

ECOLOGY AND IMPACT OF AN EMERGING INVASIVE SPECIES IN FRANCE:
WESTERN RAGWEED (*AMBROSIA PSILOSTACHYA* DC.)

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RÉSUMÉ.— *Écologie et impact d'une espèce invasive émergente en France : l'Ambroisie à épis lisses (Ambrosia psilostachya DC.).*— L'Ambroisie à épis lisses (*Ambrosia psilostachya* DC.) est une Astéragée vivace originaire d'Amérique du Nord et introduite en France à la fin du XIX^e siècle. Des observations de terrain font état d'une expansion récente et la formation de populations clonales assez denses pourrait présenter une menace pour la biodiversité dans certains habitats méditerranéens sensibles ou dégradés. Dans ce contexte, cette étude vise à identifier les habitats colonisés et les conditions écologiques favorables à son succès et à mesurer quels sont les impacts sur les communautés végétales des habitats semi-naturels envahis. *Ambrosia psilostachya* colonise principalement des milieux rudéraux (61 %), cultivés (14 %) et des habitats semi-naturels (pelouses sableuses, dunes) dégradés (12 %). Cette ambroisie vivace, si elle peut occuper les mêmes habitats qu'*Ambrosia artemisiifolia* (plante annuelle), sera présente dans les stations les plus stables de ces habitats. *Ambrosia psilostachya* présente de fortes abondances dans les végétations vivaces de début de succession (friches, bords de routes) mais est moins présente dans les habitats pionniers régulièrement perturbés ou stressants, suggérant que son optimum se situe à des niveaux de perturbations intermédiaires. La compétition interspécifique pourrait également agir comme le suggère son plus faible succès lorsqu'elle occupe des communautés composées d'espèces fonctionnellement proches, supposées utiliser les ressources de manière similaire. Aucun impact significatif sur la structure des communautés végétales occupées par *A. psilostachya* n'a été mis en évidence suggérant des conséquences limitées sur les communautés végétales. Toutefois, son développement dans les prairies à chiendents (*Elytrigia* spp.) serait à surveiller et une gestion intégrée des pâturages avec de fortes densités de plantes est à mettre en place. Ces premières données écologiques récoltées pourront permettre d'établir une meilleure cartographie du risque envahissant d'*A. psilostachya* en France.

SUMMARY.— Western ragweed (*Ambrosia psilostachya* DC.) is a perennial member of the *Asteraceae* native to North America that was introduced into France at the end of the 19th Century. Field observations have provided evidence of a recent expansion and of the emergence of dense clonal populations potentially threatening the biodiversity of certain Mediterranean sensitive or degraded habitats. This study therefore aimed to identify the habitats colonized and the ecological conditions favouring successful colonization by this species, and to determine its impact on the plant communities of the semi-natural habitats invaded. *Ambrosia psilostachya* mostly colonizes ruderal (61 %) and cultivated (14 %) environments and degraded semi-natural (sandy grassland, dunes) environments (12 %). Western ragweed occupies the same habitats as the annual species *Ambrosia artemisiifolia*, but is found at the most stable sites in these habitats. *Ambrosia psilostachya* is highly abundant in the perennial vegetation at the start of succession (wasteland, roadsides), but is less frequent in more stressful, regularly disturbed pioneer habitats, suggesting a preference for sites with an intermediate level of disturbance. Interspecific competition may also have an effect, as suggested by its lower levels of success in communities consisting of functionally similar species thought to use the available resources in a similar manner. We found no significant impact on the structure of the plant communities occupied by *A. psilostachya*. However, the development of this plant in *Elytrigia* grasslands should be monitored and integrated pasture management, including a high plant density, should be implemented. The preliminary ecological data collected in this study should make it possible to establish a more accurate map of the risk of *A. psilostachya* invasion in France.

Western ragweed (*Ambrosia psilostachya* DC., *Asteraceae*) is one of the four American ragweed species present in France. It originates from Western North America (Rydberg, 1922;

USDA, 1970), but has been accidentally introduced into several continents (including Asia and Australasia) and a dozen or so Western European countries. This perennial species survives from year-to-year through a rhizome, which propagates by means of suckers (Basset & Crompton, 1975), resulting in the establishment of clonal populations that can cover large areas rapidly. In some circumstances, *A. psilostachya* is considered to be an invasive species, both in its area of origin and in certain parts of its introduction area. In the United States, it grows as a weed on degraded rangelands (McCarty & Scifres, 1972; Gillen *et al.*, 1991), particularly in the Great Plains of the central United States (Stubbendieck *et al.*, 1994). Similarly, in Russia, *A. psilostachya* is officially classified as a quarantine species (Afonin *et al.*, 2008), indicating that its agricultural impact and current limited distribution have justified the implementation of regulatory measures to control the existing populations and to prevent new introductions.

A recent estimate of the increase in the number of new sites occupied by this species in France (Fried & Mandon-Dalger, 2013) suggested that, after a lag phase, *A. psilostachya* would have entered a more dynamic phase. The species, considered to inhabit disturbed environments in its native range (Strother, 2006), can nevertheless become established on sandy grasslands in France (Tison & de Foucault, 2014), raising questions about its possible impact on the remarkable flora of such environments (Jauzein & Nawrot, 2011). It may also have an impact on human health, through the production of allergenic pollen (Wodehouse, 1945; Ghosh *et al.*, 1994) a characteristic common to two other ragweed species already present in France: *A. artemisiifolia* L. and *A. trifida* L. (Wodehouse, 1945). The lack of information about the behaviour of *A. psilostachya* in France, and the diverse potential risks posed by this species, led us to study its ecology, the conditions associated with dense populations and its impact on the plant communities it invades.

