Received: 22 November 2017 | Revised: 19 April 2018 | Accepted: 23 April 2018

DOI: 10.1111/geb.12775

RESEARCH PAPER

WILEY Global Ecology and Biogeography A Journal of Macroecology

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

Marta Carboni*[1,2] | Irene Calderon-Sanou*[1] | Laura Pollock[1] | Cyrille Violle[3] | DivGrass Consortium | Wilfried Thuiller[1]

[1]University of Grenoble Alpes, CNRS, University of Savoie Mont Blanc, Laboratoire d'Ecologie Alpine (LECA), Grenoble, France

[2]Biological Sciences, University of Toronto-Scarborough, Scarborough, Ontario, Canada

[3]CEFE UMR 5175, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, Montpellier, France

Correspondence
Marta Carboni, Biological Sciences, University of Toronto-Scarborough, 1265 Military Trail, Toronto, ON, M1C 1A4, Canada
Email: marta.carboni@gmx.net

FUNDING INFORMATION
European Community's Seventh Framework Program, Grant/Award Number: FP7-PEOPLE-2012-IEF and IASIMOV 327616; ANR, Grant/Award Number: ANR-13-EBID-0004

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

---

*Joint first authors.

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

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, Procheş, & 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 (Rejmanek & 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 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 m^2). 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 1 Alien species used in the study, with their frequency (no. of plots), local abundance (average percentage species cover in the plots where they occur), biogeographical origin and introduction pathways, from Carboni et al. (2016)

Alien species	Family	Frequency	Local abundance (% cover ± *SE*)	Origin	Pathways
Ambrosia artemisiifolia	Asteraceae	36	3.50 ± 1.18	Americas	T
Avena sativa	Poaceae	180	7.27 ± 0.99	Eurasia	U
Cotula coronopifolia	Asteraceae	124	22.46 ± 2.31	Africa	U
Erigeron annuus	Asteraceae	249	3.16 ± 0.50	*N* America	O/H
Linum austriacum	Linaceae	36	4.10 ± 0.85	Eurasia	O/H
Linum usitatissimum	Linaceae	560	3.33 ± 0.30	Anecophyte[a]	A
Matricaria discoidea	Asteraceae	105	4.69 ± 0.89	Asia	T
Oenothera biennis	Onagraceae	75	2.53 ± 0.61	*N* America	O/H
Onobrychis viciifolia	Fabaceae	2,364	6.29 ± 0.22	Europe	A
Solidago gigantea	Asteraceae	66	3.39 ± 0.75	*N* America	O/H

Notes. A = agriculture; H = horticulture; O = ornamental; T = transportation; U = unknown. [a]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 generalism. 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 a set of 10 alien species for further modelling, which included a mix of recently introduced species (neophytes introduced after 1,500) and species of more ancient introduction (mostly through cultivation from Eurasia; Table 1). These alien plants have been introduced in France either intentionally to be used in agriculture, horticulture or as ornamentals, or unintentionally via transportation activities (Carboni et al., 2016). They have different origins involving at least three continents (Table 1), vary in their trait values (Supporting Information Appendix S1, Table S1) and are unequally distributed across French permanent grasslands (Supporting Information Appendix S1, Figure S1). This list of invasive species might appear short. However, we note that although permanent grasslands were mostly invaded in ancient times, more recently new plant invasions are occurring and are likely to be favoured in the future under ongoing global changes (e.g., Essl & Dirnböck, 2008). A better understanding of how traits modulate invasion processes in these ecosystems can thus enhance management strategies at an early stage to prevent future invasions in these threatened ecosystems (also see Supporting Information Appendix S1 for further considerations).

2.4 | Variables related to invasion processes

To model alien species distributions, we selected as explanatory variables: (a) a measure of human pressure as a proxy of propagule pressure, (b) a set of spatially continuous environmental variables considered important for plant species distribution, and (c) a biotic index estimating ecological dissimilarity to the natives.

