The role of adaptive strategies in plant naturalization

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Abstract

Determining the factors associated with the naturalization of alien species is a central theme in ecology. Here, we tested the usefulness of a metric for quantifying Grime's seminal concept of adaptive strategies – competitors, stress-tolerators and ruderals (CSR) – to explain plant naturalizations worldwide. Using a global dataset of 3004 vascular plant species, and accounting for phylogenetic relatedness and species' native biomes, we assessed the associations between calculated C, S, and R scores and naturalization success for species exhibiting different life forms. Across different plant life forms, C-scores were positively and S-scores negatively associated with both the probability of naturalization and the number of regions where the species has naturalized. R-scores had positive effects on the probability of naturalization. These effects of the scores were, however, weak to absent for tree species. Our findings demonstrate the utility of CSR-score calculation to broadly represent, and potentially explain, the naturalization success of plant species.

Introduction

Determining the factors associated with the naturalization of alien species and invasibility of recipient ecosystems is a central theme in ecology (Lonsdale 1999; Richardson & Pyšek 2006, 2012; van Kleunen *et al.* 2015a). In recent decades, a multitude of plant-species traits and environmental characteristics have been identified that promote naturalization and invasiveness, such as fast growth, early flowering (Pyšek & Richardson 2007; van Kleunen *et al*. 2010), large native range size and habitat affiliation in the native range (Rejmánek & Richardson 1996; Pyšek *et al*. 2015; Kalusová *et al*. 2017). Studies, however, have also revealed that the factors associated with plant invasions are stage (Williamson 2006; Theoharides & Dukes 2007; Dawson *et al.* 2009; Pyšek *et al.* 2009a; Moodley *et al.* 2013) or context dependent (Kueffer *et al.* 2013; van Kleunen *et al.* 2015b; Elliott-Graves 2016). Consequently, few of the characteristics explored so far appear to be universally linked to invasion success.

Given the complexities and context dependency typical of biological invasions, one possible reason why our ability to generalize and predict the outcome of particular introductions remains limited is that most studies focus on single traits rather than on trait combinations and species-ecosystem interactions, so-called invasion syndromes (Küster *et al.* 2008; Kueffer *et al.* 2013; van Kleunen *et al*. 2015b). A promising direction therefore is the ordination of species along known principal axes of functional variability, or primary trait spectra (e.g., Rejmanek & Richardson 1996; Pyšek *et al.* 2009b; Byun *et al.* 2013; Novoa *et al.* 2016). This is particularly promising where traits are integrated as suites of functional traits that jointly confer fitness in the face of selection pressures, so called 'adaptive strategies', and are thus consistent with a theory that can potentially offer additional explanatory and predictive power. To illustrate this concept: the single traits Rubisco content (carboxylation capacity), chlorophyll content (light absorption) and internal water conduction each impact on the photosynthetic rate of a leaf, but the measured value of photosynthetic rate represents the joint effects of these various functions. Similarly, overall plant fitness may ultimately depend on the optimization of trait integration, perhaps more than it does on the performance of a single trait. Therefore, an adaptive strategy is not a combination of traits *per se*, but is in essence the particular regime of resource investments across traits that achieves fitness in response to one or more selection pressures.

The main axes of plant-functional-trait variability globally are known to represent spectra of resource-investment economics (i.e., a trade-off between traits supporting resource capture and conservation; Wright *et al*. 2004; Blonder *et al.* 2015; Onoda *et al.* 2017) and organ and whole-plant sizes (Díaz *et al*. 2016). These two fundamental spectra are compatible with trait variation hypothesized by Grime (1974, 1977), and are associated with constraints imposed by major selection pressures such as stress (reduced productivity) and disturbance (biomass destruction and removal; Cerabolini *et al*. 2010; Pierce *et al*. 2012, 2013).Within Grime's framework, three fundamental or primary adaptive strategies exist: i) competitors (C) exploit conditions of high productivity where stress and disturbance are relatively unimportant selection pressures, ii) stress-tolerators (S) are adapted to survive conditions in which productivity is chronically or seasonally limited, and iii) ruderals (R) can maintain a population despite the death of individuals by relying on inherently rapid completion of the life cycle (Grime 1979). A combination of both high stress and high disturbance is untenable because severe stress prevents recovery after disturbance (Herben *et al*. 2018).

Numerous advantages are conferred by an adaptive strategy approach over the use of single traits. First, strategies integrate variation along both major plant functional spectra (plant economics and size) and represent the underlying multi-trait trade-offs. Second, strategies potentially link trait variation to causal factors meaning that they can help explain observations. Third, strategies provide a theoretical context that can be experimentally tested, and which also confers transferability and thus predictive power. The performance of a plant with a certain strategy in one environment may be expected to predict responses of functionally similar species in other similar environments. This is of clear relevance to the functional characterization and prediction of naturalization ability in plants.

