

# Impact of invasive plants in Mediterranean habitats: disentangling the effects of characteristics of invaders and recipient communities

G. Fried · B. Laitung · C. Pierre · N. Chagué ·  
F. D. Panetta

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**Abstract** While the effects of an invasive alien plant that has become dominant in a community may seem obvious, there are few studies that attempt to understand how impacts vary according to the characteristics of invaders and recipient communities. For this purpose, the vegetation of invaded and non-invaded plots was sampled for eight different invasive species in a variety of habitats within the French continental Mediterranean region. Most of the observed impact variation was species-specific, with greater effects on community-level metrics found for *Carpobrotus* spp. and *Reynoutria × bohemica* and lower effects for *Amorpha fruticosa*, *Ambrosia artemisiifolia* and *Phyla filiformis*. Some trends were consistent with competition-driven processes, with higher impact found in the presence of rhizomatous and creeping perennial invasive species compared to annuals, or in habitats with sparse

vegetation. The importance of community characteristics such as the cover of the invasive plant or the differences in cover between the invader and the native dominant species confirmed previous results obtained in Central Europe. Therefore, such variables, easy to measure and with a generic value, could be profitably integrated into risk assessment methods to improve the prediction of the most threatened habitats. Beyond the overall decline in species diversity, the presence of some invasive species was associated with significant changes in species composition, with a filtering toward more shade-tolerant and nitrophilous ruderal species. Managers should consider replacement of resident species by species with different ecological preferences together with simple community-level metrics, to decide whether management is justified.

**Keywords** Traits · Community · Biodiversity · Competition · Biotic resistance · Risk assessment

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G. Fried (✉) · C. Pierre · N. Chagué  
Laboratoire de la Santé des Végétaux, Unité entomologie  
et plantes invasives, Anses, CBGP, Campus International  
de Baillarguet, CS 30016, 34988 Montferrier-sur-Lez  
Cedex, France  
e-mail: guillaume.fried@anses.fr

B. Laitung · C. Pierre · N. Chagué  
Université de Bourgogne, UMR 1347 Agroécologie  
AgroSup/INRA/uB, 6 boulevard Gabriel, 21000 Dijon,  
France

F. D. Panetta  
Melbourne School of Land and Environment, The  
University of Melbourne, Parkville, VIC 3010, Australia

## Introduction

While it is obvious that dense stands of invasive alien plant species will lead to changes in the invaded community (Hulme et al. 2013), little is known about the factors that produce variation in invader impact at the community level. During recent decades, much theoretical effort in invasion ecology has been devoted to the concept of invasibility (Levine et al. 2003). For

example, disturbance and high resource availability are widely recognized to increase the invasibility of communities (Davis et al. 2000; Chytrý et al. 2008), while resident species diversity is generally assumed to decrease aliens' establishment success (Levine et al. 2004), although this latter question is still debated (Zeiter and Stampfli 2012; Byun et al. 2013). The identity of the dominant resident species was also found to play an important role in invasibility (Smith et al. 2004; Emery and Gross 2006), which is consistent with the fact that dominant species exert strong influence over community dynamics and ecosystem function (Grime 1998). Levine et al. (2004) have, however, suggested that such biotic resistance hypotheses may be more relevant to the regulation of the impact of invaders once they have successfully established, rather than to elucidate the process of establishment per se. Until now, the relevance of these hypotheses related to invasibility has been solely tested through the degree of establishment success of one or several alien plant species, whatever their impact. Therefore, little is known about the significance of these hypotheses for predicting the impact of a plant in a given community (Maron and Marler 2008).

In this study, we assessed the impact of eight invasive plants (sensu Richardson et al. 2000) in different plant communities of the French Mediterranean region which is the most at risk in France (Muller 2004) and where alien plant invasion is widely recognized as a major threat to biodiversity, as for other Mediterranean regions of the world (Underwood et al. 2009).

Beyond quantifying impacts for a representative range of invasive species, our interest in the present study was to understand the factors determining the magnitude of these impacts, both according to invader traits and features of the recipient community, and how this knowledge can help to anticipate risk in the framework of weed risk assessment (WRA) and early detection and rapid response (EDRR) procedure. Our first hypothesis was that some invasive species traits related to the competitive ability of the invasive plant (e.g. plant height, life form), as well as population characteristics (e.g. cover of the invasive plant), would influence the magnitude of impacts. On the other hand, we assumed that the presence of a competitive resident plant species would reduce the effects of a new invader. The total vegetation cover and the structure of

the recipient communities (i.e. the relative proportions of different life forms) might also influence impacts, with higher effects expected in communities dominated by therophytes. Finally, taking into account some general ecological theories (Tilman 2004), we assumed that abiotic conditions, in particular the level of available resources, could also be an important factor. For example, in productive sites, we could expect that a competitive invader with a better ability to use resources compared to resident species would increase its invasive success within the resident community (Godoy et al. 2012).

We asked the following questions: (1) How is the presence of invasive plants associated with the recipient community diversity, composition and life-form spectrum (i.e. the relative proportion of different life forms)? (2) what are the major determinants of the impact, i.e. how do (i) the traits of the invasive species, (ii) the features of the invaded community, and (iii) their interactions mediate the impact that an invader has on a recipient community?

## Materials and methods

### Study sites and invasive species

The impact of plant invasion was studied in various sites and habitats of the French Mediterranean region (Appendix 1). Eight exotic plant taxa, listed as invasive species with supposed impacts in Mediterranean ecosystems (Brunel et al. 2010; CBNMed 2011a), were chosen to represent four different life forms. Two species per life form were selected within shrubs (*Amorpha fruticosa* L., *Baccharis halimifolia* L.), creeping perennials rooting at nodes (*Carpobrotus* spp., *Phyla filiformis* (Schrad.) Meikle), perennials with underground rhizomes (*Artemisia verlotiorum* Lamotte, *Reynoutria × bohémica* Chrtek & Chrteková), and annuals (*Ambrosia artemisiifolia* L. and *Impatiens balfourii* Hook.f.).

*Amorpha fruticosa* (Fabaceae) is a deciduous shrub native to North America and introduced for ornamental and amenity purposes (e.g. for dune stabilisation). In France, it mainly invades water-fringing beds and sand dunes. *B. halimifolia* (Asteraceae) is a semi-deciduous shrub from North America colonizing wet coastal habitats such as upper saltmarshes, mainly along the Atlantic coast and more recently around the

Mediterranean basin. *Carpobrotus* spp. (Aizoaceae)—including both *C. edulis* (L.) N.E.Br. and *C. acinaciformis* (L.) L.Bolus and their hybrids—are ground-hugging succulent chamaephytes native to South Africa. They form extensive mats and occur in several coastal habitats, mainly in sand dunes and rocky shores. *P. filiformis* (Verbenaceae) is a mat-forming stoloniferous hemicryptophyte introduced as an ornamental from South America. It proliferates in Mediterranean salt meadows and disturbed grasslands. *A. verlotiorum* (Asteraceae) is a geophyte with rhizomes (behaving more rarely as a hemicryptophyte) originating from Eastern Asia. It occurs in a wide range of habitats but the most dense populations are found in pioneer riparian forests (with *Salix* spp. and *Populus* spp.) or in mesic grasslands. *R. × bohemica* (Polygonaceae) is a fertile hybrid between *R. japonica* Houtt. and *R. sachalinensis* (F.Schmidt) Nakai (native from Eastern Asia) spreading in various disturbed habitats but forming especially large stands in riparian habitats, including river banks and riparian forests. *A. artemisiifolia* (Asteraceae) is a spring-germinating annual originating from North America, introduced accidentally with crop seeds and invading arable fields and various human-disturbed habitats. River banks are the only natural habitat where it forms dense stands. *I. balfourii* is also a spring-germinating annual introduced for ornamental purposes from Himalaya region, which mainly invades riparian forests.

#### Vegetation survey and measured traits

Field work was done throughout spring and autumn in 2011 and 2012. For six out of the eight studied species, impacts were measured in the two main habitat types that these species are known to invade in the Mediterranean area of France (Table 1) based on the SILENE database (CBNMed 2011b). For each species within each habitat, 15 pairs of adjacent 4 m<sup>2</sup> vegetation plots were sampled with a hierarchical design including five replications per location in three different locations. Following the methodology developed by Vilà et al. (2006) and Hejda et al. (2009), for each pair of plots, one plot was placed in heavily invaded vegetation ('invaded plots') where the invader was dominant and had at least 70 % cover and the second plot in neighbouring vegetation, where the invader was absent ('non-invaded plots') or in a very few cases, where its cover did not exceed 5 %.

The non-invaded plot was chosen in close proximity in order to have as far as possible similar site conditions (e.g. same slope, same exposure) to the invaded plot. Cover of every individual plant species was estimated and canopy height of 10 individuals of both the invasive plant and the native dominant species was measured in each plot. Canopy height was recorded as the shortest distance between the highest photosynthetic tissue in the canopy and ground level (Cornelissen et al. 2003). Recorded species were classified into four life forms sensu Raunkiaer (1934): therophyte, hemicryptophyte, geophyte and chamaephyte based on the Baseflor database (Julve 1998).

