Contrasting the effects of environment, dispersal and biotic interactions to explain the distribution of invasive plants in alpine communities

Laure Gallien · Florent Mazel ·
Sébastien Lavergne · Julien Renaud ·
Rolland Douzet · Wilfried Thuiller

Abstract Despite considerable efforts devoted to investigate the community assembly processes driving plant invasions, few general conclusions have been drawn so far. Three main processes, generally acting as successive filters, are thought to be of prime importance. The invader has to disperse (1st filter) into a suitable environment (2nd filter) and succeed in establishing in recipient communities through competitive interactions (3rd filter) using two strategies: competition avoidance by the use of different resources (*resource opportunity*), or *competitive exclusion* of native species. Surprisingly, despite the general consensus on the importance of investigating these three processes and their interplay, they are usually studied independently. Here we aim to analyse these three filters together, by including them all: abiotic environment, dispersal and biotic interactions, into models of invasive species distributions. We first propose a suite of indices (based on species functional dissimilarities) supposed to reflect the two competitive strategies (resource opportunity and competition exclusion). Then, we use a set of generalised linear models to explain the distribution of seven herbaceous invaders in natural communities (using a large vegetation database for the French Alps containing 5,000 community-plots). Finally, we measure the relative importance of competitive interaction indices, identify the type of coexistence mechanism involved and how this varies along environmental gradients. Adding competition indices significantly improved model's performance, but neither resource opportunity nor competitive exclusion were common strategies among the seven species. Overall, we show that combining environmental, dispersal and biotic information to model invasions has excellent potential for improving our understanding of invader success.

Keywords Alien species · Competitive exclusion · Dispersal · Environmental filtering · Niche model · Resource opportunity

L. Gallien (✉) · F. Mazel · S. Lavergne ·
J. Renaud · W. Thuiller
Laboratoire d'Ecologie Alpine (LECA),
Univ. Grenoble Alpes, 38000 Grenoble, France
e-mail: laure.gallien@gmail.com

L. Gallien · F. Mazel · S. Lavergne · J. Renaud ·
W. Thuiller
Laboratoire d'Ecologie Alpine (LECA), CNRS,
38000 Grenoble, France

Present Address:
L. Gallien
Swiss Federal Research Institute WSL, 8903 Birmensdorf,
Switzerland

R. Douzet
Station Alpine Joseph Fourier, CNRS, Univ. Grenoble,
38000 Grenoble, France

Introduction

Understanding the processes that facilitate or prevent biological invasions in natural communities is crucial

to better anticipating their potential spread and impacts (Rejmánek et al. 2005). Even though accurate modelling and predictions of invasive species distributions remain a challenge (Gallien et al. 2010), it is generally well accepted that three major ecological processes that act as successive filters influence the outcome of invasion (Theoharides and Dukes 2007, Richardson and Pysek 2012). The species has to disperse (1st filter) into a suitable environment (2nd filter) and succeed in establishing in a recipient community through biotic interactions (3rd filter). Previous researches have demonstrated that dispersal (e.g. propagule pressure; Simberloff 2009), abiotic environment (e.g. climate matching; Thuiller et al. 2005), and biotic interactions (e.g. enemy release; Mitchell et al. 2006) are important determinants of biological invasions (Higgins et al. 2000; Roura-Pascual et al. 2009; Thuiller et al. 2012). However, it remains unclear whether interspecific competitive interactions, in particular, play a prominent role in driving invasion success and how they may interact with environmental gradients (Simberloff 2006; Seastedt and Pysek 2011).

From the coexistence theory, there are only two possible ways for an invader to succeed in the context of competitive interactions (Chesson 2000; MacDougall et al. 2009). First, the invader uses an unused resource at the community level, regardless of whether it is a good or bad competitor. This strategy, also called *resource opportunity* (or *niche differences*), is made possible due to functional differences between the invader and native species (Mayfield and Levine 2010). Second, the invader is a better competitor than at least one native species and it will tend to replace it in the communities. This strategy, also called *competitive exclusion* (or *competitive ability hierarchy* or *fitness differences*), is made possible by the hierarchical difference of functional traits between the invader and the native species (Kunstler et al. 2012; Mayfield and Levine 2010). Although the two strategies are relatively straightforward to explain, they are difficult to tease-apart using observed data or to measure with adequate community-level indices (HilleRisLambers et al. 2012).

The use of an available resource by the invader can be estimated with indices based on measures of functional dissimilarities between the potential invader and the native species of a given community (Thuiller et al. 2010). This argument obviously holds

on the premise that these functional dissimilarities depict differences in resource use. Two predictions are then typically proposed (see Fig. 1a). First, in a stressful environment, a successful invader needs to be pre-adapted to survive and therefore tends to be functionally similar to the natives. Second, in a non-stressful environment, where invasion success is mostly limited by resource competition, invaders that are functionally dissimilar from native species will be favoured (Darwin 1859; Duncan and Williams 2002; Richardson and Pyšek 2006).

