Community-level impacts of three invasive alien plants in Mediterranean coastal habitats

Nicolas Chagué¹ and Guillaume Fried^{2,*} ¹ University of Burgundy, Dijon, France ² Anses - Plant Health Laboratory, Montpellier, France

ABSTRACT: Rigorous impact assessments are of vital importance for policy makers and land managers which have to set management priorities between invasive alien species, given the limited financial resources available. Although there is a general consensus regarding the negative effects of invasive alien species, studies that quantify community-level impacts of invasive plants are still scarce. In order to build a standardised way of measuring local effects of invasive plants, the objectives of this study were i) to explore the abundance-effect relationship of invasive plants on various aspects of local communities diversity (species richness, species evenness, abundance) and ii) to analyze how these effects vary depending on the traits of the invaders and the traits of the native plants. For this purpose, the vegetation of invaded plots (invaded by *Phyla filiformis, Carpobrotus edulis* and *Amorpha fruticosa*) and uninvaded plots with similar habitat conditions was sampled during spring 2011. For *Carpobrotus* spp., the sampling covers a gradient of invasion from ~ 0% to ~ 100% coverage of the

invasive plant. The practical value of this approach for impact assessment is to move forward on the question of whether we can get a good estimate of the effect of invasive plants using both their abun-

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1 INTRODUCTION

dance and their traits.

Most territories are facing an increasing number of invasive alien plants requiring both management actions and a preventive strategy to limit new introductions. One important part of such preventive strategies includes Weed Risk Assessments (WRA), which are science-based risk analysis tools for determining the weed potential of new species introduced or detected on a territory (Pheloung et al., 1999). These assessments take into account climate matching, spread capacity and impacts on the environment or on economic activities of invasive alien plants (Fried et al., 2009).

While it is recognized that invasive alien species alter native communities and ecosystem functioning through their dominance (Richardson et al., 2000), environmental impact assessments carried out with WRA tools are often lacking precise data about changes in native species richness, in native species composition or on the effects of the invader on a particular rare species. Some WRA tools use the maximum observed cover of the invasive in a natural habitat as a proxy of its impact (Branquart, 2007; Brunel et al., 2010). Species able "to build large, dense and persistent populations (cover of at

least 80%)" (Brunel et al., 2010), in a natural or a semi-natural habitats are considered as having a high impact. Although seeming reasonable, this implies a threshold effect. This assumption seems to be correct for Lantana camara for which an Australian study indicated that native species richness remained stable below 75% cover of the invasive, but declined rapidly above this threshold level (Gooden et al., 2009). Second, this kind of impact assessment implies that all invasive species with a cover greater than 80% will be classified with the same risk while a few recent studies (Vilà et al., 2006; Hejda et al., 2009) showed that the order of magnitude of the impacts of plant invaders can vary seven fold ranging from a loss of only 12 % of species richness (Impatiens glandulifera) to a loss of 86% (Reynoutria sachalinensis) when the cover of these 2 species is effectively higher than 80%. This brief review reveals the need for more studies that would measure precisely the community-level effects of invasive alien plants in order to improve impact assessment in WRA protocols.

Besides providing precise data on the impacts of three important invasive species in the Mediterranean area, the present study aims at searching general rules linking the intensity of the impacts to the traits of the invasive species (growth forms, plant height, etc.) as well as to the characteristics of the native invaded community and traits of the native dominant species (Emery and Gross, 2006).

Corresponding author address: Guillaume Fried, Anses, Laboratoire de la Santé des Végétaux, France;

tel: + 33 467 02 25 53; fax: + 33 467 02 00 70; email: guillaume.fried@anses.fr

2 MATERIAL AND METHODS

2.1. Study sites and species

Three taxa representing different growth forms have been studied in the Mediterranean part of France: (1) Amorpha fruticosa, a North-American nanophanerophyte invading riparian habitats and sand dunes in Camargue and the Rhone valley, (2) Carpobrotus spp. (including both C. edulis and C. acinaciformis), succulent chamaephytes from south Africa, invading several coastal habitats and (3) Phyla filiformis, a stoloniferous hemicryptophyte from South America which proliferates in Mediterranean salt meadows.

