



Alien plant species invade by occupying similar functional spaces to native species[☆]



Michele Dalle Fratte^{a,*}, Rossano Bolpagni^b, Guido Brusa^a, Marco Caccianiga^c, Simon Pierce^d,
Magda Zanzottera^a, Bruno E.L. Cerabolini^a

^a Department of Theoretical and Applied Sciences, Università degli studi dell'Insubria, Via J.H. Dunant 3, I-21100, Varese, Italy

^b Department of Chemistry, Life Sciences, and Environmental Sustainability, Università degli studi di Parma, Parco Area delle Scienze 11/a, I-43124, Parma, Italy

^c Department of Biosciences, Università degli studi di Milano, Milano, via G. Celoria 26, I-20133, Italy

^d Department of Agricultural and Environmental Sciences (DiSAA), Università degli studi di Milano, Via G. Celoria 2, I-20133 Milan, Italy

ARTICLE INFO

Edited by Fei-Hai Yu

Keywords:

Competition

Exotic

Invasion

Plant functional types

Plant strategies

Universal adaptive strategy theory

ABSTRACT

Invasive alien species (IAS) are the subset of naturalized species that cause greater impacts on biodiversity, ecosystem functions and services. However, despite management actions and eradication plans, their expansion worldwide is seemingly unstoppable.

In this paper, based on a large dataset of 1039 records of IAS and native plant species representative of the extensive biogeographic diversity in Southern Europe, we tested the consistency of Grime' concept of CSR universal adaptive strategies (competitors, stress-tolerators and ruderals) to explain plant invasion across a broad elevation gradient. Accounting for phylogenetic relatedness, we tested two hypotheses. First, whether IAS occupy a different CSR space compared to native species. Second, whether the success of IAS at the regional scale is linked to higher degree of C- and/or R-selection, according to recent worldwide observations on naturalization success of alien species. We tested such hypotheses on different growth forms (trees, shrubs, long-lived herbs, short-lived herbs, hydrophytes) that are related to plant functional traits.

Except for trees, IAS and native plant species essentially occupied the same CSR space, indicating that IAS can occupy the same niches of native species. However, IAS exhibited mainly higher C- scores compared to natives, suggesting that IAS are more competitive and are associated with relatively productive habitats, involving that these sites are highly prone to invasion (and that native species in resource-poor habitats are less likely to experience pressure from IAS). Our findings confirm the utility of CSR classification to broadly represent, and explain, the invasion success of alien plant species at the regional scale. This approach emerges as a viable tool in assessment of IAS characteristics and for development of strategies and plans for their containment.

1. Introduction

Species introduction outside their natural boundaries is a rapidly increasing phenomenon fostered by globalization processes (Meyerson and Mooney, 2007; Guo et al., 2019). Despite the lack of problems caused by many of these species on introduction to new locations, some become invasive (invasive alien species, IAS) and represent one of the major anthropogenic threats to ecosystem integrity worldwide, with impacts on biodiversity, ecosystem functioning and services (Pejchar and Mooney, 2009; Vilà et al., 2011). In Europe, which has a long history of species introduction (Lambdon et al., 2008b), risk assessments, early detection and eradication plans, and management actions

have been widely implemented (e.g. Regulation No 1143/2014 of the European Parliament). Nevertheless, the expansion rate of IAS continues to increase (Pyšek et al., 2017), damaging economic and social aspects of human well-being. Thus, understanding the ecological characteristics of IAS could provide supporting information to develop more effective measures for their containment.

Among plant species, IAS are recognised as those that rapidly broaden their spatial distribution by expanding into existing native plant communities (Richardson et al., 2000). Although invasions start from natural or human induced dispersal processes, a range of biological and physical factors can provide the opportunity for IAS to rapidly outcompete native species (Rejmánek et al., 2005a). The success of IAS

[☆] This article is part of a special issue entitled: "Plant invasions" published at the journal *Flora*.

* Corresponding author.

E-mail address: michele.dallefratte@gmail.com (M. Dalle Fratte).

is often attributed to their capacity for rapid growth through high resource acquisition, particularly in non-resource limited conditions (Pyšek and Richardson, 2008; Funk, 2013). However, Leishman et al. (2010) showed that IAS and native species do not have fundamentally different carbon capture strategies, supporting the concept of community invasibility, i.e. characteristics of the resident communities favouring invasion (Richardson and Pyšek, 2006). Specifically, according to trait-environment relationships (Dalle Fratte et al., 2019), differences between IAS and native plant species can reflect environmental conditions of the sites where they occur rather than differences between species *per se* (Leishman et al., 2010).

Pyšek and Richardson (2008) reviewed the literature in an attempt to identify the traits characteristic of invasive vascular plant species, finding evidence only for some traits that are universally associated with these species: height, vigorous vegetative growth, early and extended flowering. Van Kleunen et al. (2010) demonstrated that IAS tend to outcompete native or non-invasive species due to higher values of functional traits related to growth rate and resource acquisition. Also consistent with a 'soft leaves, fast growth' strategy, the most successful alien species are those that minimize carbon investment in leaf construction, as observed both in terrestrial (Tordoni et al., 2019) and aquatic vascular flora (Lukács et al., 2017). Nevertheless, the debate concerning native vs. alien suites of traits is ongoing since patterns or common features are not always clear (Hulme and Bernard-Verdier, 2018; Funk et al., 2017). Daehler (2003) suggested that there is no unique set of traits responsible for invasiveness, but that multiple suites of traits could explain invasion success in different environments (e.g. Tecco et al., 2010; Funk et al., 2016).

Multiple adaptive traits can be summarized in terms of the ecological strategies or the group of functional traits involved in plant resource economics (determining matter and energy turnover rates) and size (denoting the absolute amount of matter and energy present within organisms and within biotic communities) (Díaz et al., 2016; Pierce et al., 2017). Grime's CSR life-strategy theory provides a conceptual framework to classify species into competitive (C), stress-tolerant (S) and ruderal (R) strategies (Grime and Pierce, 2012), and is currently the only plant strategy theory that agrees with resource economics and size as the principal axes of adaptive variation, and can place these in the context of environmental selection pressures (Pierce and Cerabolini, 2018). There are a range of advantages in using adaptive strategy theory, rather than single traits, to evaluate the interactions among alien and native species (Davis, 2009; Rejmánek et al., 2005a; Guo et al., 2018, 2019) and the effects on ecosystem services provision due to plant invasion (Vicente et al., 2013). The application of CSR strategy theory to studies at a local to regional-scale, has highlighted that amongst alien plant species, R- and C- selected species and their intermediate strategies (CR) are prevalent, while S-selected species are under-represented (Pyšek et al., 2003; Lambdon et al., 2008a; Dainese and Bragazza, 2012; Alexander et al., 2016). Despite this pattern also being evident at the global scale (Guo et al., 2018, 2019), Hulme and Bernard-Verdier (2018) raised some questions concerning the use of CSR theory to categorize alien species, since it may mask individual trait differences. Indeed, though CSR strategies can potentially provide a robust theoretical context to predict the performance of species in a definite environment (Grime and Pierce, 2012), it is necessary to experimentally validate the potential for CSR strategy theory to discriminate IAS and to predict their capacity to invade.

In this study, we used a large regional flora dataset based on IAS and native species characteristic of Southern European vegetation to test two hypotheses. 1) First we tested whether IAS and native plant species occupy the same or a different space within the ternary combination imposed by CSR strategies; hence, contrary to the habitat invasibility concept (Leishman et al., 2010), the capacity to invade depends on differences in carbon accumulation strategies. 2) A secondary hypothesis was that at the regional scale the invasion success of alien species is linked to a higher degree of C- and R- selection, according to recent

global findings of naturalization success of alien species (Guo et al., 2018). We tested these hypotheses for different growth forms (trees, shrubs, long-lived herbs, short-lived herbs, hydrophytes) using plant functional traits common across growth forms (Pierce et al., 2017).

2. Methods

2.1. Study area

The study area was the Lombardy administrative region of Italy, which covers an area of 23,870 km² ranging between latitudes 44°40' – 46°37' N, from the Apennines to the Alps, and longitudes 8°29' – 11°25' E, from Lake Maggiore to Lake Garda. The elevation spans 10 m a.s.l. in the Po Valley to approximately 4,000 m a.s.l. on Mount Bernina. The study area includes both the Alpine and Continental biogeographical regions (ETC/BD, 2006), and spans from continental to oceanic bioclimates (Pesaresi et al., 2014), although it is characterized by a highly variable mesoclimate due to its complex orography. Geological substrates consist of a wide range of litho-types, both silicate or carbonate rocks, alluvial or morainic deposits. This extensive environmental variability is consistent with the heterogeneity of vegetation communities, ranging from Mediterranean holly oak woods near Lake Garda to Alpine tundra in the highest mountain regions.