However, these indices based on functional (dis)similarity cannot disentangle competitive exclusion from environmental filtering when the considered species compete for a single resource (Fig. 1b). Indeed, when competitive exclusion is driving species coexistence, and in the absence of resource differences between species but strong differences in their competitive abilities, only the best competitor is expected to survive. However, several good competitors can also co-exist locally due for example to spatio-temporal or demographic stochasticity (i.e. neutral-like dynamics of functionally similar species; Chesson 2000). Therefore, in both cases the invader is expected to be functionally similar to the native species (Mayfield and Levine 2010). Similarly, functional (dis)similarity indices cannot disentangle competitive exclusion from resource opportunity when the considered species compete for different resources. Indeed, when the invader and the native species use different resources (either via the use of an available resource or because the invader outcompeted another native species) the invader is always expected to be dissimilar from the coexisting native species (Fig. 1a, b). Therefore, to adequately tease-apart the different coexistence mechanisms that promote invasive species presence, it is necessary to use an additional type of metric measuring the *competitive ability* of the invader in respect to natives (Fig. 1c). A simple way to do so is to use functional traits summarising species' *competitive ability* (i.e. species' probability to win resource competition; Westoby et al. 2002). Such an index can be estimated as the difference between the invader's competitive value and the values for the native species (Kunstler et al. 2012). It is expected that (1) when competitive exclusion is driving invasion, the invader is favoured in communities where it is a better competitor than the native species (i.e. a positive index value; Fig. 1c red line). Respectively,
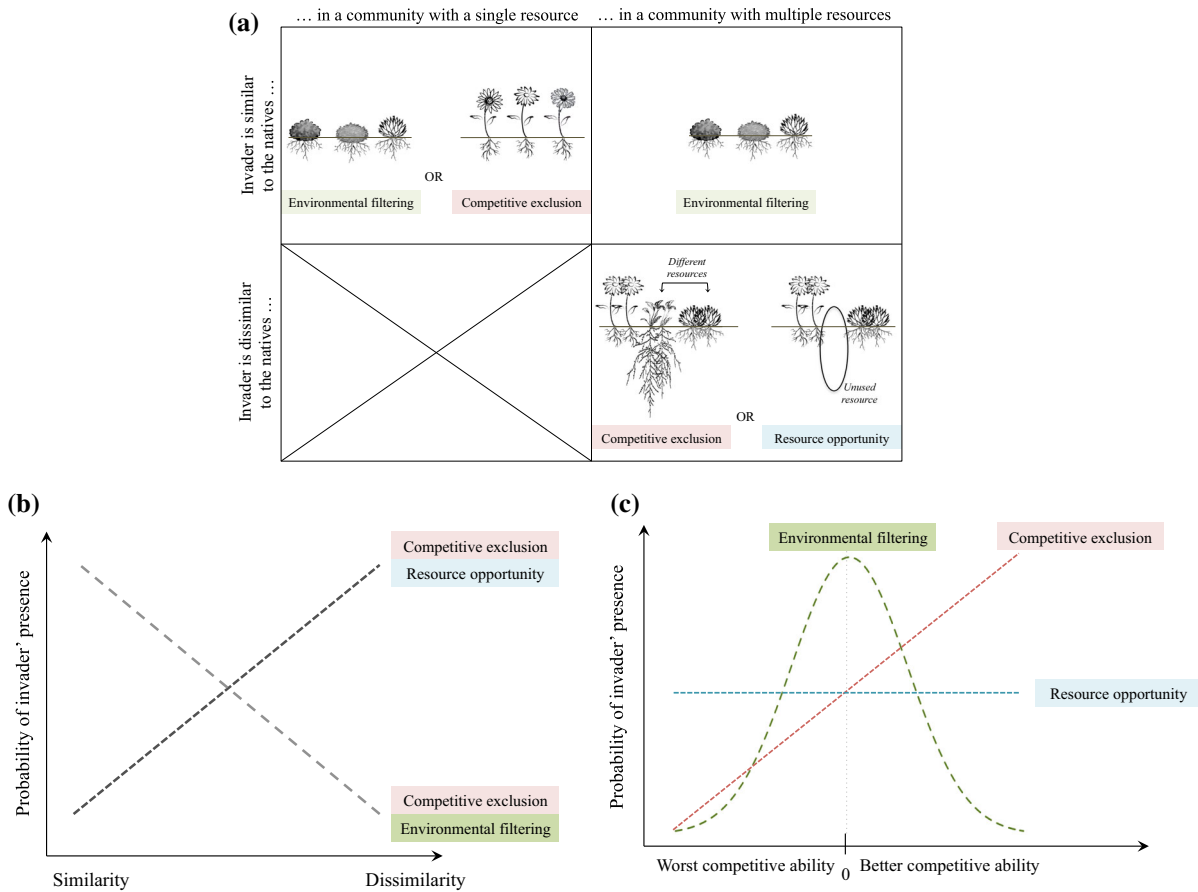
Fig. 1 Theoretical expectations on the different coexistence mechanisms at stake during invasion at a community scale (**a**), and the underlying relationships between the invader's presence and its similarity with the recipient community (**b**) or its competitive ability in regards to native species (**c**). **a** Coexistence mechanisms vary in respect to both the functional similarity between the invader and the resident native species, and the number of resources available in the community. When an invader is observed to be functionally similar to the natives, this can either be due to environmental filtering (whatever the number of resource present in the community), or competitive exclusion if all species compete for the same resource (i.e. only

the best competitors, with similar good traits can survive). In contrast, if the invader is found very dissimilar to the native species it implies that the native species exploit different resources. Therefore, the invader has either invaded communities via competitive exclusion of at least one native, or by exploiting an unused resource. **b** Expected relationship between the invader's probability of presence and its similarity to native species. Similar relationships can be expected for different mechanisms. **c** Expected relationship between the invader's probability of presence and its competitive ability in regards to native species. Here, co-existence mechanisms can be teased-apart

(2) when environmental filtering is the main driver, the invader should have a trait similar to the one of the native species, and thus a similar competitive ability (i.e. an index value close to zero; Fig. 1c green line). Finally, (3) when the invader uses an available resource in the community, its competitive ability should be independent from the native species ones (Fig. 1c blue line).

Despite these theoretical formulations, it remains difficult to conclude whether competitive interactions

are important determinants of plant invasions (see examples in Levine and D'Antonio 1999; Lonsdale 1999; Shea and Chesson 2002; Mitchell et al. 2006; Proches et al. 2008). In our point of view, past mixed results come from three essential methodological issues (additionally to the spatial scale issue that has been extensively studied; Swenson 2006; Thuiller et al. 2010; Carboni et al. 2013).

Firstly, in most published studies only one of the two of invasion strategies detailed above (i.e. resource

opportunity *vs.* competitive exclusion) are properly tested, while in fact they can both act at different locations or stages of invasion. For instance, it is possible that both resource opportunity and environmental filtering prevail in the early stages of invasion when the invader still occurs in disturbed or ruderal habitats (i.e. transport and colonisation stages), and that the importance of competitive ability increases when the invader establishes in natural communities (i.e. establishment and spread stages, Theoharides and Dukes 2007).

The second confusion arises when selecting the interacting species within the communities. Indeed, not all species in a community necessarily compete for the same resources. For example for light interception, *resource opportunity* is probably of prime importance for the coexistence of different growth forms (e.g. herbaceous *vs.* woody species), while *competitive ability* drives the outcome of assembly between woody species (e.g. Kunstler et al. 2012; but see also Fargione et al. 2003).

Finally, the change in levels of environmental stress across communities is rarely taken into account, while the relative importance of competition may vary according to the strength of the environmental stress: the stress-gradient hypothesis (Callaway et al. 2002; Meier et al. 2011; see also Welden and Slauson 1986; Kikvidze et al. 2011). For instance, the competition filter is usually expected to be less important at the niche edge where physiological constraints limit species distribution more than competition (e.g. in cold alpine environments; Callaway and Walker 1997; De Roy et al. 2013), while it can be more important at other niche edges where the distribution of the focal species is limited by negative biotic interaction with another species (e.g. presence of a predator; Wisz et al. 2013).