Field work was done between March and May 2011. For each of the three studied neophytes, impacts were measured in the two main habitat types that these species invade in the Mediterranean coastal area of France (Table 1). All these habitats, except from water-fringing reedbeds, are included in Natura 2000 sites. In each habitat, 3 sites were studied and within each site, 5 pairs of adjacent 4 m² vegetation plots were sampled. Following the methodology developed by Vilà et al. (2006) and Hejda et al. (2009), for each pair of quadrat, one plot of the pair was placed in heavily invaded vegetation ('invaded plots') where the invader was dominant and had at least 80% cover and the second plot in a neighbouring vegetation, where the invader had no cover ('non-invaded plots'). The non-invaded plot was chosen in order to have similar site conditions (e.g., same slope, same exposure) to the invaded plot. To ensure that those conditions are quite similar, the noninvaded and the invaded plot were situated in close vicinity. Cover of every plant was estimated and the height of the invasive plant as well as the height of the native dominant species was measured in each plot on ten individuals.

Forty supplementary 4 m² plots (20 in the sand dune communities and 20 in the coastal cliff communities) were sampled across a continuum of *Carpobrotus* invasion (with covers ranging between 5 and 75%), in order to test the existence of a threshold effect for this species. In total, 220 vegetation plots were sampled in Mediterranean coastal habitats.

2.2. Data analysis

For each invaded habitat type, the differences in species richness, Shannon's diversity and species evenness (i.e., how close in cover each species in a plot are) between invaded and non-invaded plots were tested using a pairwise Wilcoxon-test. Total species richness per habitat (γ -diversity) was also compared. An analysis of similarity (ANOSIM) was used to test whether there are significant differences in species composition (using the Jaccard similarity index) and to detect changes in relative covers of resident species (using the Bray-Curtis index calculated on cover abundance).

Table 1: Habitat type classification and GPS localisation of the three study sites for each studied species.

Habitats	EUNIS Code	Site locations
Carpobrotus spp.		
Mediterranean clifftop phrygana (Plantagini subulatae-Dianthetum catalaunici, Thymelaeo hirsutae- Plantaginetum subulatae)		N42 30.942 E3 08.291
	F7.115	N42 30.885 E3 08.159
		N42 31.298 E3 07.195
		N42 53.927 E3 03.223
Grey dunes Crucianellion maritimae	B1.43	N42 53.705 E3 03.077
		N42 48.711 E3 02.127
Phyla filiformis		
		N43 16.242 E3 08.147
Disturbed Mediterranean salt meadows Agropyro-Artemision coerulescentis	A2.52	N43 14.303 E3 10.639
		N43 14.319 E3 10.617
Mediterranean salt meadows Agropyro-Artemision coerulescentis		N43 16.191 E3 08.290
	A2.52	N43 16.008 E3 07.698
		N43 14.350 E3 10.589
Amorpha fruticosa		
		N43 33.233 E4 00.848
Grey dunes Crucianellion maritimae	B1.43	N43 33.361 E4 01.613
		N43 29.206 E4 08.549
Water-fringing reedbeds	C3.2	N43 35.784 E4 20.459
		N43 36.786 E4 19.670
		N42 53.927 E3 03.223

Changes in vegetation structure were assessed by comparing the coverage of each life form: therophytes, hemicryptophytes, geophytes, chamaephytes and phanerophytes (sensu Raunkiaer, 1934) per plot.

The impacts of the invaders on individual native species were assessed by analysing changes in native species cover between invaded and non-invaded plots using a pairwise Wilcoxon-test. Differences in the occurrence (i.e. number of plots occupied by each species) amongst invaded and non-invaded plots were assessed using the Fisher exact test using presence/absence data.

In order to interpret species composition changes between non-invaded and invaded plots, ecological indicator values were used by computing for each community the mean Ellenberg-values (Ellenberg et al., 1992) for light, edaphic moisture, soil reaction and nitrogen, adapted for France (Julve, 1998).