#### Data analysis

The first set of analyses aimed at quantifying the impact of the eight invasive plants. For each invaded habitat type per species, the differences in alpha species richness ( $S_\alpha$ ), Shannon's diversity ( $H'$ ) and species evenness ( $J$ ) between invaded (Inv.) and non-invaded (Non-inv.) plots were tested using a pairwise Wilcoxon test. To account for the hierarchical design (5 pairs of plots nested within 3 locations), Wilcoxon tests were performed by location. Total species richness per habitat (combining the 15 plots of each habitat), i.e.  $\gamma$ -diversity ( $S_\gamma$ ), was provided by constructing the mean species accumulation curve produced by repeating 100 times the process of randomly adding the 15 plots. The Jaccard dissimilarity index ( $D_J$ ) was used to quantify differences in species composition with  $D_J = 1 - J_{(Inv., Non-inv.)}$  where  $J_{(Inv., Non-inv.)} = \frac{a}{a+b+c}$  with  $a$  denoting the number of species occurring in both Inv. and Non-inv. plots, and  $b$  and  $c$  denoting the number of species occurring only in Inv. or in Non-inv. plots, respectively. To test the significance of these composition changes we used a Permanova test (Anderson 2001), a method similar to analysis of variance but using a distance matrix with a pseudo  $F$ -ratio test. Comparison of distances within ( $SS_W$ ) and among groups ( $SS_A$ ) is based on the formula  $F = \frac{SS_A/(a-1)}{SS_W/(N-a)}$  where  $N$  is the number of samples and  $a$  the number of groups (in our case with two groups of samples: Inv. and Non-inv,  $a = 2$ ). The  $P$  value is obtained by permutation (1,000 permutations for  $\alpha = 0.05$ ). To account for the nested design, locations were defined as strata within which to constrain permutations. In order to interpret changes in

**Table 1** The eight invasive alien plants studied in different EUNIS habitats and their impacts on community diversity

| Species                  | EUNIS habitat | Mean cover [min-max] | $\alpha$ -species richness (plot scale) $S_d$ |            |                       | Shannon diversity $H'$ |           |                      | Species evenness $J$ |             |                        | $\gamma$ -diversity (habitat scale) $S_\gamma$ |      |        |
|--------------------------|---------------|----------------------|---|------------|-----------------------|------------------------|-----------|----------------------|----------------------|-------------|------------------------|--|------|--------|
|                          |               |                      | Non-inv.                                      | Inv.       | Impact (%)            | Non-inv.               | Inv.      | Impact (%)           | Non-inv.             | Inv.        | Impact (%)             | Non-inv.                                       | Inv. |        |
| <i>A. artemisiifolia</i> | C3.5          | 82 [70-93]           | 10.6 ± 3.2                                    | 9.9 ± 3.8  | 6.6 ns                | 1.8 ± 0.4              | 1.9 ± 0.3 | -5.6 ns              | 0.77 ± 0.10          | 0.86 ± 0.06 | -11.7 ns               | 57   | 50   | 12.3*  |
| <i>I. balfourii</i>      | G1.1          | 81 [70-90]           | 7.2 ± 2.2                                     | 5.9 ± 1.6  | 18.1 ns               | 1.5 ± 0.4              | 1.4 ± 0.3 | 6.7 *                | 0.76 ± 0.14          | 0.82 ± 0.09 | -7.9 *                 | 34   | 29   | 14.7*  |
| <i>Carpobrotus</i> spp.  | B3.3          | 88 [80-100]          | 14.5 ± 2.7                                    | 7.3 ± 2.3  | 49.7 <sup>a</sup> *** | 1.9 ± 0.4              | 1.6 ± 0.4 | 15.8 <sup>a</sup> *  | 0.73 ± 0.12          | 0.82 ± 0.10 | -12.3 <sup>a</sup> *   | 63   | 34   | 46.0*  |
|                          | B1.4          | 95 [80-100]          | 14.9 ± 3.9                                    | 5.1 ± 3.4  | 65.8 <sup>b</sup> *** | 2.2 ± 0.3              | 1.4 ± 0.7 | 36.4 <sup>b</sup> ** | 0.81 ± 0.10          | 0.96 ± 0.03 | -18.5 <sup>b</sup> ns  | 63   | 47   | 25.4*  |
| <i>P. filiformis</i>     | A2.5 gr.      | 95 [92-98]           | 18.0 ± 5.1                                    | 13.3 ± 2.8 | 26.1 <sup>a</sup> *   | 2.1 ± 0.6              | 2.4 ± 0.2 | -14.3 <sup>a</sup> * | 0.74 ± 0.15          | 0.92 ± 0.02 | -24.3 <sup>a</sup> **  | 59   | 48   | 18.6*  |
|                          | A2.5          | 94 [93-95]           | 13.1 ± 3.4                                    | 11.7 ± 2.8 | 10.7 <sup>b</sup> ns  | 1.6 ± 0.5              | 1.7 ± 0.3 | -6.2 <sup>a</sup> *  | 0.65 ± 0.11          | 0.74 ± 0.18 | -13.8 <sup>a</sup> *   | 44   | 38   | 13.6*  |
| <i>A. verticillatum</i>  | G1.1          | 95 [85-100]          | 28.4 ± 6.4                                    | 12.5 ± 4.6 | 56.0 <sup>a</sup> *** | 2.9 ± 0.4              | 2.2 ± 0.4 | 24.3 <sup>a</sup> ** | 0.87 ± 0.10          | 0.90 ± 0.07 | -3.4 <sup>a</sup> ns   | 124  | 67   | 46.0*  |
|                          | E2.7          | 99 [92-100]          | 10.7 ± 1.8                                    | 4.6 ± 1.5  | 57.0 <sup>a</sup> *** | 1.3 ± 0.3              | 1.3 ± 0.3 | 0.0 <sup>b</sup> ns  | 0.56 ± 0.11          | 0.91 ± 0.09 | -62.5 <sup>b</sup> *** | 40   | 17   | 57.5*  |
| <i>R. × bohemica</i>     | C3.5          | 99 [95-100]          | 15.3 ± 5.7                                    | 7.1 ± 4.1  | 53.6 <sup>a</sup> *** | 2.3 ± 0.4              | 1.5 ± 0.8 | 34.8 <sup>a</sup> ** | 0.88 ± 0.06          | 0.88 ± 0.16 | 0.0 <sup>a</sup> ns    | 91   | 53   | 41.8*  |
|                          | G1.1          | 97 [95-100]          | 22.3 ± 6.6                                    | 13.9 ± 5.2 | 37.7 <sup>b</sup> *   | 2.6 ± 0.4              | 2.3 ± 0.5 | 11.5 <sup>b</sup> ** | 0.85 ± 0.07          | 0.90 ± 0.09 | -5.8 <sup>a</sup> *    | 93   | 66   | 29.0*  |
| <i>B. halimifolia</i>    | A2.5          | 100 [98-100]         | 8.8 ± 1.9                                     | 5.1 ± 2.0  | 42.0 <sup>a</sup> **  | 1.3 ± 0.3              | 1.0 ± 0.4 | 23.1 <sup>a</sup> *  | 0.58 ± 0.13          | 0.62 ± 0.20 | -6.9 <sup>a</sup> *    | 36   | 22   | 38.9*  |
|                          | F9.3          | 94 [87-100]          | 7.4 ± 1.5                                     | 4.2 ± 1.5  | 43.2 <sup>a</sup> *** | 1.1 ± 0.2              | 1.1 ± 0.5 | 0.0 <sup>a</sup> *   | 0.56 ± 0.10          | 0.77 ± 0.17 | -37.5 <sup>a</sup> **  | 26   | 20   | 23.1*  |
| <i>A. fruticosa</i>      | B1.3          | 90 [79-96]           | 8.7 ± 2.8                                     | 8.9 ± 2.5  | -2.3 <sup>a</sup> ns  | 1.6 ± 0.5              | 1.7 ± 0.3 | -6.2 <sup>a</sup> ns | 0.73 ± 0.16          | 0.77 ± 0.11 | -5.4 <sup>a</sup> ns   | 34   | 42   | -23.5* |
|                          | C3.2          | 85 [75-91]           | 5.7 ± 2.3                                     | 4.9 ± 1.2  | 14.0 <sup>a</sup> ns  | 1.0 ± 0.5              | 0.9 ± 0.4 | 10.0 <sup>a</sup> ns | 0.60 ± 0.25          | 0.56 ± 0.23 | 6.7 <sup>a</sup> ns    | 21   | 19   | 9.5*   |

The full nomenclature of EUNIS habitats is detailed in Appendix 1

Results for alpha species richness ( $S_d$ ), Shannon diversity ( $H'$ ) and species evenness ( $J$ ) (mean ± SD, n = 15) in non-invaded (Non-inv.) and invaded (Inv.) plots are presented at the habitat scale. Wilcoxon pairwise tests were performed at the level of each locality to take into account the hierarchical sampling design. Asterisks (\*) indicate the number of localities (0-3) where  $P$  values associated to the Wilcoxon pairwise tests were < 0.05. The relative impact on these three indices is expressed as the mean percentage reduction in invaded plots compared to non-invaded ones (100 %). A positive value indicates a higher diversity in non-invaded plots, a negative value indicates a higher diversity in invaded vegetation. Significant differences in the magnitude of the impact of a species between the two different habitats tested are indicated by different letters (a, b)

species composition and detect possible directional changes, three additional tests were performed. (1) Differences in species occurrence (i.e. number of plots occupied by each species) amongst Inv. and Non-inv. plots were assessed using the Fisher exact test in order to highlight species contributing the most to these composition changes. (2) Life form spectra of plots (i.e. the relative proportion of the mean coverage sum of each life form) and (3) cover-weighted mean Ellenberg values for light, edaphic moisture, and nitrogen (Julve 1998) were computed for each plot and compared between Inv. and Non-inv. plots using pairwise Wilcoxon tests at the level of each locality. Ellenberg values are essentially an ordinal classification of plant species according to the position of their realized ecological niche along an environmental gradient (Diekmann 2003). Weighted means at the community level are supposed to reflect the ecological conditions of each plot. The studied invasive alien species was excluded for all these community characteristics calculations.

