**RESEARCH PAPER**

**Functional traits modulate the response of alien plants along abiotic and biotic gradients**

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**Abstract**

**Aim:** It is widely recognized that the prediction of invasion success at large biogeographical scales requires jointly accounting for alien species traits and local community filters, such as abiotic conditions, biotic interactions and propagule pressure. Despite this recognition, interactions between traits and community filters are generally neglected. Here, we aim to address this limitation by developing a hierarchical framework that builds on trait-based theory to model occurrences of alien species as a function of spatially explicit variables, filtering invasions and their interactions with species traits.

**Location:** Herbaceous communities throughout France.

**Time period:** c. 1960–2012 (mostly after 1990).

**Major taxa studied:** Herbaceous plants.

**Methods:** Based on a large dataset of >50,000 community plots, we built a multispecies hierarchical model of the distribution of the 10 most widespread alien plants in French grasslands. In this model, we explicitly account for how plant height, specific leaf area (SLA) and seed mass affect the occurrence of alien species along gradients of human pressure, environmental conditions and native community composition. Finally, we contrast the results to native species responses along the same gradients.

**Results:** We show that two out of three traits significantly modulate the responses of species along these broad gradients. Alien plants with exploitative traits (i.e., tall and with high SLA) were less dependent on human pressure, more efficient in resource-rich environments and better at avoiding competition from native species. These trait-gradient interactions were often unique to alien plants (e.g., human pressure was important only for supporting alien species with low SLA), even though trait ranges of alien and native species were comparable. Ultimately, the modelling of trait-gradient interactions allows spatially explicit estimations of invasion risks by novel species with particular sets of traits.

**Main conclusions:** By taking the best from multispecies distribution modelling and trait-based theory, our framework paves the way for a generalized mechanistic...
1 | INTRODUCTION

As a consequence of the repeated introduction of alien species outside their native range, biological invasions are becoming increasingly common in natural environments, often posing a major challenge for the conservation of biodiversity (EEA, 2013). Understanding the mechanisms by which introduced plant species establish and become invasive is thus essential to anticipate their potential spread and impact on ecosystems (Bradley, Blumenthal, Wilcove, & Ziska, 2010).

Invasion success within a local community is a function of multiple factors associated with three main ecological processes: (a) introduction, (b) environmental filtering and (c) biotic interactions between the invader and the resident species (Catford, Jansson, & Nilsson, 2009). First, the human-mediated introduction of propagules (i.e., propagule pressure) determines the probability of establishment of any given alien species in a region (Lockwood, Cassey, & Blackburn, 2005). Second, local environmental conditions represent a filter for establishment, selecting only the alien species with the right physiological adaptations (Thuiller, Richardson, Rouget, Proches, & Wilson, 2006). Third, if local conditions are favourable for the survival and reproduction of the species, invasion success will finally depend on biotic interactions with the natives in the recipient community. Based on coexistence theory, introduced species can succeed either using different resources from the other species in the invaded community (resource opportunity) or by replacing the resident natives that are inferior competitors (competitive exclusion) (Gallien & Carboni, 2017; Mayfield & Levine, 2010). Overall, the local combination of propagule availability, environmental conditions and native species composition will determine whether a community is invaded or not.

However, the characteristics of the alien species also influence invasion success. Some alien species are intrinsically more invasive than others because they have more successful functional traits, associated with higher plant performance, fitness and competitive abilities than most native species (van Kleunen, Weber, & Fischer, 2010). In addition, certain ecological adaptations might be advantageous in particular environments and not in others (Catford, Morris, Vesk, Gippel, & Downes, 2014; Thuiller et al., 2006). Likewise, traits related to competitive ability might be important in competitive environments, but not in environmentally stressful ones. For example, in harsh environments (such as in extreme climatic conditions or in infertile soils) invasion might be most limited by physiological pre-adaptations to survive and reproduce in these conditions (e.g., slow growth rates, conservative stress-tolerant strategies). Conversely, in favourable environmental conditions, where more species can grow, invasion will probably be more strongly limited by competitive dynamics. Finally, functional traits can also modulate the role of propagule pressure (Maurel, Hanspach, Kühn, Pyšek, & van Kleunen, 2016; Peoples & Goforth, 2017). For example, taller alien species with small and light seeds typically have good dispersal ability and might be less reliant on local introduction sources (Rejmánek & Richardson, 1996; Thomson, Moles, Auld, & Kingsford, 2011). In summary, the traits of alien species modulate all major invasion processes (introductions, environmental filtering and biotic interactions), ultimately determining which species become invasive and which communities are invaded across environmental gradients (Richardson & Pyšek, 2006). Yet, surprisingly, these trait-process interactions are systematically neglected in most invasion studies (Catford et al., 2009).