For the analysis of threshold relationships between Carpobrotus cover and species rich-

ness the framework developed by Gooden et al. (2009) was followed. First, individual linear regressions were used to assess the relationship between *Carpobrotus* cover and species richness, employing the 15 pairs of invaded and non-invaded plots plus the 20 supplementary plots (moderately invaded) resulting in a complete set of sites (i.e. n = 50) ranging from 0 to 100% cover of the invaders. Secondly, nonlinear cubic models were also applied to detect the presence of potential impact thresholds.

The Relative Impact (RI) of an invasive species was calculated as follow: $RI = (a_{NI}-a_I)/(a_{NI}+a_I)$, where *a* is the variable of interest (e.g., species richness), *I* is the invaded plot and *NI* is the non-invaded plot.

3 RESULTS

3.1. Impacts on species richness

Impacts on the invaded communities markedly differed among the three invasive species tested (Table 2). For *Carpobrotus* spp. and to a lesser extent for *P. filiformis*, we observed a significant decrease in species richness per plot in the different types of habitats, whereas no decrease was observed in *A. fruticosa* invaded plots. Differences in γ -diversity at the habitat level followed more or less the same pattern.

The Shannon diversity index was only significantly reduced in *Carpobrotus* stands, from H=1.94 to H=1.56 in coastal cliffs (Wilcoxon test, p<0.05) and from H=2.16 to H=0.96 in grey dunes (Wilcoxon test, p<0.01). Evenness of native communities increased for *Carpobrotus* in both habitats and for *P. filiformis* only in degraded wet meadows.

Species richness declined linearly with increasing *Carpobrotus* cover (Figure 1). Cubic regressions provided no better fit to the data (R^2 =0.63, p=3.91.10⁻¹⁰). The rate of species richness loss is slightly higher in sand dune communities compared to clifftop phrygana communities.

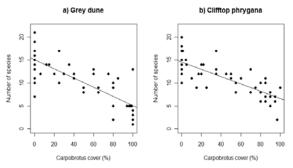


Figure 1. Relationships between *Carpobrotus* cover (%) and species richness in (a) grey dunes (R^2 =0.62, p=2.76.10⁻², slope=-0.100) and

(b) clifftop phrygana communities (R²=0.61, p= $1.24.10^{-11}$, slope=-0.079) (n=50).

3.2. Impacts on vegetation structure

Almost all life forms were affected in their coverage with some exceptions. Therophytes response to the invasion is contrasted for a given invasive alien plant or within the same habitat: *Carpobrotus* had no impact on therophytes in clifftop phrygana while they are strongly reduced in grey dunes. In this latter habitat, stands of *A. fruticosa* significantly favoured therophytes that became the dominant life form at the expense of chamaephytes and geophytes.

3.3. Impacts on species composition

Species composition varied significantly between non-invaded and invaded plots (Table 2). As shown in Fig. 2, there was a correlation between the impact on species richness and the change in species composition. However, in the present studies this link was weaker than for other studied species (Hejda et al., 2009) with for example the effect of A. fruticosa in grey dunes, that did not induce a decrease in species richness while it caused one of the highest change in species composition (Table 2). Higher dissimilarities observed with the Bray-Curtis index compared to the Jaccard index indicate a stronger effect on species relative abundance in the communities invaded by P. filiformis and in dense stands of A. fruticosa in grey dunes.

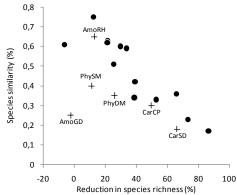


Figure 2. Correlation between the impact of the invasive species studied in Hejda et al. 2009 (●) and in our study (+) on species composition (expressed as mean Sorensen similarity between invaded and uninvaded plot in a pair) and species richness S: r= -0.65, t=-3.55, df=17, P<0.01. Abbreviations: Amo=Amorpha fruticosa, Car=Carpobrotus spp., Phy=Phyla filiformis. CP= clifftop phrygana, GD=grey dunes, RH=riparian habitat, DM=degraded salt meadows, SM=salt meadows.

