

Testing alien plant distribution and habitat invasibility in mountain ecosystems: growth form matters

M. A. Giorgis · A. M. Cingolani ·
P. A. Tecco · M. Cabido · M. Poca ·
H. von Wehrden

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Abstract Most studies focused on understanding habitat invasibility use the current levels of invasion as a direct proxy of habitat invasibility. This has shown to be biased by the influence of propagule pressure and climate. We suggest that plant growth forms need to be considered as an extra factor, as habitat preferences might not be equal for all potential invaders. We test the influence of propagule pressure, climate and habitat characteristics on the current level of invasion and habitat invasibility, specifically addressing whether an analysis focused on growth forms evidence

different patterns than the total pool of alien species. We used 499 floristic vegetation plots located in Córdoba Mountains. We used proportional alien richness of the total pool and for each growth form as response variables. We identified models that best explained current levels of invasion. We used the residuals of the models with propagule pressure and climate as the response variable. Then, we performed linear models to test the relationship between habitat characteristics and the residuals of the models. We found different drivers of current alien distribution patterns for the total pool and each growth form. Habitat invasibility was not equal when quantified for the total pool or growth forms. Shrublands and outcrops were recorded as less susceptible to woody invasion, while grasslands and native woodlands were resistant to the invasion of grasses and none habitat type was resistant to the invasion of forbs. We highlight that the current level of invasion and habitat invasibility are highly growth form dependent.

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M. A. Giorgis (✉) · A. M. Cingolani ·
P. A. Tecco · M. Cabido · M. Poca
Instituto Multidisciplinario de Biología Vegetal (IMBIV-
CONICET), Universidad Nacional de Córdoba, Av. Vélez
Sársfield 1611, C.C. 495, 5000, Córdoba, Argentina
e-mail: mgiorgis@imbiv.unc.edu.ar

M. A. Giorgis · A. M. Cingolani · P. A. Tecco ·
M. Cabido · M. Poca
Cátedra de Biogeografía, Departamento de Diversidad
Biológica y Ecología, Facultad de Ciencias Exactas
Físicas y Naturales, Universidad Nacional de Córdoba,
Av. Vélez Sársfield 1611, X5000JJC Córdoba, Argentina

H. von Wehrden
Institute of Ecology, Faculty of Sustainability, Leuphana
University Lüneburg, Scharnhorststr. 1, 21335 Lüneburg,
Germany

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Introduction

Plant invasions are altering and threatening ecosystem services and human well-being on a global scale (Mack et al. 2000; Pimentel et al. 2005; Charles and Dukes

2007). Most studies on alien species focus on a species perspective, investigating distribution patterns and the factors associated with the invasion success (e.g. Alexander et al. 2009; Blackburn et al. 2014). However, the spread of specific aliens is filtered by the habitat, which makes habitat characteristics important filters worth to be considered for understanding alien invasions (Davis et al. 2005; Chytrý et al. 2008). While the difference between a species driven perspective and a habitat driven perspective is widely established, for example, in the theoretical frame for conservation biology (Fazey et al. 2005), the discipline of invasion ecology is still widely restricted to species-driven studies (Rejmánek et al. 2013). As a consequence, habitat invasibility, defined as the intrinsic characteristics of the resident habitat to become invaded (Crawley 1987; Lonsdale 1999), has been poorly investigated to date but rather inferred from current levels of invasions (Rejmánek et al. 2013).

Since invasion processes are ongoing, and propagule pressure and environmental characteristics vary across time and space (Dietz and Edwards 2006), it is difficult to assume an equilibrium regarding the ongoing spread on a specific invasive alien species. As a consequence, the current level of invasion should not be used as a direct proxy of habitat invasibility (Eschtruth and Battles 2011). Alternatively, Chytrý et al. (2008), Rejmánek et al. (2013) proposed that habitat invasibility should be quantified by considering measures of current level of invasion but removing the effect of propagule pressure and climate (i.e. factoring out their influence). Based on this approach, Chytrý et al. (2008) proved that different habitat types vary in terms of their invasibility in Czech Republic. However, the susceptibility of certain habitat types to get invaded might not be equal for all potential invaders, given differential species' habitat preferences (Hulme 2009). Indeed, plant attributes have shown to share relevance with propagule pressure and abiotic characteristics as underlying factors of invasion success (Catford et al. 2009). Following this idea, here we propose that when inferring habitat invasibility from current levels of invasion, special consideration of invaders growth strategies should be included in addition to the control of climate and propagule pressure effect.