As a proxy of the intensity of human-mediated propagule pressure in each community plot, we used the human footprint (HF) variable that summarizes globally (30° resolution) the human influence on ecosystems by taking into account population density, land use, accessibility and electrical power infrastructure (Sanderson et al., 2002). It ranges from 0 to 100 (natural to completely transformed and unsuitable for wildlife). In the context of plant invasions, this variable has been found previously to be important for explaining alien species distributions and can be considered a reasonable proxy for propagule pressure of alien species (Gallardo, Zieritz, & Aldridge, 2015; Lockwood et al., 2005). We acknowledge that this contemporary HF metric may not fully capture human pressure at the time of first introduction (given that some of the alien species included here are of relatively ancient introduction). Nevertheless, it should be correlated with the continuous introduction pressure for propagules (e.g., from gardens or human transportation) that influences the current distribution of these alien plants in the wild (Gallardo et al., 2015). However, we also note that the HF also relates to the degree of disturbance and land transformation, which can also potentially favour invasive species (Mooney & Hobbs, 2000). Thus, we interpret HF as a measure of "human pressure" hereafter.

To assess environmental filtering, for each community plot we extracted a set of abiotic environmental variables related to climate, 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 at 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 Vesk (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 m^2/kg) and one with low SLA values (13 m^2/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

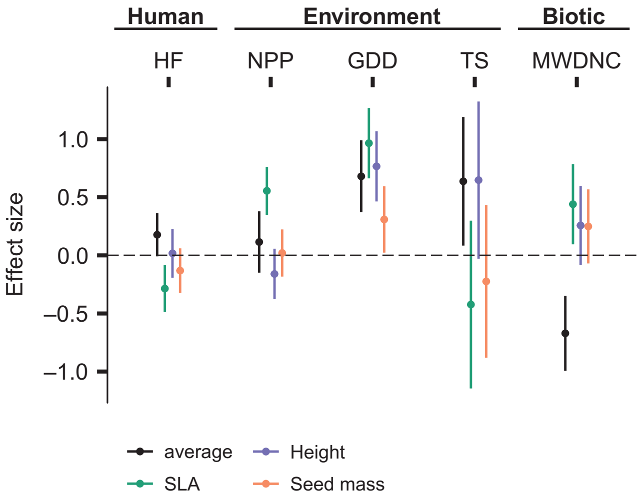

FIGURE 1 Contribution of alien species traits to partial responses to environmental variables (GDD = growing degree-days; NPP = net primary productivity; TS = temperature seasonality), human footprint (HF) and biotic interactions (MWDNC = mean weighted distance to native community). The "average" effect (black) represents the response of a hypothetical alien species with average traits to each abiotic and biotic 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]

the alien and the native species had similar ranges and distributions (Supporting Information Appendix S5, Figure S7).

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 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