Grime (1979) proposed an ordination of species in a triangular plot, reflecting the trade-offs among tolerance of competition, stress and disturbance. However, until recently a wider application and generalization based on the CSR-strategy scheme has been fraught with limitations (see the methodologies of Hodgson *et al.* 1999; Pierce *et al*. 2013), because the traits used were specific to certain plant groups, reflected phenology at particular latitudes, represented a mixture of detailed values measured on individuals (leaf traits) alongside general classes determined for the population or species (e.g. the month of flowering onset), or studies were geographically limited in scope. To overcome these limitations, Pierce *et al.* (2017) developed a CSR-classification method in which a few easily determined leaf traits are compared against the global leaf economics and size trade-offs. Extremely high values of specific leaf area (SLA) and leaf dry matter content (LDMC) are highly representative of extremes of fast and slow leaf economics, respectively, and leaf area (LA) is a fundamental determinant of the ability of species to intercept light that also correlates with plant and seed size, orthogonal to the leaf economics spectrum (Cerabolini *et al*. 2010; Pierce *et al*. 2013; Díaz *et al*. 2016). However, each of the traits – LA, LDMC and SLA – themselves do not directly represent the extent of C, S and R-selection. Instead, it is the trade-off between traits, compared against trade-offs evident globally, from which the C, S, and R scores are calculated (Pierce *et al.* 2017).

Co-inertia analysis demonstrated that this method based on the three leaf traits mentioned above is representative of variation in 14 key leaf, reproductive and whole-plant functional traits, including leaf nitrogen content, seed mass and flowering phenology (Pierce *et al.* 2017). Although this system cannot represent all of plant functioning, nor all factors that affect survival, the three leaf traits do represent a broader underlying spectrum of function and of adaptive strategies, which makes global comparisons possible.

Using the ordination tool of Pierce *et al.* (2017), a species cannot only be classified according to the traditional CSR categories of Grime, but continuous C, S, and R scores are calculated as the percentage of each main strategy (C, S, R) realized by a focal plant species. This makes the scheme quantitative and unbiased by subjective classification. The method is generally applicable to vascular plants, sufficiently precise to distinguish strategies among species within genera, among populations within species and across biomes, and its validity has been confirmed in several experiment and field studies (Li & Shipley 2017; Rosado & de Mattos 2017). Depending on the availability of robust trait measures, this objective CSR-strategy approach makes it possible to investigate primary plant functional types across a wide range of species and habitats at the global scale.

Grime's CSR categories have previously only been applied to plant invasions in local to regional-scale studies, with findings that ruderals (R), competitors (C) and the intermediate stage between C and R (CR) are prevalent, while stress-tolerators (S) are under-represented amongst alien plant species (Pyšek *et al.* 2003; Lambdon *et al.* 2008; Dainese & Bragazza 2012; Alexander *et al.* 2016). These results suggest that Grime's CSR-strategy theory is a powerful tool for studying the interactions of plant traits and species invasion success (Davis 2009; Rejmánek *et al.*, 2013). These previous local and regional studies addressing the role of adaptive strategies simply reported the proportions of aliens in each CSR category (Pyšek *et al.* 2003; Alexander *et al.* 2016), or compared the proportions of alien and native species in each CSR category (Lambdon *et al.* 2008; Dainese & Bragazza 2012). However, no global study has quantitatively assessed the adaptive strategies of species that have been able to successfully naturalize compared to those that have not (i.e., naturalization incidence), or how the strategies relate to the number of regions where a species has naturalized (i.e., naturalization extent). Furthermore, no previous study has considered the effect of phylogenetic relatedness of species, which could bias comparative analyses, as closely related species usually exhibit similar traits due to shared evolutionary history (Felsenstein 1985; Ives & Garland 2010).

To overcome these methodological constraints to a rigorous evaluation of the role of adaptive strategies in plant invasions and to assess their validity at the global scale, we used the C, S, and R scores calculated by Pierce *et al.* (2017) for 3004 species in combination with data from the Global Naturalized Alien Flora database (GloNAF; van Kleunen *et al.* 2015a; Pyšek *et al.* 2017). We asked if (i) the incidence and (ii) the extent of naturalization of alien plant species are associated with their specific C, S and R score, as calculated by this method (and while accounting for phylogeny). In addition, since plant functional traits are closely linked to life form (Faber-Langendoen *et al*. 2015; Pierce *et al*. 2017), which also influences naturalization success (e.g., Razanajatovo *et al.* 2016), we included species life form (short-lived herb, long-lived herb, shrub, tree) in our models to test whether they interact with calculated C, S and R scores to affect the incidence and extent of naturalization. Furthermore, as previous global studies revealed that geographic regions and habitats differ as donors and recipients of naturalized species (Pyšek *et al.* 2003; van Kleunen *et al.* 2015a; Kalusová *et al.* 2017; Pyšek *et al.* 2017), we also included information on the biome of the species' native range as a covariate.