In this paper we present an approach to investigate the relative importance of the three general processes driving plant invasion: environmental filtering, dispersal and competitive interactions. As a case study, we used an extensive dataset of 5,000 plant community sites over the French Alps area, and modelled the invasion success of seven notorious herbaceous plant invaders in these communities. Building on previous works demonstrating that environmental filtering and species dispersal capacities are important drivers of biological invasions, we evaluated whether including community-wide indices, potentially depicting competitive interactions, into species distribution models

increases their performance at identifying invaded sites. In order to distinguish between the two competitive interaction strategies (resource opportunity *vs.* competitive ability), we used a set of different metrics based on functional trait differences between the invaders and native species. Since we also aimed at identifying whether different types of competition occur between different sets of species, we calculated the indices for two pools of species: all species and only herbaceous species. Finally, we tested whether the effects of biotic interactions varied along the environmental gradients.

Material and methods

Data

Community data

We used an extensive database of vegetation survey plots spanning the French Alps, collected by the Alpine Botanical Conservatory (Boulangeat et al. 2012). Overall, the study area covers approximately 3.8 million hectares, encompasses a large diversity of vegetation types (including forests, grasslands, meadows or riparian areas) across long altitudinal gradients ranging from 165 m to 3,254 m a.s.l. Each vegetation plot ('community' hereafter) consists of an exhaustive survey of homogeneous plant assemblages (about 10×10 m) with species relative abundance. The total number of available communities was 15,931 including around 3,030 species. Given our interest in studying both (1) biotic interactions between the invader and all other species, but also (2) biotic interactions between the invader and the species of the same life forms (i.e. herbaceous species), we only kept 5,141 communities for which functional trait information (see below) were available for at least 70 % of species cover across all species and for herbaceous species only (according to the 'biomass ratio hypothesis', Grime 1998).

Among the 142 non-native species of the French Alps, we focused on the invaders that were either classified as "establishing" or "spreading" (*sensu* Theoharides and Dukes 2007), recorded at least 30 times within the 5,141 communities (see number of occurrence per species in "Appendix"), and for which the functional traits were available (see below).

Furthermore, in order to consider biotic interactions between species of the same life form we chose to work only with herbaceous invaders. We finally retained seven herbaceous invaders: *Ambrosia artemisiifolia* L., *Bidens frondosa* L., *Conyza canadensis* (L.) Cronquist, *Erigeron annuus* (L.) Desf., *Panicum capillare* L., *Solidago canadensis* L., and *Solidago gigantea* Aiton.

Environmental data

A set of five environmental variables (three bioclimatic, one human footprint, and one land cover) known to be important for species establishment and spread was tested to describe the main drivers of invader' distribution. We considered three climatic variables originating from the French meteorological model Aurelhy (Benichou and Le Breton 1987) based on interpolated measurements at a 100 m resolution and summarising climatic information over the last 30 years (here 1971–2000). These variables were the annual sum of degree-days with a 5.56 °C threshold (ddeg) as a measure of the environmental heat vital to plant biomass production (Prentice et al. 1992), the mean annual level of potential solar radiation as an important driver of plant growth rate, and mean annual precipitation as an indicator of water availability. Land cover information was extracted from the CORINE Land Cover map for Europe (CORINE 2006, http://www.epa.ie/whatwedo/assessment/land/corine) at 250 m resolution, and indicates the type of ecosystem in which the communities have been recorded.

Using the same methodology as Sanderson et al. (2002), we built a human footprint map of the French Alps at a 250 m resolution based on CORINE Land cover 2006, including the population density (Gallego 2010; http://www.eea.europa.eu/data-and-maps/data/population-density-disaggregated-with-corine-land-cover-2000-2), the sum of road length per pixel (BD CARTO®, Institut Géographique National), and a normalized value of light pollution (http://www.ngdc.noaa.gov/dmsp/downloadV4composites.html). This human footprint variable ranging from 0 (wild) to 1 (highly disturbed) was used to indicate the degree of disturbance in the vicinity of communities.

Functional trait information

We focused on three key functional traits that can play a role in both niche differentiation and competitive ability: the specific leaf area (SLA; light-capturing area deployed per unit of leaf dry mass), the height of the plant's canopy at maturity (Height) and the seed mass (SeedM), which are well-known components of the leaf-height-seed (LHS) syndrome of plant traits (Westoby 1998). SLA reflects species' relative growth rate, differences among species in terms of water use efficiency and competitive abilities for nitrogen (Grime 1998; Suding et al. 2005, Angert et al. 2009). Seed mass reflects on the one hand seed dispersal distances, production and longevity, which represent the chance of "successful dispersal by a species into an establishment opportunity" (Hamilton et al. 2005). On the other hand, seed mass can also been seen as indicating species competitive ability at juvenile stage, as the absolute growth rate (opposed to the relative growth rate) is higher for larger seedlings than those from smaller ones (Grotkopp et al. 2002). Height captures each species' ability to intercept light (Westoby et al. 2002).

Height and SLA values were taken from our own measurements collected over the past 10 years, together with data from Flora Indicativa and LEDA for the missing species in our database (Knevel et al. 2003, Landolt et al. 2010). For both height and SLA, several individuals were measured in different locations, usually sampled through the range of environmental conditions the species occur in the Alps (e.g. Albert et al. 2010; de Bello et al. 2013). We then took the average trait values among all sampled individuals. For seed mass we used data from Kew Garden for most species complemented with our own measurements. Note that these traits were thus not measured within each community under study here but rather represent the mean value across their range in the Alps. Trait values for invasive species were also traits measured in the invaded range in the study area.

Although other functional traits may influence species co-existence (e.g. the level of leaf nitrogen content, the degree of plasticity), they were not available for all species occurring in the 5,141 selected communities.

Biotic interaction indices

For each of the 5,141 communities we computed six *biotic interaction indices:* three indices to describe resource opportunity (one index considering all species in the communities, and two indices considering

only herbaceous species), and three indices of competitive ability (only for herbaceous species).

Resource opportunity To measure resource opportunity for the invaders in the communities, we calculated the functional relatedness between invaders for both all natives and with herbaceous natives only (Gower distance on the three traits together, Gower 1971). More specifically, we calculated (1) the Mean Distance of the invader to *all* Native Species ($MDNS_{all}$), (2) the Mean Distance of the invader to *herbaceous* Native Species ($MDNS_{herb}$), (3) the Distance of the invader to the Nearest Native Species among *herbaceous* species only ($DNNS_{herb}$). These indices are complementary as they suggest different hypotheses on how biotic interactions drive the integration of a given invader into native communities. $MDNS_{all}$ assumed that the invaders compete with all native species with the same strength, $MDNS_{herb}$ assumed that the invaders mainly compete with native species from the same growth form, while $DNNS_{herb}$ assumed that competition is strongest with the most similar species of the same growth form.