2.2. Dataset

The dataset included all records of plant functional traits for the species analysed by Dalle Fratte et al. (2019), to which we added some unpublished data. Many records are available from Authors' datasets in TRY (Kattge et al., 2011; <https://www.try-db.org/>; see datasets n. 227, 228, 229, 371, 372 and related references).

IAS are defined as naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: > 100 m / < 50 years for taxa spreading by seeds and other propagules; > 6 m / 3 years for taxa spreading by roots, rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area (Richardson et al., 2000). We established the status of native or invasive species in Lombardy according to literature (Assini et al., 2010; Galasso et al., 2018).

A rapid decrease in alien species richness with increase in elevation was detected in adjacent regions of Italy (Barni et al., 2012) and more generally in the European Alps (Becker et al., 2005). The upper montane belt was considered the highest elevation attained by alien species, beyond which they were rarely observed. Given the high elevation gradient of the study area, species exclusively growing in subalpine or alpine belts, i.e. with the ecological index of T (temperature) from 1 to 2.5 according to Landolt et al. (2010), were removed from the dataset. In the analysis, we also considered species listed as "x" for T index (Landolt et al., 2010), since they can spread along a wide portion of the elevation gradient.

The final dataset thus consisted of 1039 records, including 59 tree species, 94 shrubs, 601 long-lived herbs (perennial graminoids and forbs), 224 short-lived herbs (annual or biennial graminoids and forbs) and 61 hydrophytes (Table 1). We assigned each species to the growth forms identified by Guo et al. (2018): trees, shrubs, long-lived herbs, and short-lived herbs, but considered hydrophytes separately, given their specific ecological constraints. Finally, we computed the C-, S-, and R- scores for each species according to the *StrateFy* tool of Pierce et al. (2017).

2.3. Phylogenetic tree

We built a phylogenetic tree of the species in our dataset using the *PhytoPhylo* megaphylogeny tree implemented by Qian and Jin (2016). Following their recommendations, we used their 'Scenario 1' to solve the phylogeny at the species level in our dataset. This scenario is the most

Table 1

Summary of the number (n) and percentage of invasive alien and native species within all the dataset and each growth form.

	n	%
ALL SPECIES	1039	100.0
invasive	110	10.6
native	929	89.4
TREES	59	100.0
invasive	17	28.8
native	42	71.2
SHRUBS	94	100.0
invasive	16	17.0
native	78	83.0
LONG-LIVED HERBS	601	100.0
invasive	22	3.7
native	579	96.3
SHORT-LIVED HERBS	224	100.0
invasive	46	20.5
native	178	79.5
HYDROPHYTES	61	100.0
invasive	9	14.8
native	52	85.2

cautious, as it adds genera or species as basal polytomies within their families or genera to avoid random solutions. Before processing the phylogenetic tree, names of every taxon (family, genus and species) in our dataset were standardized according to The Plant List (www.theplantlist.org) using the R package 'Taxonstand' (Cayuela et al., 2017).

2.4. Statistical analysis

The CSR classification indicates proportion for each element (C, S and R) along each axis, and thus represents an integrated trade-off between traits, i.e. the three axes are dependent on each other (Pierce et al., 2017). We used the R package 'compositions' (van den Boogaart et al., 2018) to visualize the ternary diagrams of the CSR strategies of IAS and native species. To account for the compositional structure of the data (van den Boogaart and Tolosana-Delgado, 2013) we first transformed the dataset of CSR scores with Isometric Log-Ratio Transformation (ilr), which reduced the ternary dataset to a two dimensional image. To test the first hypothesis, i.e. whether invasive and native plant species occupy different CSR space, we computed phylogenetic multivariate analysis of variance (MANOVA) which compares native vs. invasive alien species inside the distribution provided by the ternary combination of CSR scores. In addition, to check for the second hypothesis, i.e. whether the invasion success of alien species is correlated with a higher degree of C- and R- selection, we computed a phylogenetic univariate analysis of variance (ANOVA) considering each axis (C-, S-, and R-) as independent. The *StrateFy* CSR classification method (Pierce et al., 2017) does not use each trait (leaf area, LA; leaf dry matter content, LDMC; specific leaf area, SLA) to directly represent the extent of C-, S- and R- selection, rather they are calculated using the trade-offs between traits, integrated and compared against trade-offs evident globally. Hence, to gain an immediate comparison with previous traits-based studies on IAS, we also ran a phylogenetic ANOVA on each leaf trait used for the calculation of CSR strategies (LA, LDMC and SLA). Before running the ANOVAs, we checked for normality of C-, S- and R- scores and leaf traits by means of the Shapiro-Wilk normality test. While it was not necessary to transform the C-, S- and R- scores, the transformation that best normalized the leaf traits were $\log(x+1)$ for LA and SLA, and \sqrt{x} for LDMC. We computed both phylogenetic MANOVA and ANOVA by means of the function 'aov.phylo' in the R package 'Geiger' (Harmon et al., 2007), which accounts for the phylogenetic tree produced by the 'S.PhyloMaker' R function (Qian and Jin, 2016). We used the R package 'ggplot2' (Wickham, 2016) to visualize the boxplots of the C-, S- and R- scores and then of leaf traits between IAS and native species. We ran both the analysis considering all the species together, as well as splitting the

dataset according to the growth forms. We performed all the analysis with the software R 3.4.4 (R Core Team, 2018).

3. Results

In the CSR ternary space and accounting for the phylogeny (Fig. 1 and Table 2), IAS did not show any significant divergence from native species regardless of the growth form. Considering growth forms, IAS were significantly different from native species only within trees ($p = 0.02$). Invasive alien trees showed higher C- and lower S- compared to natives, but similar R- mean values (CSR compositional mean \pm SD: 51.2 (C) : 38.0 (S) : 10.8 (R) \pm 24.7% vs 40.2 (C) : 46.3 (S) : 13.5 (R) \pm 22.5%) (Appendix A). All gymnosperm trees were classified as stress tolerant, indeed, they were clustered in the S corner of the CSR triangle; however, this did not affect the results since in our dataset gymnosperm trees were balanced between IAS and native species. Shrubs, long-lived herbs, short-lived herbs and hydrophytes did not differ between IAS and native species.

Analysing axes of CSR as independent variables and considering the phylogenetic signal (Fig. 2 and Table 3), at all species level we found higher C- scores for IAS compared to natives (mean \pm SD: 36.3 \pm 22.6% vs 29.8 \pm 21.4%), without significant differences between S- and R- scores. Trees showed the same pattern, with IAS showing higher C- scores (44.5 \pm 19.4% vs 34.6 \pm 13.7%) (Appendix B). Also shrub IAS showed a marked increase of C- scores compared to native species (43.5 \pm 13.8% vs 23.9 \pm 17.0%), but they showed significantly lower S- scores too (35.9 \pm 18.0% vs 54.8 \pm 26.0%). Among herbaceous growth forms, invasive alien short-lived herbs had higher C- scores than native species (35.5 \pm 21.5% vs 26.3 \pm 22.8%), while S- and R- scores did not show significant differences. Among long-lived herbs and hydrophytes, IAS did not show significant differences from native species along each CSR axis.

With regard to the single leaf traits, and accounting for the phylogenetic signal (Fig. 3 and Table 4), at the species level we found significant differences only for LA, being larger for IAS compared to natives (mean \pm SD: 7.4 \pm 2.2 vs. 6.6 \pm 1.9) (Appendix C). A similar pattern was observed among shrubs (mean \pm SD: 8.4 \pm 1.0 vs. 6.4 \pm 1.9) and short-lived herbs (mean \pm SD: 7.1 \pm 1.6 vs 6.0 \pm 2.0), but for the other growth forms IAS and native species did not display any significant difference for each considered leaf trait.