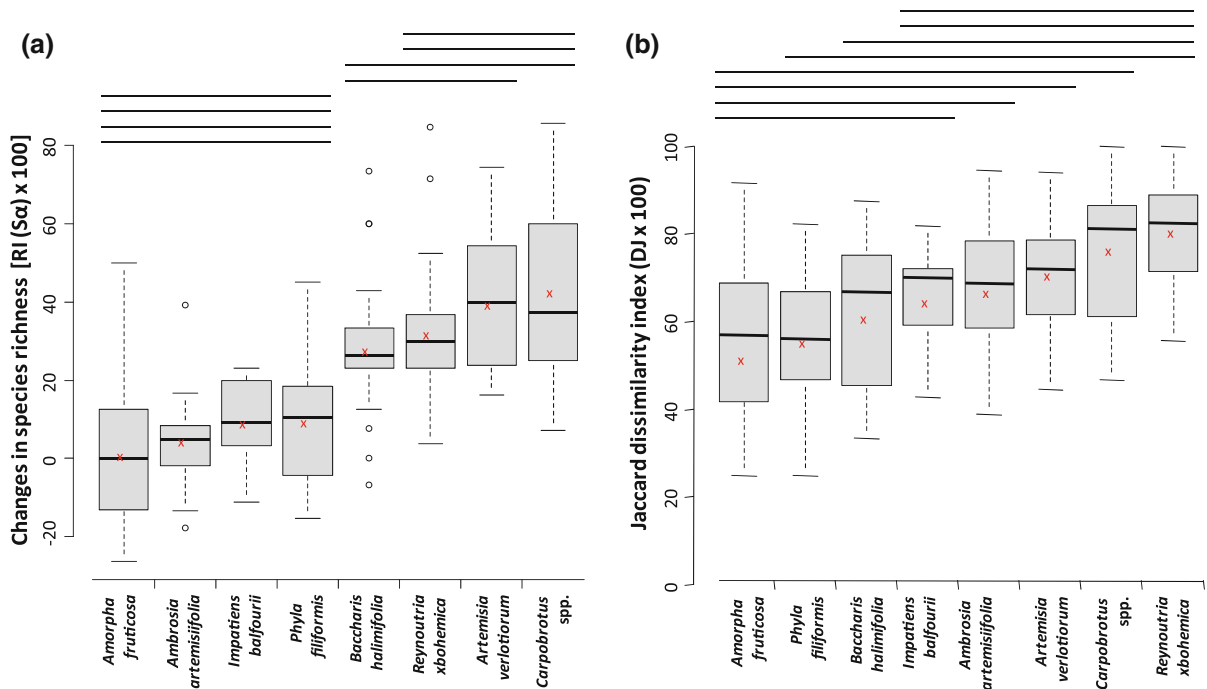
The second set of analyses aimed at measuring the relative influence of different factors presumably involved in impact variation. The difference in the magnitude of the impact of the invasive species between the two different habitats tested was analysed for six species with a Wilcoxon test. Differences in the magnitude of the impact between the eight invasive species were tested using linear mixed effect models (using the R packages lmer and lmerTest). The individual invasive species was considered as a fixed factor and habitats and locations as random factors, with locations nested within habitats and habitats nested within species. Differences in alpha species richness ( $S_{\alpha}$ ), Shannon's diversity ( $H'$ ), species evenness ( $J$ ) and Jaccard dissimilarity ( $D_J$ ) between each pair of Inv. and Non-inv. plot were the response variables. Differences in  $S_{\alpha}$ ,  $H'$  and  $J$  were expressed as a Relative Impact (RI) following Vilà et al. (2006), with  $RI(a) = \frac{a_{NI} - a_I}{a_{NI} + a_I}$ , where  $a$  is the variable of interest (e.g.  $S_{\alpha}$ ),  $I$  is the invaded plot and  $NI$  is the non-invaded plot. The advantage of using RI is that its distribution is approximately normal, it is linear and does not have discontinuities. RI is symmetrical around zero, and it has defined limits  $[-1; +1]$ , with a positive value indicating a decrease of the variable associated to the presence of the invader, and a negative value indicating an increase of the variable.

To test the effect of the growth form of the invaders, a nested ANOVA model was used, with invasive species as a factor hierarchically subordinated to growth forms (annuals, creeping perennials, perennials with rhizomes, shrubs). Tukey–Kramer post hoc tests were then used to perform multiple comparisons among means.

Finally, the relative importance of the characteristics of: (1) the invader, (2) the invaded communities and (3) their interaction in the magnitude of the impact was analyzed using an Analysis of Covariance (ANCOVA) and conditional inference trees. In ANCOVA models, the response variables were  $RI(S_{\alpha})$ ,  $RI(H')$  and  $D_J$ . The explanatory variables included individual invasive species as a factor, and (1) canopy height and cover of the invasive species, (2) canopy height and cover of the native dominant species, total vegetation cover in the non-invaded plots, relative percentage cover of different life forms in the non-invaded plots, mean cover-weighted Ellenberg values for light, soil moisture and nutrients in the non-invaded plots, and (3) differences in size and cover between invasive species and native dominant species as covariables. Prior to stepwise regression analyses, we created a correlation matrix among all variables to assess potential covariation. Predictor variables with Pearson's correlation coefficient  $r > 0.75$  were not used in the model. Dominant species cover and invasive canopy height were therefore eliminated from the initial model as these variables were highly correlated, respectively, to the differences in cover between invasive species and native dominant species ( $r = 0.97$ ), and to species identity ( $r = 0.97$ ). To find the best model, a backward stepwise process of model simplification was then used, beginning with the maximal model (including all variables) and then proceeding by eliminating the variables that improved the model the least based on Akaike Information Criterion (AIC), and repeating this process until no further improvement was possible.

To meet the assumptions of linear regression models, data were transformed as follows: canopy height was ln-transformed, all percent cover data were arcsin-square root transformed, and all covariates were standardized to zero mean and unit variance.

In order to obtain more easily interpretable results and to take into account interactions between all variables, conditional inference trees were also con-



**Fig. 1** The impact of individual invasive species on species richness  $S_{\alpha}$  (a) and Jaccard dissimilarity index  $D_J$  (b), measured with the RI index based on 30 pairs of invaded and non-invaded plots with three locations nested within two habitats nested within eight species (only 15 pairs and one habitat for *Ambrosia* and *Impatiens*). Differences in linear mixed models:  $F_{7,34} = 11.00$ ,  $P < 0.001$  (a);  $F_{7,34} = 5.64$ ,  $P < 0.001$  (b). The random effect of habitat nested within species and the random effect of locality nested within habitat nested within

species are detailed in Appendix 1. For each box plot, top bar is maximum observation, lower bar is minimum observation, top of box is third quartile, bottom of box is first quartile, middle bar is median value and circles are possible outliers. Means are represented by a cross. Lines above the box plots show groups of species not significantly different; lines that do not overlap with others show means significantly ( $P < 0.05$ ) different in a posteriori Tukey–Kramer tests

structured (using the `ctree` function in R package `party`). The procedure for `ctree` construction is described elsewhere by Hothorn et al. (2006). Compared to classical regression trees, conditional inference trees avoid the problems of overfitting data, selection of variables and stopping by estimating a regression relationship by binary recursive partitioning in a conditional inference framework. This statistical approach ensures that the right-sized tree is grown. All statistical analyses were performed under R software version 3.0.1.

## Results

### Impact on species diversity

In nine invaded sites out of the 14 studied, a significant decline in  $\alpha$ -species richness was observed, with an

overall mean decrease of 34 % in the number of species within invaded plots (Table 1). Changes in  $\alpha$ -species richness ranged from a non-significant increase of 2.3 % for *A. fruticosa* in sand dunes to a significant decrease of 65.8 % for *Carpobrotus* spp. in sand dunes. Two main groups of invasive species were detected (Fig. 1a), contrasting species with no or low impact on species richness (*A. fruticosa*, *A. artemisiifolia*, *I. balfourii*, *P. filiformis*) with values of  $RI(S_{\alpha})$  between 0.01 and 0.10, and species with higher impact (*B. halimifolia*, *R. × bohemica*, *A. verlotiorum*, *Carpobrotus* spp.) with  $RI(S_{\alpha})$  between 0.28 and 0.43.

Ten sites, involving six species exhibited a significant decline in Shannon's Diversity in at least one location, with an overall mean decrease of 9 % in invaded plots (Table 1). The largest impact was observed for *Carpobrotus* spp. in sand dune communities (36.4 % decrease) and for *R. × bohemica* in river bank communities (34.8 % decrease).

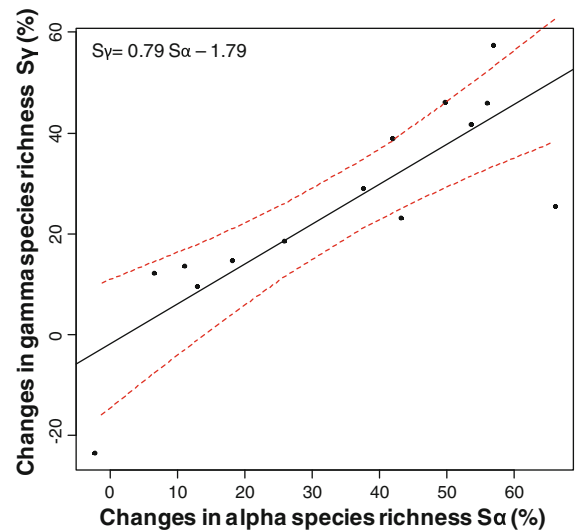
Differences between invasive species were only marginally significant (Appendix 2).

Species evenness was found to be higher in invaded plots for six species in eight sites, while no impact was found for *A. artemisiifolia* and *A. fruticosa* (Table 1). Evenness increased, especially under stands of *A. verlotiorum* in mesic grasslands (62.5 %) while almost no change was observed for *R. × bohemica* in river banks and a slight but non-significant decrease (6.7 %) occurred for *A. fruticosa* in sand dunes. No significant differences were found between invasive species (data not shown).

At the habitat scale, comparison of species accumulation curves showed that  $\gamma$ -diversity was significantly reduced in 13 out of 14 sites, with the smallest effect in invaded communities for *A. artemisiifolia* (12.3 %), *P. filiformis* (13.6 % in ungrazed salt marshes) and *I. balfourii* (14.7 %) and the largest one for *A. verlotiorum* (57.5 % in mesic grasslands and 46 % in riparian forests) and *Carpobrotus* spp. (46 % in rocky shores). *A. fruticosa* in sand dunes was the only case studied showing a significant increase of 23.5 % in the total number of recorded species. Decline at the habitat scale ( $S_{\gamma}$ ) was proportional to that at the plot scale ( $S_{\alpha}$ ) but the magnitude of impact was generally lower (Fig. 2).

#### Impact on vegetation composition and structure

In 11 sites out of 14, community composition was also markedly altered (Table 2: Jaccard dissimilarity index). The greatest changes in species composition were recorded for *R. × bohemica* in river bank communities (0.86), *Carpobrotus* spp. in sand dunes (0.81) and *A. verlotiorum* in pioneer riparian forests (0.78). On the other hand, changes for three species (*A. artemisiifolia*, *I. balfourii* and *A. fruticosa* in water-fringing beds) were not significant (and ranged from 0.40 to 0.67). The Tukey–Kramer tests showed that the effects of *R. × bohemica* and *Carpobrotus* spp. on species composition were significantly larger than those of *B. halimifolia*, *P. filiformis* and *A. artemisiifolia* (Fig. 1b). According to the Fisher's exact test on species occurrence, 61 species significantly contributed to composition differences (Appendix 3). There was a clear asymmetry, with many cases of species excluded by the invaders (92 %) and very few cases where some species were favored under stands of the invasive plants (8 %). There was no significant



**Fig. 2** Correlation between changes in  $\gamma$ -species richness at the habitat scale and  $\alpha$ -species richness at the plot scale associated with the presence of the invasive species (expressed in % of changes compared to richness in non-invaded plots). Dotted lines represent the 95 % confidence interval. S:  $r = 0.84$ ,  $t = 5.44$ ,  $df = 12$ ,  $P < 0.001$ .  $S_{\gamma} = 0.79 S_{\alpha} - 1.79$

trend toward a specific life form being more excluded (Chi squared Test,  $P = 0.72$ ,  $df = 4$ ).

