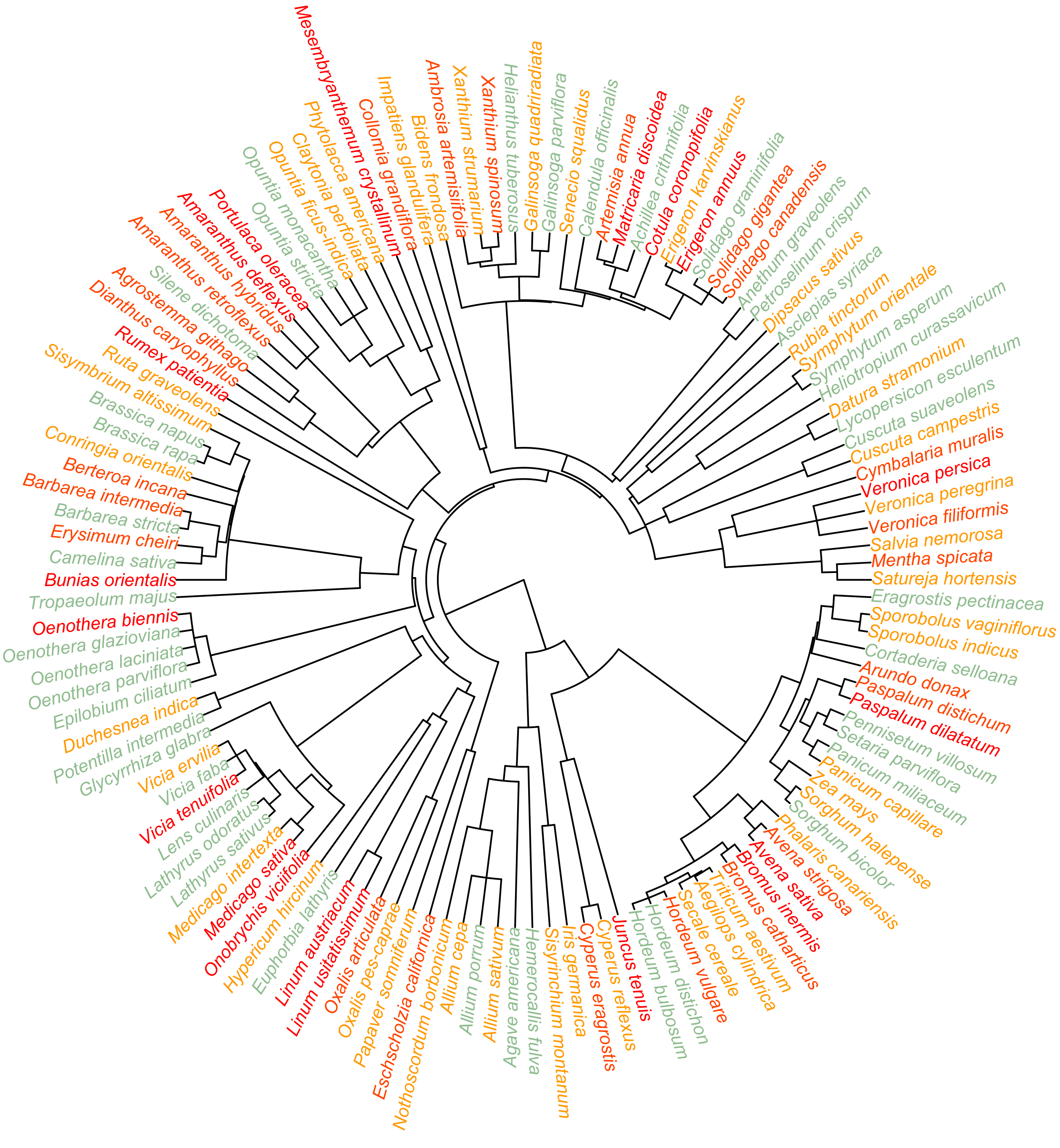


Figure 3 Phylogenetic tree of alien species in 50 000 French grassland plots with the corresponding commonness class. Colour scheme follows the one in the contingency table in Fig. 1.

determinant. Thereby, the most successful alien species were introduced long ago and had smaller seeds, greater SLA and lower height than the natives co-occurring within plots (Fig. 5c, d and f; Fig. S2). Importantly, while the relative trait hierarchy of alien and native species contributed to invasion success, intrinsic trait values of aliens species did not. Overall, this set of historical, functional and invasibility variables explained well the invasion success of alien species in French grasslands (R^2 = 0.571).