Populations of a species introduced into a new area lie somewhere on the introduction-naturalization-invasion continuum (Richardson & Pyšek, 2006), based on its capacity i) to form stable populations (naturalization) and/or ii) to spread rapidly over large areas (invasion). The passage between these stages depends, in particular, on the ability of a species to breach different types of environmental filters. Introduction and secondary dispersal are frequently linked to human activities, whereas the stages of establishment and dominance over the existing communities are controlled by abiotic (pedoclimatic conditions, disturbance regime, etc.) and biotic (biological regulation, competition with the existing flora, Davis *et al.*, 2005) filters. Most introduced species can be considered opportunists, in that they preferentially occupy environments disturbed by human activity (the “passengers” concept, MacDougall & Turkington, 2005). Nevertheless, some species manage to establish in natural or semi-natural communities subject to little interference from humans. Such species may have a greater impact, particularly if they are “transformer” species capable of modifying the properties of the ecosystem (the “drivers” concept; MacDougall & Turkington, 2005).

If *A. psilostachya* behaves as an opportunistic species, then it should develop better within communities in which it uses an ecological niche that would otherwise be partly vacant. Conversely, if this species is highly competitive, then its development may be independent of both the identity of the neighbouring species and the level of niche overlap. These hypotheses can be tested indirectly, by considering functional traits (Violle *et al.*, 2007) and focusing on the functional niche (Rosenfeld, 2002). The exploitation of this niche may involve the use of different strategies to gain access to resources, resulting in distinctive trait values. A conceptual framework based on three functional traits — specific leaf area, plant height and seed mass, abbreviated to LHS, for leaf-height-seed) — can be used to describe the behaviour of species in the principal environmental gradients (Westoby, 1998), particularly as concerns the levels of resources available and the degree of disturbances. We used this model to evaluate the degree of similarity between

A. psilostachya and the communities colonized, as a function of the colonization success of *A. psilostachya*.

“Environmental impact” is a key issue in biological invasions (Blackburn *et al.*, 2011). The Mediterranean biome is among the richest biomes in the world in terms of the species it contains, but its biodiversity is also expected to be one of the most affected by species introduction (Sala *et al.*, 2000). The effects of invasive plants that have become dominant on species and/or on ecosystem functioning are clear (Hulme *et al.*, 2013), but the variability of their impact raises questions about the extent to which the presence and abundance of *A. psilostachya* might affect the diversity of Mediterranean plant communities. The identity and life form of species have been shown to be determinants of the magnitude of this impact (Fried *et al.*, 2014), and perennial species, particularly those propagating by means of a rhizome, have a greater impact than annuals (Herrera & Dudley, 2003).

We investigated the ecological impact of *A. psilostachya* by evaluating its interaction with the plant communities of three different habitats with contrasting levels of human disturbance. The sampling was based on a plant cover gradient of *A. psilostachya*, in order to study how an increasing cover of this species was associated with species richness, Shannon diversity, equitability and total plant cover (Kumschick *et al.*, 2015). The study aimed to detect potential impact thresholds defined as the discontinuity where the community response variable decreased dramatically with increasing invader cover (Gooden *et al.*, 2009). We aimed i) to determine the ecological characteristics of *A. psilostachya* in France, ii) to identify the abiotic and biotic factors associated with dense populations and iii) to investigate the possible impact of this species on plant communities.

MATERIALS & METHODS

ECOLOGY AND RESPONSE TO THE ENVIRONMENT

We analysed the ecological features of *A. psilostachya* at three levels of precision. We assessed the presence and abundance of this species with respect to (i) the type of habitat colonized, (ii) the abiotic conditions (climate, soil), and (iii) the conditions underlying interactions with the other species present (through the calculation of functional distance). Data on the ecology of *A. psilostachya* were compiled from different sources, including the main herbaria of France, published studies and the databases of national botanical conservatories. In a first step, we were able to identify 245 sites at which this species had been recorded, from 1891 to 2013, and 30 *départements* (a French administrative area roughly equivalent to a county). Almost 60 % of the observations were in the *départements* Bouches-du-Rhône, Gard, Hérault, Var and Vaucluse, in the Mediterranean area in which this species was present locally at high densities. In a second step, we were able to analyse the range of habitats colonized by *A. psilostachya* for 172 observations using ecological information recorded in herbarium notes ($n = 106$) and our own observations in the field ($n = 66$). Habitats were then assigned, on the basis of this information, to one of the categories defined in the EUNIS classification system levels 1, 2, 3 and 4 (Davies *et al.*, 2004).

We selected 48 observation sites for which we had precise geolocation co-ordinates from the SILENE database (CBNMed, 2014) or from publications. At each site, a 4 m² quadrat was used to record all the plant species co-occurring with *A. psilostachya*. According to the situation, either the quadrat included the only colony of *A. psilostachya* present or, at sites where several separate colonies were present, the quadrat was placed randomly on one of the colonies. All the species present within the quadrat were identified and the percentage of the ground they covered was estimated visually as a percentage of the quadrat area. Nomenclature follows Tison & de Foucault (2014). Plant height (h), defined as the minimum distance between the photosynthetic tissues furthest from the ground and the ground itself (Cornelissen *et al.*, 2003) was measured for 10 individuals of *A. psilostachya* and for 10 individuals of representative species in the assembly. The 10 individuals of *A. psilostachya* were also used to measure the maximum width (mw). Percentage ground cover (Cover) and an approximation of the mean biovolume of the stems (defined as $BV = h \times mw$) were used to assess the colonization success of *A. psilostachya*.