Variation across plant ecological strategies in resource acquisition, dispersal, establishment and competitive ability is well captured by Westoby’s (1998) leaf-height-seed (LHS) scheme. Specific leaf area (SLA), defined as the light-catching area deployed per dry mass, is correlated with relative growth rates (Wright, Reich, & Westoby, 2001) and can be used as a predictor of plant response to resource availability (Grime, 1977). High SLA is associated with exploitative, fast-growing species and low SLA is associated with conservative species with lower metabolic rates but enhanced efficiency of nutrient and water use. Plant height reflects the ability of species to intercept light and to dominate vegetation layers (Violle et al., 2009), in addition to dispersal ability (Thomson et al., 2011). Seed mass partly captures dispersal ability, seed production, longevity and competitive ability at the seedling stage (Moles & Westoby, 2006; Tamme et al., 2014). These three traits have been shown previously to correlate with alien species invasiveness (van Kleunen et al., 2010) and are also likely to be important in modulating the establishment of alien species along broad biogeographical gradients.

Here, we propose building upon hierarchical generalized linear modelling to understand, quantify and, ultimately, predict how LHS traits modulate alien species distributions along environmental gradients. We combine this framework with proxies of human-mediated propagule pressure and trait-based indices of biotic interactions, in order to reveal the role of functional traits in influencing alien species responses not only to environmental filtering but also to all major invasion filters at biogeographical scales. We apply our approach to a large dataset of herbaceous communities that spans broad environmental gradients across the entire country of France. We specifically aim: (a) to demonstrate

understanding of how traits influence the success of alien plants and their spatial distributions.

**KEYWORDS**

biotic interactions, environmental filtering, functional traits, hierarchical model, plant invasion, propagule pressure, trait-based theory, trait-environment interactions
how functional traits modulate the responses of alien species to abiotic and biotic gradients, focusing on the LHS scheme; (b) to forecast the invasion probability of potential new alien species based on their traits; and (c) to compare the mechanisms shaping distributions of alien and native species. For example, we expect that: (a) strong propagule pressure should be more important for alien species with poor dispersal ability (short and large-seeded species); (b) productive and generally favourable environmental conditions should be more important for exploitative species (tall and high SLA species); and (c) biotic interactions should be more important for competitive alien species of productive environments (tall and high-SLA species).

2 | MATERIALS AND METHODS

2.1 | Community data for French permanent grasslands

Data on alien species distributions and on plant communities in French herbaceous communities were obtained from the DIVGRASS database on permanent grasslands (Violle et al., 2015), a compilation of >50,000 vegetation plots (50–100 m²). Permanent grasslands are semi-natural herbaceous ecosystems used to produce forage and maintained through grazing and/or cutting regimes (Silva, 2008). In France, they cover >20% of total land area (Violle et al., 2015). This database contains community information (visually estimated relative cover of all species present in plots) for 4,282 species. These community plots belong to four grassland types (or habitats), which span broad environmental gradients and include dry calcareous grasslands, mountain grasslands, mesic grasslands and ruderal and trampled grasslands (for details on habitat categories, see Carboni et al., 2016). In the following analyses, out of all available community plots, we excluded cases that we suspected might represent instances of resampling of the same plot, as a conservative approach to avoid potential pseudo-replication.

2.2 | Functional traits

We used information for the three functional traits corresponding to Westoby’s (1998) LHS scheme: SLA, plant maximal height at maturity (plant height) and seed mass. Average values of these traits were available per species through the DIVGRASS project for most herbaceous species, including both aliens and natives, and were originally collated from TRY (Kattge et al., 2011) and a number of local databases (for details about the original sources, see Violle et al., 2015). In the dataset, the mean number of independent observations for trait values available per species was 5.71, 3.35 and 3.63 for SLA, height and seed mass, respectively (Borgy, Violle, Choler, Garnier, et al., 2017). For alien species, this included individual measurements from both the native and the non-native range (i.e., the global range). Previous analyses with this dataset have shown that, in spite of a certain degree of intraspecific variation, species and community rankings for trait values measured locally in French grasslands and in TRY were generally consistent (Borgy, Violle, Choler, Garnier, et al., 2017; Violle et al., 2015). We thus assumed that using the average trait value per species would be acceptable to detect trait–environment interactions at the biogeographical scale of our study. However, we acknowledge that through this simplification we might miss patterns related to local adaptations or plasticity (also see Discussion and Perspectives sections).