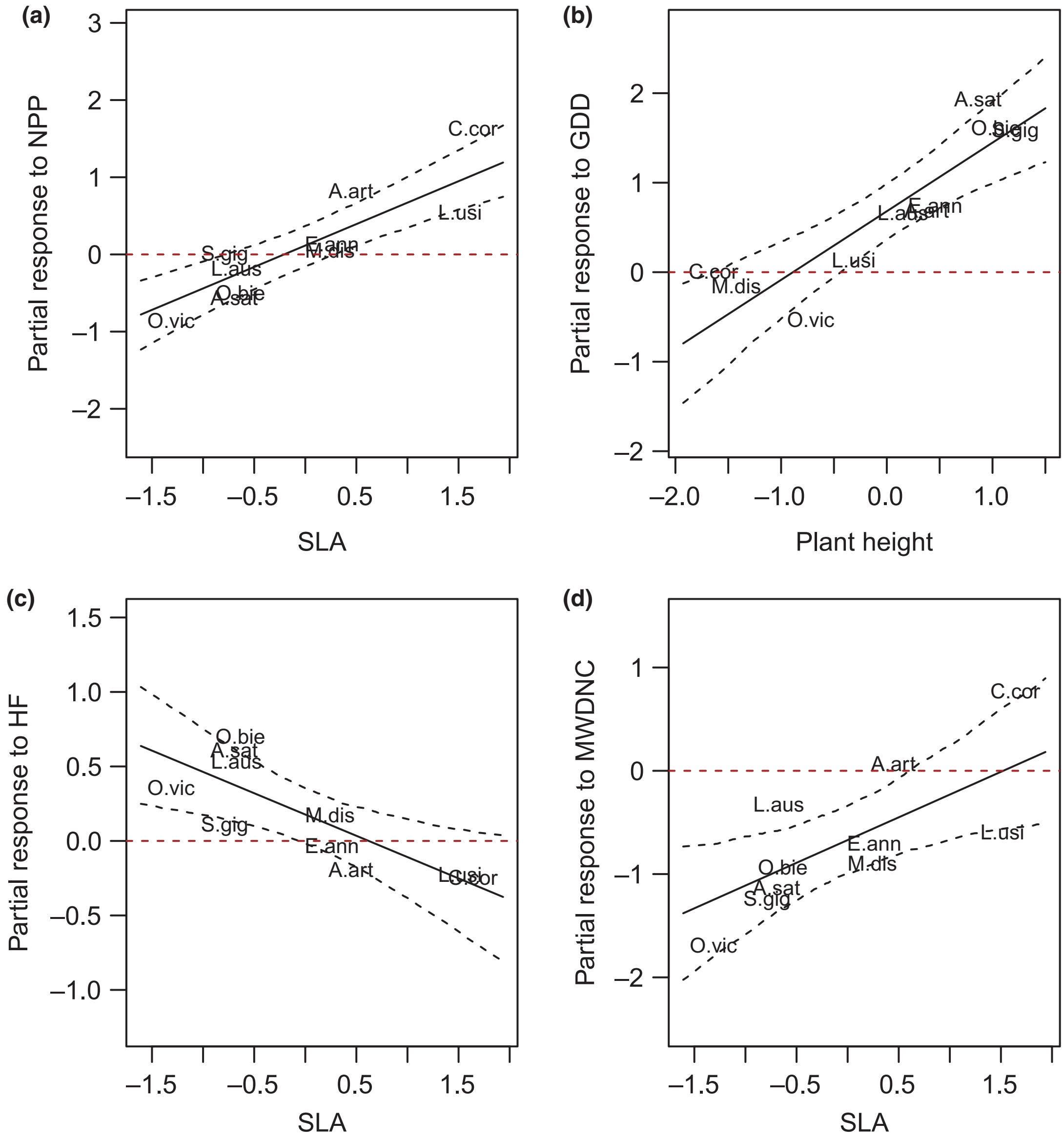

FIGURE 2 Partial responses of species to some of the explanatory variables as a function of their specific leaf area (SLA) and plant height values (centred and scaled). (a) Net primary productivity (NPP). (b) Growing degree-days (GDD) over a 5.56°C threshold. (c) Human footprint (HF). (d) Mean weighted distance to native community (MWDNC). Continuous lines represent the average response expected by the model, and dashed lines are 95% confidence intervals that represent uncertainty of the average response. Species shown are as follows: *Ambrosia artemisiifolia* (A.art), *Avena sativa* (A.sat), *Cotula coronopifolia* (C.cor), *Erigeron annuus* (E.ann), *Linum austriacum* (L.aus), *Linum usitatissimum* (L.usi), *Matricaria discoidea* (M.dis), *Oenothera biennis* (O.bie), *Onobrychis viciifolia* (O.vic) and *Solidago gigantean* (S.gig) [Colour figure can be viewed at wileyonlinelibrary.com]