4. Discussion

Our results, based on a large regional dataset of plant species characterizing the vegetation of contrasting biogeographic situations of Southern Europe, underline the relevance of CSR strategy theory (Grime and Pierce, 2012) to assess the invasiveness ability of IAS. We can confirm that there are clear patterns of CSR strategies at the regional scale (Pyšek et al., 2003; Lambdon et al., 2008a; Dainese and Bragazza, 2012; Alexander et al., 2016), which confirm and emphasize recent observation at the global scale concerning species naturalization incidence and extent based on similar approach (Guo et al., 2018). Nevertheless, we observed some different responses among growth forms and with regard to the CSR space.

Our first hypothesis was that IAS and native plant species occupy a different region of CSR space. We detected clear differences only for trees, while robust patterns were not evident when all growth forms were considered together, or separately, for non-tree growth forms (Fig. 1 and Table 2). In other words, except for trees, the space occupied by IAS and native species in the CSR classification was practically identical. This finding suggests that IAS occupy a similar strategic position to native species and that other factors operate in concert with carbon accumulation strategies to drive the local success of invasion (Funk et al., 2017). For example, these factors could be linked to the phylogenetic similarity of alien and native species, which involves that IAS prefer to occupy existing phylogenetic space in native communities

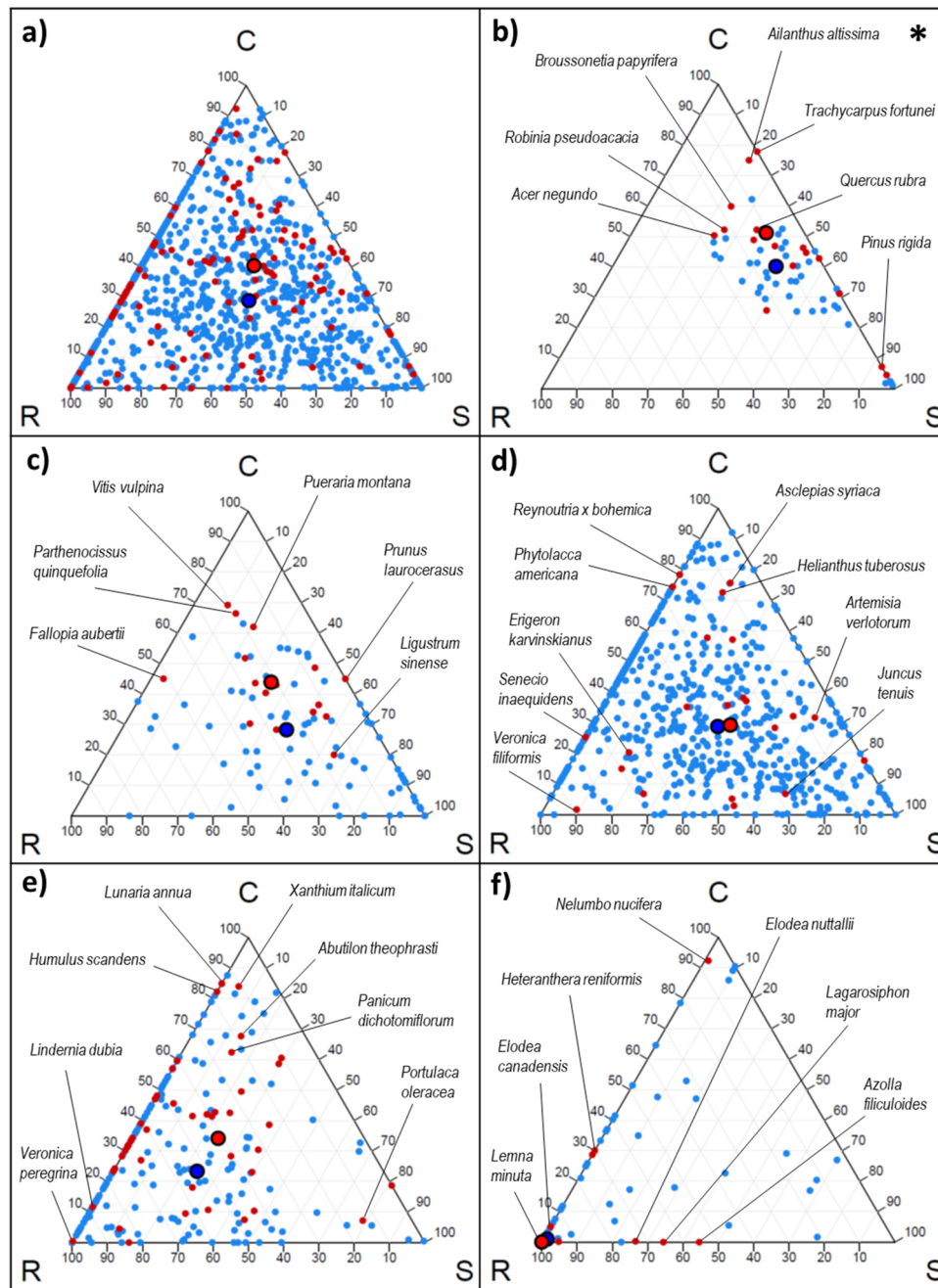


Fig. 1. Invasive alien (red dots) and native (blue dots) species within the CSR strategies triangle. Legend: a) all species, b) trees, c) shrubs, d) long-lived herbs, e) short-lived herbs, f) hydrophytes. Star indicates statistically significant difference between invasive and native species ($p < 0.05$).

Table 2

Results of the phylogenetic multivariate analysis of variance (MANOVA) among invasive alien and native species CSR compositional data within all species and each growth form, indicating Wilk's statistics, F-values and phylogenetic p-values. Coefficients in bold are statistically significant ($p < 0.05$).

	Wilks	F	p-value
all species	0.998	0.92	0.60
trees	0.862	4.50	0.02
shrubs	0.960	1.87	0.25
long-lived herbs	0.999	0.37	0.85
short-lived herbs	0.978	2.46	0.27
hydrophytes	0.935	2.01	0.38

(Ordóñez, 2014; Loiola et al., 2018). Furthermore, native communities can determine the entry of IAS depending by intrinsic habitat properties such as habitat filtering (Carboni et al., 2016) and invasibility (Leishman et al., 2010; Richardson and Pyšek, 2006; Rejmánek et al., 2005b), or to biogeographical context (Pyšek and Richardson, 2006). Hence, with the exception of trees, when different environmental gaps are available for colonization within a plant community, IAS and native species should have the same probability to colonize them. Such findings are consistent with difficulties encountered in the management of IAS, as they respond to multiple components of global change (Bradley et al., 2010) and do not differ solely with regard to plant functional types or strategies.

Consequently, IAS management must be integrated into the framework of whole vegetation management, since it is context-dependent (Daehler, 2003) and may differ across communities (Funk et al., 2017).