According to the Fisher's exact test on species occurrence and the Wilcoxon test on the mean species cover, some species significantly contributed to compositional differences (Table 4). There was a clear asymmetry with many cases of species excluded by the invaders (89%) and very few cases where a species was favored (11%).

These changes in species composition were not random (Fig. 3), especially in grey dune communities. The mean Ellenberg-L values decreased under stands of *A. fruticosa*, while the mean Ellenberg-N values increased in invaded plots of *A. fruticosa* and *Carpobrotus* to a lesser extent. No significant changes were detected in the other habitats.

Table 2. The invasive alien plants studied and their impacts on community characteristics. The number of species (mean ± SD, n=15) in invaded (S inv) and uninvaded plot is shown (S non-inv). At the plot scale, the impact on species richness S is expressed as the mean percentage reduction of species number in invaded plot compared to uninvaded ones (100%). A positive value indicates a higher species number in uninvaded plots, a negative value indicated a higher richness in invaded vegetation. At the larger scale, the impact is expressed as the percentage reduction of the total number of species recorded in invaded (Stot inv) plots and related to that recorded in uninvaded plot (Stot uninv = 100%). Mean Jaccard and Bray-Curtis dissimilarity indexes, calculated as an average value for the 15 pairs of plots, indicate the impact on the species composition; the higher the dissimilarity, the more dissimilar is the invaded and the uninvaded vegetation. Significant differences between invaded and non-invaded plots in species richness S (tested by Wilcoxon paired test) and species composition (tested by ANOSIM) are shown: *P<0,05, **P<0,01 and ***P<0,001.

3.4. Characteristics of the native communities influencing the impacts

The relative impact (RI) on native species richness and native species composition was positively correlated with species richness of the non-invaded plots (Spearman rank tests, rho=0.56, p<0.001 and rho=0.34, p<0.001, respectively) meaning that initially species-poor communities suffer less from the impact of plant invasions than species-rich communities. The RI on species richness and composition is also negatively correlated with the mean plant height of the dominant species in the non-invaded plot (Spearman rank tests, rho=-0.58, p<0.001, rho=-0.62, p<0.001).

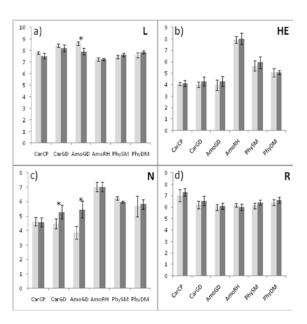


Figure 3. Ellenberg mean values for noninvaded (clear grey) and invaded plots (dark grey) a) for light (L), b) edaphic moisture (HE), c) nitrogen (N), d) soil reaction (R) and for each species in each habitat.

Invasive species	Habitats	S non inv	S inv	Impact on S (%)	Stot non inv	Stot inv	Impact on Stot (%)	Jaccard	Bray-Curtis
Carpobrotus spp.	Clifftop phrygana	$14{,}5\pm2{,}7$	$7,3\pm3,3$	49,7***	63	33	47,6	0,89***	0,7**
Carpobrotus spp.	Grey dunes	$14{,}9\pm4{,}0$	$5,1 \pm 3,4$	66,1***	63	47	25,4	0,89***	0,82***
Phyla filiformis	Salt meadows	$13,1\pm5,7$	$11{,}7\pm3{,}0$	11,1*	44	38	13,6	0,57*	0,6***
Phyla filiformis	Disturbed salt meadows	$18 \pm 4,6$	$13{,}3\pm3{,}1$	25,9**	59	48	18,6	0,54	0,65***
Amorpha fruticosa	Grey dunes	$8{,}7\pm2{,}8$	$8{,}9\pm2{,}5$	-2,3	34	42	-23,5	0,63*	0,75***
Amorpha fruticosa	Water-fringing reedbeds	$5,7\pm2,3$	$4{,}9\pm1{,}2$	12,9	21	19	9,5	0,39	0,35

Table 4. Summary of significant variations in frequency of occurrence and abundance for 33 species amongst invaded and non-invaded plots of the three invasive and five habitats. Occurrences are the sum of species presence in 4 m² invaded or non-invaded plots (n=15). Mean cover is the average cover over all plots. Legend for P-values: * P<0.05, **P<0.01, ***P<0.001.