We evaluated the regional abiotic conditions, using 19 bioclimatic variables (BIO) recorded in and available from the WorldClim database at a 30 seconds resolution i.e., ~ 1 km² (Hijmans *et al.*, 2005). In order to use this information in a model explaining the variation of cover and biovolume of *A. psilostachya*, we carried out a principal component analysis (PCA; data not shown) on these 19 variables (with the “ade4” package; Dray *et al.*, 2007) with the aim of obtaining a reduced number of orthogonal factors. The first two components of the PCA were retained, accounting for 60.3 % and 28.0 % of the variance, respectively. The first principal component was linked to precipitation levels during wet periods

(BIO13: precipitation during the wettest month; BIO14: precipitation during the three wettest months) and mean and minimum temperatures (BIO1: annual mean temperature; BIO5: minimum temperature of the coldest month) and contrasts the most thermomediterranean zones (*Var département*), which have minimum and mean temperatures of 3.2°C and 14.5°C, respectively, with medioeuropean zones (*Marne département*), which have minimum and mean temperatures of -1.1°C and 9.8°C, respectively. The second principal component essentially related to daily and seasonal temperature ranges (BIO2: diurnal difference between maximum and minimum temperatures, BIO4: temperature seasonality), contrasting the sites nearest the coast with the most continental sites. The coordinates of the sites with respect to these two PCA axes were retained as climatic variables. The synthetic variable corresponding to the first principal component is referred to hereafter as “Precipitation” (or “Prec” for short) and that corresponding to the second principal component is referred to as “Thermal amplitude” (“Th. Amp.”). The local abiotic conditions (at the site concerned) were assessed with the Ellenberg indicators of soil humidity (Ellenberg-He) and nutrient richness (Ellenberg-N), as adapted for France in Baseflor (Julve, 1998). The mean values of these indicators, weighted for the percentage cover of each species (except *A. psilostachya*), were calculated for each set of measurements. The lifeform (Raunkiaer, 1934) of each species was determined, making it possible to determine the percentage of annual species for each community, as an indicator of environmental disturbance.

To estimate the functional distances between *A. psilostachya* and each of the other species, we carried out a principal component analysis of the variation of the following traits: maximum height (Hm), thousand-seed weight (SW), specific leaf area (SLA) and start of flowering (SF), representative of the position of the species on gradients of disturbance and fertility (Grime, 1974; Westoby, 1998). Maximum height (Hm) was extracted from Tison & de Foucault (2014), mean thousand-seed weight (SW) was obtained from the Seed Information Database (Royal Botanic Gardens Kew, 2015), specific leaf area (SLA) was obtained from the LEDA database (Kleyer *et al.*, 2008) and the date of the start of the flowering seasons was extracted from the Baseflor database (Julve, 1998). Phanerophytes (essentially shrubs and trees) were excluded from this analysis because they occurred as juveniles with traits values (height, SLA) strongly differing from mean traits values available in databases. The first two axes of the PCA based on functional traits accounted for 62.15 % of the variation. The first axis (38.24 %) expressed a gradient positively correlated with plant height (0.77) and the beginning of the flowering period (0.75) and negatively correlated with specific leaf area (-0.48). Axis 2 was positively correlated with thousand-seed weight (0.92). The Euclidian distance between each species on the first two PCA axes defined their functional distance. Then, for each studied plots, the functional distance of *A. psilostachya* to each co-occurring species was weighted by the percentage cover of those latter to define the mean functional distance of *A. psilostachya* to the community.

RELATIONSHIP BETWEEN ABUNDANCE AND BIODIVERSITY

We used a hierarchical sampling protocol (Gooden *et al.*, 2009; Ramula & Pihlaja, 2012; Fried *et al.*, 2014) to investigate the diversity and structure of plant communities as a function of the percentage ground cover by *A. psilostachya* and habitat type, at the ‘Domaine du Petit Saint-Jean’ (Saint-Laurent-d’Aigouze, Gard *département*; 43.63° N – 4.19° E), in an area representative of *A. psilostachya* infestation in Camargue, mainly in semi-natural habitats (sandy grasslands) and secondary successions after vineyards abandonment. The three principal types of habitat invaded by *A. psilostachya* were i) grassland of sandy pine forests clearings (or sandy grassland for short), ii) subhalophile grassland, iii) wasteland. We obtained 30 sets of measurements for each of these types of habitat, as described above, encompassing a range of plant cover percentages for *A. psilostachya* of 0 to 80 % (median = 26.5, mean = 24.0), reflecting the invasion of the site by this species. The effects of other dominant species were taken into account by classifying quadrats retrospectively into three categories: i) ragweed-dominated (maximum cover by this species at least 10 % higher than that for the second most abundant species); ii) ragweed-codominated (difference in cover between ragweed and the resident dominant species between -10 % and +10 %) and iii) other species-dominated (ragweed cover at least 10 % lower than that of the resident dominant species).

STATISTICAL ANALYSIS

We evaluated the habitat preference of *A. psilostachya*, by analysing percentage cover by this species for each of the major habitats of the EUNIS classification, in Kruskal-Wallis tests. Post-hoc tests were then carried out to determine which habitats displayed significantly different levels of cover.

The data for *A. psilostachya* cover and biovolume were subjected to logarithmic transformation and then analysed with a mixed linear regression model (lmer function of the “lme4” package (Bates *et al.*, 2014)). As several sets of measurements were obtained from the same town or village in some cases, the samples were not completely independent (pseudoreplicates). We therefore considered these localities (Loc) as a random effect in the model. The variables Prec., Th. Amp., Ellenberg-He, Ellenberg-N, proportion of therophytes (essentially annuals) and functional distance were considered to be fixed factors. The model can be expressed as follows:

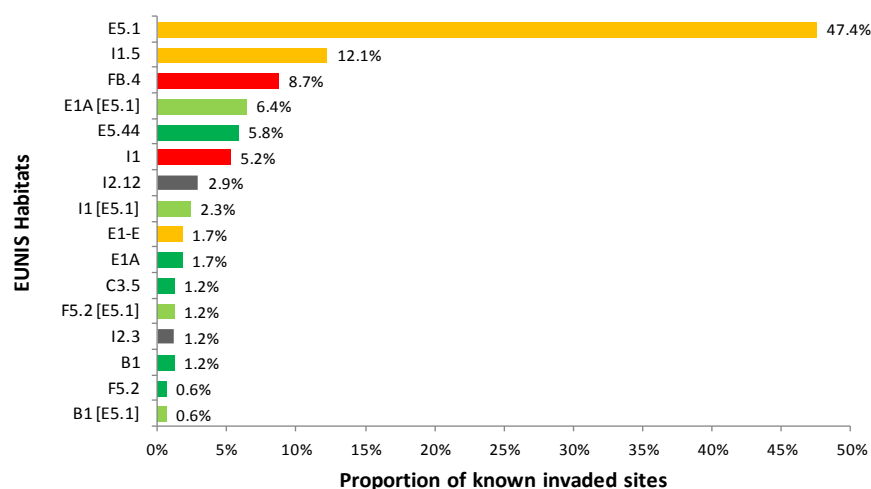
$$\text{Resp. var.} \sim \text{Prec.} + \text{Th. Amp.} + \text{Ellenberg-He} + \text{Ellenberg-N} + \% \text{therophytes} + \text{functional distance} + (1|\text{Loc}) + \epsilon$$

Likelihood-ratio tests based on the Chi2 distribution were used to evaluate the significance of the additional effect of each variable in the models after first including all other variables (i.e. type III analysis of deviance). We applied sum to zero contrasts before fitting models. We evaluated the relative importance of the various parameters of the model by variance partitioning analysis (with the hier.part package of R software; MacNally, 2000).

We investigated the possible impact of *A. psilostachya* invasion with mixed linear models to analyse the relationship between *A. psilostachya* cover and plant community structure. Ragweed cover and the three types of habitat were considered to be fixed factors, whereas dominance status (dominant, codominant, non-dominant) was considered to be a random factor. The dependent variables were the diversity indices (species richness (S), Shannon's diversity index (H')), Piélou equitability (J') and total plant cover (Cover):

$$\text{Dependent variable} \sim \text{Cover} * \text{Habitat} + (1|\text{Dominance}) + \epsilon$$

Species richness and total plant cover were subjected to logarithmic transformation and the Piélou equitability index was subjected to arcsine transformation to satisfy the conditions for regression analysis (normal distribution of the residuals). The variables for which an effect of *A. psilostachya* cover was detected were subjected to an additional analysis, with the aim of identifying thresholds beyond which ragweed cover had a stronger impact on the structure of plant communities. These analyses were based on the construction of trees by conditional inference approaches (Hothorn *et al.*, 2006, ctree function of the party package). The trees were constructed solely as a function of *A. psilostachya* cover or as a function of habitat type and dominance status. All statistical analyses were carried out with R software (version 3.1.1).



- : FB.4, I1 - cultivated environments
- : E5.1, I1.5, E1-E - habitats under strong anthropic influence
- : I1[E5.1], F5.2[E5.1], B1[E5.1] - semi-natural habitats in various stages of degradation
- : E5.44, EA1, C3.5, B1, F5.2 - semi-natural habitats displaying little or no degradation
- : I2.12, I2.3 - habitats in which *A. psilostachya* has been cultivated (botanic gardens)

Figure 1.— Relative frequencies of the principal EUNIS habitats colonised by *Ambrosia psilostachya* in France (based on $N = 172$ sites including 106 herbarium data and 66 field observations). The EUNIS habitats codes that are followed by [E5.1] correspond to sites where a semi-natural habitat was degraded favouring ruderal species typical of anthropogenic herb stands (E5.1) but showing still the main features of the original habitat.

RESULTS

DISTRIBUTION AND ABUNDANCE OF *A. PSILOSTACHYA* IN THE MAJOR HABITAT TYPES

Ambrosia psilostachya was identified in 12 different types of EUNIS habitats covering four of the eight level 1 units: coastal habitats (B), inland surface waters (C), grasslands (E) and regularly or recently cultivated agricultural, horticultural and domestic habitats (I). The distribution of sites at which *A. psilostachya* was detected between habitat types (Fig.1) indicated a clear predominance (47.1 %) in anthropogenic herb stands (E5.1), including the grass verges alongside roads (70 %), urban wasteland (26 %) and field margins (4 %). Fallows or recently abandoned arable lands (I1.5) were the second most frequently invaded habitats (12.1 %), followed by vineyards (FB.4: 8.6 %). This plant was also present in open Mediterranean dry

[sandy] grasslands (E1.A), which were often degraded (6.3 %), Mediterranean grasslands on alluvial river banks dominated by *Elytrigia* spp.(E5.44: 5.7 %) and arable land and market gardens (I1: 5.2 %). Other habitats including coastal dunes and sandy shores (B1), periodically inundated shores with pioneer and ephemeral vegetation (C3.5) and scrubland vegetation (maquis) (F5.2) accounted for less than 5 % of the infested sites.

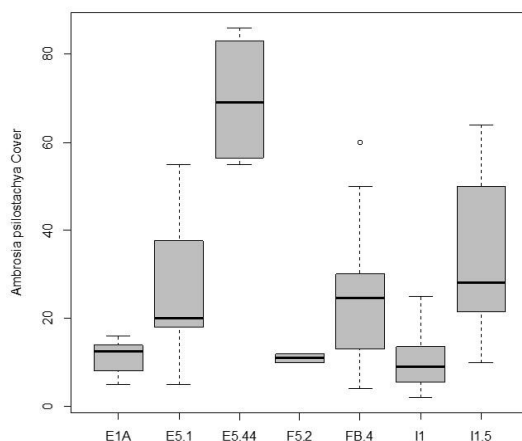


Figure 2.— Median *A. psilostachya* cover for the seven principal habitats occupied by this species ($N=48$ sites). E1A: open Mediterranean dry [sandy] grasslands; E5.1: anthropogenic herb stands; E5.44: Mediterranean grasslands on alluvial river banks dominated by *Elytrigia campestris*; F5.2: scrubland vegetation (maquis); FB.4: vineyards and olive groves; I1: arable land and market gardens; I1.5: fallow or recently abandoned arable land.