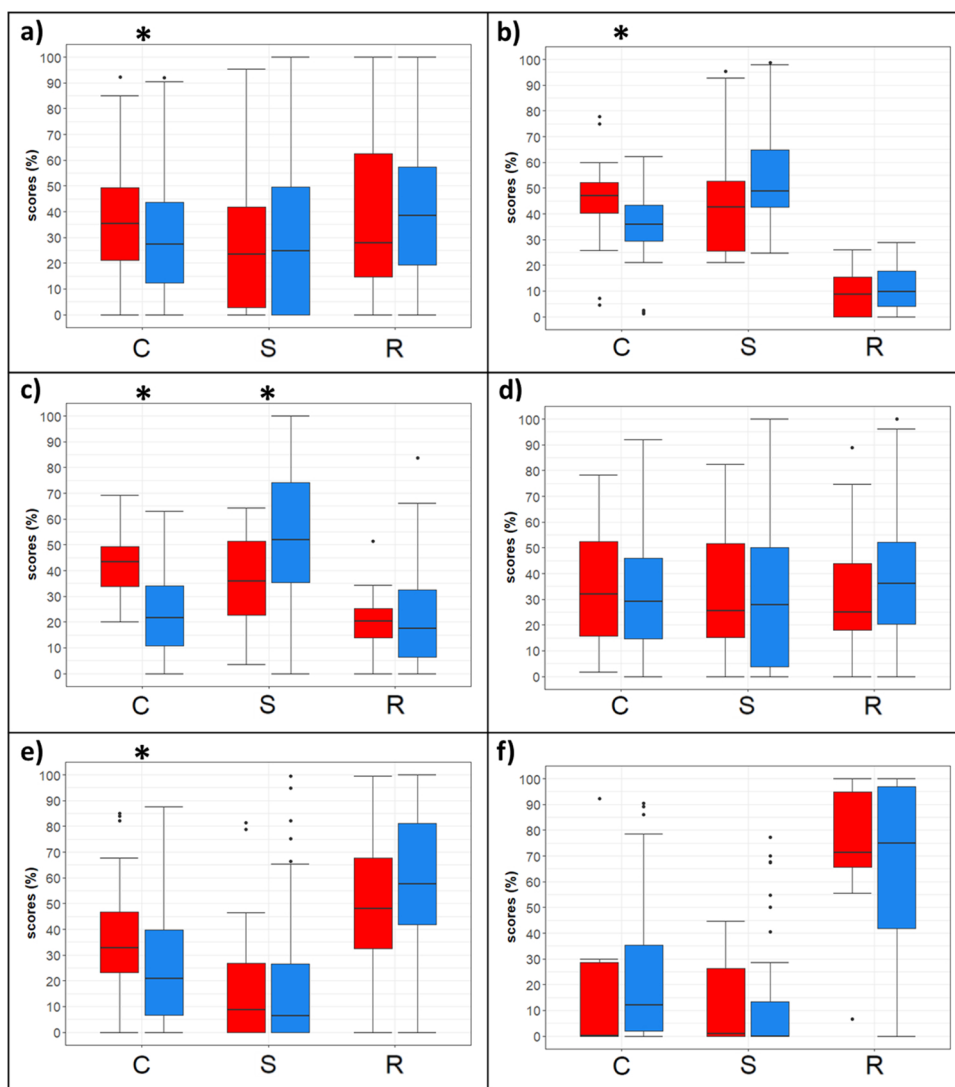


Fig. 2. Boxplots of C-, S-, R- strategy scores of invasive alien (red) and native (blue) species displaying the median (line in the middle of the boxes), the interquartile range (boxes), ± 1.5 times the interquartile range (whiskers) and outliers (circles) for all species and each growth form. Legend: a) all species, b) trees, c) shrubs, d) long-lived herbs, e) short-lived herbs, f) hydrophytes. Star indicates statistically significant difference between invasive alien and native species ($p < 0.05$).

Table 3

Results of the phylogenetic univariate analysis of variance (ANOVA) among invasive alien and native species C-, S-, and R- scores, within all species and each growth form, indicating F-values and phylogenetic p-values. Coefficients in bold are statistically significant ($p < 0.05$).

	C	p-value	S	p-value	R	p-value
	F		F		F	
all species	9.09	0.03	1.76	0.27	1.17	0.47
trees	4.91	0.05	1.68	0.29	0.88	0.50
shrubs	18.70	0.01	7.68	0.02	0.02	0.89
long-lived herbs	0.26	0.66	0.01	0.96	0.38	0.69
short-lived herbs	6.08	0.05	0.00	0.98	5.01	0.15
hydrophytes	0.25	0.82	0.00	0.97	0.14	0.83

The markedly different patterns between trees and the other growth forms within the CSR space (Fig. 1), underline that regional efforts to control plant invasion should focus on tree IAS as a priority. Indeed, while non-tree IAS confirm the ‘join-the locals’ hypothesis (Thompson et al., 1995), according to which the filtering of environmental factors led to strong similarities between IAS and natives (e.g., Tecco et al., 2010), patterns among trees indicated divergence, following the ‘try-

harder’ hypothesis (Crawley et al., 1996). This latter hypothesis maintains that successful aliens should be able to deal better with the local conditions than resident species. Specifically, tree IAS were more competitive compared to natives in resource-rich habitats (favouring the C- selection strategy), in line with observations for woody species by Tecco et al. (2010). The ‘try-harder’ hypothesis should work symmetrically on the other side of the nutrient gradient, i.e. towards resource-poor habitats, where IAS possessing attributes associated with resource conservation and slow growth should succeed over native species with similar strategies (Funk and Vitousek, 2007). According to CSR classification, both IAS and native coniferous species are classified at the most conservative extreme of the S- selection gradient, but due to the few species data available we unfortunately could not provide a statistically confirmation of a trend.

The second hypothesis was that the invasion success of IAS at the regional scale is associated with a high degree of C- and R- selection strategies, according to recent global findings of naturalization success of alien species (Guo et al., 2018). Analysing each axis of CSR as independent variables, we found broad evidence in support of the hypothesis that IAS tend to be competitors (Fig. 2). Efficient competitors for available resources are likely to be the best invaders in natural and semi-natural ecosystems (Pyšek et al., 1995; Rejmánek et al., 2005a).

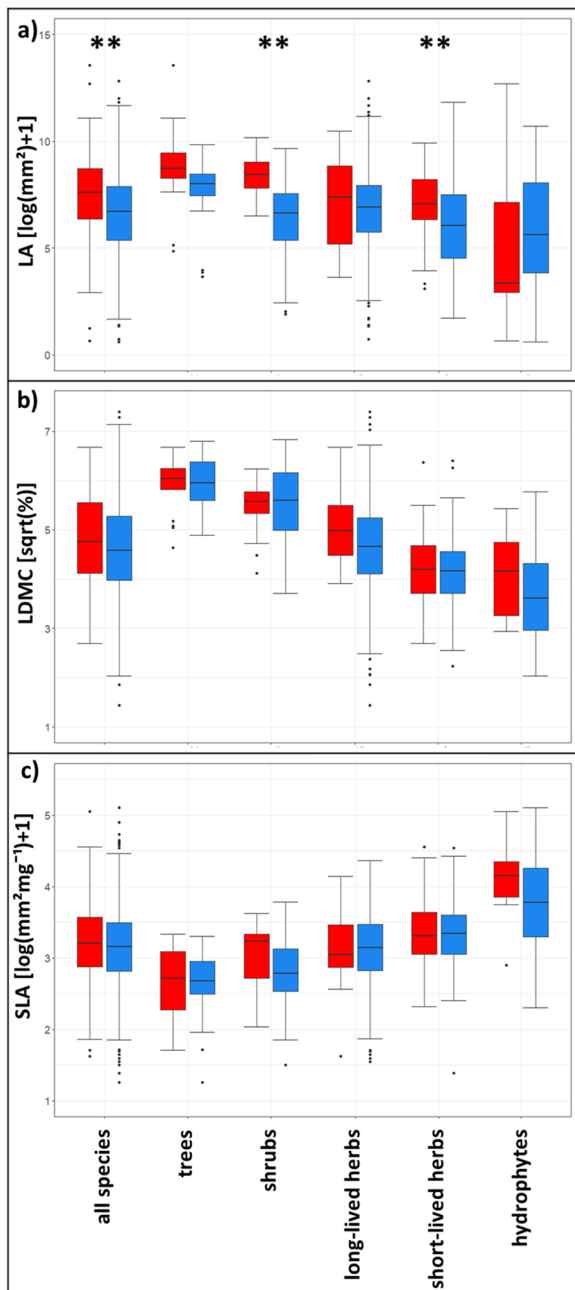


Fig. 3. Boxplots of a) leaf area (LA), b) leaf dry matter content (LDMC), and c) specific leaf area (SLA) of invasive alien (red) and native (blue) species displaying the median (line in the middle of the boxes), the interquartile range (boxes), ± 1.5 times the interquartile range (whiskers) and outliers (circles) for all species and each growth form. Stars indicate statistically significant difference between invasive alien and native species ($p < 0.01$).

Moreover, our findings underlines that the evident selection of IAS toward a higher competitive ability is reflected in larger leaves of IAS compared to native species (Fig. 3), LA being the only trait showing significant differences. This pattern is significant when considering all species together, as well as among trees (not for LA), shrubs and short-lived herbs, but not among long-lived herbs and hydrophytes (Tables 3 and 4). Competitors are characterized by traits that enhance photosynthetic rate and rapid growth, larger leaves, high flowering frequency and nutrient rich leaves (Wright et al., 2004; Reich, 2014) and some of them (the most competitive) have been associated also to a high efficiency of clonality (Song et al., 2013). All these traits have been frequently linked with invasive plant species (Pyšek and Richardson,

Table 4

Results of the phylogenetic univariate analysis of variance (ANOVA) among invasive alien and native species leaf traits (leaf area, LA; leaf dry matter content, LDMC; specific leaf area, SLA), within all species and each growth form, indicating F-values and phylogenetic p-values. Coefficients in bold are statistically significant ($p < 0.01$).