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

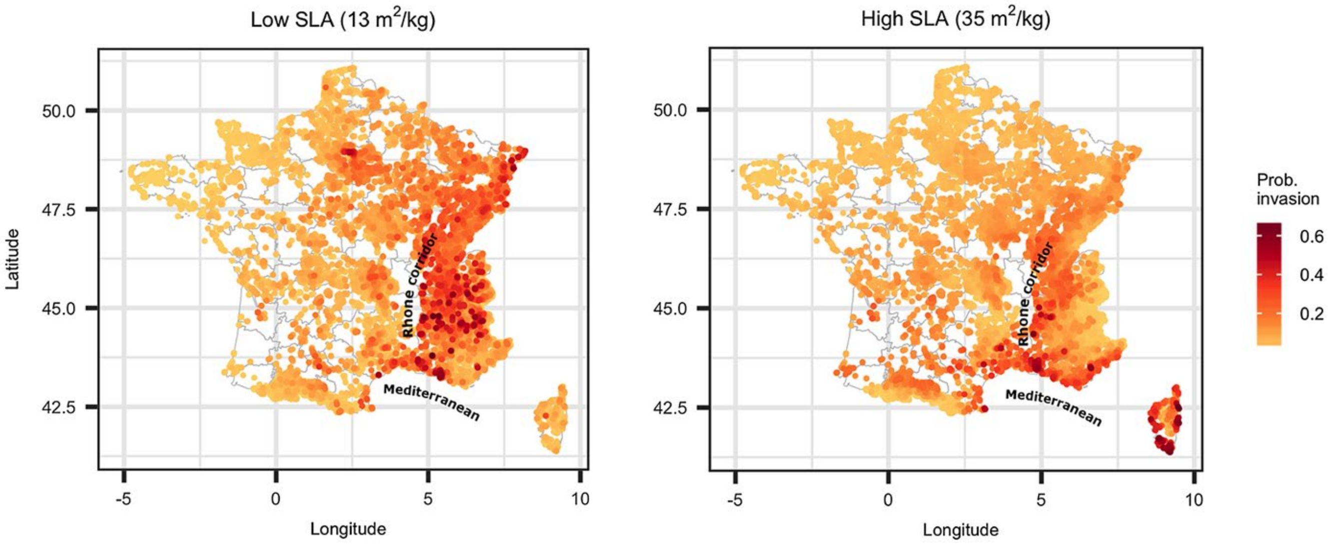

FIGURE 3 Predicted probability of invasion of hypothetical species with low (13 m^2/kg; left panel) or high (35 m^2/kg; right panel) specific leaf area (SLA) values in French permanent grasslands, with average values of height and seed mass. The two areas most at risk of invasion mentioned in the text are marked (Mediterranean basin and Rhone corridor) [Colour figure can be viewed at wileyonlinelibrary.com]

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.

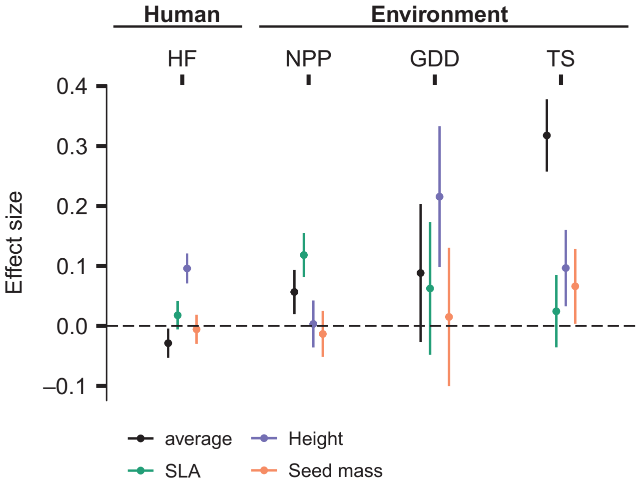

FIGURE 4 Contribution of native species traits to partial responses to environmental variables and human pressure. The "average" effect (black) represents the response of species with average traits to each environmental and human gradient variable. The interaction coefficients describe how traits modulate 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]

Although SLA clearly modulated the dependence of invasion success on human pressure, we unexpectedly did not observe a significant interaction either with height or with seed mass, both of which are correlated with species dispersal ability. Specifically, we 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, Violle, 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, & Lavorel, 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 multitrophic 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.