On average, the cover of all life forms was reduced in invaded plots (Table 2) but their relative importance in the community was conserved except in two cases. Under *A. fruticosa* stands in sand dunes, the community was dominated by therophytes (22.8 %) and hemicryptophytes (16.5 %) while it was initially dominated by geophytes (20.3 %) and chamaephytes (15.1 %). In mesic grasslands invaded by *A. verlotiorum* and originally dominated by hemicryptophytes (67.9–3.5 %), therophytes became the most dominant life form (9.7–4.7 %).

Changes in mean cover-weighted Ellenberg values were not significant for *A. artemisiifolia*, *I. balfourii* and *Carpobrotus* spp. on rocky shores (Fig. 3). Consistent changes were observed for other species, with increasing values of Ellenberg-N (eight cases), Ellenberg-H (nine cases) and decreasing values of Ellenberg-L (four cases) associated with the presence of the invader.

#### Factors affecting impact on community diversity and composition

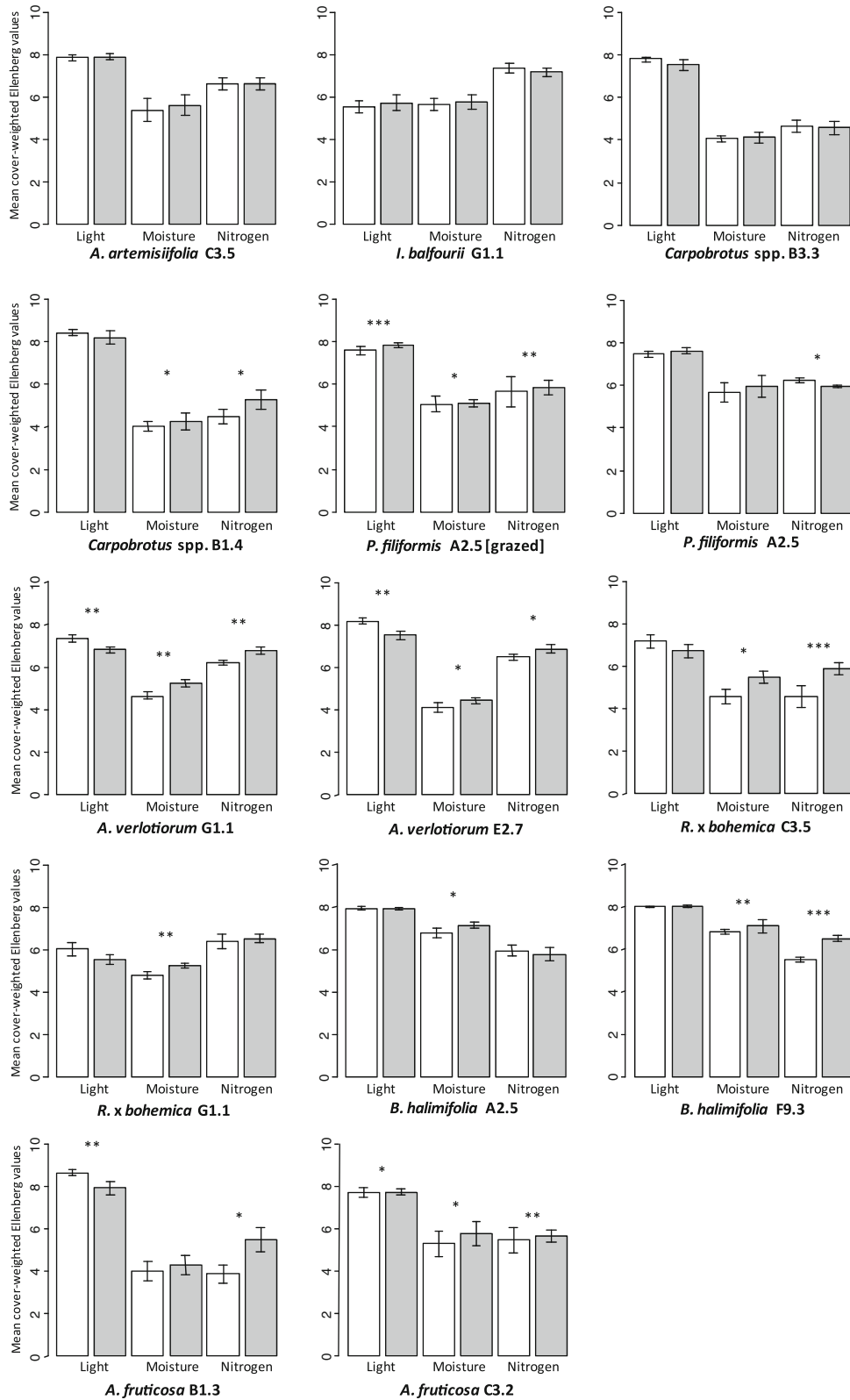
Although the effect of species identity was largely significant, the mixed effects models also indicated a

**Table 2** The eight invasive alien plants studied in different EUNIS habitats and their impacts on community composition and life form spectra

| Species                  | EUNIS habitat | Jaccard dissimilarity index (D <sub>j</sub> ) | Chamaephytes |             |               | Hemipterophytes |             |                | Geophytes   |             |               | Therophytes |             |                |
|--------------------------|---------------|---|--------------|-------------|---------------|-----------------|-------------|----------------|-------------|-------------|---------------|-------------|-------------|----------------|
|                          |               |   | Non-inv.     | Inv.        | RI            | Non-inv.        | Inv.        | RI             | Non-inv.    | Inv.        | RI            | Non-inv.    | Inv.        | RI             |
| <i>A. artemisiifolia</i> | C3.5          | 0.67 ± 0.17 ns                                | 0            | 0           | NA            | 17.7            | 10.1        | 27.4           | 0.9         | 0.4         | 40            | <b>37.3</b> | <b>20.1</b> | <b>29.9*</b>   |
| <i>I. balfourii</i>      | G1.1          | 0.65 ± 0.12 ns                                | 6.5          | 1.5         | 61.7          | 27.1            | 21.8        | 10.9           | <b>12.5</b> | <b>4.6</b>  | <b>46.3*</b>  | 0.9         | 0.6         | 21.7           |
| <i>Carpobrotus</i> spp.  | B3.3          | 0.72 ± 0.18 <sup>a***</sup>                   | <b>35.1</b>  | <b>12.2</b> | <b>48.6**</b> | <b>59.4</b>     | <b>24.8</b> | <b>41.1**</b>  | <b>1.3</b>  | <b>0.5</b>  | <b>42.9*</b>  | 5.5         | 3.8         | 18.1           |
|                          | B1.4          | 0.81 ± 0.11 <sup>b***</sup>                   | 1            | 0.3         | 50.0          | <b>29.6</b>     | <b>3.8</b>  | <b>77.2**</b>  | 2.7         | 1.1         | 42.9          | <b>24.3</b> | <b>1.9</b>  | <b>85.7**</b>  |
| <i>P. fliformis</i>      | A2.5 gr.      | 0.54 ± 0.14 <sup>a***</sup>                   | 0            | 0.1         | -100          | <b>44.2</b>     | <b>22.9</b> | <b>31.8*</b>   | <b>25.9</b> | <b>5.7</b>  | <b>64.1**</b> | <b>30.2</b> | <b>12.5</b> | <b>41.3*</b>   |
|                          | A2.5          | 0.57 ± 0.13 <sup>a***</sup>                   | 0.07         | 0.2         | -50.0         | <b>40.3</b>     | <b>21.1</b> | <b>31.2*</b>   | <b>55.7</b> | <b>23.7</b> | <b>40.3*</b>  | 20.3        | 20.7        | -1             |
| <i>A. verticillatum</i>  | G1.1          | 0.78 ± 0.09 <sup>a***</sup>                   | <b>1.5</b>   | <b>0.07</b> | <b>91.7*</b>  | <b>26.1</b>     | <b>9.1</b>  | <b>48.2**</b>  | 0.7         | 1.1         | -18.5         | <b>30.5</b> | <b>8.9</b>  | <b>54.7***</b> |
|                          | E2.7          | 0.64 ± 0.13 <sup>b***</sup>                   | 0            | 0           | NA            | <b>67.9</b>     | <b>3.5</b>  | <b>90.1***</b> | 43.2        | 1.9         | 91.4          | <b>9.7</b>  | <b>4.7</b>  | <b>35.2*</b>   |
| <i>R. × bohemica</i>     | C3.5          | 0.86 ± 0.10 <sup>a***</sup>                   | 1.7          | 0.2         | 79.3          | <b>29.7</b>     | <b>7.6</b>  | <b>59.3**</b>  | 1.8         | 0.9         | 31.7          | <b>3.5</b>  | <b>1.5</b>  | <b>38.7*</b>   |
|                          | G1.1          | 0.75 ± 0.12 <sup>b***</sup>                   | 2.7          | 2.3         | 6.70          | <b>48.3</b>     | <b>16.5</b> | <b>49.0***</b> | 5.9         | 4           | 19.5          | <b>21.9</b> | <b>8.1</b>  | <b>46.1**</b>  |
| <i>A. fruticosa</i>      | B1.3          | 0.64 ± 0.17 <sup>a*</sup>                     | <b>15.1</b>  | <b>2.5</b>  | <b>71.8*</b>  | 12.9            | 16.5        | -12.4          | <b>20.3</b> | <b>4.8</b>  | <b>61.9**</b> | <b>4.8</b>  | <b>22.8</b> | <b>-65.2*</b>  |
|                          | C3.2          | 0.40 ± 0.28 <sup>a</sup> ns                   | 0.07         | 0.07        | 0.00          | 28.8            | 11.3        | 43.5           | 36.7        | 41.9        | -6.7          | 0.27        | 0.53        | -33.3          |
| <i>B. halimifolia</i>    | A2.5          | 0.62 ± 0.16 <sup>a***</sup>                   | 2.5          | 0.07        | 94.9          | <b>27.6</b>     | <b>4.1</b>  | <b>73.9**</b>  | <b>68.3</b> | <b>37</b>   | <b>29.7**</b> | <b>1.07</b> | <b>0</b>    | <b>100*</b>    |
|                          | F9.3          | 0.60 ± 0.15 <sup>b***</sup>                   | 1.4          | 4.3         | -51.2         | <b>20.1</b>     | <b>4.1</b>  | <b>65.8**</b>  | 24.3        | 19.1        | 12            | 1.7         | 0.5         | 51.5           |

Mean Jaccard dissimilarity index, calculated as an average value for the 15 pairs of plots, indicates the impact on species composition; the higher the dissimilarity, the more dissimilar is the invaded to the non-invaded community. Significant differences in the magnitude of the impact of a species between the two different habitats tested are indicated by different letters (a, b). Changes in the life form spectrum according to the cover of chamaephytes, hemipterophytes, geophytes and therophytes in non-invaded (Non-inv.) and invaded (Inv.) plots at the habitat scale. RI gives the relative impact on cover expressed as percentages [-100, 100]. Wilcoxon pairwise tests were performed at the level of each locality to take into account the hierarchical sampling design. Asterisks (\*) indicate the number of localities (0–3) where *P* values associated to the Wilcoxon pairwise tests were <0.05. Values in bold indicate that significant changes in the cover of the corresponding life form occurred at least in one locality. See Table 1 for additional legend





**Fig. 3** Mean cover-weighted Ellenberg values for non-invaded (white bars) and invaded plots (grey bars) for light (L), edaphic moisture (HE), and nitrogen (N), for each species in each habitat. The number of asterisks (\*) refers to the number of locations (0–3) where significant differences ( $P < 0.05$ ) were found between invaded and non-invaded plots tested by Wilcoxon paired tests. Letters followed by numbers refer to different EUNIS habitats

significant effect of locality, while no influence of the habitat was found at this scale (Appendix 2). However, when considering each species individually, the magnitude of impact significantly differed according to the type of invaded habitat for four species (Table 1). Higher impact of *R. × bohemica* was recorded in river bank communities (C3.5) compared to riparian forest (G1.1). Sand dunes were more impacted in terms of  $\alpha$ -species richness (*Carpobrotus* spp.) or species composition (*A. fruticosa*) compared to the second habitat tested for these species. The impact of *A. verlotiorum* was stronger in riparian forest (G1.1) compared to mesic grasslands (E2.7).