	LA F	p-value	LDMC F	p-value	SLA F	p-value
all species	14.44	0.01	2.43	0.14	1.05	0.42
trees	4.77	0.08	0.16	0.73	0.32	0.64
shrubs	17.63	0.01	0.54	0.52	4.53	0.06
long-lived herbs	0.57	0.61	3.24	0.24	0.20	0.74
short-lived herbs	12.02	0.01	0.10	0.77	0.49	0.62
hydrophytes	1.10	0.41	1.92	0.36	1.79	0.36

2008; van Kleunen et al., 2010; Roiloa et al., 2016). While very few alien species are able to invade plant communities at advanced successional stages (Rejmánek et al., 2005a), IAS tend to accumulate in early successional stages (Crawley et al., 1996), i.e. following disturbance or as part of secondary succession. In particular, early succession on fertile substrates typically promotes dominance of high-resource demanding species (Grime, 2006). Indeed, high-resource ecosystems tend to accumulate more exotic species than low-resource ecosystems (e.g. Huenneke et al., 1990; Gross et al., 2005; Stohlgren et al., 2008). After that IAS are released into new environments, usually because they naturalize from cultivated gardens (Guo et al., 2019), such sites may be the gateway through which alien species invade a target region (Crawley et al., 1996; Rejmánek and Richardson, 1996; Pyšek et al., 2017),

Despite the fact that Guo et al. (2018) found a positive relation of R-selection with the incidence of naturalization worldwide, we did not find such evidence for IAS at the regional scale in our study system. It is possible that such differences are caused by the more specific subset of species that we used compared to the global dataset. Indeed, our analysis might be considered a specific focus of part of the study by Guo et al. (2018), as IAS are the subset of naturalized species already having extensive impact on the structure of communities and ecosystems (Pejchar and Mooney, 2009). Moreover, focusing on IAS we removed the naturalized species from our analyses, which constitutes a large proportion of the local flora (e.g., Galasso et al., 2018) that is more likely to contain a high degree of ruderals. Often such invasions start from disturbed sites (Crawley et al., 1996; Richardson et al., 2000; Pyšek et al., 2017), where species with a ruderal life strategy thrive (Rejmánek and Richardson, 1996). Hence, IAS act on ecosystem that are already modified, characterized by a lower disturbance. Furthermore, a global analysis such as that of Guo et al. (2018) represents a greater range of very specialized environments. For example, they highlighted that the high R- degree of shrubs and long-lived herbs was due to the presence of Mediterranean species, which are absent in our local flora. In addition, Guo et al. (2018) studied the naturalization capacity of species worldwide, and it is possible that some of the species we classified as native in our geographic region are classified as naturalized elsewhere in the world.

With regard to the degree of S- selection, we did not find differences either within or between growth forms. Only invasive alien shrubs displayed significant lower values of S-scores compared to natives, confirming that species with a greater S-score are less likely to become naturalized (Pyšek et al., 2003; Alexander et al., 2016). Usually stress-tolerators are very long-lived, have a long leaf life-span, grow slowly, fruit later and produce fewer seeds with respect to competitors and ruderals (Grime, 1979; Grime and Pierce, 2012). All of these traits contrast with those commonly reported to be associated with successful invaders (Pyšek and Richardson, 2008; van Kleunen et al., 2010), and could make stress-tolerators less likely to be selected by humans as horticultural or gardening plants (van Kleunen et al., 2018; Guo et al.,

2019). In general, stress-tolerant plants rely heavily on vegetative rather than sexual reproduction and rarely show extensive morphological plasticity, which limits their potential to spread (Grime, 1979, 1988). In addition, the chance of a stress-tolerant plant to be introduced into an environment with a stress regime comparable to the one it is adapted to in its native range is relatively low, given that stressful environments are relatively rare in general, and often characterised by idiosyncratic and restricted environmental regimes (Alexander et al., 2016; Funk, 2013). Native species appear to have a competitive advantage over IAS in low-resource ecosystems (Alpert et al., 2000; Daehler, 2003), and communities become more susceptible to invasion when resource availability is increased (Davis et al., 2000; Funk, 2013).

According to Grime (2001), woody species occupy the S-C region of the CSR triangle, while trees with high R-scores do not exist (Pierce et al., 2013, 2017). In the S- corner we found a cluster of gymnosperm tree species, while broad-leaved trees were classified towards higher C (see also Pierce et al., 2013). Two IAS, i.e. *Ailanthus altissima* and *Trachycarpus fortunei*, exhibited the highest C-scores. In general, among IAS we found a solid signal towards more competitive species, considering both the CSR ternary combination, and the dimension of each single axis. Indeed, above all growth forms, trees were the only one to show significant differences within the CSR space. For trees, it is likely that IAS are fast-growing species that can more rapidly fill empty gaps following clear-cuts, while late-successional species have not been imported, except for a few exceptions (e.g. *Quercus rubra*). Guo et al. (2018) found that the naturalization incidence and extent of trees is not, or is only weakly, affected by their C-, S-, and R- scores. Differences with our findings could be due, once again, to the fact that we have considered IAS, i.e. the portion of naturalized species that are already well established in new environments. Indeed, the naturalization of trees may occur over longer periods of establishment, long generation time, relatively low proportions of resources invested in seed production (Grime, 1979), and the long time lag following introduction to new ranges (Kowarik, 1995; Pyšek et al., 2017). Shrubs also prevail in the S-C region of the triangle (Grime, 2006; Pierce et al., 2013). However, in this case we found robust patterns only considering each axis as independent. The highest C-scores were associated with climber IAS such as *Vitis vulpina* and *Parthenocissus quinquefolia* as well as to *Pueraria montana*; the latter is a clonal species, which highlights that high clonality can correspond to greater invasive capacity (Song et al., 2013; Roiloa et al., 2016). In our dataset, the shrubs with the highest R- score were native species, i.e. *Thymus vulgaris* and *Myricaria germanica* (Fig. 1).

With regard to herbaceous growth forms, short-lived IAS showed high C-scores compared to natives according to Guo et al. (2018). Accordingly, short-lived herbs do not exhibit extensive ruderalism, probably because they are successfully invaders only under conditions of relatively low disturbance, while under continuous disturbance, the seed production of ruderal species does not compensate for the mortality rate, and they eventually fail to establish (Grime, 1979, 1988). Regarding long-lived herbs, it must be considered that in our dataset IAS represent only 3.7% of the total (Table 1), which may have affected outcomes; anyway, invasive alien long-lived herbs are homogeneously distributed in the CSR space (Fig. 1), without forming clusters, similarly to natives. However, competitive and large-leaved invasive herbs capable of forming monospecific stands in productive habitats were classified towards the C-selected corner, for example *Phytolacca americana*, *Reynoutria x bohemica*, or *Helianthus tuberosus* (Pierce et al., 2013). Aquatic plants displayed clear preferences towards ruderal strategies,

for both IAS and native species (Fig. 1), confirming previous observations (Pierce et al., 2012, 2013). Aquatic species were either small, fast growing and with extremely acquisitive leaves (highly R-selected) or CS to C-selected species with large, broad leaves, such as water lilies, in agreement with previous conclusions (Pierce et al., 2012). Among IAS, *Nelumbo nucifera* displayed the highest C-scores, and in the CSR spectrum clustered together with other native *Nymphaeiden* (Pierce et al., 2012). Several traits of this species may form part of the C- selected syndrome (Bornette et al., 2008), including moderate relative growth rates, limited vegetative dispersal and seeds that sink immediately. Many aquatic species are R selected in the extreme, as they mainly rely on rapid generation to face disturbance, indeed most hydrophytes are typical of disturbed habitats, as they colonize areas where seasonal flooding washes away the existing vegetation (Bornette et al., 2008). No hydrophyte species in our study exhibited selection toward the extreme of conservative S- corner, also confirming that hydrophyte IAS may not include stress tolerators *sensu* Grime (1979) (Kautsky, 1988; Pierce et al., 2012). Previous observations of functional traits of hydrophytes (Lukács et al., 2017) found that traits of IAS are linked to competitive ability ('soft leaves faster'). However, we cannot confirm such differences because the functional traits of alien aquatic plants depend strongly on their growth-form (see Lukács et al., 2017).