ACKNOWLEDGMENTS

We thank J. Renaud for his help with the preparation of the environmental data. M.C. was supported by a Marie Curie Intra European Fellowship within the European Community's Seventh Framework Program (FP7-PEOPLE-2012-IEF; IASIMOV 327616) and by the ERA-Net BiodivERsA, with the national funders ANR (ANR-13-EBID-0004), part of the 2013 BiodivERsA call (project "WhoIsNext"). The Laboratoire d'Ecologie Alpine (LECA) is part of Labex OSUG@2020 (ANR10 LABX56). Data were obtained from the DIVGRASS database supported by the French Foundation for Research on Biodiversity (FRB; www.fondationbiodiversite.fr) in the context of the Centre de Synthèse et d'Analyse sur la Biodiversité (CESAB) project "Assembling, analysing and sharing data on plant functional diversity to understand the effects of biodiversity on ecosystem functioning: a case study with French Permanent Grasslands", and from the TRY initiative on plant traits (https://www.try-db.org). The TRY database is hosted at the Max Planck Institute for Biogeochemistry, Jena, Germany, and currently supported by DIVERSITAS/Future Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle–Jena–Leipzig. M.C., W.T. and L.P. conceived the ideas. C.V. contributed and processed data. I.C.S. performed all statistical analyses and produced the figures. All authors contributed to the writing, which was led by M.C.

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).

ORCID

Marta Carboni http://orcid.org/0000-0002-9348-4758

REFERENCES

Albert, C., & Thuiller, W. (2008). Favourability functions against probability of presence: Advantages and misuses. *Ecography*, *31*, 417–422.

Barney, J. N., Ho, M. W., & Atwater, D. Z. (2016). Propagule pressure cannot always overcome biotic resistance: The role of density-dependent establishment in four invasive species. *Weed Research*, *56*, 208–218. https://doi.org/10.1111/wre.12204

Bartoń, K. (2013). *MuMIn: Multi-model inference* (R package version 1.9.13). https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M., & Courchamp, F. (2013). Will climate change promote future invasions? *Global Change Biology*, *19*, 3740–3748. https://doi.org/10.1111/gcb.12344

Bénichou, P., & Le Breton, O. (1987). AURELHY: Une méthode d'analyse utilisant le relief pour les besoins de l'hydrométéorologie. In *Deuxièmes journées hydrologiques de l'ORSTOM à Montpellier* (pp. 299–304). Paris: ORSTOM, Colloques et Séminaires.

Bivand, R. S., Hauke, J., & Kossowski, T. (2013). Computing the Jacobian in Gaussian spatial autoregressive models: An illustrated comparison of available methods. *Geographical Analysis*, *45*, 150–179. https://doi.org/10.1111/gean.12008

Borgy, B., Violle, C., Choler, P., Denelle, P., Munoz, F., Kattge, J., … Garnier, E. (2017). Plant community structure and nitrogen inputs modulate the climate signal on leaf traits. *Global Ecology and Biogeography*, *26*, 1138–1152. https://doi.org/10.1111/geb.12623

Borgy, B., Violle, C., Choler, P., Garnier, E., Kattge, J., Loranger, J., … Viovy, N. (2017). Sensitivity of community-level trait–environment relationships to data representativeness: A test for functional biogeography. *Global Ecology and Biogeograpy*, *26*, 729–739. https://doi.org/10.1111/geb.12573