The species most frequently co-occurring with *A. psilostachya* were *Cynodon dactylon* (48 %), *Lolium perenne* (35 %), *Avena barbata* (31 %), *Crepis foetida* (31 %), *Elytrigia campestris* (29 %), *Plantago lanceolata* (29 %), *Chenopodium album* (25 %), *Chondrilla juncea* (25 %), *Anisantha diandra* (23 %) and *Bromus hordeaceus* (23 %).

The percentage cover of *A. psilostachya* cover differed considerably between habitats (Fig. 2, Kruskal-Wallis test, KW chi-squared = 22.180, $df = 6$, p -value = 0.001). The median percentage *A. psilostachya* cover was significantly higher in grasslands dominated by *Elytrigia campestris* (E5.44: 69 %) than in dry grasslands (E1A: 12.5 %) and crops (I1: 9 %). Anthropogenic herb stands (E5.1: 20 %) and habitats associated with perennial crops (FB.4 vineyards and olive groves: 24.5 %) and fallows (I1.5: 28 %) displayed intermediate, more variable levels of cover.

RESPONSES TO ABIOTIC AND BIOTIC FACTORS

The linear mixed model indicated that *A. psilostachya* cover varied significantly with the functional distance to the co-occurring species, the proportion of annual species in the community and thermal amplitude (Tab. I). Variance partitioning analysis (Fig. 3a) indicated that functional distance independently accounted for 33.3 % of the variance, versus 27.8 % and 18.4 % for thermal amplitude and the proportion of annuals in the plant community, respectively. Water-related factors (rain, water reserves) had no effect on *A. psilostachya* cover (Fig. 3a). The

biovolume depended on the nitrogen content of the environment, precipitation and temperature levels (Prec.), and the proportion of annuals in the plant community (Tab. I).

TABLE I.

Mixed-models of the effects of abiotic and biotic factors determining *A. psilostachya* cover and biovolume based on N=48 sites. Statistical significance is indicated by asterisks: * $P < 0.05$, with significant values in bold.

Dependent variables	Explanatory variables	Estimate	Std. Error	Chi ²	P(> z)	
<i>A. psilostachya</i> Cover	Th. Amp.¹	-3.459	2.239	3.933	0.047	*
	Prec. ²	0.424	1.633	0.059	0.808	ns
	Ellenberg-He	-0.031	3.192	0.009	0.921	ns
	Ellenberg-N	4.514	3.493	2.157	0.142	ns
	%Therophytes	-0.271	0.128	4.925	0.026	*
	Functional distance	15.130	5.604	6.094	0.014	*
Biovolume of <i>A. psilostachya</i>	Th. Amp. ¹	-0.043	0.117	0.079	0.779	ns
	Prec.²	0.221	0.098	3.927	0.047	*
	Ellenberg-He	-0.094	0.129	1.398	0.237	ns
	Ellenberg-N	0.453	0.136	6.070	0.014	*
	%Therophytes	-0.012	0.005	4.657	0.031	*
	Functional distance	0.420	0.241	3.523	0.061	ns

¹ The thermal amplitude variable (Th. Amp.) increases with the monthly mean difference in temperature between the day and the night (BIO2) and with the mean standard deviation of mean monthly temperature (BIO4).

² The variable Precipitation (Prec.) is linked to precipitation levels during the wettest periods (BIO13: precipitation during the wettest month; BIO14: precipitation during the wettest three-month period) and mean and minimum temperatures (BIO1: mean annual temperature, BIO5: minimum temperature for the coldest month).

TABLE II

Mixed-models of the effects of *A. psilostachya* cover and habitat type on species richness (*S*), Shannon's diversity (*H'*), species evenness (*J*) and total vegetation cover of the invaded communities based on 90 plots. Significant factors are indicated in bold

Dependent variables	Explanatory variables	Chi ²	df	P(>Chi ²)
<i>S</i>	Cover	1.813	1	0.176
	Habitat	4.750	2	0.093
	Cover:Habitat	2.973	2	0.226
	Dominance		2	1
<i>H'</i>	Cover	0.104	1	0.746
	Habitat	3.480	2	0.176
	Cover:Habitat	0.042	2	0.979
	Dominance		2	<0.001
<i>J</i>	Cover	2.537	1	0.111
	Habitat	5.420	2	0.066
	Dominance		2	0.288
Total Vegetation Cover	Cover	11.348	1	<0.001
	Habitat	12.151	2	0.002
	Cover:Habitat	5.185	2	0.075
	Dominance		2	<0.001

Variance partitioning analysis indicated that the richness of the environment in nutrients (33.8 %) and climatic conditions relating to precipitation and temperature (23.4 %) significantly and independently accounted for the variation of biovolume (Fig. 3b).

The mean height of *A. psilostachya* was significantly correlated with the mean height of the plant community ($\rho=0.560$, $P < 0.001$), but *A. psilostachya* was generally shorter (mean difference = - 6.8 cm +/- 14.0). Finally, the height of *A. psilostachya* plants was strongly correlated with the nutrient content of the environment (Spearman's rank correlation analysis; $\rho=0.354$, $P=0.015$), whereas no such correlation was observed for the mean height of the vegetation sampled ($r = 0.217$, $P = 0.138$).