Competitive ability The differences in competitive ability between species were calculated separately for each of the three functional traits (SLA, Ht and SeedM) because these traits represent different competitive strategies. SLA contrasts fast growing (high SLA) vs. slow growing or stress resistant species (low SLA; Wright et al. 2004; Westoby and Wright 2006). SeedM separates species with high seed production, long dispersal distances but low juvenile growth rates (low SeedM; i.e. dispersal and propagule pressure advantages) vs. species with low seed production but high juvenile growth rates (high SeedM; i.e. juvenile competition advantage), and Ht is a key component of competition for light (Westoby et al. 2002). Competitive ability indices were calculated as the standardised mean differences in trait value between the invader and each herbaceous species in a given community (Kunstler et al. 2012). Only herbaceous species were used to calculate these indices to avoid the comparison of traits between trees and herbaceous species, which may reflect broad life histories and niche differences more than competitive abilities. When the index equals 0, it means the invader has the same trait value as the average trait value of the community; it is negative or positive when

the invader has a lower or higher value than the community mean respectively (see also Fig. 1c).

These indices differ from the resource opportunity indices because for each trait the invader's hierarchical position in one trait gradient of the community is emphasised, rather than the multi-trait absolute difference. For example, in the case of invasion by competitive exclusion for light interception, the invader is expected to invade natural communities only when it is taller than the native species (i.e. it cannot outcompete taller plants for light interception). In this case, resource opportunity indices would fail at detecting the right process because they would consider the departure of the invader compared to the community mean: both positive (the invader is taller) and negative departures (the invader is smaller). In contrast, competitive ability indices are able to tease apart these two cases because they explicitly quantify the difference between invader and mean community traits.

It can be noted that species abundances or cover was not taken into account in these indices, (although probably influencing competitive interactions). The main reason for not taking abundance into account was that the observed abundance in already invaded communities is very likely to have changed following invasion, and was therefore not directly comparable to species' abundances in non-invaded communities.

Teasing apart the mechanisms: summarizing the different cases In order to identify the coexistence mechanisms driving invasions, we propose to regress the presence and absence of each invasive species as a function of the biotic indices. Here we summarize the different cases on how the regression coefficients and shapes of the relationships (i.e. linear vs. quadratic) can inform us on the underlying mechanisms (Fig. 1).

(1) Environmental filtering should be expected when functional dissimilarity indices are negatively correlated to invader's presences in a linear case (i.e. invaders occur in functionally similar communities, grey curve in Fig. 1b), or when competitive ability indices show hump-shaped relationships to the invader's presences (i.e. a negative coefficient of the quadratic term) that are centred on zero (green curve in Fig. 1c).

(2) Resource opportunity should be expected when functional similarity indices are positively correlated to the invader's presence in a linear case (i.e. invaders occur in functionally dissimilar communities, black

curve in Fig. 1b), while no significant relationship is expected when considering competitive ability indices (blue curve in Fig. 1c).

(3) Competitive exclusion can be expected when functional similarity indices are positively correlated to the invader's presence in a linear case (i.e. invaders occur in functionally dissimilar communities, black curve in Fig. 1b), and when competitive ability indices are also positively correlated to the invader's presence (red curve in Fig. 1c).

Dispersal index

Dispersal limitations can lead to the spatial clustering of invader presences, also called spatial autocorrelation (i.e. spatial autocorrelation of occurrences, hereafter SAC; Dormann et al. 2007). Unsuitable sites can indeed be invaded when they are close enough to source sites (false presences), while suitable sites can be spared from colonisation if they are too distant (false absences). However, apparent spatial autocorrelation of individuals also emerges when the abiotic, and even the biotic, environments are themselves spatially autocorrelated. As the effects of biotic and abiotic environment are directly modelled in our framework, we suggest that when SAC is identified as a significantly important variable in the model (i.e. selected at the end of the AIC step-wise selection procedure) it mainly reflects species dispersal limitations (although they may also emerge from unknown local environmental configurations). To model this spatial autocorrelation, we used an autocovariate variable (Augustin et al. 1996). This modelling approach is the simplest and least computationally intensive method to account for SAC. Although other methods (e.g. Eigenvector Mapping, Dormann et al. 2007) are likely to provide a better estimation, the use of an autocovariate term was the only option here because of computational limitation for more than 5,000 sites. The autocovariate term D_i was then defined as (Augustin et al. 1996):

$$D_i = \frac{\sum_{j=1}^{k_i} f(d_{ij}) y_j}{\sum_{j=1}^{k_j} f(d_{ij})}$$

where D_i at site i depends of $f(d_{ij})$ a function of the Euclidian distance between sites i and j (here: $f(d_{ij}) = 1/d_{ij}$), k_i is the number of sites within the vicinity of the site i, and y_j is the response variable (here presence and absences) of the site j. This index measures, for each site, the potential effect, weighted by the inverse of the distance, of the surrounding sites (up to 10 km, that is an approximation of the maximal natural long distance dispersal of the seed rain; see anthropochory in Engler et al. (2009). We did not include rare long distance dispersal events due to their highly stochastic and idiosyncratic nature.

Statistical analyses

To study the importance of the different competition processes via different competition indices, we used generalized linear models (GLMs). For each species, we built three nested models: (1) an intercept model, (2) a model with environmental and dispersal variables, and (3) a full model including environmental, dispersal and biotic interaction variables. The variables tested in these models include: (i) five environmental variables in their simple and quadratic forms (except for land use as it is a categorical variable), (ii) a dispersal variable based on the spatial autocorrelation of the species presence, (iii) six biotic interaction variables in their simple and quadratic forms (three of resource opportunity and three of competitive exclusion, see the section *Biotic interaction indices* for more details), and (iv) the interaction between the environmental and biotic variables.

Since the full model could potentially include 118 variables, we could not test the performance of all possible sub-models ($\sim 10^{35}$ models). We thus used a forward-backward step-wise variable selection procedure based on the BIC criterion (i.e. Bayesian Information Criterion), a more conservative criterion than the Akaike Information Criterion (Akaike 1974), as it penalises the model score by the number of observations. As first step and for each species, we identified among the environmental, dispersal and biotic indices variables the ones that significantly improved model performance, and kept the model with the lowest BIC score. In a second step, we added to the previous model all interaction terms between the selected environmental and biotic interaction variables and ran a new stepwise variable selection to identify the final best model (based on BIC scores). We finally corrected the model intercepts for unequal sampling of presences and absences following the suggestion of Maddala (2001; but not the parameter estimates since they are not affected by prevalence). Thus, the model intercept was decreased by

Table 1 Statistics representing the performance of the model *without biotic* interaction variables, and the model *with biotic* interaction varaibles, based on BIC, AUC and D^2 scores for each species

	AUC		BIC		D^2	
	Without biotic	With biotic	Without biotic	With biotic (delta)	Without biotic	With biotic
Ambrosia artemisiifolia	0.89	0.94	226	211 (−15)	0.23	0.28
Bidens frondosa	0.96	0.99	228	144 (−74)	0.35	0.62
Conyza canadensis	0.90	0.93	371	334 (−37)	0.23	0.32
Erigeron annuus	0.86	0.91	579	522 (−57)	0.16	0.26
Panicum capillare	0.90	0.97	239	184 (−55)	0.20	0.39
Solidago Canadensis	0.95	0.96	228	183 (−45)	0.35	0.47
Solidago gigantea	0.92	0.98	689	462 (−227)	0.34	0.57

$(\ln p_1 - \ln p_0)$, where p_1 and p_0 are the proportion of observed presences and absences respectively.