Bradley, B. A., Blumenthal, D. M., Wilcove, D. S., & Ziska, L. H. (2010). Predicting plant invasions in an era of global change. *Trends in Ecology and Evolution*, *25*, 310–318. https://doi.org/10.1016/j.tree.2009.12.003

Carboni, M., Guéguen, M., Barros, C., Georges, D., Boulangeat, I., Douzet, R., … Thuiller, W. (2018). Simulating plant invasion dynamics in mountain ecosystems under global change scenarios. *Global Change Biology*, *24*, e289–e302. https://doi.org/10.1111/gcb.13879

Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C., … Thuiller, W. (2016). What it takes to invade grassland ecosystems: Traits, introduction history and filtering processes. *Ecology Letters*, *19*, 219–229. https://doi.org/10.1111/ele.12556

Catford, J. A., Downes, B. J., Gippel, C. J., & Vesk, P. A. (2011). Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands: Flow regulation drives wetland invasion. *Journal of Applied Ecology*, *48*, 432–442. https://doi.org/10.1111/j.1365-2664.2010.01945.x

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*, 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Catford, J. A., Morris, W. K., Vesk, P. A., Gippel, C. J., & Downes, B. J. (2014). Species and environmental characteristics point to flow regulation and drought as drivers of riparian plant invasion.

Diversity and Distributions, *20*, 1084–1096. https://doi.org/10.1111/ddi.12225

Davidson, A. M., Jennions, M., & Nicotra, A. B. (2011). Do invasive species show higher phenotypic plasticity than native species and if so, is it adaptive? A meta-analysis: Invasive species have higher phenotypic plasticity. *Ecology Letters*, *14*, 419–431. https://doi.org/10.1111/j.1461-0248.2011.01596.x

Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, *88*, 528–534. https://doi.org/10.1046/j.1365-2745.2000.00473.x

Díaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., … Zak, M. R. (2004). The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, *15*, 295–304. https://doi.org/10.1658/1100-9233(2004)015[0295:TPTTDE]2.0.CO;2

EEA. (2013). *The impacts of invasive alien species in Europe*. Luxembourg: Publications Office of the European Union.

Essl, F., & Dirnböck, T. (2008). Diversity of native and alien vascular plant species of dry grasslands in central Europe. *Applied Vegetation Science*, *11*, 441–450. https://doi.org/10.3170/2008-7-18527

Funk, J. L., Larson, J. E., Ames, G. M., Butterfield, B. J., Cavender-Bares, J., Firn, J., … Wright, J. (2017). Revisiting the Holy Grail: Using plant functional traits to understand ecological processes. *Biological Reviews*, *92*, 1156–1173. https://doi.org/10.1111/brv.12275

Gallardo, B., Zieritz, A., & Aldridge, D. C. (2015). The importance of the human footprint in shaping the global distribution of terrestrial, freshwater and marine invaders. *PLoS One*, *10*, e0125801. https://doi.org/10.1371/journal.pone.0125801

Gallien, L., & Carboni, M. (2017). The community ecology of invasive species: Where are we and what's next? *Ecography*, *40*, 335–352. https://doi.org/10.1111/ecog.02446

Gaucherand, S., Liancourt, P., & Lavorel, S. (2006). Importance and intensity of competition along a fertility gradient and across species. *Journal of Vegetation Science*, *17*, 455–464. https://doi.org/10.1111/j.1654-1103.2006.tb02466.x

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, *111*, 1169–1194. https://doi.org/10.1086/283244

Grime, J. P. (2006). Trait convergence and trait divergence in herbaceous plant communities: Mechanisms and consequences. *Journal of Vegetation Science*, *17*, 255–260. https://doi.org/10.1111/j.1654-1103.2006.tb02444.x

Harrell, F. E., & Dupont, M. C. (2007). *The Hmisc package* (R package version 4.0-3). https://biostat.mc.vanderbilt.edu/Hmisc

Imhoff, M. L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R., & Lawrence, W. T. (2004). *HANPP collection: Global patterns in net primary productivity (HANPP)*. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC).