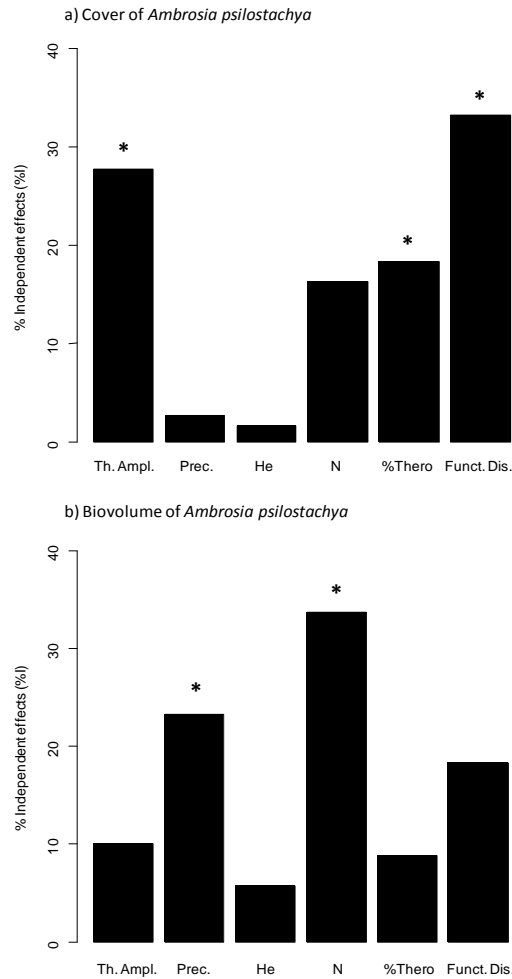


Figure 3.— The independent contributions (given as the percentage of the total explained variance) of each predictor variable estimated from hierarchical partitioning for *A. psilostachya* (a) cover, (b) biovolume. Variables marked with an asterisk independently explained a greater proportion of variance than would be expected by chance (with $P < 0.05$ level).

Th. Ampl.=Thermal amplitude, Prec.=Precipitation, He=mean cover-weighted Ellenberg score for edaphic moisture, N=mean cover-weighted Ellenberg score for soil nutrient richness, %Thero=proportion of therophytes in the community, Funct. Dis.= mean functional distance between *A. psilostachya* and co-occurring species.

IMPACT ON PLANT COMMUNITIES

The linear mixed models revealed no effect of *A. psilostachya* cover on species richness, Shannon diversity index or equitability. By contrast, *A. psilostachya* cover was correlated with total plant cover, which was also dependent on habitat type (Tab. II). The regression trees (Fig. 4a) indicated a threshold effect at 14% *A. psilostachya* cover. Beyond this threshold, total plant cover was lower with respect to *A. psilostachya* cover (Fig. 5).

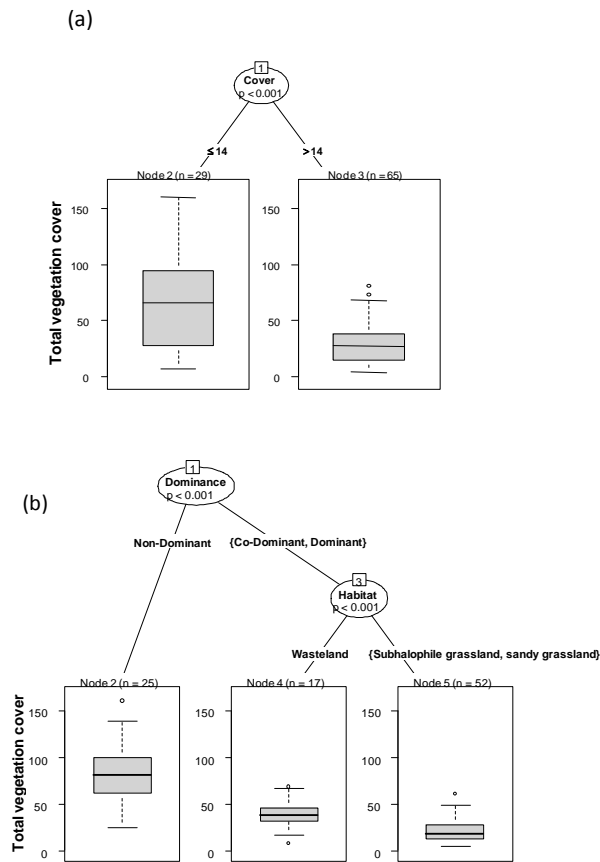


Figure 4.— Conditional inference tree describing the effects of a) *A. psilostachya* cover and b) *A. psilostachya* dominance status and habitat type on total vegetation cover. Inner nodes (ovals) indicate which variables were used for splitting and threshold values are given on the line; n is the number of plots falling in each terminal node; the box plots show the distribution of total vegetation cover.

However, the changes in community structure were better explained by dominance status and type of habitat when these variables were included in the tree (Fig. 4b). Total cover was greater when *A. psilostachya* was not dominant and lower on subhalophile grasslands and on sandy grasslands than on wastelands when *A. psilostachya* was dominant or codominant.

DISCUSSION

The objective of this study was to improve our understanding of the ecology of *A. psilostachya*, to determine the extent to which this species of unknown invasiveness potential in France is dependent on anthropic habitats or habitats degraded by human activity. We also estimated its impact on natural plant communities as a function of colonisation levels.

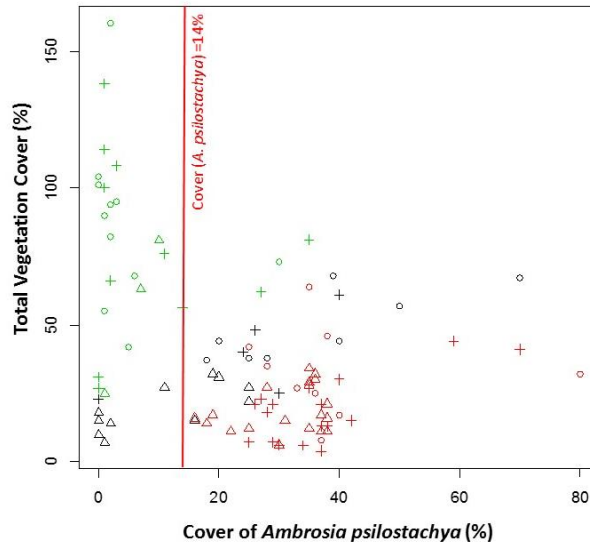


Figure 5.— Total plant cover as a function of *Ambrosia psilostachya* cover in three different habitats (N=90 plots). Green: quadrats in which *A. psilostachya* was not dominant; black: quadrats in which *A. psilostachya* was codominant; red: quadrats in which *A. psilostachya* was dominant; circle= wasteland, cross = sandy grassland, triangle= coastal grassland.

