



Comparing an exotic shrub's impact with that of a native life form analogue: *Baccharis halimifolia* L. vs *Tamarix gallica* L. in Mediterranean salt marsh communities

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Keywords

Biotic resistance; Impact thresholds; Nestedness; Risk assessment; Shrub invasion; Species richness; Species turnover; Vegetation cover

Nomenclature

Tison & de Foucault (2014) for vascular plants, Julve (<http://philippe.julve.pagesperso-orange.fr/catminat.htm>, Accessed 6 July 2015) for plant communities

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Abstract

Questions: To what extent may impact vary according to the invaded community, region or sites? Do impact thresholds exist, above which native species richness and/or cover declines rapidly? Does impact following invasion by the exotic shrub *Baccharis halimifolia* differ from that of a native shrub (*Tamarix gallica*) during natural successions?

Location: Mediterranean coast, SE France.

Methods: Vegetation was sampled on 120 4-m² quadrats, half of which were in areas invaded by *B. halimifolia* and the other half in nearby non-invaded areas, in two distinct community types nested in three sites in each of two regions. Mixed models were built to explain variations in impacts on native vegetation according to community types, sites and regions. Next, 85 additional plots variously invaded by *B. halimifolia* were used to assess the nature of the relationships between *B. halimifolia* cover and impact in *Juncus* communities. Linear regressions were compared to polynomial regressions, and when relevant, regression trees were built to identify threshold values. Finally, we compared the vegetation from 90 plots either dominated by *B. halimifolia*, by *T. gallica* (a native shrub) or without a shrub layer (control) using dissimilarity indices in wet meadows.

Results: The magnitude of *B. halimifolia* impacts depended mainly on community type, with no differences between regions. Community structure (species richness, Shannon's diversity) declined linearly with increasing cover of *B. halimifolia*, with the most rapid decline in annual species. Native species cover fitted better with a cubic regression, with an impact threshold of around 86% cover of *B. halimifolia*. Impact of *B. halimifolia* on community diversity was higher than that of the native shrub *T. gallica*. While the magnitude of species composition changes was comparable for both shrubs, the higher nestedness component of dissimilarity found for *B. halimifolia* may indicate a higher short-term impact.

Conclusion: Improved understanding of the impacts of exotic shrubs on community structure and composition can be gained via comparisons with the impacts caused by native shrubs. Higher impacts of the exotic *B. halimifolia* on Mediterranean salt marsh vegetation are likely explained by a denser canopy, shorter juvenile period and more frequent recruitment.

Introduction

Invasion ecology has long focused on the mechanisms of spread and establishment of invasive species, while their

impacts have often been assumed rather than quantified. Perhaps because of the difficulties associated with obtaining quantitative estimates of the various types of impact caused by invasive plant species (Parker et al. 1999),

researchers have generally been content to assume that if a species is capable of reaching very high levels of cover, substantial amounts of impact will occur. During the last decade a growing number of studies have measured the impacts of invasive plants (Vilà et al. 2011), but several questions remain poorly addressed. For example, how do impacts vary across sites or regions (but see Pyšek et al. 2012) and how do impacts scale with cover abundance of the invader?

Among the most significant impacts are those produced by the invasions of open habitats by exotic shrubs, which greatly modify vegetation physiognomy by adding a woody layer to herbaceous communities (Miller & Gorchoff 2004). In many vegetation types, however, natural succession from grasslands to shrublands and, eventually, to forests is also associated with decreases in species diversity (Tatoni et al. 1994; Saïd et al. 2003), raising the question as to whether the effects of invasion by exotic shrubs differ from those of natural succession. The answer depends more generally on whether these shrubs have a different effect upon community composition. Changes in species composition can result from two different phenomena: nestedness and turnover (Baselga 2010). Nestedness can occur when the species assemblages of invaded sites are subsets of the assemblages of non-invaded sites, reflecting a non-random process of species loss. This could be expected for a strong competitor that would displace the most sensitive species without being associated with other species colonizing at the same time or afterwards. Turnover implies the replacement of some species by others as a consequence of a directional environmental filtering, such as vegetation succession, or spatial and historical constraints. For invasive plants, this could be expected when a species introduces new functional traits (Drenovsky et al. 2012), e.g. N fixation or a canopy layer that more effectively intercepts light, which can affect the direction and/or the rate of succession.

A further consideration is whether the impacts of invasive plants increase as a function of their abundance, in particular whether the relationship between invasive plant abundance and impact is sigmoid or linear (Vilà et al. 2011), and how this relationship may differ according to the identity of the resident species. The negative association between invader cover and community diversity can be explained by two contrasting concepts: post-invasion competitive displacement of resident species and biotic resistance (Thiele et al. 2010). Under the post-invasion displacement model, it is expected that low-growing and/or less competitive species will show linear rather than nonlinear responses, i.e. the invader will have an impact even at low cover. Where resident

species are stronger competitors, such biotic resistance may result in nonlinear responses to invader abundance, with impact detectable only at higher levels of invader cover.

In this study, we investigated the effects of *Baccharis halimifolia*, a North American shrub invading European coastal salt marshes (Caño et al. 2014; Fried et al. 2014), comparing its impacts with those of the native Mediterranean *Tamarix gallica*. The latter species, whose ecological niche partially overlaps that of *B. halimifolia*, forms shrublands that are considered as the climax vegetation in parts of the salt marshes where salinity is low and flooding is frequent (Mesléard et al. 1991). The present study addresses more specifically the following questions: (1) how do *B. halimifolia* impacts vary across space and what is the relative importance of the identity of the invaded community, sites and regions in these variations; (2) how do impacts scale with cover abundance of *B. halimifolia*, is it possible to identify thresholds for impact, and how might these relationships differ according to the life forms of affected species; and (3) do the impacts of *B. halimifolia* differ from those of a native shrub in communities where the latter is considered as the dominant species in the climax stage?