When grouped by growth forms, the nested ANOVA model showed that rhizomatous perennials and mat-forming creeping perennials exhibited the strongest impact, while annual species always had a minimal effect on community diversity and composition (Table 3).

The minimum adequate model for relative impact on species richness  $RI(S_x)$ , retained seven of the 12 variables tested and showed that decreases in species richness depended mainly on invasive species identity (37 %) but also on invader cover (11 %) and differences in cover between the invader and the dominant native species (Table 4). The conditional inference for  $RI(S_x)$  (Fig. 4a) was first split according to the identity of the invading species. The taxa with the largest impact further split based on differences in invasive canopy height and cover, with larger impact in situations where canopy height was  $<140$  cm and cover  $>96$  % (Fig. 4a). For species with lower effect, the magnitude of impact depended on the relative cover of hemicryptophytes, with larger impact when this life form exceeded 16.7 %.

Six variables were retained in the best model for  $RI(H')$  (Table 4). Decrease of Shannon diversity  $H'$  mainly depended on the differences in cover between the invader and the dominant native species (18 %) and the identity of the invader (12 %), as well as canopy height of the dominant native species (4 %).

The conditional inference tree attributed most variations to cover differences between the invader and the native dominant species (Fig. 4b). When the cover difference was  $\geq 40$  %, the data were further split according to the cover of the invasive species and the cover of the dominant native species, with higher impacts either if the cover of the invasive was  $>96$  % or if the cover of the dominant native species was  $<7$  %.

According to the best ANCOVA model, changes in species composition significantly depended on the identity of the invasive species (25 %), total vegetation cover (5 %) and the proportion of therophytes within the community (4 %) (Table 4).

The conditional inference tree (Fig. 4c) for changes in species composition first split the data according to species identity, with higher impact for *A. artemisiifolia*, *A. verlotiorum*, *Carpobrotus* spp. and *R. × bohemica*, and secondly according to differences in cover, with higher impact when the invasive species had 60 % more cover than the native dominant species and if the canopy height of the native dominant species was  $\leq 25$  cm.

## Discussion

Our results showed that although, on average, the presence of invasive plants is associated with a significant change in resident community diversity and composition, the magnitude and sometimes the direction of some impacts strongly vary, first according to invader identity, then according to invasive population characteristics and features of the recipient community. Impacts also varied according to the invader growth form and the type of invaded habitats, although the present design could not estimate their relative importance.

### Impact of plant invaders in Mediterranean habitats

As might be expected, the magnitude of the impact differed among the eight studied species, with *Carpobrotus* spp. and *R. × bohemica* exhibiting the largest impact for most of the studied indices while *A. fruticosa* was almost always associated with the lowest effects and even was associated with an increase in  $\gamma$ -diversity at the habitat scale. The huge effect of invasion by both *Carpobrotus* spp. and

**Table 3** Hierarchical general linear model used to examine the mean relative impacts (RI) of invasive plants grouped in growth forms

|                              | S ( $\alpha$ -species richness)              | H' (Shannon's diversity)                    | D <sub>j</sub> (Jaccard dissimilarity index) |
|------------------------------|--|---|--|
| <i>Anova table</i>           |  |   |  |
| Species (life forms)         | F <sub>4,202</sub> = 23.95; <i>P</i> < 0.001 | F <sub>4,202</sub> = 6.69; <i>P</i> < 0.001 | F <sub>4,202</sub> = 8.94; <i>P</i> < 0.001  |
| Life forms                   | F <sub>3,202</sub> = 25.44; <i>P</i> < 0.001 | F <sub>3,202</sub> = 2.87; <i>P</i> = 0.037 | F <sub>3,202</sub> = 14.11; <i>P</i> < 0.001 |
| <i>Mean RI per life form</i> |  |   |  |
| Rhizomatous perennials       | 0.36 ± 0.17 <sup>a</sup>                     | 0.12 ± 0.21 <sup>a</sup>                    | 0.76 ± 0.13 <sup>a</sup>                     |
| Creeping perennials          | 0.26 ± 0.25 <sup>a</sup>                     | 0.07 ± 0.24 <sup>ab</sup>                   | 0.66 ± 0.17 <sup>b</sup>                     |
| Shrubs                       | 0.14 ± 0.22 <sup>b</sup>                     | 0.04 ± 0.25 <sup>ab</sup>                   | 0.56 ± 0.21 <sup>c</sup>                     |
| Annuals                      | 0.07 ± 0.01 <sup>b</sup>                     | −0.01 ± 0.01 <sup>b</sup>                   | 0.66 ± 0.15 <sup>bc</sup>                    |

Similar single letter (a, b, c) indicates groups that are not significantly different (*P* < 0.05, Tukey–Kramer post hoc tests)

*R. × bohemica* was also associated with changes in species composition toward more nitrophilous species in invaded plots, especially for *R. × bohemica*. These results are in accordance with previous studies showing changes in the upper soil profile attributed to the abundant litter produced (Maurel et al. 2010; Santoro et al. 2011). Stems and leaves of *Reynoutria* spp. decay slowly, resulting in an increase of litter thickness and the depth of the underlying soil horizon A. These new soil conditions with increasing organic matter content would therefore be more favourable to nutrient-demanding species.

While several recent reviews (Vilà et al. 2011; Hulme et al. 2013; Pyšek et al. 2012) identified that impacts remain unquantified for most alien plants, our study provides the first comparative quantitative impact estimation for a number of invasive species. Even though *A. verlotiorum* has been the object of less attention by land managers, our study shows that this invasive species has a comparable or even stronger community-level impact than *R. × bohemica* in pioneer riparian forest (see Table 1 for G1.1). Furthermore, our study confirms the major impact of *B. halimifolia*, especially on therophytes and on endemic saltmarsh species (e.g. *Sonchus maritimus*, *Dorycnium pentaphyllum* subsp. *gracile*) as observed in the Basque country in Spain, where a substantial part of subhalophilous communities initially dominated by *J. maritimus* has been replaced by monospecific stands of *B. halimifolia* (Caño et al. 2013). Although significant for species richness at the habitat scale ( $S_{\gamma}$ ) and for Shannon's diversity (H') in one location, the low magnitude of impact found for *I. balfourii* is consistent with the results obtained for other annual species of the *Impatiens* genus, including *I. glandulifera* (Hejda and

Pyšek 2006; Hejda et al. 2009) or *I. parviflora* (Hejda 2012). Similarly, common ragweed (*A. artemisiifolia*), which is mainly known for its impact on human health and crop yield, does not exhibit significant impact in invaded communities of river banks.

Contrary to theoretical expectations (Olden 2006) and previous studies (Hejda et al. 2009), we found that species evenness was rather increased under stands of invasive plants. As suggested by Powell et al. (2011), such a pattern is possible when invasive species affect more common species and/or drive rare species to local extinction, leading to more even abundances amongst the remaining species. This is confirmed by our study, where under the invaded plots of *A. verlotiorum* (which increased species evenness the most), we regularly recorded only one or very few individuals for each remaining species, which led to a high species evenness, tending to  $J = 1$ .

#### Factors determining the magnitude of impacts

The effect of invasion is largely species-specific, with the identity of the invader accounting for the majority of variations in the relative impact on species diversity and species composition. However, growth form, as well as the height and cover reached by the invasive plant, also play a significant role for the most impacting species. As expected, invasive species with an annual life cycle (e.g. *A. artemisiifolia* and *I. balfourii*) have a lower effect, probably because even dense populations of these species reach lower cover compared to the other studied species (only averaging 81–82 % in our dataset, see Table 1), do not form homogeneous stands and therefore lead to less competition for resources. In