Jiménez-Valverde, A., Lobo, J., & Hortal, J. (2009). The effect of prevalence and its interaction with sample size on the reliability of species distribution models. *Community Ecology*, *10*, 196–205. https://doi.org/10.1556/ComEc.10.2009.2.9

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., … Wirth, C. (2011). TRY – A global database of plant traits. *Global Change Biology*, *17*, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Leffler, A. J., James, J. J., Monaco, T. A., & Sheley, R. L. (2014). A new perspective on trait differences between native and invasive exotic plants. *Ecology*, *95*, 298–305. https://doi.org/10.1890/13-0102.1

Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, *20*, 223–228. https://doi.org/10.1016/j.tree.2005.02.004

Loveys, B. R., Scheurwater, I., Pons, T. L., Fitter, A. H., & Atkin, O. K. (2002). Growth temperature influences the underlying components of relative growth rate: An investigation using inherently fast- and slow-growing plant species. *Plant, Cell and Environment*, *25*, 975–988. https://doi.org/10.1046/j.1365-3040.2002.00879.x

Maurel, N., Hanspach, J., Kühn, I., Pyšek, P., & van Kleunen, M. (2016). Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. *Global Ecology and Biogeography*, *25*, 1500–1509. https://doi.org/10.1111/geb.12520

Mayfield, M. M., & Levine, J. M. (2010). Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, *13*, 1085–1093. https://doi.org/10.1111/j.1461-0248.2010.01509.x

Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., … Leishman, M. R. (2009). Global patterns in plant height. *Journal of Ecology*, *97*, 923–932. https://doi.org/10.1111/j.1365-2745.2009.01526.x

Moles, A. T., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, *113*, 91–105. https://doi.org/10.1111/j.0030-1299.2006.14194.x

Mooney, H. A., & Hobbs, R. J. (2000). *Invasive species in a changing world*. Washington, DC: Island Press.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.

Peoples, B. K., & Goforth, R. R. (2017). The indirect role of species-level factors in biological invasions. *Global Ecology and Biogeography*, *26*, 524–532. https://doi.org/10.1111/geb.12567

Pollock, L. J., Morris, W. K., & Vesk, P. A. (2012). The role of functional traits in species distributions revealed through a hierarchical model. *Ecography*, *35*, 716–725. https://doi.org/10.1111/j.1600-0587.2011.07085.x

Pollock, L. J., Tingley, R., Morris, W. K., Golding, N., O'Hara, R. B., Parris, K. M., … McCarthy, M. A. (2014). Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). *Methods in Ecology and Evolution*, *5*, 397–406. https://doi.org/10.1111/2041-210X.12180

Pyšek, P., Lambdon, P. W., Arianoutsou, M., Kühn, I., Pino, J., & Winter, M. (2009). Alien vascular plants of Europe. In Daisie (Eds.), *Handbook of alien species in Europe* (Invading Nature – Springer Series in Invasion Ecology, Vol. *3*, pp. 43–61). Dordrecht: Springer.

R Development Core Team. (2016). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org

Rejmanek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology*, *77*, 1655–1661. https://doi.org/10.2307/2265768

Richardson, D. M., & Pyšek, P. (2006). Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, *30*, 409–431. https://doi.org/10.1191/0309133306pp490pr

Ricotta, C., La Sorte, F. A., Pyšek, P., Rapson, G. L., Celesti-Grapow, L., & Thompson, K. (2009). Phyloecology of urban alien floras. *Journal of Ecology*, *97*, 1243–1251. https://doi.org/10.1111/j.1365-2745.2009.01548.x

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The human footprint and the last of the wild. *BioScience*, *52*, 891–904. https://doi.org/10.1641/0006-3568(2002)052[0891:THFATL]2.0.CO;2

Sheppard, C. S., Carboni, M., Essl, F., Seebens, H., & Thuiller, W. (2018). It takes one to know one: Similarity to resident alien species increases establishment success of new invaders. *Diversity and Distributions*, *24*, 680–691. https://doi.org/10.1111/ddi.12708

Silva, J. P. (Ed.). (2008). *LIFE and Europe's grasslands: Restoring a forgotten habitat*. Luxembourg: Office for Official Publications of the European Community.