Methods

Study species

Baccharis halimifolia is a dioecious shrub growing up to 4 m high. Native to North America, it has been introduced as an ornamental in several parts of the world, including Asia, Australia and Western Europe (mainly in N Spain and W and S France). The species reproduces mainly by seed; shrubs are mature within 2 yr, flower every year and are highly fecund (Panetta 1979), producing seed dispersed by wind, but also by water. *B. halimifolia* colonizes a wide range of open disturbed habitats (roadsides, wastelands), but concerns about this species are based on its ability to invade coastal wetlands, often in protected natural areas (Caño et al. 2013).

Tamarix gallica is an evergreen shrub of 1–6 m in height, native to the western part of the Mediterranean (France, Spain). It reproduces both by vegetative means (root suckers and resprouting at the base of the stem) and by seed. Compared to *B. halimifolia*, estimation of maximum seed production per individual is lower (600 000 against 1 500 000), sexual maturity is reached later (from 3 yr onwards), and above all, seeds are viable only for 2 months (Willm et al. 2012). This strongly reduces seedling recruitment and prevents the formation of a viable seed bank, in contrast to *B. halimifolia* (Panetta 1979). In its native range, *T. gallica* can become dominant, with 80–100% cover, and forms shrubby woodland in temporarily flooded

and moderately saline wetlands, where it is considered as the climax stage (*Tamaricetum gallicae*).

Study sites and dynamics of studied communities

We studied the invasion of *B. halimifolia* in Mediterranean salt marshes of the SE coast of France, where it has mainly spread in two distinct estuarine regions: Camargue, a large wetland area located in the Rhone delta, with meso-mediterranean climatic conditions, and Roussillon, a coastal region where several rivers from the Pyrenees flow into the Mediterranean Sea, in a warmer thermo-mediterranean area. For both regions, we chose one main study location (Domaine de la Palissade 43°21.734' N, 4°49.584' E, and Réserve naturelle de la Ribère 42°45.121' N, 3°01.945' E) and several sites within these locations (see below). Both locations are positioned very close to river mouths in protected natural areas integrated in the European Natura 2000 network. The Domaine de la Palissade (integrated in the FR9301592 – Camargue Natura 2000 site) occupies 702 ha on the west side of the Rhone River estuary and has been protected since 1977. *B. halimifolia* was first observed there in 1982 and started to spread in the mid-1990s (Charpentier et al. 2006). The area, including the studied sites, is grazed by horses, with low grazing pressure. The Réserve Naturelle de la Ribère (integrated in the FR9101463 - Complexe lagunaire de Salses Natura 2000 site) extends over 67 ha on the north side of the Bourdigou River, and since 1982 has no longer experienced direct disturbances. It is thought that *B. halimifolia* escaped from cultivation in this area in the early 1980s (Amigo 1983). The two regions can therefore be considered to have approximately the same history of invasion, differing only in land use (\pm grazing) and mesoclimate. In both locations, populations of *B. halimifolia* are generally scattered but locally form populations of high density over several hundred square meters.

Mediterranean coastal wetlands constitute a mosaic of habitats where successional development is strongly dependent on ecological constraints involving water and salinity (Mesléard et al. 1991). Hence, natural salt marsh communities dominated by *Juncus maritimus* (*Juncetalia maritimi*) are not dynamic and do not change along a seral vegetation succession (Braun-Blanquet et al. 1952). Locally, the salinity of the water table can decrease in sites exposed to frequent flooding resulting from rainfall. Under these circumstances, *T. gallica*, a moderately salt-tolerant species (typically on oligohaline soils with 1–5 g-NaCl·l⁻¹), can establish and progressively transform wet meadows into a shrub community. *B. halimifolia* is relatively more tolerant of salinity and occurs typically on mesohaline soils (around 10 g-NaCl·l⁻¹) but can also grow on hyperhaline soils (>23 g-NaCl·l⁻¹). It is therefore able to establish in a

wider range of communities, from non-saline riverine forests to highly saline *Sarcocornia* communities where it is more sporadic, its optimum occurring in sub-halophilous communities (Caño et al. 2013).

Vegetation surveys

During summer 2012 and 2014, vegetation surveys were performed in areas variously colonized by *B. halimifolia* or *T. gallica*. We used 4-m² plots, in which the percentage cover of every vascular plant species was measured with an approximation of $\pm 5\%$. Plot size was chosen as a compromise between a sufficiently small size to measure changes related to the presence of the invasive shrub (based on the fact that individual plants interfere with their closest neighbours) and a sufficiently large size to encompass the whole range of cover of *B. halimifolia*, from young individuals of 1–2 yr and <1 m high to mature shrubs up to 2–3-m tall. Three complementary surveys were arranged.

The aim of the first survey (S1) was to determine how the impact of *B. halimifolia* varies according to region, sites and communities. In each region, we focused on the two community types most frequently invaded by *B. halimifolia*. The first comprises the sub-halophilous *Juncetalia maritimi* communities, mainly dominated by rushes (*J. maritimus*, *J. acutus*), grasses (*Elytrigia acuta*) and sedges, but including forb species (*Iris reichenbachiana*, *Sonchus maritimus*) typical of these communities. According to the weighted means of the values of indicator species for salinity (Julve 1998), we assumed that the salinity of the studied plots in this community ranged between 7 and 12 g-NaCl·l⁻¹. This community type corresponds to the optimum for *B. halimifolia*, where it can form dense stands, while *T. gallica* is hardly found or only as scattered individuals. The second comprised small depressions that are currently occupied by a wet meadow (included in *Holoschoenetalia vulgaris*) dominated by *Phragmites australis*, *Scirpoides holoschoenus*, *Lotus jordani* and *Althaea officinalis*. The salinity in this community is assumed as lower according to Julve (1998), ranging between 1 and 8 g-NaCl·l⁻¹. *B. halimifolia* also frequently colonizes this community, and thus both shrubs can co-occur in dense thickets and likely compete for the same resources. For each community, we selected areas invaded by *B. halimifolia* and nearby (~3–5 m) non-invaded areas where *B. halimifolia* is not yet present but could establish, based on a preliminary survey designed to identify areas with similar soil and topography. We assumed that the close proximity of the plots ensured that abiotic conditions were similar and that non-invaded areas can be considered as the state of the community prior to invasion by *B. halimifolia*. For each of the two community types and each of the two regions

surveyed, 15 replications consisting of paired invaded and non-invaded plots were used with a hierarchical design, including five replications per site in three different sites ($N_{S1} = 120$ plots, two types of plot (inv. vs non-inv.) \times five replications \times three sites \times two communities \times two regions). The distances between pairs ranged between 10–80 m, while distances between sites (within a region) ranged between 400–950 m.