2.3 | Alien species selection

We identified all herbaceous species in DIVGRASS that were recorded in the DAISIE database as alien to France and naturalized there (Pyšek et al., 2009), for a total of 162 herbaceous alien species occurring in c. 8,000 plots. These species were classified by Carboni

<table>
<thead>
<tr>
<th>Alien species</th>
<th>Family</th>
<th>Frequency</th>
<th>Local abundance (% cover ± SE)</th>
<th>Origin</th>
<th>Pathways</th>
</tr>
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<tbody>
<tr>
<td><em>Ambrosia artemisiifolia</em></td>
<td>Asteraceae</td>
<td>36</td>
<td>3.50 ± 1.18</td>
<td>Americas</td>
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<tr>
<td><em>Avena sativa</em></td>
<td>Poaceae</td>
<td>180</td>
<td>7.27 ± 0.99</td>
<td>Eurasia</td>
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<tr>
<td><em>Cotula coronopifolia</em></td>
<td>Asteraceae</td>
<td>124</td>
<td>22.46 ± 2.31</td>
<td>Africa</td>
<td>U</td>
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<tr>
<td><em>Erigeron annuus</em></td>
<td>Asteraceae</td>
<td>249</td>
<td>3.16 ± 0.50</td>
<td>N America</td>
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<tr>
<td><em>Linum austriacum</em></td>
<td>Linaceae</td>
<td>36</td>
<td>4.10 ± 0.85</td>
<td>Eurasia</td>
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<tr>
<td><em>Linum usitatissimum</em></td>
<td>Linaceae</td>
<td>560</td>
<td>3.33 ± 0.30</td>
<td>Anecophyte</td>
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<tr>
<td><em>Matricaria discoidea</em></td>
<td>Asteraceae</td>
<td>105</td>
<td>4.69 ± 0.89</td>
<td>Asia</td>
<td>T</td>
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<tr>
<td><em>Onoethera biennis</em></td>
<td>Onagraceae</td>
<td>75</td>
<td>2.53 ± 0.61</td>
<td>N America</td>
<td>O/H</td>
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<tr>
<td><em>Onobrychis vicifolia</em></td>
<td>Fabaceae</td>
<td>2,364</td>
<td>6.29 ± 0.22</td>
<td>Europe</td>
<td>A</td>
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<tr>
<td><em>Solidago gigantea</em></td>
<td>Asteraceae</td>
<td>66</td>
<td>3.39 ± 0.75</td>
<td>N America</td>
<td>O/H</td>
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Notes. A = agriculture; H = horticulture; O = ornamental; T = transportation; U = unknown. Anecophytes are species that have been created from their wild ancestors by plant breeding and have subsequently become alien; they thus have no native range in the strict sense.
et al. (2016) into different categories of invasion success based on their degree of geographical spread, local abundance and general-ism. Here, we restricted our analysis to those species that were classified as both geographically widespread and locally abundant (c. 20 species; Carboni et al., 2016). In addition, only alien species that were present in >30 plots were selected for modelling, considering this as a minimal sample to explain species distribution in a model at this scale. We excluded species with missing values for functional traits or for which introduction status was uncertain. We obtained this scale. We excluded species with missing values for functional variables: (a) a measure of human pressure as a proxy of propagule pressure, (b) a set of spatially continuous environmental variables related to invasion processes, (c) a biotic index, and (d) soil, slope and productivity and thought to be closely linked to physiological functioning. We then selected an uncorrelated subset of environmental variables to avoid multicollinearity in further modelling (see Supporting Information Appendix S1). Of this subset, two variables, growing degree-days (GDD) and temperature seasonality (TS), reflect gradients of favourable climatic conditions in plant establishment. The GDD corresponds to the annual sum of degree-days over a 5.56°C threshold (that corresponds to the baseline for growth of most herbaceous plants; e.g., Trudgill, Squire, & Thompson, 2000) and is positively correlated with annual mean temperature and negatively with annual precipitation (Supporting Information Appendix S2, Figure S3). Temperature seasonality is a measure of temperature change over the course of the year, and we calculated it as the standard deviation of monthly temperature averages. Furthermore, net primary productivity (NPP) is the net amount of solar energy converted to plant organic matter through photosynthesis and is measured in units of elemental carbon (Imhoff et al., 2004). It represents a resource-availability gradient for plant establishment. All bioclimatic variables were available at 1 km resolution from the French meteorological model AURELHY, downscaled to 100 m resolution (Bénichou & Le Breton, 1987; Supporting Information Appendix S2). The NPP was calculated based on a model that incorporates satellite and climate data to estimate the fixation and release of carbon and was obtained from the Columbia University Center for International Earth Science Information Network (Imhoff et al., 2004).