Moreover, contrasting phylogenetic similarity patterns at the habitat scale suggests distinct underlying drivers for the different components of success (Fig. 5a). When considering variation across the Rabinowitz's classes (Fig. S3), we found that different strategies could favour different components of invasion success. In congruence with the BRT results, alien species closely related to natives became both widespread and abundant (classes A and E; Fig. S3, left panel). By contrast, alien species that were phylogenetically most distant from

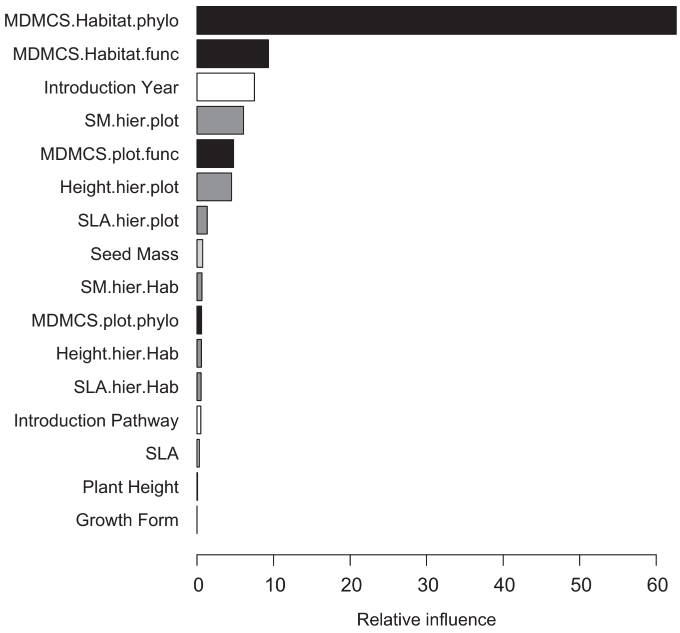


Figure 4 Variable importance in the boosted regression trees analysis. Bar colours indicate symmetric invasibility metrics (black), hierarchical competition metrics (dark grey), species traits (light grey) and introduction history (white). MDMCS.Habitat.phylo = mean phylogenetic distance to the most often co-occurring species at habitat level; MDMCS.Habitat.func = mean functional distance to the most often co-occurring species at habitat level; MDMCS.plot.func = mean functional distance to the most often co-occurring species at plot level; MDMCS.plot.phylo = mean phylogenetic distance to the most often co-occurring species at plot level; SM.hier.plot = mean (signed) difference in seed mass at plot level; Height.hier.plot = mean (signed) difference in height at plot level; SLA.hier.plot = mean (signed) difference in SLA at plot level; SM.hier.Hab = mean (signed) difference in seed mass at habitat level; Height.hier.Hab = mean (signed) difference in height at habitat level; SLA.hier.Hab = mean (signed) difference in SLA at habitat level. Also see Table 1.

natives became widespread regionally but not locally abundant (class B). In other words, the species in class A were those indicating high invasion success of close relatives to the natives in the BRT response curve (left part of Fig. 5a), while species in class B corresponded to the moderate invasion success obtained by distantly related species (right part of Fig. 5a). Finally, the species with very low invasion success (rare aliens) had intermediate phylogenetic distances to the natives (central part of Fig. 5a).

Predicting invasion success

While our framework is mainly designed for identifying the factors driving the success of invasions in grassland ecosystems, we found that our model also had a reasonable predictive performance to estimate invasion success of newly introduced species (Pearson $R = 0.56$ and R-squared = 0.33; Tables S3, Appendix S6). In particular, frequent, abundant and generalist species were on average correctly predicted as having greater invasion success than the rare ones (Fig. S9). The highest prediction errors and under-predictions occurred for the invaders of class C (regionally scarce, but locally abundant and generalist) and for some of the species of class A (Fig. S10).