Plant growth form (e.g. tree, shrub, grass, forb) is a soft trait often correlated with other more specific functional traits, such as relative growth rate, height or above-ground biomass, which are related to longevity,

fecundity and competitive ability (Díaz and Cabido 1997; Lavorel et al. 2007). In line with this, plant growth form has shown to be related to differential alien success across ecosystems (Cronk and Fuller 1995; Tecco et al. 2010). For instance, the proportion of invasive grass species in closed forest is typically low, while it is expected to be higher in open environments (Williams and Baruch 2000; Rejmánek et al. 2013). Since alien growth forms might respond differently to local environment and climatic pressures (but see Marini et al. 2012), we propose that measuring invasibility of certain habitat types in a given system though recognizing and discriminating all growth forms, might not led to the same results as when inferred from the total pool of alien species (i.e. as in most studies, Chytrý et al. 2008; Stohlgren et al. 1999; Alexander et al. 2011).

Mountain systems provide steep climatic gradients, broad variability in local habitats (Körner 2007), as well as uneven propagule pressure of alien species (i.e. generally decreasing from surrounding lowlands towards higher elevations, Pauchard et al. 2009; Alexander et al. 2009, 2011; Giorgis et al. 2011a). As a consequence, mountain areas constitute ideal systems to assess and compare current levels of invasion with invasibility while identifying the relevance of climate, propagule pressure and habitat types for the invasion success. In this paper, we test the influence of different growth forms of alien species, and propagule pressure, climate and habitat characteristics on the current level of invasion and habitat invasibility using a community dataset sampled through a comparable protocol across a mountainous region from central Argentina (South America). We hypothesize that the relative role of propagule pressure, climate and habitat characteristics on the invasion success might vary depending on the growth form of the alien species. Consequently, we predict different influence of climate, propagule pressure and habitat characteristics on the actual level of invasion, as well as different estimations of habitat invasibility when considering the total species pool or each growth form.

Methods

Study area

The study was conducted in the mountains of Córdoba, central Argentina. These mountains consist of three main ranges extended along 430 km from North to

South (29°00'S–33°12'S), and 110 km from East to West (64°18'W–65°29'E), and their altitude ranges from 500 to 2790 m a.s.l.

Precipitation decreases from the southeast to the northwest, and temperature decreases with both altitude and latitude and increases with longitude. In the centre of the study area at 500 m a.s.l. mean annual temperature is 17 °C, while at 1800 m a.s.l. is 11.2 °C, and at 2700 m a.s.l. is 7.4 °C (De Fina 1992; Marcora et al. 2008).

Plant invaders are abundant and widespread particularly at mid and low elevations (500–1000 m asl), affecting ecosystems biodiversity and functioning (Giorgis et al. 2011a, b, 2013; Gavier-Pizarro et al. 2012; Furey et al. 2014). A large proportion of woodlands have been transformed into shrublands and grasslands, while the remaining patches show different levels of degradation in terms of floristic composition and physiognomy (Zak and Cabido 2002; Cingolani et al. 2008). As a result, the mountain landscape is a mosaic of open and closed woodlands, shrublands and grasslands in different successional stages with variable levels of plant invasion (Zak and Cabido 2002; Giorgis et al. 2013). Agriculture is concentrated in the lowlands outside of our study area or in small valley bottoms with deeper soils (Zak and Cabido 2002).

Vegetation sampling

The data source consisted of 499 complete floristic vegetation relevés, sampled from 2006 to 2011. Most data were taken from Giorgis et al. (2011b) and Cingolani et al. (2010), and from unpublished sources (M. Poca unpublished data). Vegetation plots below 1800 m a.s.l. had 20 × 20 m while most of the vegetation plots situated above this altitude had 10 × 10 m. Relevés were performed in the most representative floristic and physiognomic types at each altitude (Cingolani et al. 2010; Giorgis et al. 2011b, 2013). For the distinction between native and alien species we followed the criteria established in Tecco et al. (2010) and Giorgis et al. (2011b). We divided the species into three growth forms: tree and shrub (woody species), grass and forbs species.

Response variables

The response variable was the proportional richness of alien species (i.e. current level of invasion) quantified

for the following groups: (1) the total pool of alien species, (2) alien woody species (3) alien grasses and (4) alien forbs. We used the proportional richness of aliens in order to avoid any site size effect. Therefore, any reference to actual levels of invasion hereafter will refer to the proportional richness of alien species and not to the absolute richness. Though lacking data on residence time of each alien species, all can be considered neophytes as their introduction occurred after Columbus arrival to south America in 1492 (Chytrý et al. 2008).