Variable importance

We estimated the variable importance using a permutation accuracy importance algorithm, as suggested by Strobl et al. (2007; we used 500 permutations). The principle was to apply a random permutation of each variable in order to mimic the absence of the variable in the model. Then, importance is estimated according to the difference in prediction accuracy (i.e. mean squared error) without and with the permutation. For each species we extracted the median variable importance for both models: the model without biotic interaction variables (model 2), and the model including them (model 3).

Model evaluation

Models were evaluated with three complementary indices: BIC as it allows to account for model complexity, the Area Under the relative operating Characteristic curve (AUC) which measures the predictive accuracy of the models, and the adjusted D^2 measuring the goodness-of-fit of the model. The AUC ranges from 0.5 (prediction not better than random) to 1 (perfect prediction). A model with an AUC that is higher than 0.8 is usually classified as relatively good (Swets 1988; e.g. Araújo et al. 2005; Engler et al. 2011). The adjusted D^2 was calculated as the proportion of explained deviance corrected by the number of degrees of freedom (*df*) of the final model.

We finally controlled for remaining spatial autocorrelation in the residuals of the model using Moran's I index (Cliff and Ord 1981; see "Appendix"). If no residual spatial autocorrelation is detected, it means

that the species dispersal limitations were well captured by the dispersal index.

All statistical analyses were carried out in R 2.15 (Development Core Team 2012; http://www.R-project.org).

Results

Model performance

For all modelled invasive species both models sets—without and with biotic interaction indices—performed well with respectively AUC scores ranging from 0.86 to 0.96 and 0.91 to 0.99 (Table 1). Based on AUC, BIC and D^2 scores, for every species the inclusion of biotic interaction indices improved model accuracy (Table 1).

Environment and spatial autocorrelation

Amongst the abiotic variables, growing degree-days (ddeg) and precipitation variables were often selected as important predictors of the invader's presences and absences (in linear and/or quadratic forms), while radiation and the human footprint index were only selected for two species (Table 2). For these seven herbaceous invaders the land use type was never selected as a good predictor. The spatial autocovariate was also important for four species (Table 2), and residual SAC was not significant for any of the species ("Appendix").

Biotic interaction indices

The biotic interaction indices significantly improved model performance for all species (Table 1) and

contributed to more than 60 % of the model performances (except for *E. annuus*; Fig. 2), but the indices selected change across species (Table 2). In general, the functional dissimilarity indices: MDNS$_{all}$, MDNS$_{herb}$ and DNNS$_{herb}$, were worst indicators of invader presence than the indices of competitive ability (i.e. functional dissimilarity indices were less often selected and have less importance in the models; Fig. 2). More specifically, among the competitive ability indices, metrics based on plant height and SLA were better indicators of invader's presence than the ones based on seed mass (Table 2 and Fig. 2). For only two species, the resource opportunity indices were selected in the final model (Table 2). *E. annuus* showed a positive coefficient for DNNS (i.e. it occurs in communities where there is always a native species highly functionally similar), while *S. canadensis* showed both a positive coefficient for MDNS when considering all species and a negative coefficient when considering only the herbaceous strata. For competitive ability indices, we found in all cases (except for *C. canadensis*) a hump shaped relationship (Fig. 3) that was centred on zero (i.e. the invader is present in communities where it has a trait value similar to the mean community trait). In the case of *C. canadensis*, the sign of the coefficient for the competitive ability on seed mass is positive (Table 2).

Interactions between environmental and biotic variables

We found significant interactions between some of the abiotic and biotic predictors for most of the species (Table 2). For instance, *S. gigantea* is present for intermediate levels of solar radiations, and within these conditions it is only present in communities where the native species have a similar height as itself (Fig. 4). Overall, it was clear that for every interaction between important variables (identified in Fig. 2), the biotic indices were systematically more influential towards the core of the invader environmental niches (i.e. when the probability of invader presence was high in the abiotic gradient).

Discussion

The general aim of our work was to identify the respective influence of the three potential processes driving invasion success: environmental filtering, dispersal, and competitive interactions. Including a palette of different variables

Table 2 Best selected models (based on the lowest BIC scores) including biotic interaction variables

	Ddeg ^2	Radia ^2	Precip ^2	Hum Fp ^2	LU	SAC	MDNS h	MDNS t	DNNS h	Height h	Height ^2	SLA h	SLA ^2	SeedM h	SeedM ^2	Interactions	No. of variables
Ambrosia artemisiifolia	+	+				+				−		−	−				4
Bidens frondosa	−	+	−							−	−	+	−			Ddeg:SLA (+); ddeg:Height^2 (−)	9
Conyza canadensis			+	+		+				−				+		HumFP:Height (+)	6
Erigeron annuus	+	+	+	+					+							Precip:DNNS (−)	7
Panicum capillare	−	+			−						−		−		−	Ddeg:Height^2 (+)	5
Solidago Canadensis	+	+	+			+	−	+			−						5
Solidago gigantea	+	+	−	+		+				−		−	−			Radia:Height^2 (+)	9