Methods

Global database compilation

Pierce *et al*. (2017) compiled a global dataset of 3068 vascular plant species for which they calculated C, S and R scores using data on specific leaf area (SLA), leaf area (LA) and leaf dry matter content (LDMC) of species from the TRY global plant functional traits database (Kattge *et al.* 2011; www.try-db.org). The calculation involved two main steps: an initial Principal Component Analysis (PCA) of the three leaf traits, followed by a regression of trait values against PCA axes to obtain the regression equations, which were used to assign the species' C, S, and R scores (Pierce *et al.* 2017). We used the calculated C, S and R scores of the 3068 plant species (Table S1 of Pierce *et al*. 2017) and merged these with the GloNAF database (version 1.1; van Kleunen *et al.* 2015a; Pyšek *et al.* 2017). GloNAF is the most comprehensive global database of naturalized alien plants, comprising information on the naturalization status of vascular plant species in 843 regions. The database includes 13,168 naturalized alien species, and the regions range in area from 0.03 to 2.5 × 10^6 km^2, with a mean of 1.3 × 10^5 km^2 and cover *c*. 83% of the world's ice-free land area. In GloNAF, the criterion for naturalization follows the widely accepted definition that the species forms self-reproducing populations in the wild (Richardson *et al*. 2000; Blackburn *et al*. 2011). As species names in the GloNAF database were standardized according to The Plant List (http://www.theplantlist.org), we standardized the species names provided by Pierce *et al.* (2017) via the R package *plantlist* (https://github.com/helixcn/plantlist) before merging the two databases. After name checking, several species were identified as synonyms of other species in the list and were thus removed. Subspecies and varieties were included under the binomial species name in the final list. The final dataset therefore included 3004 instead of 3068 species from 60 orders and 198 families (see Figs. S1 & S2 for the numbers of species belonging to each order and family).

Naturalization success was first measured as the *incidence of naturalization*, i.e., whether a species was listed as a naturalized alien in the GloNAF database. Of the 3004 species, 1515 were reported to be naturalized alien species somewhere in the world. As a second measure of naturalization success (for the subset of naturalized species), we estimated the *extent of naturalization* as the number of GloNAF regions for which the species is recorded as naturalized. The extent of naturalization could also be measured as the cumulative area of the regions in which the species is naturalized. However, because a species does not necessarily occur in all parts of a region, and because the number and cumulative area of regions are strongly correlated (Pyšek *et al*. 2017), we used only the number of regions.

Data on the life history and growth form of each species were taken from Table S1 of Pierce *et al*. (2017). Due to low numbers of biennial species (only 83 naturalized alien and 11 non-naturalized species), we combined annuals and biennials in the group of *short-lived* species, and perennials formed the group of *long-lived* species (Figs. 1 & S3). The species originally belonged to seven growth forms (as classified in Pierce *et al*. 2017), but as some groups consisted of only a few species (e.g., liana, herbaceous vine), which could limit statistical power, we created a broader classification of four life forms. These life-form categories largely correspond to those of Raunkiær (1934), and include *short-lived herbs* (annual and biennial herbs, which merges the graminoid, forb, herbaceous vine and aquatic categories of Pierce *et al.* 2017), *long-lived herbs* (perennial graminoids and forbs), *shrubs* (shrubs and lianas) and *trees* (as used in FGDC, 1997; Qian *et al.* 2017).

The native distribution range of species was assigned to geographic continents following the Biodiversity Information Standards TDWG (TDWG level 1; Brummitt 2001). Geographic continents were assigned using several online databases: the World Checklist of Selected Plant Families (WCSP, http://apps.kew.org/wcsp/), the Germplasm Resources Information Network (GRIN, http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl). The

Global Biodiversity Information Facility database (GBIF, http://www.gbif.org) was used for some non-naturalized species, if no other distribution data were available. To account for a potential effect of species' biogeographic origins, we further assigned each species' native distribution range to biomes, i.e., biogeographic units of representative habitats and species assemblages (*sensu* Olson *et al*. 2001). We obtained species' biome information from Pierce *et al*. (2017). The native ranges of the 3004 species investigated in this study covered eight of the nine TDWG continents (Antarctica was not covered; Fig. S4), and covered all the 14 world biomes (Pierce *et al*. 2017). The 1489 non-naturalized species belonged to 50 orders and 160 families, and the 1515 naturalized alien species belonged to 53 orders and 141 families (Figs. S1 & S2).