Species	Occurrenœ			Mean cover				
	Inv	Non-inv	Р	Inv	Non-inv	Р		
Carpobrotus spp.	Medi	terranea	ın cli	fftop phr	ygana			
Sedum sediforme	1	12	***	0,067	3,667	**		
Euphorbia terracina	2	10	**	0,133	1,200	**		
Pallenis spinosa	0	6	*	0,000	0,533	*		
Lobularia maritima	0	5	*	0,000	1,400			
Daucus carota	6	12		2,300	5,067	*		
Sonchus tenerrimus	4	10		0,333	3,600	**		
Dactylis glomeratasubsp.hispanica	5	9		0,667	2,333	*		
Brachypodium retusum	11	10		11,333	31,133	*		
Carpobrotus spp.	Grey dunes							
Erodium cicutarium	2	11	**	0,133	1,267	**		
Echium calycinum	0	7	**	0,000	0,800	*		
Lobularia maritima	4	12	**	0,333	1,733	**		
Andryala integrifolia	1	8	*	0,067	1,000	*		
Senecio vulgaris	0	6	*	0,000	0,600	*		
Hypochaeris glabra	1	7	*	0,133	1,600	*		
Anthemis mixta	0	5	*	0,000	0,733			
Silene nicaeensis	0	5	*	0,000	1,000			
Trifolium cherleri	0	5	*	0,000	6,000			
Plantago lagopus	2	8		0,200	3,667	*		
Paronychia argentea	6	12		0,600	12,600	**		
Medicago littoralis	3	9		0,400	1,800	*		
Bromus madritensis	2	7		0,133	0,733	*		
Amorpha fruticosa	Grey	dunes						
Artemisia campestris	7	14	*	2,300	16,000	**		
Helichrysum stæchas	6	9		2,333	10,067	*		
Bromus sterilis	11	8		13,200	1,800	**		
Carduus pycnocephalus	7	0	**	4,633	0,000	*		
Amorpha fruticosa	Wate	r-fringin	gree	dbeds				
Poa trivialis	0	5	*	0,000	3,867			
Phyla filiformis	Saltmeadows							
Elytrigia repens	3	11	**	0,533	29,733	**		
Geranium dissectum	7	14	*	1,800	2,667			
Sonchus asper	1	7	*	0,333	0,800			
Limoniumnarbonense	6	9		0,800	1,667	*		
Trifolium fragiferum	7	7		2,267	5,867	*		
Plantago lanœolata	11	4	*	2,333	0,600	*		
Phyla filiformis	Distu	rbed sal	t me	adows				
Medicago minima	3	9		0,4	3,33333	*		
Linum bienne	1	6		0,0667	1,13333	*		
Elytrigia repens	6	9		2	22,1333	*		
Trifolium fragiferum	11	12		3,2	20,8667	**		
Limoniumnarbonense	10	7		4	1,66667	**		

4 DISCUSSION

Measuring the impacts of invasive species on native communities in several habitat types by comparing invaded and non-invaded sites makes it possible to compile lots of information directly useful for WRA and can enable to improve WRA protocols.

4.1. Impacts of plant invaders on Mediterranean coastal communities

As might be expected, the magnitude of the impact differed among the three species, with *Carpobrotus* exhibiting the largest impact (- 66% in species loss) and *Amorpha* the least (+ 2%).

Our study confirms the huge impact of *Carpobrotus* on Mediterranean native communities (Vila et al., 2006) with a similar order of magnitude as *Fallopia* x *bohemica* in central Europe (Hejda et al., 2009). Increasing Ellenberg-N values in invaded sand dunes can be interpreted as a result of the important amount of litter produced by *Carpobrotus* spp., which increases organic N (Vila et al., 2006) at the expense of specialists of poor sandy conditions (e.g., *Hypochaeris glabra*). A significant impact of *Carpobrotus* has also been detected on a regionally protected species (*Euphorbia terracina*) and on another species considered rare at the regional scale (*Silene nicaeensis*).