The second survey (S2) aimed to identify how increasing *B. halimifolia* cover affects the structure of the invaded communities; with 85 additional plots variously invaded by *B. halimifolia* (0–100% cover) investigated in *Juncetalia maritimi* communities of both regions. Plots were selected via stratified random sampling, with strata comprising *B. halimifolia* cover categories of 0–20, 20–40, 40–60, 60–80 and 80–100%.

Finally, the third survey (S3) was intended to determine more precisely the extent to which *B. halimifolia* modifies the herbaceous vegetation layer compared to natural succession with *T. gallica*. In each region, we selected 15 additional sites in wet meadows (included in *Holoschoenetalia vulgaris*) where it was possible to compare side-by-side three plots: (1) non-invaded wet meadow communities considered as control plots of open vegetation, (2) areas already colonized by *T. gallica*, and (3) areas invaded by *B. halimifolia* ($N_{S3} = 90$ plots, three types of plot \times 15 sites in two regions). The selection of the 15 sites was random based on a previous survey that identified a list of sites where open vegetation contained (outside survey plots) young individuals of *T. gallica* and *B. halimifolia*, suggesting possible colonization of the communities.

Statistical analyses

Plant community structure was characterized as species richness (S), Shannon's diversity index (H'), species evenness (J) and total cover of the herbaceous layer (Cov). The cover of species grouped in three main life forms was also distinguished: annual species, perennial graminoid species (Gram.Cov; including grasses, sedges and rushes) and perennial forb species (Forb.Cov; including all other herbs). Within the studied communities, we assume that annuals, perennial forbs and perennial graminoids represent life forms of increasing competitive ability based on mean plant height, relative proportion of Grime's CSR strategies (Grime 1977) and dominance of perennial graminoids (e.g. *J. maritimus* and *E. acuta* often reach >50% cover).

In the first study (S1), differences in plant community structure between paired invaded and non-invaded plots were analysed with Wilcoxon signed-rank tests at the level of each site ($n = 3$ sites \times 2 communities \times 2 regions = 12 sites), each based on five paired plots. Following Hulme et al. (2013), we computed the impact

frequency and reliability. Impact frequency is the proportion of cases (i.e. the 12 sites in our study) where a significant change in the response variable was found between invaded and non-invaded plots at the site scale. Impact reliability is the proportion of sites with significant changes that were in the most frequently observed direction. Since this method of computing impact reliability always led to values equal to 1 (maximum reliability), we also performed an additional calculation to provide a complementary understanding of the variation of impact direction, based on the differences at the paired plot scale ($n = 60$), although there was no possible distinction of significant changes at this scale.

Differences in S, H' , J and Cov between invaded and non-invaded plots were expressed as a relative impact (RI) with $= \frac{a_{NI} - a_I}{a_{NI} + a_I}$ where a is the variable of interest, I is the invaded plot and NI is the non-invaded plot. Differences in RI according to the identity of the community (*Juncetalia maritimi* or *Holoschoenetalia vulgaris*), the region (Camargue, Roussillon) and sites nested within regions were tested using linear mixed effect models. Community types and regions were considered as fixed factors. Sites were considered as a random factor, and *B. halimifolia* canopy cover was added as a covariate. Moreover, plots were nested within sites and sites were nested within region to account for non-independence in SE estimates. The final model was: $RI \sim$ Community type + Region + Sites nested within Region + Plot identity nested within Sites nested within Region + *B. halimifolia* cover + error. P -values for the fixed effects were calculated from F -tests based on Sattethwaite's approximation, while P -values for the random effects were derived from likelihood ratio tests based on the χ^2 distribution (i.e. type III analysis of deviance) using the R packages lme4 and lmerTest (R Foundation for Statistical Computing, Vienna, AT).

In the second study, to analyse how impacts scale with cover abundance of *B. halimifolia* and to determine impact thresholds, we followed the methodology developed in previous studies (Gooden et al. 2009; McAlpine et al. 2015). A threshold was defined as the discontinuity where the community response variable decreased dramatically with increasing invader cover. In addition to S, H' , J and Cov, we also considered cover of annual, perennial forbs and perennial graminoids, with the assumption that the latter categories are more competitive. To determine impact thresholds, we first compared linear and polynomial models using the Akaike information criterion (AIC). When the polynomial model provided the best fit (as indicated by the lowest AIC, P and residual errors, as well as the highest R^2), we consider that a threshold might exist. To confirm the thresholds, we used conditional inference trees (using the R package party), which explain variation in the response variable (native species richness or

cover) by defining a split in the data based on the predictor variable specified (*B. halimifolia* cover).