Phylogenetic tree

To account for phylogenetic relatedness in our statistical analyses, we constructed a phylogenetic tree of the 3004 species in our final dataset. This was done using a dated supertree initially constructed by Zanne *et al.* (2014), and corrected and extended by Qian and Jin (2016). This tree includes 31,749 species and was generated based on several genetic markers. Qian and Jin (2016) also provided an R function, *S.PhyloMaker*, to generate phylogenies for subsets of species. Following their recommendations, we used their Scenario 3 approach, which adds absent species to their families or genera using the same approach as used in Phylomatic and BLADJ (Webb *et al.* 2008). The phylogenetic tree was visualized using the *ggtree* package (Figs. S5 & S6; Yu *et al.* 2017).

Statistical analysis

All analyses were done in R 3.3.3 (R Core Team 2017). We used the *ggtern* package (Hamilton 2015) to visualize the triangular plots of the C, S, and R scores of species. We standardized the C-, S-, and R-scores to means of zero and standard deviations of 1 to facilitate comparisons between models (Schielzeth 2010). We used phylogenetic logistic regression (Ives & Garland 2010, 2014), as implemented in the R package *phylolm* (Ho & Ane 2014), to analyze the relationships between naturalization incidence and each of the C-, S- and R-scores, while accounting for phylogenetic relatedness. We included species' life form (i.e., short-lived herb, long-lived herb, shrub and tree) and its interaction with each of the three CSR-strategy scores to test if the relationship between each strategy score and naturalization incidence was different for species in different life-form categories. We ran a similar set of models to test for associations between naturalization extent and each strategy score, and the interaction of life form with each of the three strategy scores using Phylogenetic Generalized Least Squares regression in the *phylolm* package (Ho & Ane 2014). We included biome and its interactions with each strategy score in both the naturalization-incidence and naturalization-extent models. For each predictor variable in each model, Wald tests were performed to determine if its main effect or interactions were significant, using the *aod* package (Lesnoff & Lancelot 2012). To show the general effect of biome and its interactions with the C, S, and R scores, we ran Wald tests for the 14 biomes. We calculated R^2 to assess the amount of variation explained by each regression model using the *rr2* package (Ives 2017).

Results

The C, S and R scores were all negatively correlated to each other (Pearson's correlations, C *vs* S: -0.47; C *vs* R: -0.32; S *vs* R: -0.68; all $p < 0.001$). Without accounting for life form, biome and phylogeny, the naturalized species had, compared to the non-naturalized species, higher R (mean ± SD: 39.2 ± 25.4% *vs* 26.6 ± 25.0%) and lower S scores (29.3 ± 26.7% *vs* 42.2 ± 27.7%), whereas the C scores were similar (31.5 ± 21.8% *vs* 31.2 ± 21.6%) (Fig. 2a). Among the naturalized alien species, those with high C and R scores occupied a greater number of regions outside of their native range (i.e., had a larger naturalization extent), especially when compared to species with high S scores (Fig. 2b).

When life form, biome and phylogeny were accounted for, the results were slightly different. Averaged across the four different life forms, the C score was significantly positively related to naturalization incidence and extent, and the S score was significantly negatively related to naturalization incidence and extent (Table 1, Fig. 3). The R score was significantly positively related to naturalization incidence, but had no significant effect on naturalization extent (Table 1, Fig. 3). However, the effects of most scores on naturalization differed significantly among the four life-form categories (Table 1, Fig. 3). This reflects in particular that for trees, none of the C, S and R scores was significantly related to naturalization incidence and extent (Fig. 3). On the other hand, for short-lived herbs, long-lived herbs and shrubs, having a relatively high C score or having a relatively low S score was associated with increased naturalization incidence and extent (Fig. 3). For long-lived herbs and shrubs, having a relatively high R-score increased the naturalization incidence (Fig. 3a).

Species' native biome significantly affected naturalization incidence and extent, and species originating from certain biomes had a higher naturalization success than those from other biomes (Table 1, for details see Tables S1 & S2). Moreover, the effects of the S-score on naturalization incidence and extent, and the effect of the R-score on naturalization incidence varied among biomes (Table 1).

Discussion

Based on a large dataset of 3004 vascular plant species of different life forms, we used the CSR-calculation method of Pierce *et al.* (2017) – which is in agreement with the theoretical context of Grime's (1974, 1977) adaptive strategy scheme – to test the relationships between a species' C-, S- and R-scores and its naturalization incidence (i.e., whether or not it has naturalized somewhere) and extent (i.e., in how many regions of the world it is naturalized). While previous studies, using Grime's CSR categories, revealed some general trends at the regional scale (Pyšek *et al.* 2003; Lambdon *et al.* 2008; Dainese & Bragazza 2012; Alexander *et al.* 2016), our study using quantitative C, S and R scores provides the first global test for these relationships, and of the relative importance of the different adaptive-strategy axes. Across different plant life forms, C scores were positively and S scores negatively associated with naturalization incidence and extent, whereas R scores had positive effects on the naturalization incidence only. These effects of the strategy scores were, however, weak or even absent for tree species. Our results thus demonstrate the divergent associations between adaptive strategy spectra and naturalization success among life forms.