The table shows the variables selected in the models and the sign of the coefficients (an empty case means that the variable was not selected in the model). Note that MDNS$^2_{all}$, MDNS$^2_{herb}$ and DNNS$^2_{herb}$ were also tested in the models, but because they were never selected we do not represent them in the table. ddeg: annual sum of degree-days with a 5.56 °C threshold, radia: mean annual level of potential solar radiation, precip: mean annual precipitation, HumFP: human footprint, LU: Land use, SAC: spatial auctocorrelation (dispersal index)
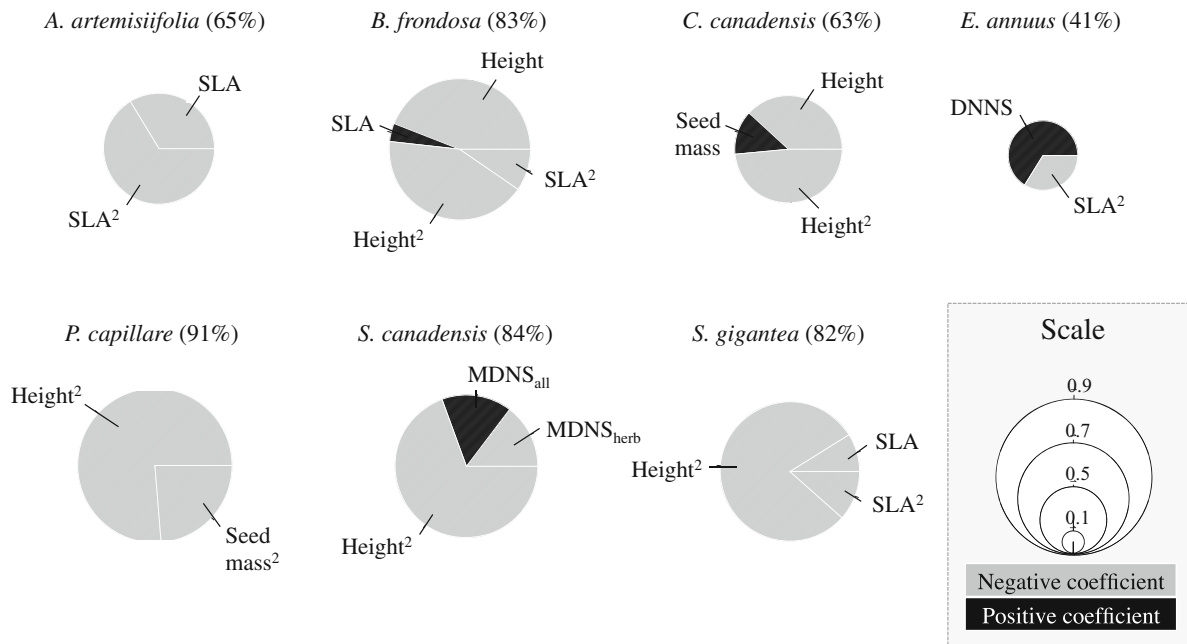
Fig. 2 Relative importance of the selected biotic interaction indices for each species. For each biotic index, the sign of the coefficient associated is indicated with a *black colour* for positive values, and *grey colour* for negative values. The size of the *pie charts* represents the proportion of the model performance (based on AUC scores) due to the biotic variables. The contribution of all biotic indices together to model performances is indicated next to the species names

and indices into species distribution models, we were able to provide a framework that can link theoretical expectations with empirical patterns. We then applied this framework on a large community dataset, where several invaders occur. Overall, we show that including biotic interaction indices can significantly improve the performance of traditional distribution models (Table 1), even though environmental filtering seems to be the main driver of invasion in the French Alps.

Environmental variables

In general, the sum of degree-days and the level of precipitation were the best predictors of our studied invader distributions. This outcome corresponds to the commonly identified abiotic drivers of invasion (e.g. Vila and Pujadas 2001; Pysek et al. 2010). The human footprint was also important for *Conyza canadensis* and *Erigeron annuus* that are currently at an establishment stage, and are probably more associated to disturbance regimes. Indeed, the human footprint is both an indicator of the intensity of site disturbance and a proxy for the level of propagule pressure (Sanderson et al. 2002). However, it is important to

keep in mind that the level of human footprint in the alpine landscape is partly linked to the temperature gradient, as human populations tend to mainly settle in lowland areas. Nonetheless, this variable is still highly descriptive of the species presence. Interestingly, the type of land use was never selected as an important variable. This can seem surprising since it is notorious that the invaders studied here have particular habitat preferences: some preferring wetlands (e.g. *B. frondosa*) while others occur more in arable lands (e.g. *C. canadensis*, *E. annuus*) or grasslands (e.g. *P. capillare*). However, it is possible (i) that the resolution of the land cover variable was not precise enough to well relate the true habitat types with the invader's presences, or (ii) that the invaders occur in many different types of habitats (as soon as they are disturbed, even temporarily) lowering the descriptive power of this categorical variable.

