

The role of adaptive strategies in plant naturalization

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3 59 **Abstract**
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7 61 Determining the factors associated with the naturalization of alien species is a central theme
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9 62 in ecology. Here, we tested [the usefulness of a metric for](#) quantifying Grime's seminal
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11 63 concept of adaptive strategies – competitors, stress-tolerators and ruderals (CSR) – to explain
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13 64 plant naturalizations worldwide. Using a global dataset of 3004 vascular plant species, and
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15 65 accounting for phylogenetic relatedness and species' native biomes, we assessed the
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17 66 associations between [calculated C, S, and R scores](#) and naturalization success for species
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19 67 exhibiting different life forms. [Across different plant life forms, C-scores were positively and](#)
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21 68 [S-scores negatively associated with both the probability of naturalization and the number of](#)
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23 69 [regions where the species has naturalized. R-scores had positive effects on the probability of](#)
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25 70 [naturalization. These effects of the scores were, however, weak to absent for tree species. Our](#)
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27 71 findings demonstrate the utility of CSR-score calculation to broadly represent, and potentially
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29 72 explain, the naturalization success of plant species.
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73 Introduction

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75 Determining the factors associated with the naturalization of alien species and invasibility of
76 recipient ecosystems is a central theme in ecology (Lonsdale 1999; Richardson & Pyšek 2006,
77 2012; van Kleunen *et al.* 2015a). In recent decades, a multitude of plant-species traits and
78 environmental characteristics have been identified that promote naturalization and
79 invasiveness, such as fast growth, early flowering (Pyšek & Richardson 2007; van Kleunen *et al.*
80 2010), large native range size and habitat affiliation in the native range (Rejmánek &
81 Richardson 1996; Pyšek *et al.* 2015; Kalusová *et al.* 2017). Studies, however, have also
82 revealed that the factors associated with plant invasions are stage (Williamson 2006;
83 Theoharides & Dukes 2007; Dawson *et al.* 2009; Pyšek *et al.* 2009a; Moodley *et al.* 2013) or
84 context dependent (Kueffer *et al.* 2013; van Kleunen *et al.* 2015b; Elliott-Graves 2016).
85 Consequently, few of the characteristics explored so far appear to be universally linked to
86 invasion success.

87 Given the complexities and context dependency typical of biological invasions, one
88 possible reason why our ability to generalize and predict the outcome of particular
89 introductions remains limited is that most studies focus on single traits rather than on trait
90 combinations and species-ecosystem interactions, so-called invasion syndromes (Küster *et al.*
91 2008; Kueffer *et al.* 2013; van Kleunen *et al.* 2015b). A promising direction therefore is the
92 ordination of species along known principal axes of functional variability, or primary trait
93 spectra (e.g., Rejmanek & Richardson 1996; Pyšek *et al.* 2009b; Byun *et al.* 2013; Novoa *et al.*
94 2016). This is particularly promising where traits are integrated as suites of functional **traits**
95 **that jointly confer fitness in the face of selection pressures, so called ‘adaptive strategies’,** and
96 are thus consistent with a theory that can potentially offer additional explanatory and
97 predictive power. **To illustrate this concept: the single traits Rubisco content (carboxylation**

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3 98 capacity), chlorophyll content (light absorption) and internal water conduction each impact on
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5 99 the photosynthetic rate of a leaf, but the measured value of photosynthetic rate represents the
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7 100 joint effects of these various functions. Similarly, overall plant fitness may ultimately depend
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9 101 on the optimization of trait integration, perhaps more than it does on the performance of a
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11 102 single trait. Therefore, an adaptive strategy is not a combination of traits *per se*, but is in
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13 103 essence the particular regime of resource investments across traits that achieves fitness in
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15 104 response to one or more selection pressures.

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18 105 The main axes of plant-functional-trait variability globally are known to represent
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20 106 spectra of resource-investment economics (i.e., a trade-off between traits supporting resource
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22 107 capture and conservation; Wright *et al.* 2004; Blonder *et al.* 2015; Onoda *et al.* 2017) and
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24 108 organ and whole-plant sizes (Díaz *et al.* 2016). These two fundamental spectra are compatible
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26 109 with trait variation hypothesized by Grime (1974, 1977), and are associated with constraints
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28 110 imposed by major selection pressures such as stress (reduced productivity) and disturbance
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30 111 (biomass destruction and removal; Cerabolini *et al.* 2010; Pierce *et al.* 2012, 2013). Within
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32 112 Grime's framework, three fundamental or primary adaptive strategies exist: i) competitors (C)
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34 113 exploit conditions of high productivity where stress and disturbance are relatively unimportant
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36 114 selection pressures, ii) stress-tolerators (S) are adapted to survive conditions in which
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38 115 productivity is chronically or seasonally limited, and iii) ruderals (R) can maintain a
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40 116 population despite the death of individuals by relying on inherently rapid completion of the
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42 117 life cycle (Grime 1979). A combination of both high stress and high disturbance is untenable
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44 118 because severe stress prevents recovery after disturbance (Herben *et al.* 2018).