DISCUSSION

By explicitly considering different components of invasion success we were able to unravel the drivers of plant invasions in French permanent grasslands. We found support for many classical hypotheses relating invasion success to species' traits and introduction history. Moreover, we were able to identify signals of competition at large spatial extent and for highly diverse communities. But more importantly, we showed that functional and phylogenetic similarities to natives were by far the most important features, suggesting that they are excellent proxies for processes of environmental filtering and competition driving invasion success. Specifically, environmental conditions filtered aliens similar to the natives at the habitat scale, while a combination of hierarchical competition and limiting similarity led to greater success of shorter aliens with smaller seeds and faster growth rates than the natives at fine scale.

We confirmed that most alien species introduced in French grasslands remained rare and failed to establish large and successful populations (Richardson & Pyšek 2006). Interestingly, certain aliens considered a threat in other habitats or countries (e.g. *Cortaderia selloana*, one of the 100 worst invasive species in Europe; Pyšek *et al.* 2009), appear to still be rare in French grasslands demonstrating the importance of the native community and of the historical context. Still, we identified 20 alien species as highly successful (Fig. 2). Several of them, including *Erigeron annuus*, *Oenothera biennis* and *Paspalum dilatatum*, are already known to be invasive elsewhere, causing negative environmental impacts in a number of different regions and habitats (Weber & Gut 2004; Pyšek *et al.* 2009; Kumschick *et al.* 2015). A few species, such as *Avena sativa* and *Linum usitatissimum*, were instead species that are, or have formerly been, cultivated, suggesting that they profited from high propagule pressure, but are unlikely to cause negative impacts.

In accordance with earlier work we found that invasion success was highest for species with a long residence time, which was the third most important factor predicting alien species success (Hamilton *et al.* 2005; Wilson *et al.* 2007; La Sorte & Pysek 2009; Dawson *et al.* 2011a). For example, *Veronica persica*, an archaeophyte in Europe, turned out to be among the most successful alien species. Residence time correlates with a number of factors such as propagule pressure or the overcoming of an initial lag phase in the process of invasion (Richardson & Pyšek 2006; Wilson *et al.* 2007), particularly by allowing time for acclimatisation and local adaptation (Lavergne & Molofsky 2007). Conversely, we found no strong relationship between invasion success and introduction pathways. This is a surprising result given that most of the naturalised alien plants considered in this study (*ca.* 50%) have been introduced as ornamental or horticultural plants. These are often suggested to spread faster than other alien species (Wilson *et al.* 2007) due to selective breeding and hybridisation in the cultivation process, high propagule pressure and repeated introduction of new genetic material through the