Finally, to account for biotic interactions with the natives we calculated a biotic index called the mean weighted distance to the native community (MWDNC; Gallien & Carboni, 2017). This index measures the functional differences between the alien and the native community, based on the combination of traits described above (height, SLA and seed mass). For each focal alien species, it was calculated as the Euclidean distance of the alien species traits to the mean of native species traits in each community plot, weighted by their abundance. There were generally only a few other alien species in the plot (average alien species richness was 1.2 across plots where aliens occurred), and these were excluded for the index calculation. The MWDNC is often interpreted as a measure of resource use in the community (or more generally, of shared requirements, such as for mutualists). If an alien species tends to be dissimilar functionally to the co-occurring natives (high MWDNC), this is likely to be because it takes advantage of a resource opportunity by filling an empty niche in the community (i.e., adopting a niche differentiation strategy) or because it adopts more successful resource acquisition strategy than the resident natives thanks to more competitive traits (Gallien & Carboni, 2017). In contrast, if the successful alien species tends to be similar functionally to the native community (low MWDNC), this is likely to be because environmental filtering favours
the establishment of aliens that can exploit similar resources to the residents (or that can share the same mutualists) and have equally competitive traits.

Overall, all explanatory variables selected for the model (environmental, biotic and human) were weakly correlated with each other (Pearson correlation <0.6; Supporting Information Appendix S2, Figure S4), so that multicollinearity was not an issue.

2.5 | Hierarchical modelling framework

We built a hierarchical mixed-effects model of species occurrence as a function of human, environmental and biotic variables and their interaction with species traits, as described by Pollock, Morris, and Vesek (2012) and using the "lme4" package (Bates, Mächler, Bolker, & Walker, 2015). In the model, the response was the probability of alien species occurrence in a community plot (with a binomial error distribution and logit-link), and the fixed-effect explanatory variables were the human footprint (HF), the environmental variables (NPP, GDD and TS) and the biotic index (MWDNC), which were included both as main effects and in interaction with species traits (SLA, plant height and seed mass; Supporting Information Appendix S3). All explanatory variables and traits were centred with respect to the mean and scaled by 1 SD. We then included alien species identity as a random effect, allowing slope and intercept parameters to vary for each species. Importantly, this hierarchical structure allows species distributions to be determined primarily by the main-level explanatory variables, and for the species trait values to modulate those responses through interaction terms, as in Pollock et al. (2012). Positive trait–environment interactions indicate that a high value of the trait increases the probability of occurrence of the species in high values of the environmental gradient. In the same way, trait interactions with HF and MWDNC convey information on the modulating role of traits for species responses to human pressure and to biotic interactions. Note that we did not include traits as a main-level effect here because, given that we preselected only the alien species that are the most widespread and abundant in the study area, we do not expect traits further to influence the overall probability of occurrence of these species.

Given the high number of plots available in the database (>50,000; leading to many observed absences compared with presences), we used an absence-selection procedure to avoid having low prevalence for species occurring at low frequencies in the database (also see Sheppard, Carboni, Essl, Seebens, & Thuiller, 2018). Very low prevalence (i.e., a very small proportion of presence records) can have a strong impact on model performance when modelling the probability of occurrence of a species (Albert & Thuiller, 2008; Jiménez-Valverde, Lobo, & Hortal, 2009). Thus, for each alien species we subsampled the total available absences to use in the model by randomly selecting only 500 of the plots in which the species did not occur (to avoid prevalence <0.05). For alien species occurring in >500 plots (frequency > 500), we selected a larger subset of absences, matching the number of plots in which the species occurred. In order to avoid biases introduced through random selection and to ensure correct capturing of the full environmental gradients, in this absence-selection procedure we selected an equal number of absence plots across the four grassland habitat types represented in the database (e.g., 125 absence plots in each habitat, for a total of 500 absences). Then, the multispecies hierarchical model for the probability of alien occurrence was fitted using the obtained subset of the data, which included all alien species presences and their subsampled absences (the sensitivity of model results to the absence selection procedure was checked for across 10 absence selection runs; Supporting Information Appendix S4, Figure S6). Given that variance in species abundance was low (Supporting Information Appendix S1, Figure S2), we did not include a separate model with abundance data.

To evaluate the model, we calculated the overall variance explained (conditional $R^2$, following Nakagawa & Schielzeth, 2013) using the package "MuMIn" (Bartoń, 2013), and the area under the curve (AUC) for the full dataset, which measures the predictive accuracy of the model, using the "Hmisc" package (Harrell & Dupont, 2007). The AUC varies from 0.5 (equivalent to the prediction from a random model) to 1 (perfect predictions). All analyses were carried out using R version 3.3.2 (R Development Core Team, 2016). We checked for any residual spatial autocorrelation with a plot of Moran's I across spatial lags of increasing distance using the library spdep (Bivand, Hauke, & Kossowski, 2013; Supporting Information Appendix S4, Figure S5).