Predictor variables

The predictor variables were divided into three groups:

Proxy variables of propagule pressure (PP)

Using Google earth® we measured the cover of alien woodlands in a circle of 100 m diameter (31,415.93 m²) centered in each of the 499 sampling sites. This cover type included both *Pinus* spp. plantations and monospecific stands of invasive trees (e.g. *Ligustrum lucidum* W.T. Aiton, *Gleditsia triacanthos* L., *Ulmus pumilla* L.). An additional 500 m diameter (785,398.16 m²) circle was established around each sampling site, within these larger circles we estimated the proportional area of urban land and we recorded the number of houses. We also measured the distance to the nearest permanent river, nearest village (we defined villages as a group of more than 20 houses), nearest town (we considered as cities settlements with more than 10,000 inhabitants, INDEC 2012), nearest land road and land paved road.

All these variables were then correlated in order to reduce redundancy and selecting the most important predictor variables. The final selected variables were: the distance to permanent rivers, the distance to villages, the distance to land paved roads and the cover of alien woodlands.

Climate (C)

We obtained 19 Worldclim (www.worldclim.org) variables per site and performed a PCA in order to reduce redundancy of variables. Axis 1 was positively related to the annual mean temperature, the mean temperature of the wettest quarter, and the mean

temperature of the warmest quarter. Axis 2 was negatively related to the precipitation of the wettest quarter, the precipitation of the wettest month and the precipitation of the warmest quarter (Supplementary material 1). Both axes were used as proxies of climate characteristics.

Habitat characteristics (H)

Habitat characteristics of each site were sampled within a radius of 100 m. We recorded the proportion (%) cover of grasslands, shrublands, native woodlands, outcrops/bare soil. Percent cover of alien woodlands and urbanization were also estimated but not included as habitat characteristics since they were considered as proxies of propagule pressure. We correlated these variables, except for alien woodland cover and urbanization, in order to reduce redundancy and selected the most relevant ones. The final variables selected as proxies of habitat characteristics were cover percentages of grasslands, shrublands, native woodlands, outcrops/bare soil.

Data analyses

Current level of invasion

We used a theoretic information approach for model selection to identify models that best explained the proportional number of alien species (Burnham and Anderson 2002) for the total pool of species and for each growth form (woody, grasses, and forbs).

We constructed eight alternative candidate models arising from all possible combinations of the three groups of variables mentioned above: 1. H, 2. PP, 3. C, 4. H + C, 5. C + PP, 6. H + PP, 7. H + PP + C and 8. the null model. We used the R package ‘AICmodavg’ to rank the candidate models. We considered a binomial distribution and used AICc values to account for small-sample bias. Models considered best had an AICc difference (DAICc) of less than two from the model with the lowest AICc. All model residuals were tested for spatial autocorrelation, yet in the case of significant spatial autocorrelation we constructed mixed effect models with a spatial error term that showed no different estimates compared to the original GLMs. Therefore, we opted for GLMs to generate more parsimonious models.

Habitat invasibility

Habitat invasibility was evaluated both for the total pool of alien species (proportional alien richness of the total pool) and for the major growth forms (proportional alien richness of woody species, grasses and forbs). To control the effect of climate and propagule pressure we obtained the residuals of the model with climate and propagule pressure (5. C + PP). Using the residuals of this model as the response variable (here after named as ‘habitat invasibility’), we performed a linear model in order to test if habitat characteristics were related to the proportion of the total alien richness and/or of each growth form.

All analyses were performed in R 2.15.1 (R Development Core Team 2014).

Results

Alien species occurred on 430 out of the 499 vegetation plots (Table 1). Most species of the alien pool were represented by forbs, which was the most numerous and frequent growth form. In turn, alien grasses showed the lowest absolute richness but were more frequent than woody species (Table 1). The total number of alien species for the total pool and for each growth form is summarized in the Supplementary material 2. Most vegetation plots had less than six alien species while the maximum value was of 16 alien species per site. Most plots with woody aliens had a single species, while only one vegetation plot showed a maximum of 8 species. Similarly, most plots with alien grasses had a single species, finding a maximum of 5 species in a plot. Finally, most of the vegetation plots with alien forbs had just one or two species but we registered a maximum of 11 species in one vegetation plot (Supplementary material 2). The mean total richness of native species per vegetation plot was 63.3 species (12.2 woody species, 9.9 grasses and 38.2 forbs).