The habitats occupied by *A. psilostachya* clearly indicate that this plant is a ruderal species. The principal habitats colonized are strongly disturbed by human influence (roadside verges, wasteland, crops), such habitats accounting for 75 % of the known infested sites (Fig. 1). These habitats presumably correspond to zones of introduction (although no clear information about the vectors of introduction were available for the studied sites) from which *A. psilostachya* seems to be able to spread to semi-natural habitats — sandy grasslands, dunes, the edges of scrubland, the grasslands occupying river floodplains — some of which (10.5 %) correspond to plant communities subject to little disturbance (Fig. 1). This distribution is consistent with the behaviour of an opportunist species taking advantage of disturbances to establish itself (Didham *et al.*, 2007). Based on what we know about the optimal habitat for this species and the ecological indications provided by identification of the species most frequently growing alongside it, *A. psilostachya* seems to be a characteristic species of the pioneer flora of disturbed wasteland; this pioneer flora includes plants with various lifeforms, from annuals to perennials, subnitrophytes, and Mediterranean to submediterranean plants (*Elytrigietalia intermedio – repentis*, *Brometalia rubenti – tectorum* communities).

Populations of *A. psilostachya* were less abundant in stable environments with high levels of abiotic stress (sandy grasslands, dunes) or man-made environments with high disturbance (crops), than in habitats with intermediate levels of disturbance well supplied with nutrients (ruderal habitats, perennial crops, wasteland, *Elytrigia campestris*-dominated grassland). *Ambrosia psilostachya* thus seems to prefer intermediate levels of disturbance. Unlike annual species of the genus *Ambrosia* (*A. artemisiifolia* and *A. trifida*), which prefer environments with high levels of soil disturbance (Maryushkina, 1991; Chauvel *et al.*, 2006), the thin rhizomes of *A. psilostachya* do not seem to tolerate deep soil cultivation. This limits the presence of this plant to crop margins and vine rows, where cultivation is more superficial. Given the mechanical and chemical weed

control methods currently used, *A. psilostachya* does not seem to be a major weed of crop habitats. The lower levels of success observed for this species in the driest Mediterranean environments (sandy grasslands, dunes, scrubland) are consistent with American observations that *A. psilostachya* is unable to survive severe drought (Pavek, 1992).

The ecological positions of the two species *A. psilostachya* and *A. artemisiifolia*, on the edges of roads and rivers, confirm their different responses to the level of soil disturbance. The annual *A. artemisiifolia* occupies the verges immediately adjacent to the road, whereas *A. psilostachya* preferentially colonizes the less disturbed grass verge (or embankment). Similarly, alongside rivers, *A. artemisiifolia* occupies the banks emerging from the river, as part of the community of annual species subjected to the direct effects of floods. By contrast, *A. psilostachya* occupies the higher, less disturbed terraces with a denser vegetation (*Elytrigia*-dominated grasslands). This suggests that *A. psilostachya* could belong to a more ‘late-successional’ phasis within the pioneer stage.

Ambrosia psilostachya cover and biovolume respond to abiotic (climate, soil, disturbances) and biotic (functional distance to other plant species present in the community) factors. The response to macroclimatic factors seems to indicate better success in coastal conditions or in areas subject to oceanic influence (small diurnal and seasonal thermal amplitudes, high levels of precipitation in the wettest month) and in the warmest conditions (high mean minimal and annual temperatures). Biovolume seems to respond more strongly to precipitation regime (Fig. 3b). The rhizomes responsible for ensuring the survival of the species during unfavourable conditions are reputed to be cold-resistant (Afonin *et al.*, 2008). Nevertheless, the date on which suckers emerge and their growth rate may be strongly influenced by temperature at the end of winter. In continental conditions, the suckers do not emerge until May (Bassett & Crompton, 1975; Afonin *et al.*, 2008), whereas they begin to develop in February in the Mediterranean coastal zone (Fried, personal communication). This difference in the timing of sucker production may enable *A. psilostachya* to take advantage over the other species and may lead to increasing differences in cover and biovolume at the end of the season. It was not possible to include infestation sites from the entire distribution zone of *A. psilostachya* in France in this preliminary study. Nevertheless, the trends revealed in this study confirm the available data. Atlantic coastal region sites (*départements* of Landes, Manche, Loire-Atlantique, Pas-de-Calais) appeared to be stable, whereas several sites in regions with a continental climate around Lyon (J.-M. Tison, personal communication) and Strasbourg (H. Tinguay, personal communication) appeared to be highly unstable.

The inverse relationship between *A. psilostachya* cover and biovolume on the one hand, and the proportion of annuals in the community on the other, confirms the poorer success of this species in highly disturbed crop environments or recently disturbed environments in other contexts. In the most stable environments, the success of *A. psilostachya*, particularly when assessed by measuring biovolume, responds strongly to the fertility of the site, as assessed with the Ellenberg-N index. Given that the mean height of the dominant species of the communities sampled does not respond to soil fertility, *A. psilostachya* may be considered to display greater plasticity than its principal competitors, a potential advantage in favourable conditions (a ‘master-of-some’ species; Richards *et al.* 2006). Such opportunist behaviour is also observed in American prairies, in which ragweed is the first species to recolonize sites subjected to drought once water becomes available again (Reece *et al.*, 2004). This point out the ‘R-C’ strategy of this species rather than a ‘R-R’ strategy according to the Grime’s terminology.