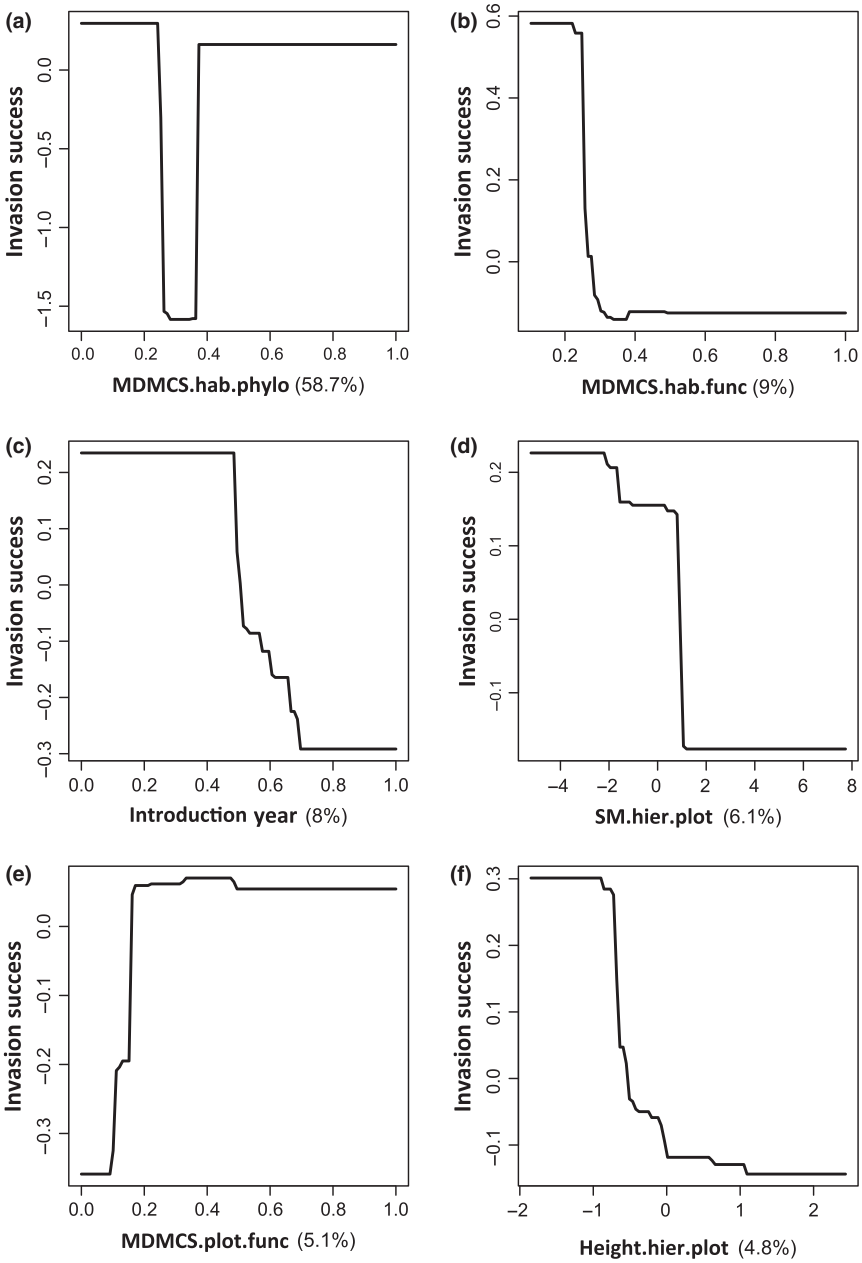


Figure 5 Response curves of invasion success to the five most important variables in the BRT. All variables are rescaled between zero and one (apart from the hierarchical indices to highlight positive vs. negative trait differences). Invasion success is expressed by the first axis of a PCA. Negative values relate to low invasion success while positive values relate to high invasion success. MDMCS.hab.phylo = mean phylogenetic distance to the most often co-occurring species within habitats MDMCS.hab.func = mean functional distance to the most often co-occurring species within habitats; MDMCS.plot.func = mean functional distance to the most often co-occurring species within plots; SM.hier.plot = mean (signed) difference in seed mass at plot level; Height.hier.plot = mean (signed) difference in height at plot level.

ornamental trade (Lavergne & Molofsky 2007). However, our finding may result from repeated introductions diluting adaptations to new environments.

The most interesting results from our study are those linking invasion success to similarity patterns between plant invaders and native communities. Many studies have already demonstrated the existence of non-random similarity patterns in invasions (Diez *et al.* 2008; Kraft & Ackerly 2010; Carboni *et al.* 2013; Pellock *et al.* 2013; Gallien *et al.* 2014b). However, here we showed that even when accounting for traits and introduction history, phylogenetic and functional similarity metrics were by far the most important correlates of plant invasion success in French grasslands.

In accordance with the filtering model of invasion biology (Richardson & Pyšek 2006), whether successful aliens co-occurred with similar or dissimilar natives depended on the spatial scale (habitat vs. plot). Specifically, the most successful alien species (both widespread and locally abundant) were those sharing habitat preferences with close relatives and functionally similar species in the native species pool (Cadotte *et al.* 2009; Lemoine *et al.* 2015). This finding suggests that alien species share ecological adaptations with natives when they successfully spread within a particular habitat type. It also implies that widespread, locally abundant and generalist aliens are not competitively limited at the habitat scale. The reason may be either that these very successful species are better competitors than natives, or that they avoid co-occurrence with closely related native competitors at fine scales. The fact that the most successful aliens tended to co-occur with functionally distinct natives at the plot scale (having high MDMCS.plot values, smaller seeds and lower height, Fig. 5) supports the latter hypothesis. These results corroborate previous findings showing that filtering mechanisms differ with the scale of observation (Kraft & Ackerly 2010; Thuiller *et al.* 2010; Carboni *et al.* 2013). Here, we find evidence of multiple hierarchical filters at an unprecedented spatial extent, thanks to the use of three dimensions of invasion success, rather than just based on dichotomous contrasts of aliens vs. natives or invasive vs. naturalised species.