Finally, in order to demonstrate how the approach can help to assess invasion risks for newly introduced species, we predicted the probability of invasion in France at varying trait values. Using the estimated model parameters, we predicted the probability of occurrence of two hypothetical species in French grassland communities differing in their SLA values: one with high SLA values (35 m²/kg) and one with low SLA values (13 m²/kg), relative to the range in SLA of the alien species studied here. In both cases, plant height and seed mass values were kept constant using the average value. We focused on SLA because it was the most influential trait in our model (see Results section). We projected this probability of occurrence on a map of France.

2.6 | A comparison with natives

As a reference and to assess whether alien species responded to gradients in a different manner from native species with similar frequencies, we applied the same modelling procedure to a selection of natives occurring in French permanent grasslands. We selected native species for which all three traits were available and that had a similar range of frequencies to the modelled alien species in our database (i.e., occurring in 100–2,400 plots). We obtained a set of 661 native species, on which we applied exactly the same modelling procedure described for the aliens, using the same fixed and random factors. However, we did not include MWDNC as a biotic index, as this index is specific to alien species (because for native species we have no information on the order of arrival to assume filtering from an already resident community). Note that overall trait values of
3 | RESULTS

On average, alien species had a positive response to GDD and TS, were moderately favoured by human pressure (high HF) and had a higher probability of establishing in functionally similar native communities (low MWDNC; Figure 1). However, as expected, individual alien species responded differently to environmental gradients, human pressure and biotic interactions, and these different responses were explained by their traits. All traits significantly modulated the response of alien species to environmental variables, whereas only SLA influenced the response of alien species to human pressure and biotic interactions (Figure 1).

3.1 | Traits modulating alien species responses

The SLA and plant height had a strong modulating influence on occurrence of alien species along the resource availability gradients (GDD and NPP). The interactions of GDD with SLA and with plant height were the strongest effects (e.g., roughly twice as strong as the effect of the interaction GDD-seed mass; Figure 1). Specifically, higher SLA and plant height values led to much more positive responses of alien species to GDD (Figures 1 and 2b). For example, the probability of occurrence of the tallest alien species, *Solidago gigantean*, increased much more rapidly along the GDD gradient than that of the more average-sized species, *Erigeron annuus* (twice as strong effect in Figure 2b). Larger seed mass had a similarly positive but less important effect for alien occurrence along the same GDD gradient (Figure 1). Furthermore, the responses of alien species to NPP ranged from negative for species with low SLA values to positive for species with high SLA values (Figure 2a). In contrast, although we found that a hypothetical average alien species would respond positively to TS (i.e., it would be more likely to occur under fluctuating climatic conditions), alien occurrence along this gradient was neither dependent on SLA nor on seed mass and was influenced by plant height to only a moderate extent (highly variable effect; Figure 1).

The responses of alien species to HF differed depending on their SLA values (Figure 2c). Species with low SLA had a positive response to HF, suggesting that their probability of establishment increased with human pressure and potential introduction sources. In contrast, the relationship with HF was much weaker for species with higher SLA values, suggesting that alien species with high SLA had an equal chance of establishing both close and far away from human sources of introduction.

The negative average effect of MWDNC in the model illustrates that the probability of establishment of alien species declined with increasing functional distance to the resident natives (Figure 1). In other words, alien species preferentially occurred in functionally similar native communities and seemed generally more limited by environmental filtering than by biotic interactions. However, aliens with higher SLA also had greater probability of occurring in functionally dissimilar communities (i.e., they had equal chances of occurring in both functionally similar and dissimilar communities), suggesting that they were either at least as competitive as most of the resident natives or capable of taking advantage of resource opportunities (Figure 2d).

3.2 | Invasion risks based on model predictions

Overall, the hierarchical model of alien species distribution had a good performance, with an overall explained deviance of 72.3% (conditional $R^2$) and an AUC of 0.92. Based on predictions from the fitted model, the grassland communities most at risk of invasion occurred in the Mediterranean basin and in the Rhone corridor in the east of France (Figure 3). However, alien species with low SLA also had higher probability of invasion in the north and east of France, whereas the probability of invasion in the Mediterranean south of France and along the coast of Corsica was higher for species with high SLA.