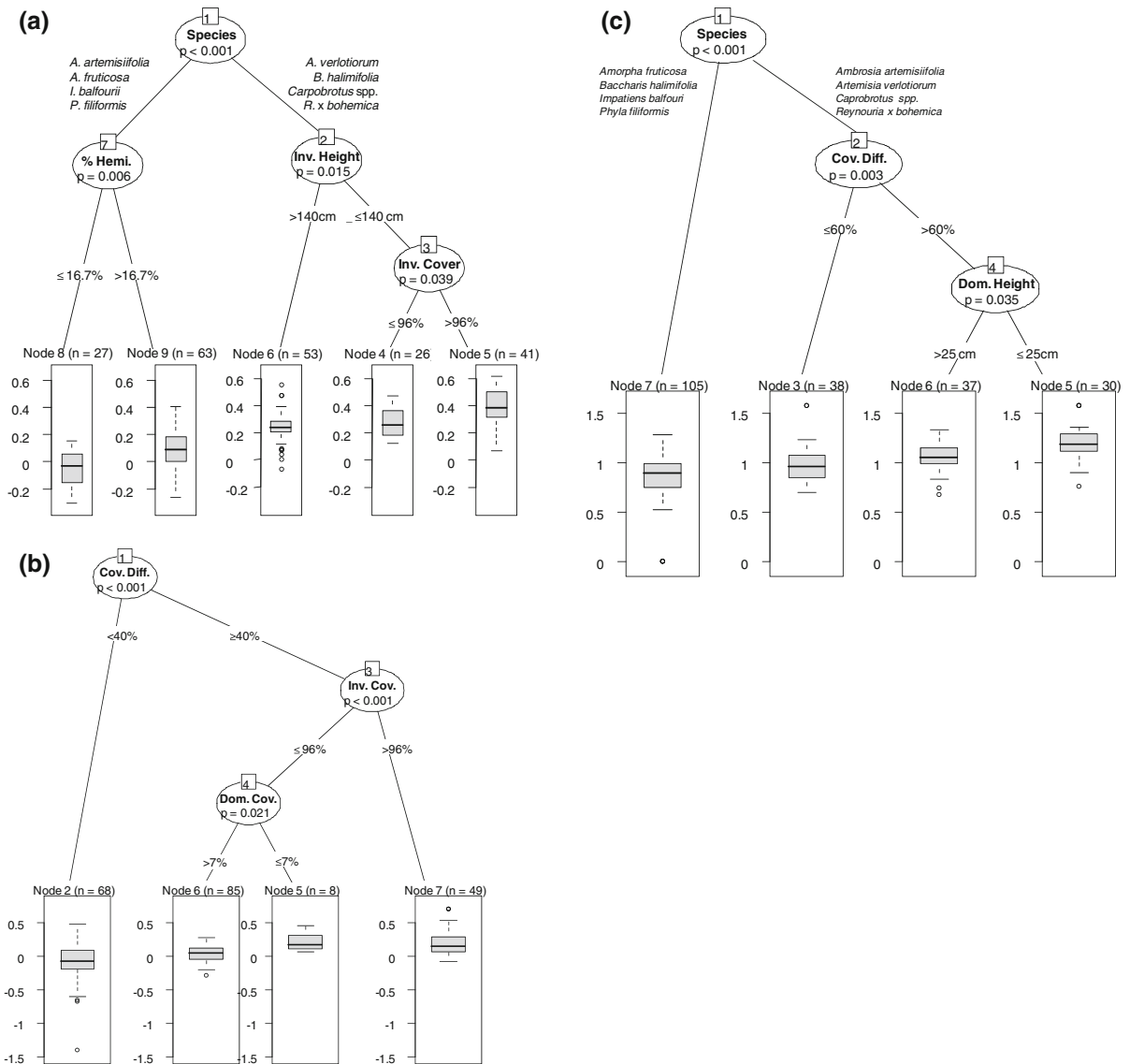
**Table 4** Analysis of variance table for the minimum adequate model of ANCOVAs obtained by stepwise selection

| Source of variation                                    | Df  | SS     | MS    | F      | P      | R <sup>2</sup> (R <sup>2</sup> adj.) | lmg   |
|--|-----|--------|-------|--------|--------|--------------------------------------|-------|
| <i>Impact on species richness (S<sub>x</sub>)</i>      |     |        |       |        |        |                                      |       |
| Species  | 8   | 11.03  | 1.38  | 90.32  | <0.001 |                                      | 37.00 |
| Invasive cover   | 1   | 0.16   | 0.16  | 10.57  | 0.001  |                                      | 10.61 |
| Differences in cover                                   | 1   | 0.11   | 0.11  | 7.25   | 0.008  |                                      | 5.21  |
| Total vegetation cover                                 | 1   | 0.13   | 0.13  | 8.58   | 0.004  |                                      | 2.06  |
| Ellenberg-H  | 1   | 0.25   | 0.25  | 16.66  | <0.001 |                                      | 1.98  |
| Ellenberg-N  | 1   | 0.12   | 0.12  | 8.08   | 0.005  |                                      | 1.67  |
| Ellenberg-L  | 1   | 0.07   | 0.07  | 4.30   | 0.040  |                                      | 0.82  |
| Residuals  | 196 | 3.01   | 0.02  |        |        |                                      |       |
| Total  | 210 |        |       |        |        | 0.80 (0.78)                          |       |
| <i>Impact on Shannon diversity (H')</i>                |     |        |       |        |        |                                      |       |
| Species  | 8   | 1.78   | 0.22  | 7.02   | <0.001 |                                      | 11.93 |
| Dominant height  | 1   | 0.62   | 0.62  | 19.61  | <0.001 |                                      | 3.88  |
| Differences in height                                  | 1   | 0.62   | 0.62  | 4.37   | 0.038  |                                      | 0.82  |
| Differences in cover                                   | 1   | 1.74   | 1.74  | 38.06  | <0.001 |                                      | 18.23 |
| Total vegetation cover                                 | 1   | 0.32   | 0.32  | 10.78  | 0.001  |                                      | 3.33  |
| Ellenberg-H  | 1   | 0.33   | 0.33  | 14.69  | 0.002  |                                      | 2.20  |
| Residuals  | 197 | 6.19   | 0.03  |        |        |                                      |       |
| Total  | 210 |        |       |        |        | 0.43 (0.39)                          |       |
| <i>Impact on Jaccard dissimilarity (D<sub>J</sub>)</i> |     |        |       |        |        |                                      |       |
| Species  | 8   | 197.50 | 24.69 | 647.41 | <0.001 |                                      | 25.18 |
| Total vegetation cover                                 | 1   | 0.49   | 0.49  | 12.72  | <0.001 |                                      | 4.93  |
| Ellenberg-L  | 1   | 0.27   | 0.27  | 7.13   | 0.008  |                                      | 1.41  |
| % Therophytes  | 1   | 0.12   | 0.12  | 3.32   | 0.070  |                                      | 4.09  |
| Residuals  | 199 | 7.57   | 0.04  |        |        |                                      |       |
| Total  | 210 |        |       |        |        | 0.96 (0.96)                          |       |

The relative importance of the variables is given by lmg, which is the R<sup>2</sup> contribution averaged over orderings among regressors (Chevan and Sutherland 1991)

contrast, rhizomatous perennials (e.g. *A. verlotiorum* and *R. × bohemica*) and to a lesser extent creeping perennials, caused the largest effects, with RI(S<sub>x</sub>) = 36 and 26 % respectively. The strong impact of the first group may be explained by their dense rhizome systems and the associated underground competition but also by the high density of stems (personal observation), resulting in stands with a very high cover (averaging 95–99 % in our dataset). The effect of shrubs was less consistent and probably also depended on other traits. For example, among shrubs, the larger impact of *B. halimifolia* compared to *A. fruticosa* may be due to more branching at the base of the shrub in the former, resulting in a more bushy habit. A recent meta-analysis of invasive plant impact in Mediterranean

regions of the world (Gaertner et al. 2009) also stressed the greater effect of creeping species. In contrast to our results, annual species were classified among high impacting species. However these results concerned particular cases of shrublands disturbed by human activities (therefore logically favouring annual species) or dry lowland fynbos where limiting resources may also favour introduced annual plants able to capture pulses of resources at the expense of resident perennial plants (Everard et al. 2010). Although our analysis highlighted consistent differences of impact between certain life forms (e.g. annuals vs. rhizomatous perennials), these results should be considered with caution and followed up by investigation of a wider range of species and across a fertility-disturbance gradient.



**Fig. 4** Conditional inference trees describing the impact of invading species on **a**  $\alpha$ -species richness ( $S\alpha$ ), **b** Shannon's diversity ( $H'$ ) and **c** Jaccard dissimilarity index ( $D_j$ ) in invaded plots. 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 changes in species richness [ $RI(S\alpha)$ ], Shannon diversity [ $RI(H')$ ] and species composition ( $\arcsin \sqrt{D_j}$ ), respectively

Contrary to expectation (Violle et al. 2009), the impact of the invasive plant did not necessarily increase with increasing canopy height. The positive relationship between canopy height and impact may be true to a certain extent in a group of herbaceous plants with a homogeneous habit (Hejda et al. 2009). Including different life forms and growth habits resulted in a different pattern, with larger impact

found for canopy height  $< 140$  cm (Fig. 4a). This effect might be driven by the high impact of *Carobrotus* spp. which are also the invasive species with the smallest size (amongst species with high impacts). To a lesser extent, this effect could also result from small bushes of *B. halimifolia* and *R. x bohemica* which exhibited higher cover densities compared to older individuals usually with another plant habit (with

fewer ramifications at the base) that may enable more light to reach the ground, favouring resident species in the second case.

Previous similar studies comparing the impact of several invasive plants did not explicitly account for differences between habitats. Our results showed that for a given invasive species all habitats did not undergo the same level of impact. A rough analysis showed that habitats with sparse vegetation, such as sand dunes (B1.3 and B1.4) invaded by *Carpobrotus* spp. and *A. fruticosa* or river banks (C3.5) invaded by *R. × bohemica* are more susceptible to impacts than more densely vegetated habitats. Coastal sediments (B1 and B2) and riverine habitats (C3 and D5) were also shown to be among the most invulnerable habitats, based on the proportion of alien species observed (Chytrý et al. 2008), while a previous analysis in the Mediterranean region also found greater impacts in dune vegetation (Gaertner et al. 2009). This result would indicate that in these habitats, the same factors allowing greater invasibility would presumably also lead to higher impacts.

The strong effect of locality in explaining differences in the impact observed, as shown by the mixed models (Appendix 2), may indicate the influence of the structure of the resident community or of the local abiotic properties of the environment. First, native communities already including a dominant species with high cover (or high canopy to a lesser extent) are less impacted (Table 4). Our study therefore confirmed some previous results found in Central Europe (Hejda et al. 2009), highlighting the importance of cover differences between the invasive species and the native dominant species. Thus, lower impacts are found in terms of Shannon's diversity or species composition when differences in cover between the invasive and the native dominant species do not exceed 40 or 60 % respectively (Fig. 4b, c). In such situations, the effect of adding a dominant alien invader is not much different from the competitive influence of the dominant native species. In other words, in these communities, the resident dominant species may already exert a strong influence limiting the number of species and filtering species already adapted to competition (Chesson 2000; Grime 2006). This is consistent with studies showing the role of the identity of the dominant native species on invasibility (Smith et al. 2004). Second, beyond the role of the dominant species, the total vegetation cover of the

community was also retained in all models, which confirms the higher vulnerability of habitats with sparse vegetation.

Abiotic properties of sites (light, water and nutrient resource) showed less influence although cover-weighted mean Ellenberg values were retained in all three models (species richness, diversity and composition), showing that the level of available resources does matter to a certain extent (Table 4). However, the importance of these variables was low and contrasting results were found regarding species and the influence of water and nutrients. Larger impacts were recorded in sites with higher soil moisture, which is consistent with the hypothesis of better performance of invaders (associated with higher growth rate) when water availability is high (Reever and Rice 2006). This was especially the case for *A. verlotiorum*. On the other hand, sites with lower nutrient resources were associated with higher invasive species impact, which is consistent with more efficient use of limited resources by invaders, resulting in faster competitive exclusion in unproductive sites (Tilman 2004). This was observed for *P. filiformis*, *R. × bohemica* and *B. halimifolia* to a lesser extent.