5. Conclusions

In the ternary space determined by CSR classification, IAS and native species cover almost the same region, indicating that IAS can occupy the same niches and have the same requirements of native species. This supports the idea that a complex of factors, which act in conjunction with the carbon accumulation strategies, mediates the mechanisms that regulate the invasion of empty gaps in vegetation communities. Several authors stressed that the spread of IAS is linked to the pivotal contribution of: 1) the phylogenetic similarity between alien and native species (Ordóñez, 2014; Loiola et al., 2018); 2) the capability of habitat features to drive IAS establishment (Carboni et al., 2016); 3) habitat invasibility (Richardson and Pyšek, 2006; Leishman et al., 2010; Rejmánek et al., 2005b), 4) as well as the role of biogeographical context (Pyšek and Richardson, 2006). Analysing each axis of CSR independently, as well as separate leaf traits (LA, LDMC and SLA), we found broad evidence that IAS are mainly true competitors, suggesting that traits that can describe the invasiveness ability of alien plants at the regional scale are those underlined by the C-selection strategy. Moreover, contrary to Hulme and Bernard-Verdier (2018), the CSR scores, being calculated using the trade-off between traits, provide more robust differences between IAS and native species compared to individual trait variation.

Further studies are necessary to implement our findings; in particular, we need to understand differences among distinct environments and habitats according to Grime's theory and the ecology of invasive plants (Rejmánek et al., 2005b; van Kleunen et al., 2018). Global changes and the flora globalization will promote the establishment of competitive alien functional types in Southern Europe (Walther et al., 2002; Ciappetta et al., 2016; Najberek et al., 2017; Dalle Fratte et al., 2019). In this context, CSR theory can be a viable tool for the risk assessment of IAS (Vicente et al., 2013), implementing the current approaches of prioritization methods and horizon scanning (Carboneras et al., 2018), and the development of non-invasive ideotypes of crops and horticultural plants (Anderson et al., 2006; van Kleunen et al., 2018; Guo et al., 2019).

Appendix A. CSR compositional mean (mean \pm standard deviations) within all species and the analysed growth forms

		C:S:R \pm sd
ALL SPECIES	invasive	40.4:32.0:27.5 \pm 25.1
	native	28.9:36.3:34.8 \pm 25.8
TREES	invasive	51.2:38.0:10.8 \pm 24.7
	native	40.2:46.3:13.5 \pm 22.5
SHRUBS	invasive	43.9:34.6:21.6 \pm 17.4
	native	28.2:46.7:25.0 \pm 26.0
LONG-LIVED HERBS	invasive	40.4:32.0:27.5 \pm 23.9
	native	29.0:36.6:34.4 \pm 25.1
SHORT-LIVED HERBS	invasive	34.2:24.3:41.5 \pm 25.6
	native	23.4:23.8:52.9 \pm 29.2
HYDROPHYTES	invasive	0.1:0.0:99.9 \pm 36.7
	native	0.3:0.0:99.7 \pm 35.6

Appendix B. C-, S-, and R-scores (mean \pm standard deviations) within all species and the analysed growth forms

		C (%) \pm sd	S (%) \pm sd	R (%) \pm sd
ALL SPECIES	invasive	36.3 \pm 21.4	26.4 \pm 27.8	37.3 \pm 26.3
	native	29.8 \pm 21.6	30.0 \pm 27.4	40.2 \pm 26.5
TREES	invasive	44.5 \pm 19.4	46.4 \pm 22.8	9.1 \pm 9.0
	native	34.6 \pm 13.7	53.9 \pm 19.1	11.5 \pm 8.7
SHRUBS	invasive	43.5 \pm 13.8	35.9 \pm 18.0	20.6 \pm 11.9
	native	23.9 \pm 17.0	54.8 \pm 26.0	21.3 \pm 19.4
LONG-LIVED HERBS	invasive	34.4 \pm 25.1	31.6 \pm 23.3	34.0 \pm 24.7
	native	32.0 \pm 21.2	31.0 \pm 27.2	37.0 \pm 22.1
SHORT-LIVED HERBS	invasive	35.5 \pm 21.5	15.9 \pm 20.0	48.6 \pm 24.2
	native	26.3 \pm 22.8	15.7 \pm 20.8	58.0 \pm 25.5
HYDROPHYTES	invasive	17.4 \pm 30.7	12.4 \pm 17.8	70.3 \pm 28.3
	native	22.1 \pm 25.3	11.9 \pm 21.2	65.9 \pm 32.9

Appendix C. Values of leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA) (mean \pm standard deviations) within all species and the analysed growth forms. Values refer to transformed data: $\log(x+1)$ for LA and SLA, \sqrt{x} for LDMC

		LA \pm sd	LDMC \pm sd	SLA \pm sd
ALL SPECIES	invasive	7.4 \pm 2.2	4.8 \pm 1.0	3.2 \pm 0.6
	native	6.6 \pm 1.9	4.6 \pm 1.0	3.2 \pm 0.5
TREES	invasive	8.7 \pm 2.0	5.9 \pm 0.6	2.6 \pm 0.5
	native	7.7 \pm 1.4	6.0 \pm 0.5	2.7 \pm 0.4
SHRUBS	invasive	8.4 \pm 1.0	5.4 \pm 0.6	3.1 \pm 0.4
	native	6.4 \pm 1.9	5.6 \pm 0.8	2.8 \pm 0.5
LONG-LIVED HERBS	invasive	7.1 \pm 2.1	5.0 \pm 0.7	3.1 \pm 0.5
	native	6.8 \pm 1.8	4.6 \pm 0.9	3.1 \pm 0.5
SHORT-LIVED HERBS	invasive	7.1 \pm 1.6	4.2 \pm 0.8	3.4 \pm 0.5
	native	6.0 \pm 2.0	4.2 \pm 0.6	3.3 \pm 0.4
HYDROPHYTES	invasive	4.8 \pm 3.7	4.1 \pm 0.9	4.1 \pm 0.6
	native	5.8 \pm 2.4	3.6 \pm 0.9	3.8 \pm 0.7

References

- Alexander, J.M., Lembrechts, J.J., Cavieres, L.A., Daehler, C., Haider, S., Kueffer, C., Liu, G., McDougall, K., Milbau, A., Pauchard, A., Rew, L.J., Seipel, T., 2016. Plant invasions into mountains and alpine ecosystems: current status and future challenges. *Alpine Bot.* 126 (2), 89–103.
- Alpert, P., Bone, E., Holzapfel, C., 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspect. Plant. Ecol.* 3 (1), 52–66.
- Anderson, N.O., Gomez, N., Galatowitsch, S.M., 2006. A non-invasive crop ideotype to reduce invasive potential. *Euphytica* 148 (1–2), 185–202.
- Assini, S., Banfi, E., Brusca, G., Galasso, G., Gariboldi, L., Guiggi, A., 2010. *La Flora Esotica Lombarda*. Museo di storia naturale di Milano, Milano [In Italian].
- Barni, E., Bacaro, G., Falzoi, S., Spanna, F., Siniscalco, C., 2012. Establishing climatic constraints shaping the distribution of alien plant species along the elevation gradient in the Alps. *Plant Ecol.* 213 (5), 757–767.
- Becker, T., Dietz, H., Billeter, R., Buschmann, H., Edwards, P.J., 2005. Altitudinal distribution of alien plant species in the Swiss Alps. *Perspect. Plant Ecol.* 7 (3), 173–183.
- Bornette, G., Tabacchi, E., Hupp, C., Puijalón, S., Rostan, J.C., 2008. A model of plant strategies in fluvial hydrosystems. *Freshwater Biol.* 53 (8), 1692–1705.
- Bradley, B.A., Blumenthal, D.M., Wilcove, D.S., Ziska, L.H., 2010. Predicting plant invasions in an era of global change. *Trends Ecol. Evol.* 25 (5), 310–318.
- Carboneras, C., Genovesi, P., Vilà, M., Blackburn, T.M., Carrete, M., Clavero, M., D'hondt, B., Orueta, J.F., Gallardo, B., Galdes, P., González-Moreno, P., Gregory, R.D., Nentwig, W., Paquet, J., Pyšek, P., Rabitsch, W., Ramírez, I., Scalera, R., Tella, J.L., Walton, P., Wynde, R., 2018. A prioritised list of invasive alien species to assist the effective implementation of EU legislation. *J. Appl. Ecol.* 55, 539–547.
- Carboni, M., Münkemüller, T., Lavergne, S., Choler, P., Borgy, B., Violle, C., Essl, F., Roquet, C., Munoz, F., Consortium, Div Grass, Thuiller, W., 2016. What it takes to invade grassland ecosystems: traits, introduction history and filtering processes. *Ecol. Lett.* 19 (3), 219–229.
- Cayuela, L., Stein, A., Oksanen, J., 2017. Taxonstand: Taxonomic Standardization of Plant Species Names. R Package Version 2.0. R Foundation for Statistical Computing.
- Ciappetta, S., Ghiani, A., Gilardelli, F., Bonini, M., Citterio, S., Gentili, R., 2016. Invasion of *Ambrosia artemisiifolia* in Italy: assessment via analysis of genetic variability and herbarium data. *Flora* 223, 106–113.
- Crawley, M.J., Harvey, P.H., Purvis, A.N.D.A., 1996. Comparative ecology of the native and alien floras of the British Isles. *Philos. T. Roy. Soc. B.* 351 (1345), 1251–1259.
- Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annu. Rev. Ecol. Evol. S.* 34 (1), 183–211.