3.3 | A comparison with natives

The hierarchical model for the 661 native species had a satisfactory performance (conditional $R^2 = 0.595$; AUC = 0.81), and most tested gradients significantly affected the distribution of native species. On
average, the occurrence of native species was positively correlated with NPP and TS and negatively correlated with HF (Figure 4). In addition, positive interactions were observed between SLA and NPP, plant height and GDD, plant height and temperature seasonality and plant height and HF (Figure 4; Appendix S5, Figure S8). In sum, native species responded in a similar manner to alien species along the NPP and TS gradients, but in a different manner along the GDD and human pressure gradients. Although all alien species profited from longer favourable growing conditions (i.e., from high GDD), only native species with certain characteristics did so (those with high SLA and plant height). Furthermore, although human pressure favoured the establishment of alien species (particularly for species with low SLA), native species were on average negatively affected by human pressure and disturbance (except tall species; Figure 4).

4 | DISCUSSION

Human introductions, environmental filtering and biotic interactions are considered the most important factors driving plant invasions in natural environments. Consistent with theoretical predictions, we found significant responses of alien plants to factors related to these
three main processes across herbaceous communities in France. However, we also found that species traits modulated invasion processes across the gradients of human, abiotic and biotic filters, in some cases strongly altering invasion outcomes.

### 4.1 Traits modulating responses of alien species to human pressure

High propagule availability through human introductions is generally thought to increase the success of colonization of alien species regardless of environmental conditions and species traits (Simberloff, 2009). In contrast, here we found that HF, our proxy for human-mediated propagule pressure showed, on average, only a marginal positive association with invasion success. In fact, the importance of the human footprint for establishment of alien species was dependent on the specific characteristics of the alien species and, in particular, on their SLA values. Specifically, the human footprint had a significantly stronger influence on the establishment of alien plants with a conservative resource acquisition strategy (low SLA). This is potentially because conservative species typically have less opportunity to invade in competitive and productive environments and could therefore be more dependent on continuous introductions (Catford, Downes, Gippel, & Vesk, 2011). In addition, a conservative strategy might also be more advantageous in anthropogenic environments representing harsh abiotic conditions for plant growth (e.g., many urban habitats are characterized by hard surfaces and increased aridity and alkalinity; Ricotta et al., 2009). However, we did not observe a similar pattern for native species (Figure 4), which suggests that the importance of the human footprint for the establishment of conservative alien plants lies more in the repeated introduction of alien propagules through human activities.

**Figure 3** Predicted probability of invasion of hypothetical species with low (13 m²/kg; left panel) or high (35 m²/kg; right panel) specific leaf area (SLA) values in French permanent grasslands, with average values of height and seed mass. The two areas most at risk of invasion mentioned in the text are marked (Mediterranean basin and Rhone corridor) [Colour figure can be viewed at wileyonlinelibrary.com]

**Figure 4** Contribution of native species traits to partial responses to environmental variables and human pressure. The "average" effect (black) represents the response of species with average traits to each environmental and human gradient variable. The interaction coefficients describe how traits modulate responses to each gradient across species (given other traits and variables held at their means). A positive effect size indicates that higher values of that trait increase the probability of species occurrence along that gradient. Bars are 95% confidence intervals that represent uncertainty around effect size. We consider effects as significant if the 95% confidence intervals do not overlap zero [Colour figure can be viewed at wileyonlinelibrary.com]
expected taller species with smaller seeds, which typically disperse over larger distances, to be able to invade communities far away from their introduction origin, and species with large seeds to be more dispersal limited. Following this line of reasoning, the human footprint should have stronger effects for short and large-seeded species, because human-mediated propagule pressure where human activities are intense can compensate for poor natural dispersal ability. However, we did not find patterns consistent with this expectation, potentially because humans also mediate introductions through vegetative propagules or because both the human footprint and seed mass might be correlated with other confounding factors. For example, seed mass can enhance seedling survival, with larger seeds potentially providing an advantage in stressful anthropogenic conditions (Moles & Westoby, 2006), or might be associated with the mode of human introduction (e.g., small-seeded species primarily introduced unintentionally, and large-seeded species more related to horticulture; Maurel et al., 2016). Owing to this intrinsic complexity, our understanding of the role of seed characteristics in interaction with propagule pressure remains partial and should be investigated further in future research, preferentially using more direct measures of propagule pressure and potentially also proxies of historical introduction sources (Barney, Ho, & Atwater, 2016; Moles & Westoby, 2006).

4.2 Traits modulating environmental responses of alien species

As expected, we found that, after introduction, environmental filtering influenced the distribution of alien species across gradients of: (a) productivity (NPP); (b) favourable conditions for growth (GDD); and (c) seasonality (TS). Nevertheless, multiple traits from the LHS scheme, representing different aspects of plant performance, also influenced invasion success along these gradients.