Drivers of the current level of invasion

The best ranked models explaining the proportional alien richness of the total pool of species included the model with the three groups of variables (i.e. 7: H + PP + C), which explained 19 % of the variance (Table 2). In this model, the proportional alien

Table 1 Absolute and mean richness of alien species in the study area. The percentage of occurrence of alien species in the 499 vegetation plots is also provided, with the number of plots in brackets

	Absolute alien richness	Mean alien richness per plot	% of the plots with alien species
Total pool	125	2.95	86 (430)
Alien woody	31	0.62	27 (137)
Alien grasses	16	0.46	37 (185)
Alien forbs	78	1.86	77 (384)

richness was lower in habitats covered by shrublands and outcrops/bare soil (Fig. 2). With respect to propagule pressure, the highest proportional alien richness was observed in the proximity to villages and alien woodlands (Fig. 1). Additionally, proportional alien richness was negatively related to climatic axis *pca* 1 (but see discussion section, Fig. 1, supplementary material 3 for more details).

The relevance of propagule pressure, climate and habitat on the actual levels of invasion varied depending on the growth form considered. The proportional richness of alien woody species was best explained by the model that integrated habitat and propagule pressure (6. H + PP), explaining 80 % of the variance (Table 2). In this model, the proportional richness of woody alien was lower far away from sources of propagules (villages, rivers and alien woodlands) (Supplementary material 3 and 4). The proportional richness of alien grasses was better explained by model 4 (H + C) and the complete model (7. H + PP + C) (Table 2), but the variances explained were close to zero. In the model 4 (H + C), the proportional richness of alien grasses was lower in habitats covered by native woodlands and higher at highest temperatures (Supplementary material 3). Finally, the proportional richness of alien forbs was better explained by the complete model (H + PP + C), with a 15 % of the variance explained (Table 2). In this case alien forbs richness was not significantly related to a particular habitat type, but rather to the potential propagule pressure provided by alien woodlands and the climatic conditions towards the negative extreme of the climatic PCA axis 1 (but see discussion section, supplementary material 3 and 4).

For further details of the best model for each response variable see Supplementary material 3 and 4.

Habitat invasibility

When estimating habitat invasibility (i.e. discounting the influence of propagule pressure and climate by using model residuals of these parameters), we found a significant negative relation between the proportional alien richness of the total pool with shrublands and outcrop/bare soil cover (Table 3).

These general patterns in habitat invasibility, estimated for the total pool of alien species, differed when alien species were separated into major growth forms. For woody plants, the pattern was similar to that observed for the total pool, with lower habitat invasibility in shrublands and outcrops/bare soil (Table 3). However, grasslands and native woodlands were detected as the less susceptible for alien grasses invasion (Table 3). Finally, we did not find significant relationships in habitat invasibility for alien forbs. That is, alien forb species may be equally prone to invade habitats with different characteristics (Table 3).

Discussion

This study provides further evidence on the bias in assuming that current levels of invasion can be used as a direct proxy of habitat invasibility (Chytrý et al. 2008; Rejmánek et al. 2013). In addition, it consistently shows the importance of considering alien species growth forms when characterizing a region in terms of its actual level of invasion and habitat invasibility. In line with our hypothesis, we found that the relative role of propagule pressure, climate and habitat characteristics on the invasion success varies depending on the growth form of the alien species involved. Accordingly, estimations on habitat

Table 2 All candidate models including the drivers of current level of alien distribution for the proportional alien richness of the total pool of species and the different growth forms (woody, grasses and forbs alien species)

Model	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
<i>Proportional alien richness of the total pool of species</i>						
7. H + PP + C	12	1992.86	0	0.77	0.77	-984.11
6. H + PP	10	1995.55	2.68	0.20	0.98	-987.55
5. C + PP	8	2000.4	7.54	0.018	0.99	-992.05
4. H + C	8	2006.67	13.81	0.0008	0.99	-995.19
2. PP	6	2009.32	16.46	0.0002	1	-998.58
1. H	6	2015.69	22.83	0	1	-1001.76
3. C	4	2122.58	129.71	0	1	-1057.25
8. Null	2	2137.28	144.42	0	1	-1066.63
<i>Proportional richness of alien woody species</i>						
6. H + PP	10	786.05	0	0.84	0.813	-382.80
7. H + PP + C	12	789.30	3.25	0.16	0.973	-382.33
2. PP	6	794.22	8.17	0.014	0.987	-391.02
5. C + PP	8	794.38	8.33	0.013	1	-389.04
4. H + C	8	832.31	46.26	0	1	-408.01
1. H	6	841.74	55.69	0	1	-414.78
3. C	4	930.31	144.26	0	1	-461.11
8. Null	2	951.33	165.28	0	1	-473.65
<i>Proportional richness of alien grasses species</i>						
4. H + C	11	752.48	0	0.482	0.482	-364.97
7. H + PP + C	12	754.05	1.58	0.219	0.701	-364.71
3. C	4	754.85	2.38	0.147	0.848	-373.39
6. H + PP	10	756.05	3.57	0.081	0.929	-367.80
1. H	6	756.65	4.17	0.059	0.989	-372.24
5. C + PP	8	761.32	8.84	0.006	0.994	-372.51
8. Null	2	761.74	9.26	0.005	0.999	-378.86
2. PP	6	765.33	12.85	0.0008	1	-376.58
<i>Proportional richness of alien forbs species</i>						
7. H + PP + C	12	1660.41	0	0.868	0.869	-817.89
5. C + PP	8	1664.29	3.88	0.124	0.993	-824.00
6. H + PP	10	1671.25	10.83	0.004	0.996	-825.39
4. H + C	11	1671.50	11.09	0.003	0.999	-824.48
1. H	6	1679.70	19.29	0.0001	1	-833.77
2. PP	6	1684.04	23.63	0	1	-835.94
3. C	4	1727.56	67.15	0	1	-859.74
8. Null	2	1746.28	85.86	0	1	-871.12