In this study, we found that, in habitats subject to little disturbance, *A. psilostachya* was more successful when it occurred together with functionally distant species in terms of height, leaf specific area, thousand-seed weight and flowering phenology. These findings are consistent with those of similar studies on other invasive plant species (Diez *et al.*, 2008; Godoy *et al.*, 2011). This may be due to weaker biotic interactions (lower probability of being attacked by the same natural

enemies) and the use of different resource exploitation strategies. The species functionally most distant from *A. psilostachya* include spring annuals (*Anisantha sterilis*, *Medicago lupulina*) and, to a lesser extent, summer annuals (*Xanthium orientale* subsp. *italicum*) and biannual hemicryptophytes (plants budding at or near the soil; *Chondrilla juncea*, *Erigeron sumatrensis*). By contrast, the species functionally closest to *A. psilostachya* include perennial grasses with rhizomes (*Brachypodium phoenicioides*, *Poa trivialis*, *Elytrigia campestris*), hemicryptophytes (*Galium corrudifolium*) and chaemophytes (woody plants with perennating buds close to the soil; e.g. *Helichrysum stoechas*). Given the growth phenology and mode of resource acquisition of these plants, competitive interactions with *A. psilostachya* are probably stronger for the second group. The better colonization success of *A. psilostachya* in communities of functionally distant species can therefore be interpreted as a preferential exploitation of empty ecological niches (Maillet & Lopez Garcia, 2004) or of less exploited niches.

It has been shown that invasive species with very high percentage cover over large areas modify the communities and ecosystems that they invade (*Fallopia japonica*; Maurel *et al.*, 2010). Nevertheless, the impact of invasive species is more frequently assumed than demonstrated (Hulme *et al.*, 2013), particularly for emerging species. Here, we report that *A. psilostachya* had no effect on the structure of the plant communities invaded; this contrasts with other alien invading species with rhizomes that have been shown to form dense colonies (*Artemisia verlotiorum*, *Solidago gigantea*; Hejda *et al.*, 2009; Fried *et al.*, 2014). The absence of impacts on community diversity may be explained by the mean *A. psilostachya* cover of 25 % observed, with fewer than 10 % of sites presenting values of more than 60 % for *A. psilostachya* cover. The threshold of 14 % cover of *A. psilostachya* beyond which the total vegetation cover was found to be lower cannot be easily interpreted. This value seems too low to correspond to an impact threshold associated with the effect of interspecific competition (Thiele *et al.*, 2010). If related to the opportunistic strategy of *A. psilostachya* highlighted in the previous results, the correlation between total vegetation cover and *A. psilostachya* dominance status (Fig. 4b) may rather be explained by its preferential colonization of recently disturbed sites where vegetation cover has been reduced (Reece *et al.*, 2004). The fact that invaded communities were already impoverished by previous disturbances may also explain the absence of observed impact on community diversity.

However, as *A. psilostachya* has been present at the study sites only since the middle of the 1990s, the full consequences of its presence for plant communities may not yet be measurable, as suggested by the notion of “extinction debt” (Essl *et al.*, 2011).

The results of this study are consistent with those reported for the Great Plains of North America, where high densities of *A. psilostachya*, which is considered to be a native species undergoing range extension, are observed (Crawford & Hoagland, 2009). This plant is generally considered to be a weed, due to its deleterious effects on forage (McCarty & Scifres, 1972), although its presence has positive effects on the bird fauna (Peoples *et al.*, 1994). In these grassland environments, which may correspond to the native zones of the species, *A. psilostachya* seems to be favoured by overgrazing (excessively high herd sizes, together with long periods of use as pasture). This species thus appears to be favoured by intermediate levels of disturbance. Vermeire & Gillen (2000) and Reece *et al.* (2004) have shown that *A. psilostachya* does not appear to be particularly aggressive towards the existing plant communities; however, in cases of major disturbance (overgrazing, Berg *et al.*, 1997; microdisturbances, drought, Dahl *et al.*, 1989), its tolerance and more rapid recovery allow it to become dominant within the plant community, leading to major losses of forage productivity (Vermeire & Gillen, 2000). This raises questions about whether, in some of the environments studied in France, the high densities of *A. psilostachya* accompanied by low cover levels for other plant species observed may be a consequence of previous events that have weakened the community, rather than competition by *A. psilostachya*, with this species displaying the characteristics of a “passenger” species (MacDougall &

Turkington, 2005). This would also account for the high densities of this plant observed on a few overgrazed prairies in Camargue (G. Fried, personal communication).

CONCLUSIONS

Current knowledge suggests that *A. psilostachya* may be considered to be spreading in mainland France. The observed densities are not yet high enough to be implicated in the general pollen allergy problems known to be caused by current populations of *A. artemisiifolia* in the Rhône Valley. However, the pollen produced by *A. psilostachya* could potentially contribute to these allergies by prolonging the presence of pollen in the air, and its effects on health might be aggravated by climate change (Wan *et al.*, 2002). Ecological data on *A. psilostachya* are very rare in France and in Europe and our data show that the species seems to be having presently a weak immediate impact on the diversity of plant communities. Nevertheless, this perennial species may be more problematic in communities rendered fragile by increasingly frequent climatic incidents, by poor pasture management or by efforts to restore environments degraded by human activities. *Ambrosia psilostachya* provides an interesting example of an emerging species, which, at this stage of invasion, has no identifiable effect on biodiversity, occupies a separate ecological niche and for which the need for intervention is debatable. Preventive action would nevertheless appear necessary to prevent the promotion of its development in the Camargue and to prevent its dispersal by soil-based transport, which would facilitate the spread of rhizomes to new sites.

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