First, the resource acquisition strategy strongly modulated the affinity of alien species for productive environments. Exploitative alien species (high SLA) responded positively to the NPP gradient and were the main invaders in productive grasslands. In contrast, unproductive grasslands had a higher probability of being invaded by conservative alien plants, with low metabolic rates (low SLA). This corroborates the prediction that unproductive environments in severe abiotic conditions should be dominated by conservative plants (Grime, 1977) and productive environments by strong competitors (Borgy, Viole, Choler, Denelle, et al., 2017; Díaz et al., 2004). However, our results are interesting because the risk of invasion is generally considered to increase with resource availability related to disturbance regimes or high ecosystem productivity (Davis, Grime, & Thompson, 2000). Instead, we show that even in these conditions, invasion success depends on alien species characteristics of resource acquisition and competitive ability, and that for invasive species with low SLA, establishment in resource-rich environments is, in fact, less likely (unless it is enhanced by high propagule pressure from anthropogenic environments). This was not the case for native species, which were on average more successful in highly productive environments, even though exploitative traits with higher SLA conferred an additional advantage under high NPP. In contrast, plant height did not have a similar modulating role, even though it is correlated with productivity globally and often reflects a competitive advantage in other environments (Moles et al., 2009). This finding suggests that rapid growth and efficient use of resources, rather than competition for light at maturity, were more important limiting factors for successful invasion of productive grasslands (see also Carboni et al., 2016). Importantly, note that the strong SLA-productivity interaction resulted in no overall relationship between community productivity and average invasion success across aliens, highlighting again how the failure to account for trait-environment relationships could mask the importance of certain invasion processes.

Second, environments with higher GDD generally promoted grassland invasions. However, this positive response to warm temperatures was stronger for taller and exploitative alien species. In general, plants with high metabolic rates tend to have an advantage in warmer environments, because temperature can increase growth rates and extend favourable growing conditions (Loveys, Scheurwater, Pons, Fitter, & Atkin, 2002). Indeed, we also found a similar trait-environment interaction in our model of native species distribution (Figure 4). But in addition, warmer conditions provided a specific advantage to alien species over most native species in these grasslands (Verlinden & Nijs, 2010), because natives on average did not respond as positively to GDD as did alien species (Figure 4). This has interesting implications for the future of invasions in grasslands under predicted scenarios of climate change (Bradley et al., 2010), because alien species will be on average more favoured than natives by a rapidly warming climate, particularly in climatically harsh environments, such as mountain ranges (Carboni et al., 2018).

Finally, alien species responded positively, on average, to temperature seasonality, but variation across species in this response was not easily predictable based on the traits we examined. Invasive species often have highly plastic traits, and this feature might facilitate invasions in fluctuating climatic conditions more than specific average trait values (Davidson, Jennions, & Nicotra, 2011; Walther et al., 2009). Intraspecific trait variability might thus play a particularly important role in modulating the response of alien species to this gradient and might have helped to account for some of the variability in species responses we detected in our model (see section 4.5 Perspectives).

4.3 Traits modulating biotic responses of alien species

Finally, the biotic structure of native communities had a clear relationship with the establishment of alien species. Specifically, on average alien species co-occurred with functionally similar natives in French permanent grasslands (low MWDNC). This pattern suggests that these alien species tend to exploit similar resources to the natives, which confirms that environmental filtering is one of the main drivers of invasions in these ecosystems. However, the
characteristics of alien species also modulated the response of aliens to biotic interactions with the natives. In particular, compared with conservative alien species, species with high SLA values had a higher probability of invading communities that were functionally different. This pattern indicates that the biotic processes leading to greater functional differentiation from the natives, such as niche complementarity or competitive exclusion, are more important for fast-growing, exploitative alien species. This is congruent with our observation that exploitative species had an increased probability of occurring in highly productive communities, where biotic interactions are expected to be more important (Gaucherand, Liancourt, & LavoR, 2006). Both competitive exclusion of weaker native species and exploitation of resource opportunities are potential strategies for invading highly productive environments (Grime, 2006). Thus, our results suggest that exploitative alien species can either take better advantage of resource opportunities or are able to invade highly productive environments by being even more efficient than the already competitive resident natives (e.g., Cotula coronopifolia; Figure 2d). We should note that, although we focused here on highlighting patterns that might result from competition with the native plant community, other types of biotic interactions are also likely to influence invasion processes. Indeed, responses of alien species to the presence of herbivores, mutualists or general facilitative interactions will also be modulated by their functional traits (e.g., Traveset & Richardson, 2014) and could be explored in future research building on our framework (see section 4.5 Perspectives).