Interestingly, we did not find strong support for intrinsic functional traits defining an overall successful invader (Lemoine *et al.* 2015). By contrast, all hierarchical indices emphasising trait differences to the natives at the plot level were much more important than the trait values *per se*. In particular, successful aliens were shorter, had smaller seeds and greater SLA than natives co-occurring within plots. Small seed mass generally correlates with prolific seed output, wider dispersal (often through wind), long persistence in the seed bank, short juvenile periods and high relative growth rate of seedlings (Rejmanek & Richardson 1996; Moles & Westoby 2006; Van Kleunen *et al.* 2010). These characteristics are likely to favour rapid colonisation by alien species in sites where natives are not as fast-growing, particularly in response to grassland disturbance. Competition for light does not seem to be the main process filtering successful aliens in grasslands, as shorter species were more successful. Shorter species can spread laterally in disturbed habitats, thereby being superior competitors for space and/or soil nutrients, and are also likely to be favoured in grazed habitats, due to both grazing avoidance and better ability to deal with higher soil bulk density associated with trampling. Therefore, our data suggest that in grasslands, faster growth rates than the surrounding natives, specifically at the juvenile stage (small seed size), together with lateral spread and good dispersal ability to reach disturbed patches are more important characteristics than high competitive ability for light interception (competition–colonisation trade-off; Kneitel & Chase 2004).

On the basis of the Rabinowitz's framework, we also highlighted distinct ecological processes driving different components of invasion success. In contrast with the most successful alien species of class A (widespread, generalists and abundant), aliens of class B were widespread and generalists but remained locally sparse. Aliens of this latter group were very distantly related to the natives not only at the plot scale but also at the habitat scale. One possible explanation is that these species are poor competitors in most grasslands (e.g. they were mostly species with low height and SLA values). They may only colonise grassland sites when resources become available through resource pulses which weaken competitive exclusion (Davis *et al.* 2000) or due to continuous propagule pressure and dispersal from adjacent, more suitable habitats. Finally, the alien species in the rare categories are neither very similar nor dissimilar to co-occurring natives at the habitat scale, suggesting that rather neutral processes determine their presence in these grasslands. We argue that processes driving invasion are not the same across alien species and that specific processes are important for widespread species compared to less successful ones. Future studies should acknowledge that the relative importance of filtering processes affecting the success of alien species is likely to change along the classical introduction–naturalisation–invasion continuum (*sensu* Richardson & Pyšek 2006).

Finally, through a cross-validation procedure we highlighted that our model based on similarity to the natives also had the potential to estimate invasion success of newly introduced species. Predictive performance was generally reasonable (Appendix S6), though we found high prediction errors and under-predictions particularly for the invaders of class C. These species are locally abundant and generalist, but they are at the moment restricted to a narrow extent, potentially close to introduction sources (i.e. they may represent recent introductions). The invasion success of these species, which are likely not to be at equilibrium, is the most difficult to predict. However, it is encouraging that, while invasion success of species in class A was not always correctly identified, the most well-known invaders in this class (e.g. *O. biennis, E. annuus, B. inermis, J. tenuis*) were indeed very well predicted by the model (Appendix S6). Such a framework has thus the potential to be used in other types of systems and in other regions.

CONCLUSIONS

Using French grasslands as a study system, we showed that complementary measures of invasion success are useful to identify the driving forces of invasion across spatial scales and environmental gradients. The Rabinowitz's components originally created for assessing different forms of species' rarity represent a straightforward framework for categorising alien species and, in turn, for identifying the most successful and potentially harmful ones. In doing so, this framework provides guidance for differentiating and prioritizing alien species for management. Furthermore, our use of complementary similarity metrics based on co-occurrence patterns allowed the identification of the relevant processes of invasion at two spatial scales. The most successful alien species are specifically adapted to the habitat they invade the most, but they then express different traits than co-occurring native species at fine scale within these habitats. Together with residence time and dispersal ability, these characteristics make up the winning alien species in permanent grasslands. Moreover, we showed that these characteristics in a modelling framework are likely to give hints on the invasion success that can be attained by newly introduced species. Taken together, the set of approaches and metrics we have proposed here can be used in other ecosystems and biogeographic regions, not only to anticipate invasions but also to gain a better understanding of the processes shaping invasion success worldwide.

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AUTHORSHIP

MC, WT, TM and SL conceived the ideas. PC, CV, FM, BB and FE contributed and processed data. CR built the phylogeny. MC performed the analyses. All authors contributed to the writing, which was led by MC.

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