Interpreting our results from the viewpoint of key traits typical for each plant strategy (Grime 1979; Grime & Pierce 2012), competitors and ruderals are both characterized by rapid growth, a short leaf life-span, a high flowering frequency, and nutrient-rich leaves (thus having a higher photosynthetic rate; Wright *et al.* 2004; Reich 2014). All of these traits are frequently associated with invasive plant species (Pyšek & Richardson 2007; van Kleunen *et al.* 2010). These features are also sought after for certain kinds of cultivation activities (e.g., ornamental horticulture, bioenergy crops; van Kleunen *et al.* 2018). This implies that competitive and ruderal species might have been more likely to be introduced early and frequently by humans, which would have increased their probability of naturalization. The higher propagule pressure and longer residence time in the introduced ranges, together with higher frequency of reproduction, may in turn result in greater naturalization extent to those kinds of species (Pyšek & Jarošík 2005; Proches *et al.* 2012; Pyšek *et al.* 2015). However, such an 'introduction bias' (van Kleunen *et al*. 2015a; Maurel *et al*. 2016) could result in spurious associations between plant adaptive strategies and naturalization success, and should be accounted for in future studies.

Theoretically, a high nutrient content of tissues should make competitors and ruderals prone to higher rates of herbivory (Grime 1979, 1988; Grime & Pierce, 2012) and impair their naturalization success. As a plant's specialist herbivores are often absent in its new range (Enemy Release hypothesis; Keane & Crawley 2002; Liu & Stiling 2006), having a strategy of fast growth and low defense, instead of slow growth and high defense, may pose stronger advantages to alien species in their naturalized than in their native range (the Resource Enemy Release hypothesis, Blumenthal 2006). In addition, a high degree of morphological plasticity typical of competitors and ruderals (Grime 1979, 1988) can also provide an advantage for being able to grow in a wider range of environments (Richards *et al.* 2006; Hulme 2008).

Our results also showed that the R scores of short-lived herbs had no association with naturalization success. In theory, even though typical ruderals usually establish very quickly, flower more frequently, allocate a large proportion of resources to seed and form a persistent seed bank (Grime 1979; Gioria *et al.* 2012; Grime & Pierce 2012), their ability to compete is much weaker in undisturbed habitats. In addition, under continuous, moderate disturbance, the seed production of ruderals does not compensate for the mortality rate, and ruderals eventually fail to establish (Grime 1979, 1988). Therefore, short-lived herbs with R-selection, unlike long-lived herbs and shrubs, did not relate to the incidence of naturalization. In our dataset, however, naturalized alien long-lived herbs and shrubs tending towards a more ruderal strategy are mostly Mediterranean evergreen microphyllous species (e.g., *Santolina chamaecyparissus*, *Retama sphaerocarpa*), indicating that they may have adapted to relative stressed and human-dominated (highly disturbed) environments in the native Mediterranean range (Lambdon *et al*. 2008). Moreover, our results indicate that a Mediterranean origin was positively related to a species' naturalization success (Tables S1 & S2).

We found that species with a greater S-score were less likely to become naturalized, which supports the findings of previous studies showing that stress-tolerators were under-represented among naturalized alien plants (Pyšek *et al.* 2003; Alexander *et al.* 2016). In theory, stress-tolerators are generally very long-lived, have a long leaf life-span, grow slowly, fruit late and produce fewer seeds with respect to competitors and ruderals (Grime 1979; Grime & Pierce 2012). All these traits are the opposite of those commonly reported to be associated with successful invaders (Pyšek & Richardson, 2007; van Kleunen *et al.* 2010), and could also make stress-tolerators less likely to be selected by humans for introduction as horticultural plants. In general, stress-tolerant plants rely heavily on vegetative instead of sexual reproduction and rarely show a high morphological plasticity, which limits their spread potential (Grime 1979, 1988). In addition, the chance of a stress-tolerant plant being 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 (Alexander *et al*. 2011).