In the third study (S3), differences in the diversity and structure of the communities under *B. halimifolia*, *T. gallica* and in adjacent wet meadow communities (control) were first assessed with one-way ANOVAs. Then, in order to compare the effect of *T. gallica* or *B. halimifolia* on the structure of wet meadow communities, linear mixed models were used with differences in RI (for S, H', J, Cov, A.Cov, Forb.Cov and Gram.Cov) as the response variables. The identity of the shrub (*T. gallica*, *B. halimifolia*) and region were fixed factors, while site nested in region and plot nested within site nested within region were random factors. Since the cover of the shrub layer was partially correlated with the identity of the shrub, the cover of the shrub was added as a covariate, and we used sequential sum of squares (Type I) to account for variation due to cover before testing the effect of the shrub species identity. The final model was: RI ~ Shrub cover + Region + Identity of shrub layer (*T. gallica*, *B. halimifolia*) + Site nested within Region + Plot identity nested within Site nested within Region + error. For models in both S1 and S3 analyses, standardized residuals were checked with the Shapiro–Wilk test to check the need for transformation. Species evenness was arcsin transformed, while ForbCov and GramCov were log₁₀-transformed.

Differences in species composition were examined through calculation of the Jaccard dissimilarity index (*Jac*), including its two components: turnover (*Jtu*) and nestedness (*Jne*) using the R package betapart (Baselga & Orme 2012). For each region, Wilcoxon signed-rank tests were used to make pair-wise comparisons of the three community types in terms of dissimilarity indices (*Jtu*, *Jne* and *Jac*). All statistical analyses were performed under R (v 3.1.1).

Results

Impact frequency and influence of habitats and locations

In the first survey, we found a total of 77 species, including 24 annuals, 33 perennial forbs and 20 perennial graminoids. Only 49% of this species pool was found under *B. halimifolia* thickets, comprising 25% of the annuals, 64% of the perennial forbs and 55% of the perennial graminoids. The presence of *B. halimifolia* had significant impacts on several community characteristics (Fig. 1). The impact frequency and reliability ranged from 0.83 to 0.93 for Shannon's diversity (the most frequently and reliably affected community characteristic) to 0.42 to 0.80 for species evenness (the least frequently and reliably affected community characteristic), respectively (Table 1). The impacts of *B. halimifolia* on species richness and Shannon's diversity varied significantly according to the community

type, with higher impacts in wet depression (*Holoschoenalia vulgaris*) compared to *Juncetalia maritimi* communities (Table 1, Fig. 1). The cover of *B. halimifolia* did not differ significantly between the two communities (see Appendix S1). No significant effects were found for any of the other community features, except total vegetation cover, which varied according to sites within regions and according to *B. halimifolia* cover.

Impact thresholds

Species richness and total vegetation cover, as well as cover of different life forms, all showed negative relationships with *B. halimifolia* cover according to linear models (Appendix S2). Linear regressions provided the best models in explaining changes in species richness, Shannon's diversity and cover of annuals (Fig. 2a–c), whereas non-linear regressions were most suitable for total vegetation cover and cover of perennial species (Appendix S2), indicating potential *B. halimifolia* impact thresholds (Fig. 2d–f). With a cubic regression, 47.5% of the variation in the total herbaceous cover was explained by *B. halimifolia* cover (Appendix S2). The conditional inference trees identified a first split at 86% cover of *B. halimifolia* and a second at 23% (Fig. 2f). The cover of perennial graminoid species exhibited a comparable trend, but with a first and lower split at 3% cover of *B. halimifolia* (Fig. 2e). Quadratic regression was most suitable for explaining changes in the cover of perennial forb species, with a single split at 66% *B. halimifolia* cover (Fig. 2d).

Comparison with *T. gallica*

Baccharis halimifolia and *T. gallica* thickets both reduced species richness, cover of perennial graminoids and the total herbaceous layer cover (Fig. 3a,d,e). Only *B. halimifolia* stands significantly impacted Shannon's diversity, species evenness (Appendix S3) and perennial forb cover (Fig. 3c). Finally, *B. halimifolia* had no significant effect on the cover of annuals, while the effect of *T. gallica* was positive on these species. The comparison of RI showed that impacts were generally higher under *B. halimifolia* canopy, except for perennial graminoid and annual cover (Table 2). The mean cover of *B. halimifolia* reached a significantly higher level (93.6%, range 80–100%) than that recorded for *T. gallica* (mean 84.9%, range 70–100%; Wilcoxon test, $P < 0.001$), with especially more frequent 100% cover values (Fig. 3f). The relative impact varied significantly with shrub canopy cover, but the identity of the shrub remained significant for the same response variables, i.e. explaining remaining variations independent of canopy cover (Table 2).

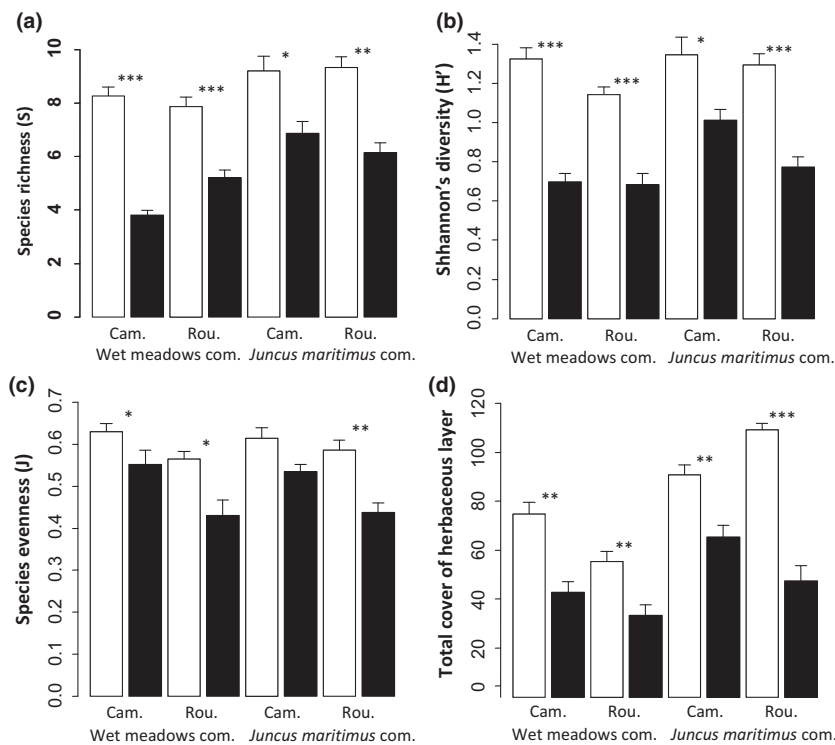


Fig. 1. Impact of *B. halimifolia* in two different communities and two different regions on (a) Species richness, (b) Shannon diversity, (c) Species evenness, (d) Total herbaceous cover. $N_{51} = 120$ paired plots. The number of asterisks (*) indicates the number of sites showing significant changes based on paired Wilcoxon tests applied on the five replicates within sites. Open and closed bars represent non-invaded and invaded plots, respectively.