Dispersal variable

Although dispersal was estimated here in the simplest manner (with an autocovariate term), it is shown to be quite an important predictor of the invader presence. It
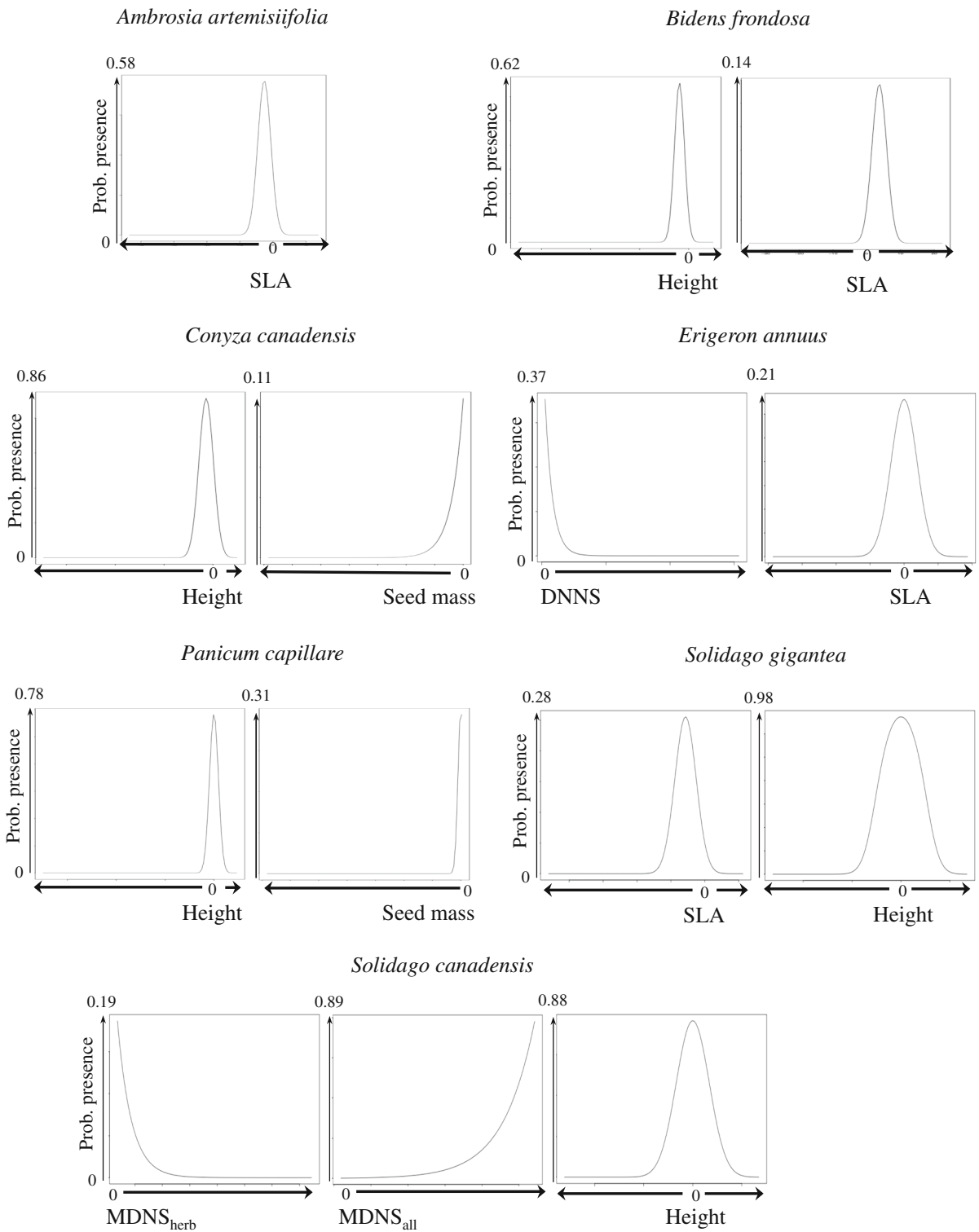
Fig. 3 Response curves of all selected biotic indices for each species (all other variables fixed at their mean). Each *curve* depicts the change in modelled probability of occurrence in function of the selected biotic variable
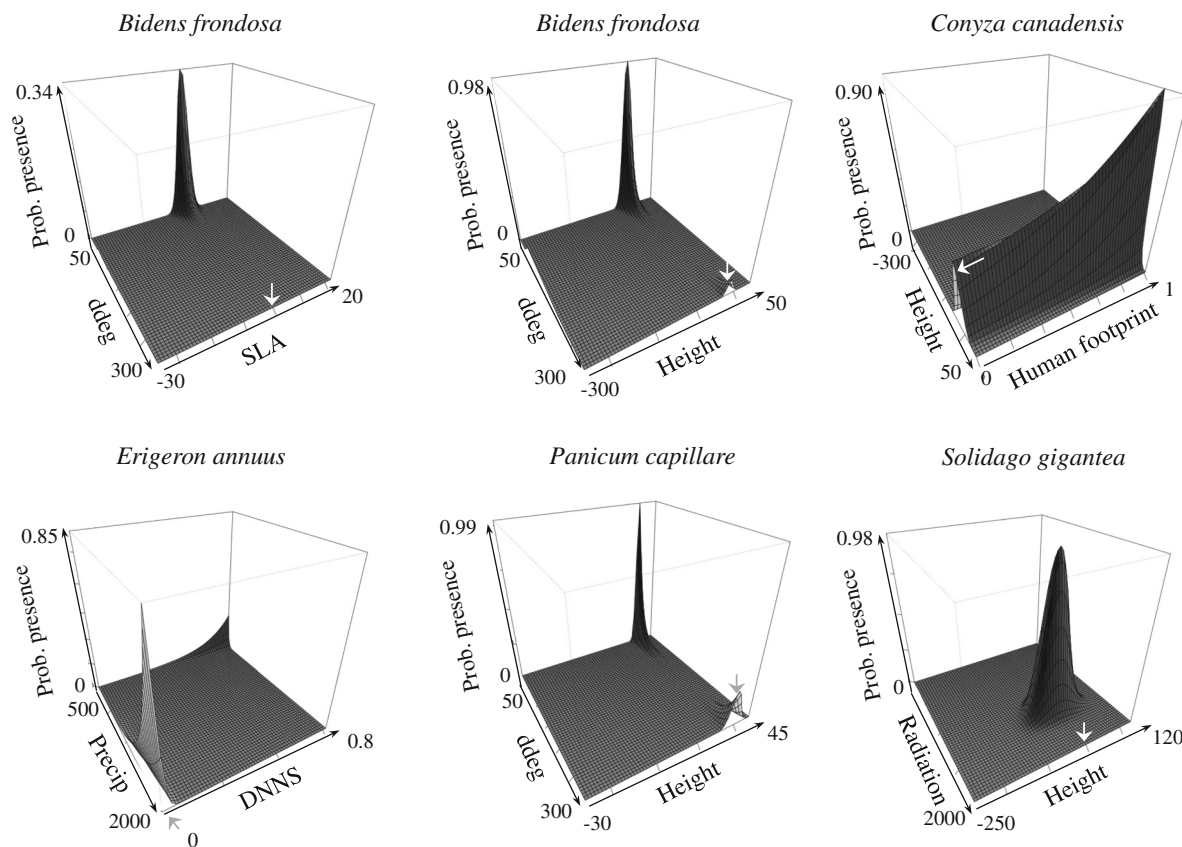
Fig. 4 3-Dimensional response curves of the probability of occurrence of each invasive species as a function of two interacting variables. The *small white* or *grey arrows* indicate the position of the 0 value on the biotic interaction indices

is particularly important for the species that have the highest seed production, as for example *A. artemisiifolia* (2,000 seeds per individual on average), *C. canadensis* (15,000 seeds per individuals on average) or *S. gigantea* (2,500 seeds per individuals on average; personal observations). Invaders producing lower seed numbers are less influenced by this dispersal variable, such as *B. frondosa* (500 seeds per individuals on average) or *P. capillare* (100 seeds per individuals on average; personal observations). This result can seem surprising as species with low fecundity are often expected to exhibit patchy distributions due to dispersal limitations. However, species producing a high number of seeds also have high probability of long distance dispersal that can as well result in patchy distributions at the regional scale. It can be noted that, although these invaders have been present in Europe for more than 100 years ("Appendix"), the number and timing of species introduction specifically in the

French Alps is likely to affect the spatial distribution of the species in our studied area, but this information was not available. Since we used a spatial autocorrelation term to represent propagule pressure and dispersal processes, it is also likely that this term reflects a missing spatially autocorrelated abiotic or biotic driver operating at the same spatial scale. In any case, if this variable is shown to be an important predictor, either as a dispersal limitation indicator or as a proxy for a missing variable, or both, it is important to include it in the modelling process, especially for predictive purposes at local scales, but also to prevent inflated type I error. In the future, once information on life history (e.g. seed production across different environments), ecological and human dispersal data will become available, it will be possible to parameterise more complex models that explicitly incorporate dispersal mechanisms (e.g. Roura-Pascual et al. 2009, Dullinger et al. 2012), and thus will permit a better understanding

on how propagule pressure impacts invasion dynamics at local and regional scales.