In contrast to the other life forms, naturalization incidence and extent of trees were not or only weakly affected by their C-, S- and R-scores (Fig. 3). Tree species with high R-scores do not appear to exist (Pierce *et al.* 2017). The absence of a clear association of naturalization success of trees with the C score could be caused by the overall lower representation of naturalized trees in our dataset (13% of all naturalized species were trees; Fig. 3). Trees are also less numerous in the global pool of naturalized plants compared to herbs (Pyšek *et al*. 2017), most likely because the global pool of tree species is much smaller than that of herbs (Beech *et al*. 2017). The lesser representation of trees and their non-significant associations of

C, S, and R scores with naturalization success may be related to the long periods needed for establishment, long generation times, the relatively low proportion of resources invested in seed production (Grime 1979), and the long time lag following introduction to new ranges (Kowarik 1995; Pyšek *et al*. 2017).

The model estimates of associations between S-score and naturalization extent showed a gradual increase from short-lived herbs to trees (Fig. 3b), indicating that among the more stress tolerant species, long-lived, big woody species tend to be naturalized in more regions than short-lived, small herbs. A possible explanation could be that stress-tolerant trees live longer than other plants, allowing them to accumulate the necessary resources to survive, grow and establish in a habitat that can be unproductive due to extreme climatic conditions or low nutrient availability (Grime 1979). In addition, increased propagule pressure resulting from forestry can significantly increase the odds of successful naturalization of trees (Křivánek *et al*. 2006; Bucharová & van Kleunen 2009; Pyšek *et al*. 2009b; Proches *et al*. 2012), thereby masking, or compensating for the effects of species characteristics, such as their adaptive CSR strategy. Furthermore, alien trees with a stress-tolerant strategy are often evergreen angiosperms (e.g., *Quercus* spp. in our data set, Table S3) or conifers (Pierce *et al*. 2017). The latter are represented by several *Pinus* species in our data set (Table S3), a genus which is known to include many invasive species (e.g., Richardson *et al.* 1994; Richardson & Rejmánek 2004; Essl *et al.* 2011; Pyšek *et al*. 2017).

Previous studies have also tested the associations of the three leaf traits used to calculate the C, S, and R scores (i.e., SLA, LA and LDMC) with naturalization and invasion success of alien plants. SLA, the most widely-examined trait among the three, is generally higher for naturalized and invasive species compared to non-naturalized species (Hamilton *et al*. 2005; Pyšek & Richardson 2007; Gallagher *et al*. 2015). However, this trend is not universal as studies have also found lower SLA for invasive species compared to non-invasive species (e.g., McDowell 2002). In addition, a recent study did not find a direct causal relationship between SLA and naturalization success, when accounting for cultivation in the introduced ranges, other species traits, propagule pressure and residence time in a path analysis (Pyšek *et al*. 2015). Studies that tested for the associations of LA and LDMC with naturalization success usually did not find any either (Pyšek & Richardson 2007; Gallagher *et al*. 2015; Pyšek *et al*. 2015). In our study, however, the C, S and R scores obtained from the trade-off among the three traits showed clear relationships with naturalization success, indicating that it is the combination of viable trait values that is associated with success. This is in agreement with the concept of adaptive strategies, and shows that the estimation of strategy scores can help to potentially explain the ability to invade.

Conclusions

With a global dataset, a dated species-level phylogeny, and accounting for life forms and species' biomes, we demonstrate that plant C, S and R scores play an important role in alien plant naturalization. This also suggests that the CSR theory has a great potential to facilitate understanding of the determinants of invasion success. For example, by taking into account the residence time of naturalized species, it should be possible to estimate, using the CSR scheme, how quickly a species can establish in the new range. Due to the ease of obtaining C, S, and R scores, the scheme can rapidly identify species with a high naturalization potential, and thus can be used in risk-assessment systems to warn and prevent future plant invasions. With ongoing accumulation and increased accessibility of field data for the relevant traits (i.e., SLA, LA, and LDMC) it will be possible to validate the generality of these results for regions and life forms that were less represented in our data set (e.g., trees), and address in greater detail the biogeographic differences in the role plant strategies play in alien species' naturalization.

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Table 1 Results of regression models of C-, S-, or R-score, life form, biome, and interaction terms in affecting naturalization incidence (n = 3004) and naturalization extent (n = 1515). Naturalization incidence models were run as phylogenetic logistic regressions, naturalization extent models were run as phylogenetic generalized least squares models, and then the significance of each variable was tested with the Wald test. Phylogenetic signal $\alpha = 0.1352, 0.1258, 0.1336$ for the three phylogenetic logistic regressions, respectively; and $\lambda = 0.3137, 0.3360, 0.3374$ for the three phylogenetic generalized least squares models, respectively.