invasibility are not equal when quantified for the total pool of alien species or when considering each growth form.

The current level of invasion

During the past years, propagule pressure has been found as one of the most important drivers of current

levels of plant invasion (Holle and Simberloff 2005; Lockwood et al. 2005; Eschtruth and Battles 2011; Giorgis et al. 2011a). Our study, considering several proxies of propagule pressure, is in line with this general pattern, but also adds new evidence on the variability of this driver among major growth forms. In the mountain range under study, the importance of propagule pressure in explaining actual levels of

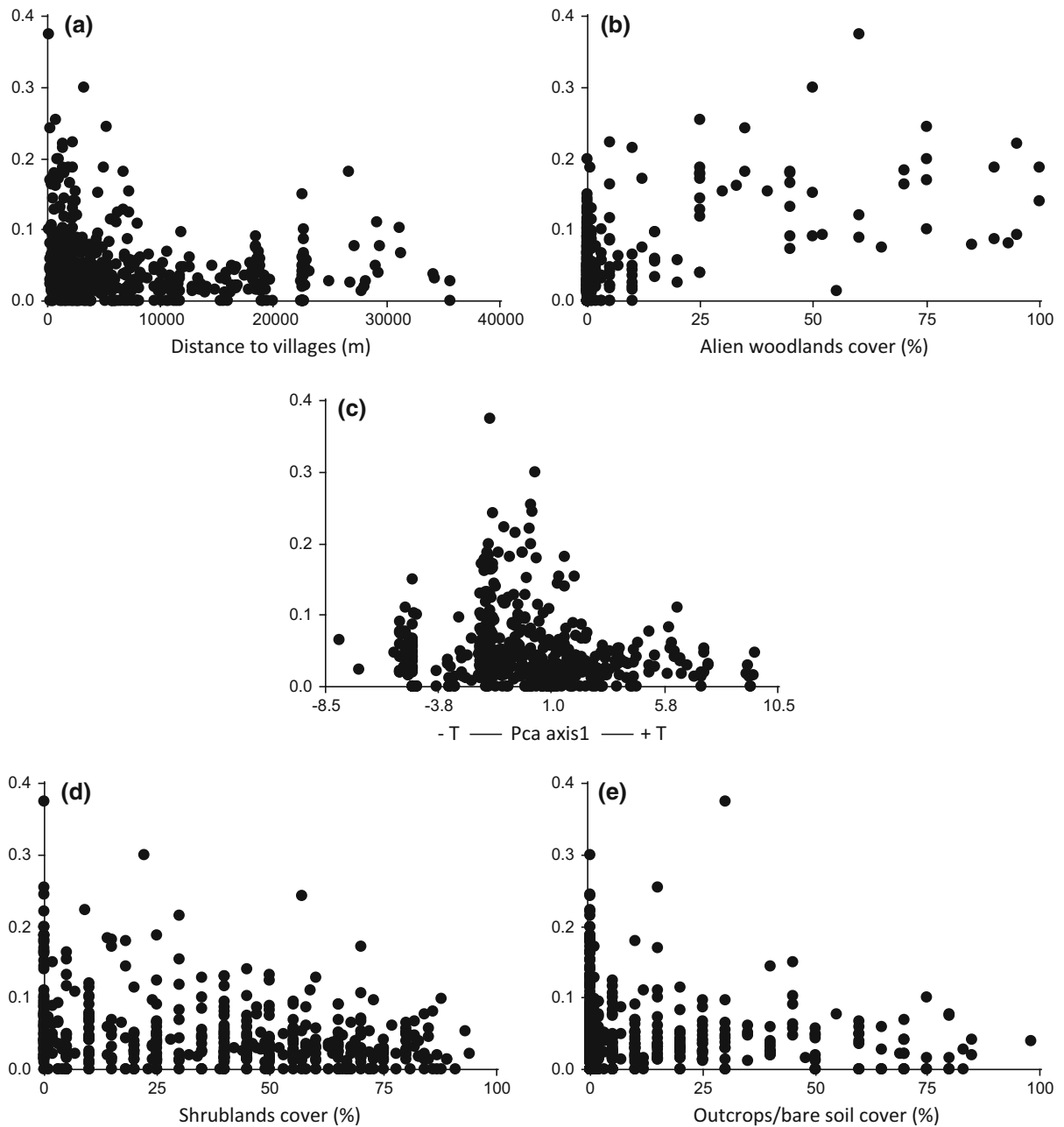


Fig. 1 Proportional alien richness of the total species pool against the significant predictor variables included in the best candidate model. Distance to village (a) and Alien woody cover (b) are indicator of propagule pressure. Pca axis 1 (c) is indicator

of climate and is positively associated with temperature. Shrubland (d) and outcrop/bare soil cover (e) are proxies of habitat characteristic

invasion seems to be high for woody species, intermediate for alien forbs and seemingly insignificant in the distribution of alien grasses. These results suggest that different alien growth forms might be under

different stages of invasion (see below). As a consequence, our results emphasize the importance of propagule pressure in the invasion process but also highlight the importance of considering a holist

Table 3 Habitat Invasibility

	Estimate	SE	t value	Pr(> t)
<i>Total pool</i>				
(Intercept)	0.156	0.192	0.813	0.42
Grassland	-0.0001	0.002	-0.044	0.96
Shrubland	-0.005	0.002	-2.516	0.01*
Native woodland	-0.001	0.003	-0.282	0.77
Outcrop/bare soil	-0.006	0.002	-2.191	0.03*
<i>Woody alien</i>				
(Intercept)	0.107	0.128	0.84	0.40
Grassland	-0.002	0.002	-1.594	0.11
Shrubland	-0.006	0.001	-3.888	0.00***
Native woodland	0.0005	0.002	0.287	0.77
Outcrop/bare soil	-0.004	0.002	-2.355	0.02*
<i>Grasses alien</i>				
(Intercept)	0.174	0.183	0.955	0.33