4.4 The many strengths of a hierarchical framework
Overall, our results highlight that considering multiple invasion processes and jointly accounting for traits through hierarchical modelling provide deeper insights on plant invasions than previous classical approaches. First, alien species with different characteristics do not necessarily respond in the same way to invasion processes, and the importance of each factor can change based on traits. For example, we found evidence that human pressure was more important for invasions by conservative alien species, whereas biotic interactions were more important for invasions by exploitative alien species. Second, we show that failure to include species traits in multispecies distribution modelling can lead to underestimation of the importance of certain processes for successful invasions (e.g., non-significant average response to productivity and human footprint). Third, our approach allows for estimation of the relative importance of each trait in different invasion processes; although all traits influenced species responses to environmental gradients, only SLA had a significant influence on responses to biotic interactions and human pressure. Overall, plant functional traits enable us to generalize findings and compare across ecosystems (Funk et al., 2017). The identification of which traits are more important for each invasion process can thus enhance models for understanding and predicting invasion risks and for comparing invasion mechanisms across gradients and ecosystems.

From a conservation perspective, knowledge of how functional traits affect the response of species to anthropogenic, environmental and biotic gradients can help to identify which local communities are more susceptible to being invaded by newly introduced species based on their traits. For example, our model highlights that grasslands from the French Mediterranean basin and the south-west of France (with high values of GDD and NPP, respectively) might be more susceptible to invasion from competitive alien species with an exploitative strategy for resource acquisition. Moreover, the French Mediterranean basin also represents a "hot spot" for propagule pressure based on the human footprint, and conservative species can take advantage even if they do not have strong competitive abilities. This combined effect means that this area is at high risk of future invasions. Likewise, the Rhone corridor, with high values of temperature seasonality, human footprint and productivity, is very susceptible to invasions from both conservative and exploitative species. This is an example of how the relative importance of each invasion process can change depending on species characteristics, and why it is important to consider traits when predicting and attempting to prevent future invasions. Simulating invasion risk for "theoretical" species with specific characteristics illustrates the added value of our approach compared with classical species distribution models that account only for environmental gradients and not for traits (e.g., Bellard et al., 2013; Bradley et al., 2010).

Finally, our framework is a valuable tool with which to compare the mechanisms shaping distributions of alien and native species. Our results suggest that shifts in the traits of alien species along productivity gradients are similar to those observed for native species according to the model of Grime (1977; Figure 4). Similar responses to environmental conditions between native and alien species have been observed before (Leffler, James, Monaco, & Sheley, 2014), supporting the premise that the same processes that influence native species assemblage also influence the success of invasion of alien species. However, we also found differences between alien and native average responses (e.g., to GDD and human footprint) and in the traits involved in their responses to environmental and human gradients. Comparison of the mechanisms shaping alien and native distribution is important because it could enable the prediction of risky species and areas susceptible to invasion based on theories and models developed for native species. Concurrently, it allows the highlighting of main differences that can help to explain why alien species manage to become dominant and pose a threat to native biodiversity.

4.5 Perspectives
Our study is a first attempt to account jointly for all main invasion processes and the modulating role of alien traits at a broad biogeographical scale. Future improvements include the consideration of additional traits (e.g., clonal growth, phenology, root system, allelopathy) in order to better capture the suite of mechanisms by which traits modulate species responses along gradients, or
the incorporation of estimates of intraspecific trait variability to account for the potential of plasticity. Moreover, the strength and mode of biotic interactions could be considered more precisely in order to obtain a better resolution of biotic dynamics. For example, potential species interactions among alien species, which have been suggested to facilitate further invasions (i.e., invasional meltdown; Simberloff, 2006), could be inferred by accounting for unexplained variation in species distributions through species co-occurrences in joint species distribution models (Pollock et al., 2014). In order to account for multitrrophic interactions (Traveset & Richardson, 2014), gradients of the intensity of grazing or of the probability of occurrence of specific important herbivores could also be included in interaction with plant traits involved in plant responses to these gradients (e.g., leaf secondary metabolites or leaf dry matter content). Finally, this modelling framework can be applied readily to the ever-growing datasets on traits and alien species distributions across habitats and continents, providing a robust test of the generality of these findings, or to focus more on species with known ecological impacts in addition to rapid spread dynamics.

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DATA ACCESSIBILITY

The dataset used to fit the alien species model with community variables, alien species occurrences and traits is available in the Figshare repository (https://doi.org/10.6084/m9.figshare.6308603.v1).

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BIOSKETCHES

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The EMABIO team investigates the ecological and evolutionary determinants of species and assemblage distributions across space and time.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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