Phyla filiformis, for which there was no prior studies on its impact in Europe, exhibited an intermediary effect on species loss ranging from 11 to 26%. According to similarity indices, P. filiformis altered more species relative abundance (Bray-Curtis) than species composition (Jaccard). P. filiformis clearly reduced the cover of dominant forage plants of salt meadows (Elytrigia repens, Trifolium fragiferum). This finding indicates that *P. filiformis* has also an impact on agricultural activities, reducing available food for cattle. Although the impacts of *P. filiformis* were not higher in degraded salt meadows, there is a trend for a more pronounced impact on species richness and composition. This result is in line with other studies showing that invasive plants are more resistant to disturbances that could favor them over native species (MacDougall and Turckington, 2005).

Surprisingly, patches of A. fruticosa caused no significant loss in species richness, which is in contradiction with the impacts of this species on permanent grasslands in central Europe (Sărăteanu, 2011). This is also contrary to other studies that have pinpointed the highest impact of invasive trees among different life forms (Gaertner et al., 2009). However, the drastic changes in species composition observed in a Natura 2000 habitats like grey dune communities (Crucianellion maritiimae) is of great concern. Our study is one of the first that illustrates the directional changes driven by this shrub. A. fruticosa had an impact on characteristic species of grey dunes communities (Artemisia campestris subsp. glutinosa, Helichrysum stoechas) which were replaced by generalist ruderal species (Bromus sterilis, Carduus pycnocephalus). This latter change could be directly related to nitrogen fixation due to root nodulation (Weber, 2003). In one of the studied site, the North-American invasive Conyza sumatrensis was always associated with invaded plots of A. fruticosa. This shows that A. fruticosa could facilitate the invasion by other neophytes.

4.2. Community-level features determining invasibility

There has been a long debate concerning the relationship between invasion success and species diversity of the recipient community (Levine et al., 2004). More (functionally) diverse communities are believed to use better available resources, leaving less resource for potential invaders (Hooper and Dukes, 2010). In our study, the relative impact of the three invaders (on species richness or on species composition) is higher in species-rich communities. A similar result has been found on Mediterranean islands by Vilà et al. (2006) which concluded that areas of higher native plant diversity are not immune to species loss. Hejda et al. (2009) suggests that the effect of Impatiens glandulifera or Helianthus tuberosus does not differ much from the competitive influence of tall native dominant species of riparian habitat. This would mean that the addition of an invasive species in a community already strongly dominated by a tall native species would have few impacts on the community. This is consistent with the negative correlation we found between the mean plant height of the dominant species of the native communities and the relative impact of the invaders. This could explain the low impact of A. fruticosa invading water-fringing reedbeds already dominated by tall competitive plants like Rubus spp. or Phragmites australis whereas, on the other side, grey dune communities dominated by small annuals (Trifolium cherleri, Medicago minima) suffered much more from new invaders. This finding confirms the importance of the identity of the dominant species in the native community that have been reported in experimental studies (Emery and Gross, 2006).

4.3. Implications for weed risk assessment

Our study showed that the effect of three major and well-known invasive species largely differs and can impact in different ways species richness or species composition (these two parameters are not necessarily correlated). Impact assessments should therefore not use too simple measures of biodiversity (using only species counts) but also consider changes in species composition, especially when characteristic species are replaced by generalist ruderal species. Prioritisation tools should also prioritise habitats where management are the most useful (e.g., *A. fruticosa* has negative impacts on grey dunes while its effect on water-fringed reedbeds is negligible).

Concerning the abundance-effect relationship, we do not find any threshold effect for *Carpobrotus*. The commonly threshold limit of 80% cover used in several prioritization tools should therefore be used with caution: a species like *Carpobrotus* causes already severe damage to native communities at 60% cover while other species would have less effect at 90% cover. This abundance-effect relationship should therefore be investigated for other species.

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