Simberloff, D. (2006). Invasional meltdown 6 years later: Important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, *9*, 912–919. https://doi.org/10.1111/j.1461-0248.2006.00939.x

Simberloff, D. (2009). The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, *40*, 81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Tamme, R., Götzenberger, L., Zobel, M., Bullock, J. M., Hooftman, D. A., Kaasik, A., & Pärtel, M. (2014). Predicting species' maximum dispersal distances from simple plant traits. *Ecology*, *95*, 505–513. https://doi.org/10.1890/13-1000.1

Thomson, F. J., Moles, A. T., Auld, T. D., & Kingsford, R. T. (2011). Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology*, *99*, 1299–1307. https://doi.org/10.1111/j.1365-2745.2011.01867.x

Thuiller, W., Richardson, D. M., Rouget, M., Procheş, Ş., & Wilson, J. R. U. (2006). Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, *87*, 1755–1769. https://doi.org/10.1890/0012-9658(2006)87[1755:IBESTA]2.0.CO;2

Traveset, A., & Richardson, D. M. (2014). Mutualistic interactions and biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, *45*, 89–113. https://doi.org/10.1146/annurev-ecolsys-120213-091857

Trudgill, D. L., Squire, G. R., & Thompson, K. (2000). A thermal time basis for comparing the germination requirements of some British herbaceous plants: Thermal requirements of British herbaceous plants. *New Phytologist*, *145*, 107–114. https://doi.org/10.1046/j.1469-8137.2000.00554.x

van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, *13*, 235–245. https://doi.org/10.1111/j.1461-0248.2009.01418.x

Verlinden, M., & Nijs, I. (2010). Alien plant species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. *Biological Invasions*, *12*, 2777–2787. https://doi.org/10.1007/s10530-009-9683-1

Violle, C., Choler, P., Borgy, B., Garnier, E., Amiaud, B., Debarros, G., … Viovy, N. (2015). Vegetation ecology meets ecosystem science: Permanent grasslands as a functional biogeography case study. *Science of the Total Environment*, *534*, 43–51. https://doi.org/10.1016/j.scitotenv.2015.03.141

Violle, C., Garnier, E., Lecoeur, J., Roumet, C., Podeur, C., Blanchard, A., & Navas, M.-L. (2009). Competition, traits and resource depletion in plant communities. *Oecologia*, *160*, 747–755. https://doi.org/10.1007/s00442-009-1333-x

Walther, G.-R., Roques, A., Hulme, P. E., Sykes, M. T., Pyšek, P., Kühn, I., … Bugmann, H. (2009). Alien species in a warmer world: Risks and opportunities. *Trends in Ecology and Evolution*, *24*, 686–693. https://doi.org/10.1016/j.tree.2009.06.008

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227.

Wright, I. J., Reich, P. B., & Westoby, M. (2001). Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology*, *15*, 423–434. https://doi.org/10.1046/j.0269-8463.2001.00542.x

BIOSKETCHES

The work leading to this paper was carried out at the Laboratoire d'Ecologie Alpine (LECA) in the Evolution, Modeling and Analysis of BIOdiversity (EMABIO) team led by **WILFRIED THUILLER.**

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.

How to cite this article: Carboni M, Calderon-Sanou I, Pollock L, Violle C, Thuiller W; DivGrass Consortium. Functional traits modulate the response of alien plants along abiotic and biotic gradients. *Global Ecol Biogeogr.* 2018;27:1173–1185. https://doi.org/10.1111/geb.12775