Table 1. Impact frequency and reliability, and mixed models of the effects of region, community type, site and *B. halimifolia* cover on the relative impact (RI) of *B. halimifolia* on four characteristics of plant communities. Impact frequency and reliability were based on the proportion of sites ($n = 12$) with significant changes based on Wilcoxon paired tests. Impact reliability was also computed at the scale of pairs of plots ($n = 60$) without reference to statistical tests.

| RI | | Species Richness | Shannon Diversity | Species Evenness | Total herb. Cover |
|--|-----------|------------------|-------------------|------------------|-------------------|
| Impact Frequency ($n = 12$) | | 0.75 | 0.83 | 0.42 | 0.75 |
| Impact Reliability ($n = 12$) | | 1.00 | 1.00 | 1.00 | 1.00 |
| Impact Reliability ($n = 60$) | | 0.88 | 0.93 | 0.80 | 0.90 |
| Analysis of Variance (type III) | | | | | |
| Fixed Factors | <i>df</i> | <i>F</i> | <i>F</i> | <i>F</i> | <i>F</i> |
| Region | 1 | 1.00 | 1.52 | 0.70 | 0.47 |
| Community | 1 | 7.41** | 5.77* | 0.03 | 0.03 |
| Covariable | | | | | |
| Cover of <i>B. halimifolia</i> | 1 | 1.47 | 1.67 | 1.03 | 7.92** |
| Random Factor | | χ^2 | χ^2 | χ^2 | χ^2 |
| Site (nested in Region) | 2 | 0.10 | 2.22 | 2.02 | 7.55** |
| Tukey contrasts | | Estimate | Estimate | | |
| <i>J. maritimi</i> comm. – Wet meadows comm. | | -0.127** | -0.099* | | |

Statistical significance is indicated by asterisks: $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, with significant values in bold.

The PERMANOVA showed that community composition differed significantly according to region ($F = 16.85$, $r^2 = 0.13$, $P = 0.001$) and to the nature of the dominant shrub ($F = 9.59$, $r^2 = 0.15$, $P = 0.001$), with a significant

effect of the interaction of region and dominant shrub ($F = 4.62$, $r^2 = 0.07$, $P = 0.003$). All pair-wise comparisons between vegetation types within each region were significant (data not shown).