#### Implications for management and weed risk assessment

Considering the ongoing debates on whether invasive plants are really a threat for natural ecosystems and considering that one third of the studies dealing with alien plant impact focused altogether only on nine species (Hulme et al. 2013), this study also considerably extends our knowledge by including six major invasive species for which no (or very few and unstandardized) quantitative assessments of community-level impacts are available. Beyond the value of these data per se, general conclusions of our study were intended to improve impact assessment in WRA (Weed Risk Assessment) and prioritization tools.

On one hand, our analysis highlighted that a large part of impact was species-specific, which means that few generalizations could be made to predict impact of a new emerging invasive species in a WRA tool. Moreover, given the variation observed across habitats and locations for a single species (Appendix 2), conclusions derived from an initially invaded habitat could hardly be extrapolated to other habitats.

On the other hand, a number of general rules can nevertheless be formulated on the basis of our results.

First, impacts varied according to the invader's life form. As already accounted for in some risk assessment tools (e.g. Weber and Gut 2004), some life forms could be more weighted than others, e.g. rhizomatous or creeping perennials compared to annuals. However, further studies are necessary to make meta-analysis possible over a wider range of life forms (Hulme et al. 2013). Second, the ability of an invasive species to form very dense populations was found to be a key characteristic. Interestingly, no real threshold was found for invasive species cover, with a significant split concerning impacts only beyond 96 % cover, almost equivalent to full cover. As not all studied species were able to reach this level of dominance, a useful follow-up to this result could be to determine which traits and which conditions make it possible for a species to reach such hyper-dominant cover.

The credibility of pre-border WRA has been recently questioned (Hulme 2012) and one alternative proposition was to combine WRA with survey data in the framework of EDRR (Early Detection and Rapid Response) when a species is at the beginning of its invasion. To make post-border WRA tools more effective for managers at the landscape level, our study showed that the assessment of the dominant native species could provide meaningful information. Our results confirmed that invasions by plants which increase the dominance in the community by approximately 40–60 % have the strongest effect (Hejda et al. 2009). By including a simple measure of cover of the native dominant species, WRA tools applied at the landscape scale could target the most endangered communities in a given location.

If such a standardized impact assessment is to be used by managers, they may also want to know on which indicator(s) they should rely to take a decision about management. Species richness or changes in species composition are simple instructive ways to capture the magnitude of impacts. However, if these are considered alone they are not totally informative. For example, *A. verlotiorum* has a comparable magnitude of impact for species richness to that of *Carpobrotus* spp.; however, impacted species in pioneer riparian forests invaded by *A. verlotiorum* include mainly other aliens (with 17 % relative cover of neophytes) or ruderal weed species (cf. Appendix 3), while *Carpobrotus* spp. excludes two species of the regional Red List (*Euphorbia terracina*, *Silene nicaeensis*) in the protected habitat 'Dune with *Euphorbia*

*terracina*', coded 2,220 in the Habitats Directive 92/43/EEC. Similarly, *A. artemisiifolia* may exhibit a stronger impact on species composition than *A. fruticosa*. However, while *A. artemisiifolia* does not affect the nature of the community, *A. fruticosa* favours annual nitrophilous and shade-tolerant species at the expense of the characteristic association of heliophilous geophytes and chamaephytes of nutrient-poor soil (Table 2 and Fig. 3). In five other cases, the mean Ellenberg-N index has increased (Fig. 3), demonstrating the selection of nitrophilous ruderal species at the expense of characteristic species of the initial community. In addition to concise indicators such as species richness or the Jaccard dissimilarity index, it is therefore necessary to take into account both the conservation interest of the invaded habitat and the direction of changes in the resulting communities filtered by invasion.

Finally, it may be argued that the impact measured at the plot scale may not be representative of the effect of an invasive species at the habitat scale. Indeed, our study showed that impact at the habitat scale tends to be lower than at the plot scale (Table 1 and Fig. 2), as already shown in other studies (Gaertner et al. 2009; Powell et al. 2011). The impacts at the two levels are nevertheless correlated, meaning that spatial diversity at the habitat scale does not completely compensate the loss of species at the plot scale. While invasive species that are able to form massive stands over more than thousands of m<sup>2</sup> (covering a whole habitat at the landscape level) are probably rare, the community-level impact remains nevertheless a good estimator of potential damage at higher spatial scales for the most extensive invasive plant species.

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## Appendix 1

See Table 5.

**Table 5** Overview of locations used in the study (with five replications per locations)

| Location | Species                             | EUNIS habitats | Latitude and longitude (WGS84) | Minimum residence time  | Known disturbances  |
|----------|-------------------------------------|----------------|--------------------------------|---|---|
| 1        | <i>Ambrosia artemisiifolia</i>      | C3.5           | N43 57.254 E4 29.237           | First occurrences in the Gardon river during the 1960s (Chauvel and Cadet 2011) | Natural (annual) disturbances by river flood              |
| 2        | <i>A. artemisiifolia</i>            | C3.5           | N43 56.306 E4 33.456           |   |   |
| 3        | <i>A. artemisiifolia</i>            | C3.5           | N43 55.921 E4 19.210           |   |   |
| 4        | <i>Amorpha fruticosa</i>            | B1.3           | N43 33.233 E4 00.848           | Early 2000s   | No known disturbances                                     |
| 5        | <i>A. fruticosa</i>                 | B1.3           | N43 33.361 E4 01.613           | Early 2000s   |   |
| 6        | <i>A. fruticosa</i>                 | B1.3           | N43 29.206 E4 08.549           | 1940s   | No known disturbances                                     |
| 7        | <i>A. fruticosa</i>                 | C3.2           | N43 35.784 E4 20.459           | 1940s   |   |
| 8        | <i>A. fruticosa</i>                 | C3.2           | N43 36.786 E4 19.670           |   |   |
| 9        | <i>A. fruticosa</i>                 | C3.2           | N42 53.927 E3 03.223           |   | Occasional grazing by horses                              |
| 10       | <i>Artemisia verlotiorum</i>        | E2.7           | N43 56.000 E4 19.151           | 1950s   |   |
| 11       | <i>A. verlotiorum</i>               | E2.7           | N43 56.005 E4 19.114           |   |   |
| 12       | <i>A. verlotiorum</i>               | E2.7           | N43 56.036 E4 19.110           |   | Natural disturbances by important river flood             |
| 13       | <i>A. verlotiorum</i>               | G1.1           | N44 01.859 E4 08.585           |   |   |
| 14       | <i>A. verlotiorum</i>               | G1.1           | N44 01.842 E4 08.520           |   |   |
| 15       | <i>A. verlotiorum</i>               | G1.1           | N43 56.035 E4 19.118           |   | No known disturbances (nature reserve)                    |
| 16       | <i>Baccharis halimifolia</i>        | A2.5           | N42 45.459 E3 01.989           | Early 1980s (Amigo 1983)  |   |
| 17       | <i>B. halimifolia</i>               | A2.5           | N42 45.285 E3 01.997           |   |   |
| 18       | <i>B. halimifolia</i>               | A2.5           | N42 45.324 E3 01.967           |   | No known disturbances (nature reserve)                    |
| 19       | <i>B. halimifolia</i>               | F9.3           | N42 45.147 E3 01.969           |   |   |
| 20       | <i>B. halimifolia</i>               | F9.3           | N42 45.242 E3 01.925           |   |   |
| 21       | <i>B. halimifolia</i>               | F9.3           | N42 45.306 E3 01.999           |   | No known disturbances                                     |
| 22       | <i>Carpobrotus</i> spp.             | B3.3           | N42 30.942 E3 08.291           | 1940s   |   |
| 23       | <i>Carpobrotus</i> spp.             | B3.3           | N42 30.885 E3 08.159           |   |   |
| 24       | <i>Carpobrotus</i> spp.             | B3.3           | N42 31.298 E3 07.195           |   | Tourist frequentation (but not enough to cause trampling) |
| 25       | <i>Carpobrotus</i> spp.             | B1.4           | N42 53.927 E3 03.223           | 1930s   |   |
| 26       | <i>Carpobrotus</i> spp.             | B1.4           | N42 53.705 E3 03.077           |   |   |
| 27       | <i>Carpobrotus</i> spp.             | B1.4           | N42 48.711 E3 02.127           |   | Natural disturbances but only by important river flood    |
| 28       | <i>Impatiens balfourii</i>          | G1.1           | N43 36.431 E3 07.209           | 1990s   |   |
| 29       | <i>I. balfourii</i>                 | G1.1           | N43 41.634 E3 33.947           |   |   |
| 30       | <i>I. balfourii</i>                 | G1.1           | N43 41.654 E3 33.931           |   | Grazing by sheeps   |
| 31       | <i>Phyla filiformis</i>             | A2.5 grazed    | N43 16.242 E3 08.147           | First occurrences during the 1920s  |   |
| 32       | <i>P. filiformis</i>                | A2.5 grazed    | N43 14.303 E3 10.639           |   |   |
| 33       | <i>P. filiformis</i>                | A2.5 grazed    | N43 14.319 E3 10.617           |   | No known disturbances (nature reserve)                    |
| 34       | <i>P. filiformis</i>                | A2.5           | N43 16.191 E3 08.290           |   |   |
| 35       | <i>P. filiformis</i>                | A2.5           | N43 16.008 E3 07.698           |   |   |
| 36       | <i>P. filiformis</i>                | A2.5           | N43 14.350 E3 10.589           |   | Natural (annual) disturbances by river flood              |
| 37       | <i>Reynoutria</i> × <i>bohemica</i> | C3.5           | N44 10.470 E3 50.663           | 1980s   |   |
| 38       | <i>R.</i> × <i>bohemica</i>         | C3.5           | N44 08.519 E3 52.279           |   |   |
| 39       | <i>R.</i> × <i>bohemica</i>         | C3.5           | N44 10.054 E3 50.661           |   | Natural disturbances but only by important river flood    |
| 40       | <i>R.</i> × <i>bohemica</i>         | G1.1           | N44 10.636 E3 50.389           |   |   |
| 41       | <i>R.</i> × <i>bohemica</i>         | G1.1           | N44 08.530 E3 52.275           |   |   |
| 42       | <i>R.</i> × <i>bohemica</i>         | G1.1           | N44 10.062 E3 50.666           |   |   |

As the exact date of introduction is usually not known, we give the minimum residence time as the first known occurrence of the species according to the literature. Except where specific reference is given, all historical data were gathered from the SILENE database (CBNMed 2011b). Known disturbances are based on the knowledge of the sites by local land managers

EUNIS Habitats A2.5 Coastal saltmarshes and saline reedbeds; B1.3: Shifting coastal dunes; B1.4: Coastal stable dune grassland (grey dunes); B3.3: Rock cliffs, ledges and shores, with angiosperms; C3.2: Water-fringing reedbeds and tall helophytes other than canes; C3.5: Periodically inundated shores with pioneer and ephemeral vegetation; E2.7: Unmanaged mesic grassland; G1.1: Riparian and gallery woodland, with dominant [Alnus], [Betula], [Populus] or [Salix]; F9.3: Southern riparian galleries and thickets



## Appendix 2

See Table 6.