Grassland	-0.004	0.002	-1.924	0.05*
Shrubland	-0.004	0.002	-1.756	0.08
Native woodland	-0.009	0.003	-3.027	0.00**
Outcrop/bare soil	-0.004	0.002	-1.666	0.09
<i>Forbs alien</i>				
(Intercept)	-0.001	0.207	-0.005	0.99
Grassland	0.001	0.003	0.33	0.74
Shrubland	-0.004	0.002	-1.588	0.11
Native woodland	0.001	0.003	0.245	0.81
Outcrop/bare soil	-0.003	0.003	-1.342	0.18

Linear relationship between each habitat characteristic and proportional alien richness of the total pool of species and woody, grass and forbs after removing the effects of propagule pressure and climate, using the residuals of the model with each response variable

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

approach in order to understand the invasion process, as Catford et al. (2009) theoretically proposes.

Woody alien species seem to be at an early stage of invasion in which the presence of alien species in the neighboring landscape is the primary determinant of alien woody distribution (Dietz and Edwards 2006; Catford et al. 2009). This is in line with Giorgis et al. (2011a) and Tecco et al. (2016) findings at local scale in the same region. In contrast, alien grasses might be at a more advanced stage of invasion, in which the presence of alien species is mainly influenced by climate and habitat characteristics (Dietz and Edwards 2006). The proportional richness of alien grasses was higher in warmer areas and lower in sites with higher cover of native woodlands. The lower occurrence of

alien grasses in native woodlands probably reflects habitat requirements for the establishment and growth of these grasses, since most were introduced for lawn gardening or grazing and are, thus, not shade tolerant (Pivello et al. 1999; Williams and Baruch 2000). The distribution of alien forbs, might be at an intermediate stage of invasion, since it was influenced by all three drivers: propagule pressure, climate and habitat characteristics. Due to the higher number of alien forbs, the model for the total pool and the model of alien forbs are almost equal, as warned by Catford et al. (2011).