Competitive interaction variables

Among the different indices developed to test the two strategies of competitive interactions (resource opportunity *vs*. competitive exclusion), the indices of individual height differences were the most influential to predict invaders presence (for all species except *A. artemisiifolia* and *E. annuus*). In all cases, height difference indicated that these invaders always co-occur with native herbaceous species of similar height but very rarely with native species of much lower or higher height. Rather than competition related processes, this pattern likely reveals high levels of environmental filtering that are not captured by the abiotic variables already included in the models. This conclusion is corroborated by the other index responses, although these are less important for model performance (Fig. 2). For instance, DNNS (e.g. *E. annuus*) and SLA indices (e.g. *A. artemisiifolia*, *B. frondosa*, *S. gigantea*) show that invaders occur more in communities where they have the same traits as the native species.

Furthermore, additional information can also be deduced for *S. canadensis* for which occurrence probability is positively correlated with $MDNS_{all}$ but negatively with $MDNS_{herb}$. This suggests that *S. canadensis* occurs in communities where it is similar to the native herbaceous species but at the same time where there are also woody species with very dissimilar traits. This result corroborates findings in the literature showing that this species mainly occurs at forest edges (Jakobs et al. 2004), probably because tree species modify the local abiotic environment toward more favourable conditions for this invader (e.g. facilitation through reduced evapotranspiration or reduced solar radiation). This finding shows the importance of accurately defining the different organisms that can interact through competitive exclusion, in order to not misinterpret the patterns of dissimilarity. As a result, models predicting this species occurrence could be largely improved by the inclusion of community metrics depicting woody and herbaceous plant communities or by remote sensing data depicting forests contours.

Overall, our results did not detect significant influences of the competitive interactions on the invasion success for our set of species in the French Alps. This finding is in agreement with the results of some studies developed in different ecological settings (e.g. Daehler 2001; Diez et al. 2009; Van Wilgen and Richardson 2011; which used phylogeny as a proxy for functional differences), but in contradiction with the results from some other ones (e.g. Davies et al. 2011; Schaefer et al. 2011; Carboni et al. 2013). In the context of our study system, it is likely that the signal of biotic resistance in communities is low because our seven herbaceous invaders are still in the establishment phase in the study region. Indeed, during this establishment phase the species tend to occur mainly in ruderal habitats, because they cannot yet survive the biotic resistance in highly competitive communities (Theoharides and Dukes 2007).

Additionally, the fact that we detected high levels of trait similarity (notably for individual height) between the invader and the native species indicates that an important variable was probably missing from the models (as trait similarity is expected to relate to environmental filtering). This variable could be abiotic, such as disturbance regime or fine-scale soil nutrient content (Lake and Leishman 2004); or it could be biotic, such as facilitation or shared pollinators (Morales and Traveset 2009). Such variable can then be brought to light by studying in more details the characteristics of the invaded communities, for instance by going back to the field and measuring the soil nutrient content, or recording the pollinator communities.

It can also be noted that, the indices were not calculated with traits measured within each community, thus ignoring intra-specific trait variability. Although such data would be more appropriate, it is impossible to get this information for 5,000 communities and around 3,000 species. However, we believe that using species mean trait values is likely to decrease the detection of the resource opportunity process due to trait displacement (i.e. when invaders tend to be dissimilar from the native species via trait plasticity), especially for invasive species that often show high plasticity (Daehler 2003). That means that using mean trait values likely decreases the probability of detecting signals of competition filtering. In the ideal case where traits are actually measured within each studied community, it could remove part of the noise in the data (as explained in Albert et al. 2012; see also van Kleunen et al. 2011).

Finally, even though our Alpine dataset did not contain the full range of the invaders we could detect a significant increase in the importance of biotic indices towards the centre of species' niches (Table 2, Fig. 4). This result cannot corroborate our expectation that stressful environments decrease the relative importance of competition (Körner 1999; Callaway et al. 2002; Graham et al. 2009), as we did not detect any. Nevertheless it appears that the patterns of functional similarity are more pronounced in highly suitable environments. Two interpretations (at least) could explain such clustering patterns. On the one hand, indirect facilitation between functionally similar species can be more important towards niche core than towards niche boundaries (i.e. net positive effects occurring via multiple negative effects: "the enemy of my enemy is my friend"; Brooker et al. 2008, McIntire and Fajardo 2013). On the other hand, if the clustering patterns were the result of a hidden abiotic factor, this would indicate a simple interaction between the niche gradient and this factor. Further investigation into the interplay between environmental stress and competitive interactions is necessary and promises to provide very interesting results.

Concluding remarks

Overall it seems that competitive interactions are not of prime importance to invader herbaceous species spread in the French Alps probably because they are essentially at an establishment stage of the invasion process. However, we have shown that proxies of biotic interactions are useful for detecting other important drivers of invader's occurrences. Consequently we suggest the further use of similarly comprehensive approaches that can mix theoretical expectations to a set of well-defined indices to better disentangle environmental filtering, resource opportunity and competitive exclusion as driving processes of invasion. Second, we also recommend the use of biotic indices when modelling invasive or native species distributions, as they have the power to significantly improve model performances. Such a comprehensive approach should pave the way for more realistic distribution models of plant invaders that integrate spatial (dispersal related) processes, environmental selection (niche related) and biotic processes (competition related) for a better prediction of their future spread.

Appendix: Test of spatial autocorrelation in the model residuals

The Moran's I index scores and randomisation tests were performed with the R package *spdep* (Bivand 2014).

See Table 3.

Table 3 Tests of spatial autocorrelation of the model residuals (models including environmental, dispersal and biotic indices variables)

Species	Moran's I	*p* value	Number of species occurrences	Estimated introduction date in France
Ambrosia artemisiifolia	−0.0011	0.54	30	1822
Bidens frondosa	−0.0017	0.79	30	1850
Conyza canadensis	−0.0009	0.47	39	1850
Erigeron annuus	−0.0013	0.76	61	1931
Panicum capillare	−0.0001	0.13	30	Unknown (1931 in Czech Republic and 1867 in UK)
Solidago Canadensis	−0.0012	0.76	30	1641
Solidago gigantea	−0.0010	0.51	101	Unknown (1900 in Germany)

The Moran's I index indicates the level of correlation between the residuals and the spatial distances between communities. The *p* values of the test indicate the significance level of the Moran's I indices (here there are only non-significant spatial autocorrelation of the residuals). The number of species occurrence used in the models, and the estimated introduction date in France (from the Daisy database and other resources; http://www.europe-aliens.org/default.do) are also indicated

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