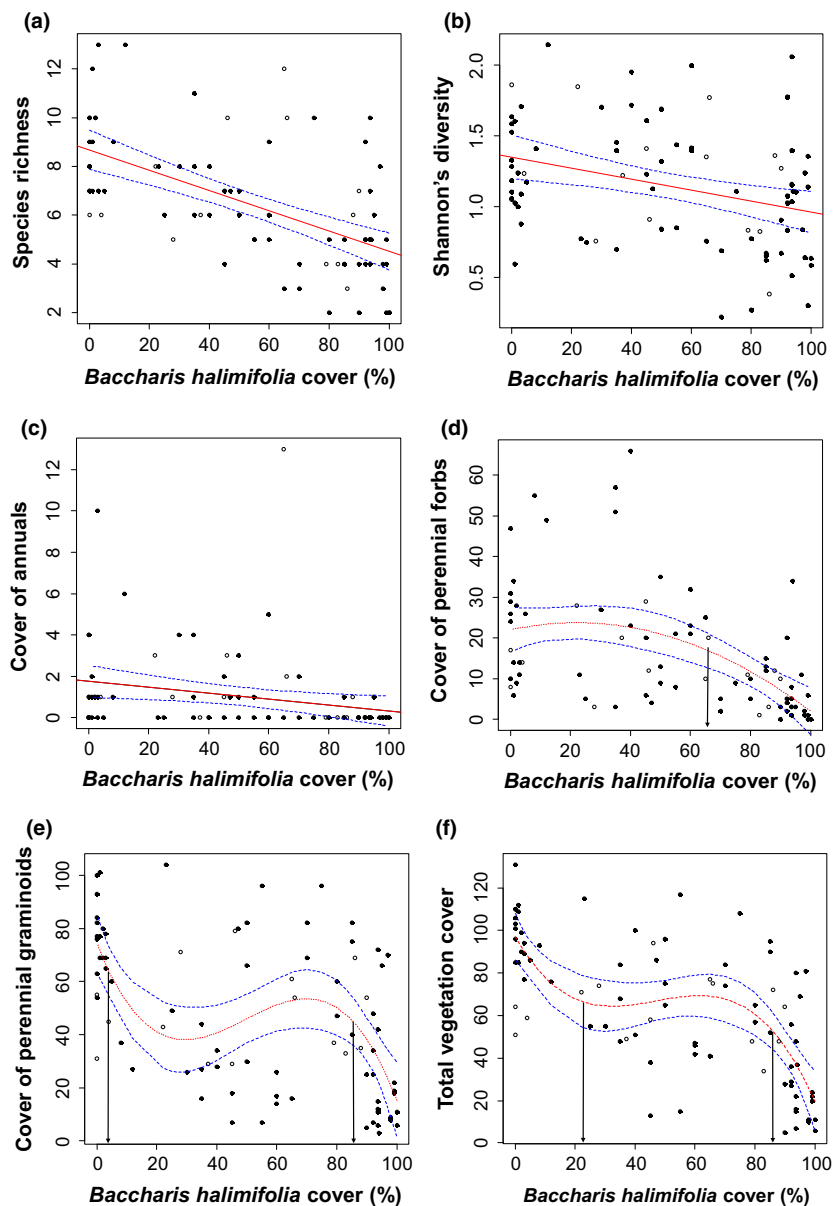


Fig. 2. Relationships between *B. halimifolia* cover (%) and community structure: (a) species richness, (b) Shannon diversity, and vegetation cover, (c) annuals, (d) perennials forbs, (e) perennial graminoids and (f) total ($n = 85$). Open and closed circles refer to Camargue and Roussillon, respectively. The external dotted lines represent the confidence intervals. Arrows indicate the location of impact thresholds as detected using conditional inference trees.

According to the Jaccard dissimilarity index, the magnitude of differences in species composition from meadows to understorey vegetation of *B. halimifolia* (0.79–0.84), or of *T. gallica* (0.76–0.86), was similar for both regions (Table 3). While the turnover component (Jtu) of dissimilarity had a larger contribution than the nestedness component (Jne) for both shrubs, the latter was significantly higher in sites invaded by *B. halimifolia* (0.26 and 0.20) compared to sites with *T. gallica* (0.04 and 0.09; Table 3).

Discussion

While the comparison of invaded and non-invaded plots is a correlative approach that does not prove impacts (Kumschick et al. 2015), the selection of invaded and nearby non-invaded plots with similar abiotic conditions (Hejda et al. 2009) makes us confident that our sampling captures the filtering effects of *B. halimifolia* on the local coastal salt marsh species pool. With this in mind, the present study demonstrates the high impact of *B. halimifolia*,

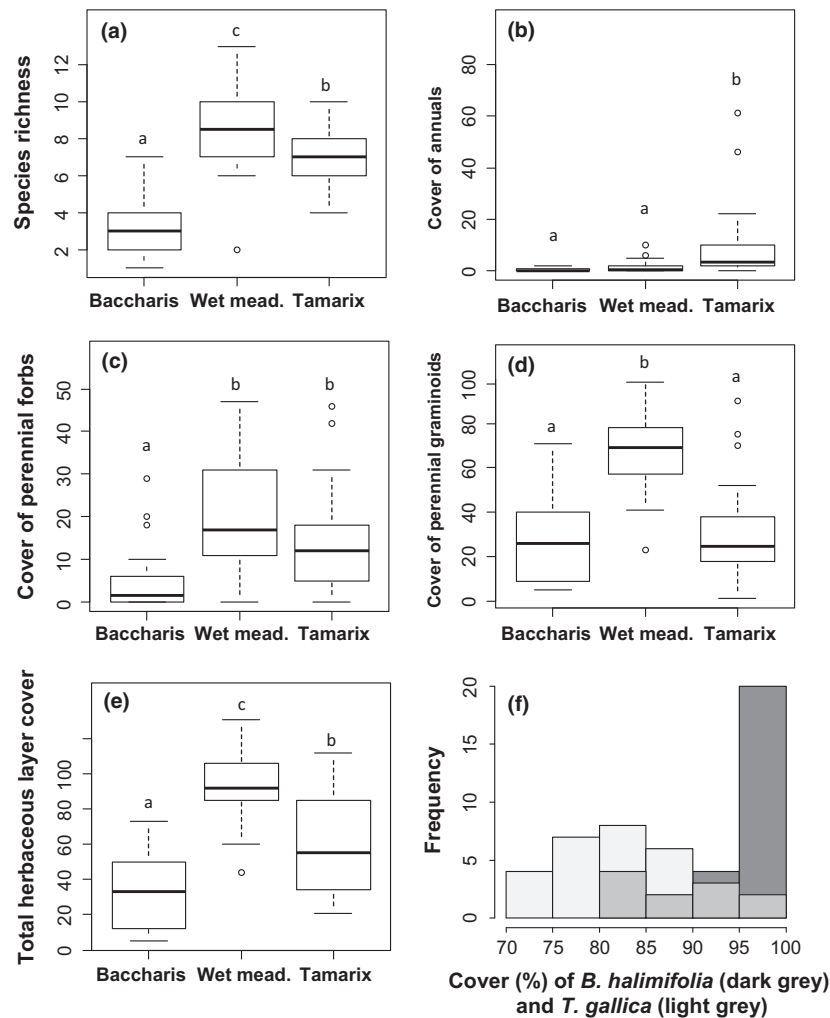


Fig. 3. Comparison of (a) species richness and (b) to (e) cover of life forms between wet meadow control plots, *B. halimifolia* and *T. gallica* thickets, and (f) the distribution of cover values of *B. halimifolia* (dark grey) and *T. gallica* (light grey), including an overlap (medium grey). Differences in one-way ANOVAs: (a) $F_{2,87} = 47.86$, $P < 0.001$; (b) $F_{2,87} = 29.14$, $P < 0.001$; (c) $F_{2,87} = 22.94$, $P < 0.001$; (d) $F_{2,87} = 25.45$, $P < 0.001$; (e) $F_{2,87} = 50.74$, $P < 0.001$. Different letters correspond to significant differences based on post-hoc Tukey tests.