Time since introduction has been proposed to underlie different stages of invasion among alien species in a given region (Wilson et al. 2007; Pyšek et al. 2009; Rejmánek et al. 2013). However, South America has a recent history of alien introduction (i.e. <500 year) and all alien species can thus be considered as neophytes (Chytrý et al. 2008). Alternatively, even if most species share similar timings of introduction, certain basic differences between growth forms, such as the amount of years to attain the reproductive stage, could partly explain the differential influence of propagule pressure. For forbs or grass species time to produce seeds is just one growing season, while for woody species it may take several seasons.

Except for woody species, all selected models had a low explained variance. It is possible that some of the predictor variables would be more important for one growth form than for other. For example, the distance to permanent rivers or to alien woodlands -as a proxy of propagule pressure-, may be more informative for woody alien species than for grasses and forbs. The absence of an important predictor variable (e.g. proxies related to habitat characteristic as disturbance history or topographic position, Catford et al. 2009) may be another possible explanation for the low explained variance. Regardless of these limitations, the approach does report the existence of different drivers of current alien distribution among alien growth forms.

It is important to highlight that PCA axis 1 (positively associated with temperature) was negatively related to the proportional alien richness of the total pool and forb species, while for grasses it was positively related. This contrasting relationship should be interpreted with caution, since our analyses test just for monotonic relationships. Indeed, the proportional alien richness of the total pool and forbs seemed to

have an unimodal response to PCA axis 1 when looking at the scatterplots (Fig. 1c, supplementary material 4), while the proportional richness of alien grasses seemed to be negatively related (see supplementary material 4). Mountain systems have strong variation of climatic conditions along the altitudinal gradient (Körner 2007). Along this gradient a pattern with opposite direction of abiotic stressors such as temperature and moisture has been described in this and other xeric mountains (e.g. Cavieres et al. 2006; Tecco et al. 2016). In this context, it seems that in this region mid-elevation might resume the most favorable condition for most alien plant species (i.e., less extreme temperatures and more water availability in the dry season; Tecco et al. 2016), while lower elevation related to highest temperatures and less water availability in the dry season are favorable condition for grass invasion. Studies around the world found negative or unimodal relationship between alien richness and altitude (Alexander et al. 2011), our results support both relationships and suggest different patterns for alien growth forms along the same environmental gradient.

Habitat invasibility

Habitat invasibility did vary along the mountain range under study, being lowest in habitats characterized by high shrubland cover. This lower susceptibility to be invaded seemed consistent for the total pool of alien species and for the proportion of woody invaders. This pattern could be interpreted as an evidence of biotic resistance (Catford et al. 2009; Rejmánek et al. 2013) since shrublands have the highest native species richness compared to other habitat types in this mountain system (Giorgis et al. 2011c). Indeed, native woody richness is even higher in this habitat type than in closed woodlands (Giorgis et al. 2011c), and could reduce its susceptibility to be invaded by woody aliens. However, this would be a misleading interpretation of our results. Other habitat types with high native richness, such as grasslands, did not follow the same pattern. On top of this, habitats with low richness did not show higher invasibility. We rather suggest that our findings are in line with the “invasion paradox” (Fridley et al. 2007) that call for caution when relating current levels of invasion with resident richness, since positive, negative and even null results

can be expected. An alternative explanation to the lower invasibility of shrublands could be the fast post disturbance recovery of the native community and the low nutrient availability in this patch type (Rejmánek et al. 2013). In our study area, most native woody species have a great sprouting capacity to overcome both fire events (Torres et al. 2014) and grazing pressure (Giorgis et al. 2010). In addition, the disturbed shrubland patches have lower nutrient availability compared with native woodlands (Giorgis et al. 2013). Nevertheless, specific research in shrublands of this system is needed to test the hypothesis of fast post-disturbance recovery or resident community and lower nutrient availability as drivers of lower invasibility (i.e. accounting for pre-established floristic composition, fire history, grazing pressure, plant traits and other confounding variables).

One of the most insightful findings of this study is the differences in habitat invasibility for different growth forms (Fig. 2). This suggests that different plant traits are filtered out in some habitats but not in others. For example, shrublands and outcrop/bare soils were recorded as resistant to the invasion by woody aliens, but not by grasses and forbs. In turn, grasslands and native woodlands were resistant to alien grasses, but not to woody or forbs invasions. The higher invasibility of open habitats versus the low invasibility of closed habitats recorded for alien grasses is in line with the above-mentioned requirements of the introduced species belonging to this growth form. The lack of relation between forbs invasiveness and habitat types could be biased by the fact that this growth form is the most diverse, both in terms of species and traits (i.e. including annual and perennial herbs, ferns, succulents and climber species, which may have different response and adaptation to biotic and abiotic conditions). This further highlights the importance of including the growth form when estimating habitat invasibility. For example, annual species may be adapted to higher disturbance frequencies, while clonal and perennial species may be adapted to extreme climatic conditions (Chytrý et al. 2008; Rejmánek et al. 2013). Our results regarding habitat invasibility for woody alien species should be taken into caution considering that the residual of the model (used to estimate habitat invasibility) had a quite low variance due to the overdriven effect of propagule pressure on the actual level of woody alien distribution (Table 1). This result emphasizes the importance of