Variable	***df***	**Naturalization incidence**			**Naturalization extent**		
		X^2	p	R^2	X^2	p	R^2
Intercept	1	0.1	0.710	0.44	37.0	< 0.001	0.83
C-score	1	15.6	< 0.001		13.2	< 0.001	
Life form	3	73.6	< 0.001		84.0	< 0.001	
Biome	14	290.8	< 0.001		107.1	< 0.001	
C-score × Life form	3	16.1	0.001		9.1	0.028	
C-score × Biome	14	13.4	0.496		21.7	0.086	
Intercept	1	75.1	< 0.001	0.43	16.1	< 0.001	0.82
S-score	1	21.7	< 0.001		6.9	0.009	
Life form	3	68.9	< 0.001		31.2	< 0.001	
Biome	14	387.3	< 0.001		96.4	< 0.001	
S-score × Life form	3	16.1	0.001		3.0	0.386	
S-score × Biome	14	34.9	0.002		25.3	0.032	
Intercept	1	3.5	0.060	0.42	28.1	< 0.001	0.82
R-score	1	0.6	0.437		0.6	0.436	
Life form	3	109.9	< 0.001		98.7	< 0.001	
Biome	14	268.1	< 0.001		147.5	< 0.001	
R-score × Life form	3	11.7	0.008		8.2	0.042	
R-score × Biome	14	47.4	< 0.001		17.1	0.253	

Figure captions

Fig. 1 Summary of naturalized and non-naturalized species numbers by life forms in the dataset used (n = 3004 species). The original seven categories of growth form in Pierce *et al*. (2017) were grouped into three categories: herb (including aquatics, forbs, graminoids and herbaceous vines), shrub (including lianas and shrubs) and tree. According to the duration of the life span, herbs were further divided into short-lived (annual and biennial) and long-lived (perennial). This resulted in a four-level life-form category, i.e., short-lived herb, long-lived herb, shrub, and tree.

Fig. 2 Naturalization incidence (a) and extent (b) within the CSR strategy triangle. (a) Competitor (C), stress-tolerant (S) and ruderal (R) scores of 1515 vascular plant species that are naturalized (orange dots) in at least one of 843 global regions outside of their native range, and of 1489 vascular plant species that are not naturalized anywhere (blue dots), according to the GloNAF database. The orange and blue triangles from interior to outward are 50%, 90% and 95% confidence levels, respectively. The black arrow indicates the shift of means from non-naturalized species to naturalized alien species. Along each axis of the ternary plot, a boxplot of the respective strategy score displays the median (line in the middle of boxes), the mean (black dot), the interquartile range (boxes), ±1.5 times the interquartile range (whiskers), and outliers (circles) for each group of species. (b) Naturalization extent (number of regions where naturalized) of the 1515 naturalized alien species. Data were log(x +1) transformed. Along each axis of the ternary plot, a heatmap shows the mean number of regions for every 10% bin of the respective strategy score.

Fig. 3 Effects of each C-, S-, or R- score on (a) naturalization incidence and (b) naturalization extent of alien plant species for each life form. Estimates of the effects and their standard errors were obtained from phylogenetic logistic/generalized linear regression models. Detailed results of models are shown in Tables 1, S1, S2.

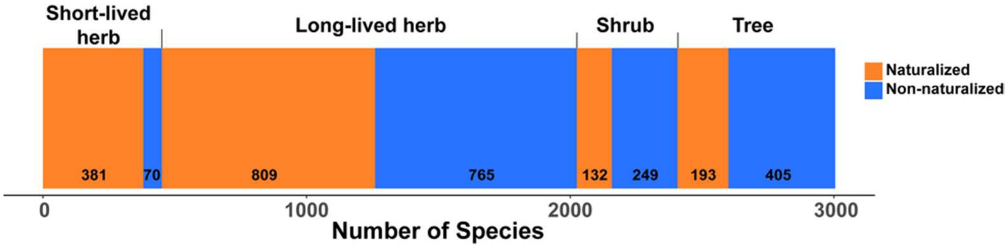

Fig. 1 Summary of naturalized and non-naturalized species numbers by life forms in the dataset used (n = 3004 species).

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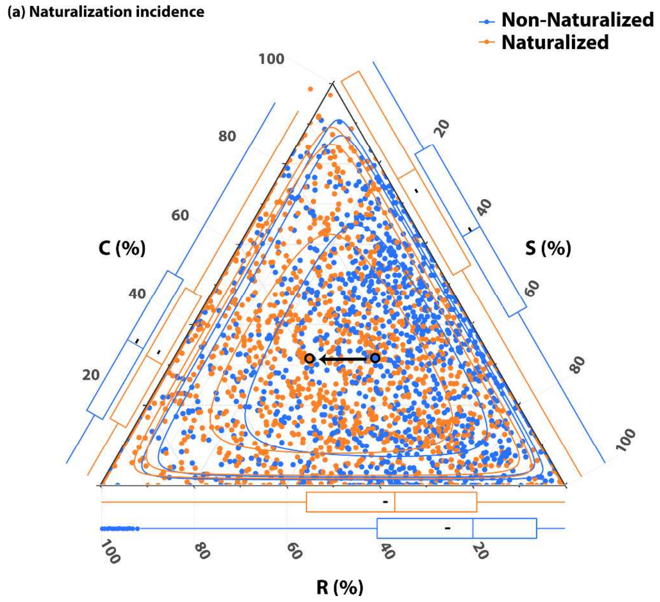
(a) Naturalization incidence