**Table 6** Summary of the linear mixed models analyses describing the effects of species, habitats (nested within species) and locality (nested within habitats nested within species) on the relative impacts on species richness (S), on Shannon's diversity (H') and on the Jaccard dissimilarity index (D<sub>J</sub>)

| Effect                           | Impact on species richness (S <sub>r</sub> ) |                     |                  | Impact on Shannon's diversity (H') |                     |                  | Impact on Jaccard dissimilarity (D <sub>J</sub> ) |                     |                  |
|----------------------------------|--|---------------------|------------------|------------------------------------|---------------------|------------------|---|---------------------|------------------|
|                                  | df, ddf                                      | F or X <sup>2</sup> | P                | df, ddf                            | F or X <sup>2</sup> | P                | df, ddf   | F or X <sup>2</sup> | P                |
| <i>Fixed term</i> <sup>a</sup>   |  |                     |                  |                                    |                     |                  |   |                     |                  |
| Species                          | 7, 34  | 11.00               | <b>&lt;0.001</b> | 7, 34                              | 2.07                | 0.074            | 7, 34   | 5.64                | <b>&lt;0.001</b> |
| <i>Random terms</i> <sup>b</sup> |  |                     |                  |                                    |                     |                  |   |                     |                  |
| Habitat (Species)                | 1  | 5.68e – 14          | 1                | 1                                  | 1.9                 | 0.200            | 1   | 0.68                | 0.400            |
| Locality [Habitat (Species)]     | 1  | 20.54               | <b>&lt;0.001</b> | 1                                  | 22.70               | <b>&lt;0.001</b> | 1   | 13.34               | <b>&lt;0.001</b> |

<sup>a</sup> The P values for the fixed effects are calculated from F test based on Satterthwaite approximation for denominator degrees of freedom (ddf)

<sup>b</sup> The tests on random effects are performed using log-likelihood ratio tests with one degree of freedom (df), which means, testing one effect in a time. Bold P values indicate significance levels smaller than 0.05

## Appendix 3

See Table 7.

**Table 7** Summary of significant variations in frequency of occurrence for 61 species amongst invaded and non-invaded plots

| Invasive species        | EUNIS habitats | Impacted species                            | Life form | Occurrence |      | P value |
|-------------------------|----------------|---|-----------|------------|------|---------|
|                         |                |   |           | Non.-Inv.  | Inv. |         |
| <i>Carpobrotus</i> spp. | B1.4           | <i>Alkanna matthioli</i>                    | T         | 7          | 0    | 0.006   |
|                         |                | <i>Andryala integrifolia</i>                | T         | 8          | 1    | 0.014   |
|                         |                | <i>Cladanthus mixtus</i>                    | T         | 5          | 0    | 0.042   |
|                         |                | <i>Erodium cicutarium</i>                   | T         | 11         | 2    | 0.003   |
|                         |                | <i>Hypochaeris glabra</i>                   | T         | 7          | 1    | 0.035   |
|                         |                | <i>Lobularia maritima</i>                   | H         | 12         | 4    | 0.009   |
|                         |                | <i>Senecio vulgaris</i>                     | T         | 6          | 0    | 0.017   |
|                         |                | <i>Silene nicaeensis</i> *                  | H         | 5          | 0    | 0.042   |
|                         |                | <i>Trifolium cherleri</i>                   | T         | 5          | 0    | 0.042   |
| <i>A. fruticosa</i>     | B3.3           | <i>Euphorbia terracina</i> *                | G         | 10         | 2    | 0.008   |
|                         |                | <i>Pallenis spinosa</i>                     | H         | 6          | 0    | 0.017   |
|                         |                | <i>Sedum sediforme</i>                      | C         | 12         | 1    | 0       |
| <i>P. filiformis</i>    | C3.2           | <i>Artemisia campestris</i>                 | G         | 14         | 7    | 0.014   |
|                         |                | <i>Carduus pycnocephalus</i>                | H         | 0          | 7    | 0.006   |
| <i>I. balfourii</i>     | A2.5           | <i>Poa trivialis</i>                        | H         | 5          | 0    | 0.042   |
|                         |                | <i>Elytrigia repens</i>                     | G         | 11         | 3    | 0.009   |
|                         |                | <i>Geranium dissectum</i>                   | T         | 14         | 7    | 0.014   |
|                         |                | <i>Plantago lanceolata</i>                  | H         | 4          | 11   | 0.027   |
|                         |                | <i>Sonchus asper</i>                        | T         | 7          | 1    | 0.035   |
| <i>I. balfourii</i>     | G1.1           | <i>Galium mollugo</i> subsp. <i>erectum</i> | H         | 5          | 0    | 0.042   |

Table 7 continued

| Invasive species             | EUNIS habitats | Impacted species                                    | Life form | Occurrence |       | P value |
|------------------------------|----------------|---|-----------|------------|-------|---------|
|                              |                |   |           | Non.-Inv.  | Inv.  |         |
| <i>A. verlotiorum</i>        | G1.1           | <i>Acer negundo</i>                                 | P         | 9          | 1     | 0.005   |
|                              |                | <i>Ambrosia artemisiifolia</i>                      | T         | 10         | 2     | 0.008   |
|                              |                | <i>Bidens frondosa</i>                              | T         | 14         | 5     | 0.002   |
|                              |                | <i>Chenopodium album</i>                            | T         | 13         | 4     | 0.003   |
|                              |                | <i>Daucus carota</i>                                | H         | 9          | 1     | 0.005   |
|                              |                | <i>Echium vulgare</i>                               | H         | 11         | 2     | 0.003   |
|                              |                | <i>Euphorbia cyparissias</i>                        | H         | 11         | 2     | 0.003   |
|                              |                | <i>Lactuca</i> sp.                                  | NA        | 8          | 0     | 0.002   |
|                              |                | <i>Oenothera</i> gr. <i>biennis</i>                 | H         | 11         | 1     | 0       |
|                              |                | <i>Picris hieracioides</i>                          | H         | 5          | 0     | 0.042   |
|                              |                | <i>Senecio inaequidens</i>                          | C         | 6          | 0     | 0.017   |
|                              |                | <i>Setaria viridis</i> subsp. <i>viridis</i>        | T         | 9          | 0     | 0.001   |
|                              |                | <i>Vulpia myuros</i>                                | T         | 5          | 0     | 0.042   |
|                              |                | <i>Xanthium orientale</i> subsp. <i>italicum</i>    | T         | 15         | 7     | 0.002   |
|                              | E2.7           | <i>Chondrilla juncea</i>                            | H         | 10         | 1     | 0.002   |
|                              |                | <i>Convolvulus arvensis</i>                         | H         | 5          | 0     | 0.042   |
|                              |                | <i>Fraxinus excelsior</i>                           | P         | 6          | 0     | 0.017   |
| <i>Orlaya grandiflora</i>    |                | T   | 5         | 0          | 0.042 |         |
| <i>Torilis arvensis</i>      |                | T   | 15        | 8          | 0.006 |         |
| <i>Vicia hybrida</i>         |                | T   | 9         | 2          | 0.021 |         |
| <i>B. halimifolia</i>        | A2.5           | <i>Dorycnium pentaphyllum</i> subsp. <i>gracile</i> | H         | 13         | 4     | 0.003   |
|                              |                | <i>Elytrigia scirpea</i>                            | H         | 13         | 2     | 0       |
|                              |                | <i>Limonium narbonense</i>                          | H         | 7          | 0     | 0.006   |
|                              | F9.3           | <i>Sonchus maritimus</i>                            | G         | 12         | 3     | 0.003   |
|                              |                | <i>Bryonia cretica</i> subsp. <i>dioica</i>         | G         | 7          | 1     | 0.035   |
| <i>R. × bohemica</i>         | C3.5           | <i>Elytrigia scirpea</i>                            | H         | 14         | 8     | 0.035   |
|                              |                | <i>Echium vulgare</i>                               | H         | 6          | 0     | 0.017   |
|                              |                | <i>Galium corrudifolium</i>                         | H         | 7          | 0     | 0.006   |
|                              |                | <i>Lactuca saligna</i>                              | H         | 8          | 0     | 0.002   |
|                              |                | <i>Ononis</i> sp.                                   | NA        | 5          | 0     | 0.042   |
|                              |                | <i>Rumex acetosella</i>                             | H         | 10         | 1     | 0.002   |
|                              | G1.1           | <i>Alliaria petiolata</i>                           | H         | 8          | 15    | 0.006   |
|                              |                | <i>Anisantha diandra</i>                            | T         | 14         | 3     | 0       |
|                              |                | <i>Artemisia verlotiorum</i>                        | H         | 7          | 0     | 0.006   |
|                              |                | <i>Cardamine hirsuta</i>                            | T         | 0          | 9     | 0.001   |
|                              |                | <i>Galium aparine</i> subsp. <i>aparine</i>         | T         | 10         | 2     | 0.008   |
|                              |                | <i>Persicaria lapathifolia</i>                      | T         | 0          | 5     | 0.042   |
|                              |                | <i>Rubus</i> sp.                                    | NA        | 11         | 1     | 0       |
| <i>Saponaria officinalis</i> | H              | 12  | 3         | 0.003      |       |         |
| <i>Stellaria holostea</i>    | H              | 8   | 1         | 0.014      |       |         |
| <i>Urtica dioica</i>         | G              | 8   | 1         | 0.014      |       |         |

Raunkiaer life form according to Julve (1998): *T* therophytes, *H* hemicryptophytes, *G* geophytes, *C* chamaephytes, *P* Phanerophytes, *NA* for species determined at the genus level including species belonging to different life forms. Occurrences are the sum of species presence in 4 m<sup>2</sup> invaded or non-invaded plots (n = 15). *P* value associated to Fisher's exact test. \* Species with a patrimonial value (either protected or listed on the Red List)

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