Table 2. Mixed models of the effect of shrub cover, region and dominant shrub species identity (*B. halimifolia*, *T. gallica*) on the variation of species richness (S), Shannon diversity (H'), species evenness (J), total herbaceous cover (Cov), annual (A.Cov), perennial forb (Forb.Cov) and graminoid (Gram.Cov) cover with sequential sum of squares (Type I) to account for the effect of the covariate.

| | | S | H' | J | Cov | A.Cov | Forb. Cov | Gram. Cov |
|---|----|-----------------|-----------------|---------------|-----------------|-----------------|---------------|-----------|
| Covariate | df | F | F | F | F | F | F | F |
| Shrub Cover | 1 | 53.15*** | 48.96*** | 7.32** | 18.56*** | 19.64*** | 8.01** | 1.49 |
| Fixed Factors | | | | | | | | |
| Region | 1 | 0.01 | 0.52 | 2.02 | 16.19*** | 0.10 | 2.68 | 3.76 |
| Shrub Species Identity | 1 | 35.96*** | 26.88*** | 4.92* | 11.30** | 31.43*** | 6.19* | 0.30 |
| Estimates of Tukey Contrasts | | | | | | | | |
| <i>B. halimifolia</i> - <i>T. gallica</i> | | 0.23*** | 0.24*** | 0.10* | 0.21*** | -0.80*** | 0.37** | 0.03 |

Statistical significance is indicated by asterisks: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, with significant values in bold.

with on average a one-third decrease in species richness and Shannon's diversity and a ~40% decrease in vegetation cover, sometimes resulting in 4-m² invaded plots with

only two or three remaining native species. Hence, invasion by *B. halimifolia* could result in the total replacement of vegetation, as has been observed in invaded estuarine

Table 3. Magnitude of changes in species composition between wet meadows (control plots) and plots with presence of *B. halimifolia* or *T. gallica* based on the Jaccard dissimilarity index (Jac), with relative contribution of turnover (Jtu) and nestedness (Jne). For each measure of species composition change (Jac, Jtu, Jne) in each region, different letters indicate significant differences between presence of *B. halimifolia* and *T. gallica* according to Wilcoxon signed rank tests.

| Region | Camargue | | Roussillon | |
|--------|--------------------------|--------------------------|--------------------------|--------------------------|
| | <i>B. halimifolia</i> | <i>T. gallica</i> | <i>B. halimifolia</i> | <i>T. gallica</i> |
| Jac | 0.84 ± 0.13 ^a | 0.86 ± 0.11 ^a | 0.79 ± 0.08 ^a | 0.76 ± 0.12 ^a |
| Jtu | 0.57 ± 0.34 ^a | 0.82 ± 0.12 ^b | 0.60 ± 0.21 ^a | 0.68 ± 0.21 ^a |
| Jne | 0.26 ± 0.26 ^a | 0.04 ± 0.06 ^b | 0.20 ± 0.18 ^a | 0.09 ± 0.11 ^b |

communities in northern Spain, where *B. halimifolia* formed monospecific stands in ~10% of the 153 surveys where it was present (Caño et al. 2013). On the other hand, species evenness was less impacted. This could be explained by higher stability of the few dominant species (e.g. *J. maritimus* and *P. australis*), which can persist at relatively high cover under *B. halimifolia* stands, together with a few other species at very low cover, maintaining the classical log series species abundance distribution. These effects are valid over a broad range of conditions, as evidenced by high impact reliability (≥ 0.8 for all indices) and the absence of a significant region effect, meaning that the impacts of *B. halimifolia* are highly comparable in the Camargue and Roussillon.

Variations in the magnitude of impact may be explained through different responses of community types, with, for example, species richness in wet meadows on oligohaline soils (*Holoschoenetalia vulgaris*) appearing to be more impacted than in *Juncetalia maritimi* communities on mesohaline soils. While some habitats or communities are considered more vulnerable to exotic species establishment than others (Chytrý et al. 2008), our results suggest that different communities may also experience different magnitudes of impact when colonized by the same invader. Such variations could be associated with different abiotic conditions, as observed in the study of Caño et al. (2014), who found higher impact of *B. halimifolia* on native species richness in medium and high salinity community types. The opposite pattern was observed in our study, with higher impacts on communities developing on low salinity soils. This result is, however, consistent with higher cover of *B. halimifolia* on low salinity soil types (Caño et al. 2014), or a higher proportion of 100% cover in wet meadows (see Appendix S1), and a linear decrease of community diversity with increasing cover. The observed 'community effect' can also result from differences in the resident community composition or in functional diversity, which can lead to different levels of

biotic resistance (Byun et al. 2013). For example, several studies found lower impacts when the cover of the dominant resident species was high (Hejda et al. 2009; Fried et al. 2014). Therefore, the higher mean cover of the native herbaceous dominant species in *Juncetalia maritimi* communities (48%) compared to wet meadow communities (33%) might explain different levels of impact.

There have been few other attempts to determine impact thresholds for plants in natural ecosystems. In one of these Gooden et al. (2009) found native species richness in native plant communities invaded by the invasive shrub *Lantana camara* was more or less stable below 75% weed cover, but declined rapidly as the cover of *L. camara* increased further. All major structural groups (ferns, herbs, shrubs and trees) exhibited significant losses of species, although trees and shrubs were most impacted.

In the present study we found both linear (e.g. species richness) and nonlinear responses (e.g. total vegetation cover) to increasing cover of *B. halimifolia*, with different responses according to life form. The linear negative response found for annuals indicated that these species exhibited individual plant losses at all stages of *B. halimifolia* invasion, indicating a higher sensitivity to competition. This could be a conservation issue for rare and protected annual species such as *Crypsis aculeata* in Camargue or *Matricaria maritima* in the Basque country, where Campos et al. (2004) have already stressed the threat of *B. halimifolia* to the small heliophilous species typical of salt marshes. For perennial species, non-linear responses suggest a more complex effect. Low and medium cover of *B. halimifolia* had no effects, reflecting native species resistance to invasion (Collinge et al. 2011). This is consistent with our hypotheses that perennials have more resources to withstand a certain level of competition. Perennial graminoids showed a very low first inflexion point at 3%, a cover level of *B. halimifolia* that usually corresponded to one to two young individuals of ~60-cm high. This might be interpreted as a result of biotic resistance (Thiele et al. 2010): the establishment of such young individuals of *B. halimifolia* would only be possible in areas where these tall perennial graminoids (including *P. australis*, *J. acutus* and *J. maritimus*) have cover <85% (which is the case for *B. halimifolia* cover >3%), i.e. in gaps within resident vegetation. This is confirmed by observations that *B. halimifolia* rarely establishes in intact, undisturbed vegetation and is also consistent with a pioneer strategy documented for this shrub (Westman et al. 1975). The second inflexion point at 86% *B. halimifolia* cover corresponds well to that observed for total vegetation cover. This is not surprising, as perennial graminoids comprise the dominant vegetation in the studied communities. Above this threshold, non-*B. halimifolia* vegetation cover declined very rapidly. At