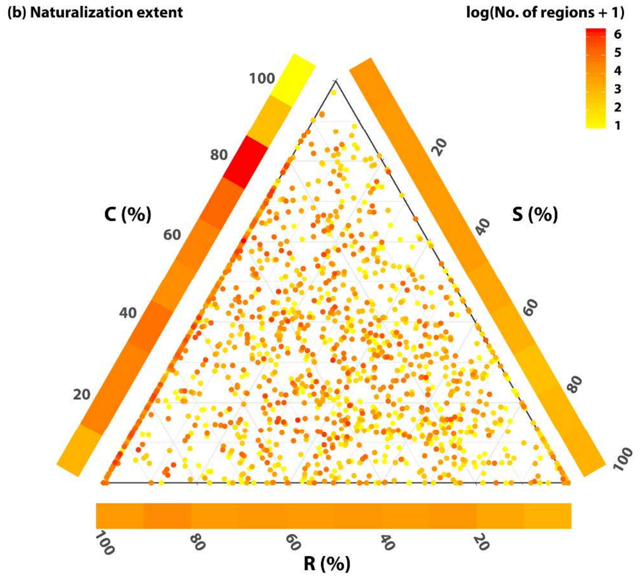
(b) Naturalization extent

Fig. 2 Naturalization incidence (a) and extent (b) within the CSR strategy triangle.

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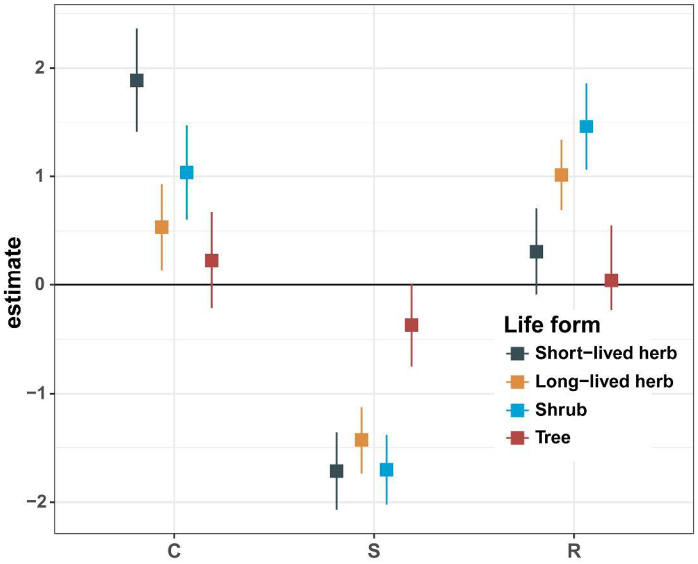
(a) Naturalization incidence



(b) Naturalization extent

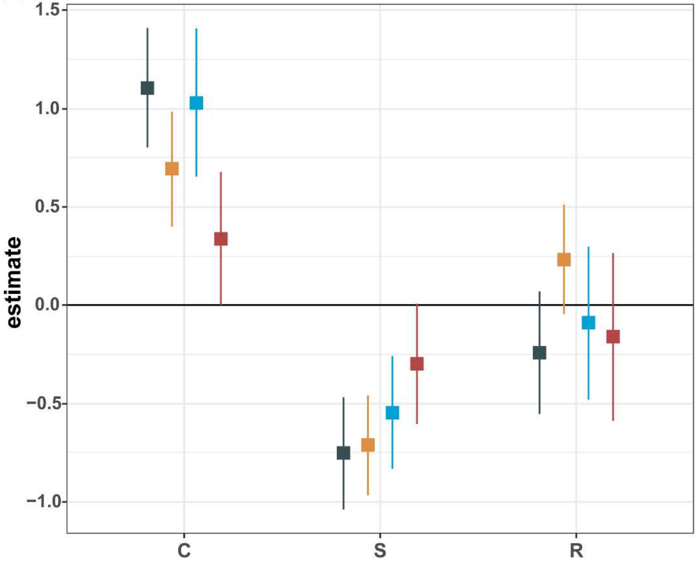


Fig. 3 Effects of each C-, S-, or R- score on (a) naturalization incidence and (b) naturalization extent of alien plant species for each life form.

259x439mm (300 x 300 DPI)