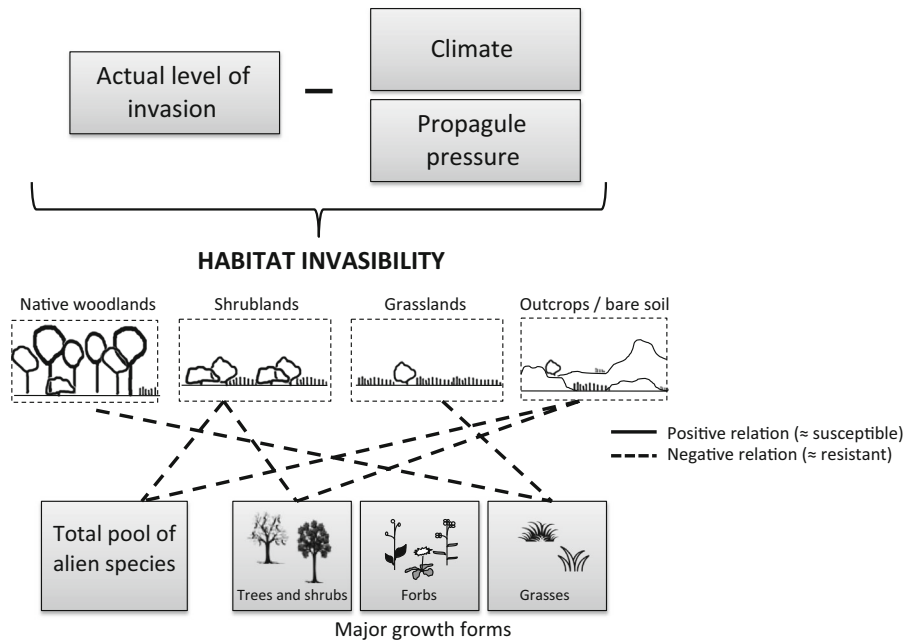


Fig. 2 Conceptual model that highlights that plant growth forms need to be considered as an extra factor together with propagule pressure and climate (Chytrý et al. 2008; Rejmánek et al. 2013) when aiming at testing invasibility from actual alien distribution patterns. The *diagram* illustrates how patterns of habitat invasibility are not equal when quantified for the total pool of alien species or when considering each growth form. In the case of the present mountainous ecosystem, both shrublands

and outcrop/bare soils were recorded as resistant to the invasion by woody aliens, but not by grasses and forbs. In turn, grasslands and native woodlands were resistant to alien grasses, but not to woody or forbs invasions. Finally, although neither of the habitats appeared as highly invasible for any growth form (i.e., absence of positive relations), none of them seem to resist forbs invasion

considering propagule pressure as confounding effect in order to test habitat invasibility from the current level of invasion (Eschtruth and Battles 2011).

All in all, the variability in habitat invasibility found in this study when accounting for the different alien growth forms supports the importance of the alien plant traits as the primary determinant to the establishment and growth of alien species in a particular habitat, as many studies have already pointed out (e.g. Chytrý et al. 2008; Catford et al. 2009, 2011). However, to our best knowledge, this is the first study to test how growth forms may condition habitat invasibility.

Conclusion

Testing habitat invasibility from the actual level of invasion is still a challenge. Chytrý et al. (2008) proposed the use of residuals of the model between the actual level of invasion and propagule pressure and

climate as explanatory variables. However, here we showed that this relationship is highly growth form dependent. For instance, forbs might drive general patterns when pooling all growth forms (Catford et al. 2011 and this study). For that reason, when aiming at testing invasibility from actual alien distribution patterns, we highlight that plant growth forms and/or attributes must be considered separately (Chytrý et al. 2008; Rejmánek et al. 2013).

Understanding habitat invasibility is a key point for planning adequate management action. However, comparatively most efforts have been directed to predict which are the most invasive alien species (Rejmánek et al. 2013; Blackburn et al. 2014; Kumschick et al. 2015; van Kleunen et al. 2015). Since management actions are focused on habitat types rather than species (Fazey et al. 2005), here we highlight the importance of understanding habitat invasibility as a proxy to develop adequate management strategies and future studies.

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