- Dainese, M., Bragazza, L., 2012. Plant traits across different habitats of the Italian Alps: a comparative analysis between native and alien species. *Alpine Bot.* 122 (1), 11–21.
- Dalle Fratte, M., Brusa, G., Pierce, S., Zanzottera, M., Cerabolini, B.E.L., 2019. Plant trait variation along environmental indicators to infer global change impacts. *Flora* 254, 113–121.
- Davis, M.A., 2009. *Invasion Biology*. Oxford University Press on Demand.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88 (3), 528–534.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Prentice, I.C., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Chave, J., Wright, S.J., Sheremet'ev, S.N., Jactel, H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.S., Günther, A., Falczuk, V., Rüger, N., Mahecha, M.D., Gorné, L.D., 2016. The global spectrum of plant form and function. *Nature* 529, 167–171.
- ETC/BD, 2006. The Indicative Map of European Biogeographical Regions: Methodology and Development. European Topic Centre on Biological Diversity, Paris.
- Funk, J.L., 2013. The physiology of invasive plants in low-resource environments. *Conserv. Physiol.* 1 (1).
- Funk, J.L., Nguyen, M.A., Standish, R.J., Stock, W.D., Valladares, F., 2017. Global resource acquisition patterns of invasive and native plant species do not hold at the regional scale in Mediterranean type ecosystems. *Biol. Invasions* 19 (4), 1143–1151.
- Funk, J.L., Standish, R.J., Stock, W.D., Valladares, F., 2016. Plant functional traits of dominant native and invasive species in mediterranean-climate ecosystems. *Ecology* 97 (1), 75–83.
- Funk, J.L., Vitousek, P.M., 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446, 1079–1081.
- Galasso, G., Conti, F., Peruzzi, L., Ardenghi, N.M.G., Banfi, E., Celesti-Grapow, L., Albano, A., Alessandrini, A., Bacchetta, G., Ballelli, S., Bandini Mazzanti, M., Barberis, G., Bernardo, L., Blasi, C., Bouvet, D., Bovio, M., Cecchi, L., Del Guacchio, E., Domina, G., Fascetti, S., Gallo, L., Gubellini, L., Guiggi, A., Iamonicò, D., Iberite, M., Jiménez-Mejías, P., Lattanzi, E., Marchetti, D., Martinetto, E., Masin, R.R., Medagli, P., Passalacqua, N.G., Peccenini, S., Pennesi, R., Pierini, B., Podda, L., Poldini, L., Prosser, F., Raimondo, F.M., Roma-Marzio, F., Rosati, L., Santangelo, A., Scoppola, A., Scortegagna, S., Selvaggi, A., Selvi, F., Soldano, A., Stinca, A., Wagensommer, R.P., Wilhalm, T., Bartolucci, F., 2018. An updated checklist of the vascular flora alien to Italy. *Plant Biosyst.* 152 (3), 556–592.
- Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Ltd., Chichester, New York, Brisbane, Toronto.
- Grime, J.P., 1988. The CSR model of primary plant strategies—origins, implications and tests. In: Gottlieb, B.D., Jain, S.K. (Eds.), *Plant Evolutionary Biology*. Springer, Dordrecht, pp. 371–393.
- Grime, J.P., 2006. *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons, Ltd., Chichester, New York, Brisbane, Toronto.
- Grime, J.P., Pierce, S., 2012. *The Evolutionary Strategies That Shape Ecosystems*. John Wiley & Sons, Ltd., Chichester, New York, Brisbane, Toronto.
- Gross, K.L., Mittelbach, G.G., Reynolds, H.L., 2005. Grassland invasibility and diversity: responses to nutrients, seed input, and disturbance. *Ecology* 86 (2), 476–486.
- Guo, W.Y., van Kleunen, M., Pierce, S., Dawson, W., Essl, F., Krefth, H., Maurel, N., Pergl, J., Seebens, H., Weigelt, P., Pyšek, P., 2019. Domestic gardens play a dominant role in selecting alien species with adaptive strategies that facilitate naturalization. *Glob. Ecol. Biogeogr.* <https://doi.org/10.1111/geb.12882>.
- Guo, W.Y., van Kleunen, M., Winter, M., Weigelt, P., Stein, A., Pierce, S., Pergl, J., Moser, D., Maurel, N., Lenzner, B., Krefth, H., Essl, F., Dawson, W., Pyšek, P., 2018. The role of adaptive strategies in plant naturalization. *Ecol. Lett.* 21 (9), 1380–1389.
- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E., Challenger, W., 2007. GEIGER: investigating evolutionary radiations. *Bioinformatics* 24 (1), 129–131.
- Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., Vitousek, P.M., 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71 (2), 478–491.
- Hulme, P.E., Bernard-Verdier, M., 2018. Comparing traits of native and alien plants: can we do better? *Funct. Ecol.* 32 (1), 117–125.
- Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönsch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J., Cornelissen, J.H.C., Violle, C., Harrison, S.P., van Bodegom, P.M., Reichstein, M., Enquist, B.J., Soudzilovskaia, N.A., et al., 2011. TRY – a global database of plant traits. *Glob. Change Biol. Bioenergy* 17, 2905–2935. <https://www.try-db.org/>.
- Kautsky, L., 1988. Life strategies of aquatic soft bottom macrophytes. *Oikos* 126–135.
- Kowarik, I., 1995. Time lags in biological invasions with regard to the success and failure of alien species. In: Pyšek, P., Prach, K., Rejmánek, M., Wade, M. (Eds.), *Plant Invasions: General Aspects and Special Problems*. SPB Academic Publishing, Amsterdam, The Netherlands, pp. 15–38.
- Lambdon, P.W., Lloret, F., Hulme, P.E., 2008a. Do non-native species invasions lead to biotic homogenization at small scales? The similarity and functional diversity of habitats compared for alien and native components of Mediterranean floras. *Divers. Distrib.* 14 (5), 774–785.
- Lambdon, P.W., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., Hejda, M., Jarošík, V., Pergl, J., Winter, M., Anastasiu, P., Andriopoulos, P., Bazos, I., Brundu, G., Celesti-Grapow, L., Chassot, P., Delipetrou, P., Josefsson, M., Kark, S., Klotz, S., Kokkoris, Y., Kühn, I., Marchante, H., Perglová, I., Pino, J., Vilà, M., Zikos, A., David, R., Hulme, P.E., 2008b. Alien flora of Europe: species diversity, temporal trends, geographical patterns and research needs. *Preslia* 80 (2), 101–149.
- Landolt, E., Baumler, B., Erhardt, A., Hegg, O., Kleotzli, F., Lammler, W., Nobis, M., Rudmann-Maurer, K., Schweingruber, F.H., Theurillat, J.P., Urmi, E., Vust, M., Wohlgenuth, T., 2010. *Flora Indicativa*. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt ed., Bern.
- Leishman, M.R., Thomson, V.P., Cooke, J., 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. *J. Ecol.* 98 (1), 28–42.
- Loiola, P.P., de Bello, F., Chytrý, M., Götzenberger, L., Carmona, C.P., Pyšek, P., Lososová, Z., 2018. Invaders among locals: alien species decrease phylogenetic and functional diversity while increasing dissimilarity among native community members. *J. Ecol.* 106 (6), 2230–2241.
- Lukács, B.A., Vojtkó, A.E., Mesterházy, A., Molnár, V.A., Süveges, K., Végvári, Z., Brusa, G., Cerabolini, B.E.L., 2017. Growth-form and spatiality driving the functional difference of native and alien aquatic plants in Europe. *Ecol. Evol.* 7 (3), 950–963.
- Meyerson, L.A., Mooney, H.A., 2007. Invasive alien species in an era of globalization. *Front. Ecol. Environ.* 5 (4), 199–208.
- Najberek, K., Nentwig, W., Olejniczak, P., Król, W., Baś, G., Solarz, W., 2017. Factors limiting and promoting invasion of alien *Impatiens balfourii* in Alpine foothills. *Flora* 234, 224–232.
- Ordóñez, A., 2014. Functional and phylogenetic similarity of alien plants to co-occurring natives. *Ecology* 95 (5), 1191–1202.
- Pejchar, L., Mooney, H.A., 2009. Invasive species, ecosystem services and human well-being. *Trends Ecol. Evol.* 24 (9), 497–504.
- Pesaresi, S., Galdenzi, D., Biondi, E., Casavecchia, S., 2014. Bioclimate of Italy: application of the worldwide bioclimatic classification system. *J. Maps* 10 (4), 538–553.
- Pierce, S., Brusa, G., Sartori, M., Cerabolini, B.E.L., 2012. Combined use of leaf size and economics traits allows direct comparison of hydrophyte and terrestrial herbaceous adaptive strategies. *Ann. Bot. Lond.* 109 (5), 1047–1053.
- Pierce, S., Brusa, G., Vagge, I., Cerabolini, B.E.L., 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Funct. Ecol.* 27 (4), 1002–1010.
- Pierce, S., Cerabolini, B.E.L., 2018. *Plant Economics and Size Trait Spectra Are Both Explained by One Theory*. The Plant Press, Milan, Italy.
- Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright, S.J., Soudzilovskaia, N.A., Onipchenko, V.G., van Bodegom, P.M., Frenette-Dussault, C., Weiher, E., Pinho, B.X., Cornelissen, J.H.C., Grime, J.P., Thompson, K., Hunt, R., Wilson, P.J., Buffa, G., Nyakunga, O.C., Reich, P.B., Caccianiga, M., Mangili, F., Ceriani, R.M., Luzzaro, A., Brusa, G., Siefert, A., Barbosa, N.P.U., Chapin III, F.S., Cornwell, W.K., Fang, J., Fernandes, G.W., Garnier, E., Le Stradic, S., Peñuelas, J., Melo, F.P.L., Slaviero, A., Tabarelli, M., Tampucci, D., 2017. A global method for calculating plant CSR ecological strategies applied across biomes worldwide. *Funct. Ecol.* 31, 444–457.
- Pyšek, P., Pergl, J., Essl, F., Lenzner, B., Dawson, W., Krefth, H., Weigelt, P., Winter, M., Kartesz, J., Nishino, M., Antonova, L.A., Barcelona, J.F., Cabesaz, F.J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Dullinger, S., Ebel, A.L., Figueiredo, E., Fuentes, N., Genovesi, P., Groom, Q.J., Henderson, L., Inderjit Kupriyanov, A., Masciadri, S., Maurel, N., Meerman, J., Morozova, O., Moser, D., Nickrent, D., Nowak, P.M., Pagad, S., Patzelt, A., Pelsler, P.B., Seebens, H., Shu, W., Thomas, J., Velayos, M., Weber, E., Wieringa, J.J., Baptiste, M.P., van Kleunen, M., 2017. Naturalized alien flora of the world. *Preslia* 89 (3), 203–274.
- Pyšek, P., Prach, K., Smilauer, P., 1995. Relating invasion success to plant traits: an analysis of the Czech alien flora. In: Pyšek, P., Prach, K., Rejmánek, M., Wade, M. (Eds.), *Plant Invasions: General Aspects and Special Problems*. SPB Academic Publishing, Amsterdam, The Netherlands, pp. 39–60.
- Pyšek, P., Richardson, D.M., 2006. The biogeography of naturalization in alien plants. *J. Biogeogr.* 33 (12), 2040–2050.
- Pyšek, P., Richardson, D.M., 2008. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig, W. (Ed.), *Biological Invasions*. Springer, Berlin, Heidelberg, pp. 97–125.
- Pyšek, P., Sádlo, J., Mandák, B., Jarošík, V., 2003. Czech alien flora and the historical pattern of its formation: what came first to Central Europe? *Oecologia* 135 (1), 122–130.
- Qian, H., Jin, Y., 2016. An updated megaphylogeny of plants, a tool for generating plant phylogenies and an analysis of phylogenetic community structure. *J. Plant Ecol.* 9 (2), 233–239.
- R Core Team, 2018. *R: a Language and Environment for Statistical Computing*. URL: R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reich, P.B., 2014. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102 (2), 275–301.
- Rejmánek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? *Ecology* 77 (6), 1655–1661.
- Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J., Grotkopp, E., 2005a. Ecology of invasive plants: state of the art. In: Mooney, H.A., Mack, R.M., McNeely, J.A., Neville, L., Schei, P., Waage, J. (Eds.), *Invasive Alien Species: Searching for Solutions*. Island Press, Washington, DC, pp. 104–161.
- Rejmánek, M., Richardson, D.M., Pyšek, P., 2005b. Plant invasions and invasibility of plant communities. In: Van der Maarel, E. (Ed.), *Vegetation Ecology*. Blackwell Science, Oxford, Blackwell Publishing Ltd, pp. 332–355.
- Richardson, D.M., Pyšek, P., 2006. Plant invasions: merging the concepts of species invasiveness and community invasibility. *Prog. Phys. Geog.* 30 (3), 409–431.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6 (2), 93–107.
- Roiola, S.R., Retuerto, R., Campoy, J.G., Novoa, A., Barreiro, R., 2016. Division of labor brings greater benefits to clones of *Carpobrotus edulis* in the non-native range: evidence for rapid adaptive evolution. *Front. Plant Sci.* 7, 349.
- Song, Y.B., Yu, F.H., Keser, L.H., Dawson, W., Fischer, M., Dong, M., van Kleunen, M., 2013. United we stand, divided we fall: a meta-analysis of experiments on clonal integration and its relationship to invasiveness. *Oecologia* 171 (2), 317–327.
- Stohlgren, T.J., Barnett, D.T., Jarnevich, C.S., Flather, C., Kartesz, J., 2008. The myth of plant species saturation. *Ecol. Lett.* 11 (4), 313–322.