this stage of invasion, a number of *B. halimifolia* individuals began to form a continuous thicket. In addition to higher light interception, this also would limit recolonization through immigration of native plants from the surroundings. Finally, perennial forbs showed a lower impact threshold at 66%. This further supports the displacement of resident species through competition, with more sensitive species disappearing first.

Beyond quantification of the absolute impact of *B. halimifolia*, our study intended to provide a series of measures related to how the colonization of wet meadows by this exotic shrub might differ in its effect when compared to the natural succession that leads to dominance of *T. gallica*, thus yielding a measure of *relative impact* of *B. halimifolia*. On one hand, the understorey vegetation associated with both species showed a reduction in species richness and plant cover (total and perennial graminoids) and significant changes in species composition compared to neighbouring meadows. In addition, the understorey of *B. halimifolia* and *T. gallica* in the Roussillon had a very similar species composition. To a certain degree, therefore, the effects of *B. halimifolia* on salt marsh communities may not be fundamentally different from natural succession occurring with *T. gallica*. On the other hand, the magnitude of decrease was always much greater under *B. halimifolia* and the level of nestedness was also higher. This means that the development of *B. halimifolia* infestations will more often result in impoverished subsets of existing meadows communities than in the case of increasing dominance of *T. gallica*, where extinction of meadows species is more often compensated by immigration of new species typical of tamarisk thickets. This may be related to a simple effect of competition for light, with the fine and short leaves of *T. gallica* allowing more light to pass through its canopy, compared to the denser *B. halimifolia* foliage, as reflected in differences measured in canopy cover. A similar difference has been found on sand dune communities invaded by *Rosa rugosa* in Northern Europe, where the native *Hippophaë rhamnoides* was not as strongly shading (Isermann 2008). The significant effect of the identity of the shrub, independent of canopy cover, suggests the involvement of additional mechanisms. It may reflect the different invasion histories of the shrubs in the studied sites, with the more dynamic, fast-growing *B. halimifolia* causing a short-term, strong impact (nestedness changed), while *T. gallica*, occurring for longer, caused a similar or larger turnover but over a longer period, perhaps in a number of small steps.

In summary, *B. halimifolia* had stronger impacts on community diversity and vegetation cover than *T. gallica*, whereas the latter modified species composition more. Therefore, where their ecological niches overlap

(colonization of *Holoschoenetalia vulgaris* wet meadows), the effect of the exotic shrub *B. halimifolia* should not be expected to be comparable to the effect of natural succession leading to the dominance of *T. gallica*. It is likely that when traits of exotic shrubs differ sufficiently from those of native shrubs, their impacts will differ (te Beest et al. 2015).

Implications for management

Given the potential impacts of serious plant invaders, there is an imperative to manage these species in such a way as to avoid irreversible changes to invaded plant communities (Vilà et al. 2011). If feasible (see Panetta 2015), eradication might be the most cost-effective management strategy, but a number of prerequisites must be satisfied before adopting this approach, one of which is that re-invasion is unlikely to occur, at least in the medium term. Otherwise, so-called maintenance control (Simberloff 2003) is recommended, whereby the impacts of the invader are kept below an acceptable threshold. As evidenced in the present and other studies (Gooden et al. 2009; McAlpine et al. 2015), different vegetation characteristics of natural ecosystems may respond differently to the particular invader concerned, as well as at different stages of invasion.

Cousens (1987) makes an important distinction between thresholds that may be observed in damage functions and 'action thresholds', which are points at which decisions are made to implement control. Because of difficulties associated with aggregating the various types of damage caused by weeds in natural ecosystems, problems in predicting future invasion dynamics (Panetta & James 1999) and the sometimes dramatic increases in control costs with increasing woody weed density (Goodall & Naudé 1998; Marais et al. 2004; Buddenhagen & Yáñez 2005), action thresholds may need to be conservative in order to meet conservation objectives. Implementing control at relatively low weed densities will also serve to reduce impacts that are linearly related to weed cover. Results from the present study (see Fig. 2f) suggest that action should occur before 20% *B. halimifolia* cover has developed.

Quantitative assessment of species impact, as provided here, should ensure that resources spent on management are prioritized to target the most affected ecosystem at the landscape level (Hulme et al. 2013). If management resources are limited, and if community diversity is considered worthy of conservation at the current level, our study indicates that an objective prioritization in coastal salt marshes invaded by *B. halimifolia* would lead to a control effort first oriented in wet meadows (*Holoschoenetalia vulgaris*), which are consistently more impacted across regions than *Juncetalia maritimi* communities.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Comparison of the distribution of the cover of *B. halimifolia* in wet meadows (red) and in *Juncus maritimi* communities (green).

Appendix S2. Comparison of linear and non-linear regression analyses for community structure (species richness, Shannon's diversity, species evenness) and vegetation cover (total, annuals, perennial graminoids, perennial forbs) against percentage cover of *B. halimifolia* ($n = 85$) using the Akaike Information Criterion (AIC), and impact thresholds as detected by splits in conditional inference trees.

Appendix S3. Comparison of Shannon's diversity (left) and species evenness (right) between wet meadow control plots, *B. halimifolia* and *T. gallica* thickets.