- Tecco, P.A., Díaz, S., Cabido, M., Urcelay, C., 2010. Functional traits of alien plants across contrasting climatic and land-use regimes: do aliens join the locals or try harder than them? *J. Ecol.* 98 (1), 17–27.
- Thompson, K., Hodgson, J.G., Rich, T.C., 1995. Native and alien invasive plants: more of the same? *Ecography* 18 (4), 390–402.
- Tordoni, E., Petruzzellis, F., Nardini, A., Savi, T., Bacaro, G., 2019. Make it simpler: alien species decrease functional diversity of coastal plant communities. *J. Veg. Sci.* <https://doi.org/10.1111/jvs.12734>.
- van den Boogaart, K.G., Tolosana-Delgado, R., 2013. *Analyzing Compositional Data with R*. Springer, Heidelberg.
- van den Boogaart, K.G., Tolosana-Delgado, R., Bren, M., 2018. *Compositions: Compositional Data Analysis. R Package Version 1*. pp. 40–42. <https://CRAN.R-project.org/package=compositions>.
- Van Kleunen, M., Essl, F., Pergl, J., Brundu, G., Carboni, M., Dullinger, S., Early, R., González-Moreno, P., Groom, Q.J., Hulme, P.E., Kueffer, C., Kühn, I., Máguas, C., Maurel, N., Novoa, A., Parepa, M., Pyšek, P., Seebens, H., Tanner, R., Touza, J., Verbrugge, L., Weber, E., Dawson, W., Kreft, H., Weigelt, P., Winter, M., Klöner, G., Talluto, M.V., Dehnen-Schmutz, K., 2018. The changing role of ornamental horticulture in alien plant invasions. *Biol. Rev.* 93 (3), 1421–1437.
- Van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* 13 (2), 235–245.
- Vicente, J.R., Pinto, A.T., Araújo, M.B., Verburg, P.H., Lomba, A., Randin, C.F., Guisan, A., Honrado, J.P., 2013. Using life strategies to explore the vulnerability of ecosystem services to invasion by alien plants. *Ecosystems* 16 (4), 678–693.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14 (7), 702–708.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J., Fromenti, J., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. *Nature* 416, 389.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin III, F.S., Cornelissen, J.H.C., Villar, R., 2004. The worldwide leaf economics spectrum. *Nature* 428, 821–827.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.