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48 119 Numerous advantages are conferred by an adaptive strategy approach over the use of
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50 120 single traits. First, strategies integrate variation along both major plant functional spectra
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52 121 (plant economics and size) and represent the underlying multi-trait trade-offs. Second,
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54 122 strategies potentially link trait variation to causal factors meaning that they can help explain
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3 123 observations. Third, strategies provide a theoretical context that can be experimentally tested,
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5 124 and which also confers transferability and thus predictive power. The performance of a plant
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7 125 with a certain strategy in one environment may be expected to predict responses of
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9 126 functionally similar species in other similar environments. This is of clear relevance to the
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11 127 functional characterization and prediction of naturalization ability in plants.

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13 128 Grime (1979) proposed an ordination of species in a triangular plot, reflecting the
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15 129 trade-offs among tolerance of competition, stress and disturbance. However, until recently a
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17 130 wider application and generalization based on the CSR-strategy scheme has been fraught with
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19 131 limitations (see the methodologies of Hodgson *et al.* 1999; Pierce *et al.* 2013), because the
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21 132 traits used were specific to certain plant groups, reflected phenology at particular latitudes,
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23 133 represented a mixture of detailed values measured on individuals (leaf traits) alongside
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25 134 general classes determined for the population or species (e.g. the month of flowering onset),
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27 135 or studies were geographically limited in scope. To overcome these limitations, Pierce *et al.*
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29 136 (2017) developed a CSR-classification method in which a few easily determined leaf traits are
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31 137 compared against the global leaf economics and size trade-offs. Extremely high values of
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33 138 specific leaf area (SLA) and leaf dry matter content (LDMC) are highly representative of
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35 139 extremes of fast and slow leaf economics, respectively, and leaf area (LA) is a fundamental
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37 140 determinant of the ability of species to intercept light that also correlates with plant and seed
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39 141 size, orthogonal to the leaf economics spectrum (Cerabolini *et al.* 2010; Pierce *et al.* 2013;
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41 142 Díaz *et al.* 2016). However, each of the traits – LA, LDMC and SLA – themselves do not
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43 143 directly represent the extent of C, S and R-selection. Instead, [it is the trade-off between traits,](#)
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45 144 compared against trade-offs evident globally, from which the [C, S, and R scores](#) are
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47 145 calculated (Pierce *et al.* 2017).

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49 146 Co-inertia analysis demonstrated that this method based on the three leaf traits
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51 147 mentioned above is representative of variation in 14 key leaf, reproductive and whole-plant
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3 148 functional traits, including leaf nitrogen content, seed mass and flowering phenology (Pierce
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5 149 *et al.* 2017). Although this system cannot represent all of plant functioning, nor all factors that
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7 150 affect survival, the three leaf traits do represent a broader underlying spectrum of function and
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9 151 of adaptive strategies, which makes global comparisons possible.

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11 152 Using the ordination tool of Pierce *et al.* (2017), a species cannot only be classified
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13 153 according to the traditional CSR categories of Grime, but continuous C, S, and R scores are
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15 154 calculated as the percentage of each main strategy (C, S, R) realized by a focal plant species.
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17 155 This makes the scheme quantitative and unbiased by subjective classification. The method is
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19 156 generally applicable to vascular plants, sufficiently precise to distinguish strategies among
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21 157 species within genera, among populations within species and across biomes, and its validity
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23 158 has been confirmed in several experiment and field studies (Li & Shipley 2017; Rosado & de
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25 159 Mattos 2017). Depending on the availability of robust trait measures, this objective CSR-
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27 160 strategy approach makes it possible to investigate primary plant functional types across a wide
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29 161 range of species and habitats at the global scale.

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31 162 Grime's CSR categories have previously only been applied to plant invasions in local
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33 163 to regional-scale studies, with findings that ruderals (R), competitors (C) and the intermediate
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35 164 stage between C and R (CR) are prevalent, while stress-tolerators (S) are under-represented
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37 165 amongst alien plant species (Pyšek *et al.* 2003; Lambdon *et al.* 2008; Dainese & Bragazza
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39 166 2012; Alexander *et al.* 2016). These results suggest that Grime's CSR-strategy theory is a
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41 167 powerful tool for studying the interactions of plant traits and species invasion success (Davis
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43 168 2009; Rejmánek *et al.*, 2013). These previous local and regional studies addressing the role of
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45 169 adaptive strategies simply reported the proportions of aliens in each CSR category (Pyšek *et*
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47 170 *al.* 2003; Alexander *et al.* 2016), or compared the proportions of alien and native species in
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49 171 each CSR category (Lambdon *et al.* 2008; Dainese & Bragazza 2012). However, no global
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51 172 study has quantitatively assessed the adaptive strategies of species that have been able to
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3 173 successfully naturalize compared to those that have not (i.e., naturalization incidence), or how
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5 174 the strategies relate to the number of regions where a species has naturalized (i.e.,
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7 175 naturalization extent). Furthermore, no previous study has considered the effect of
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9 176 phylogenetic relatedness of species, which could bias comparative analyses, as closely related
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11 177 species usually exhibit similar traits due to shared evolutionary history (Felsenstein 1985; Ives
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13 178 & Garland 2010).

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16 179 To overcome these methodological constraints to a rigorous evaluation of the role of
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18 180 adaptive strategies in plant invasions and to assess their validity at the global scale, we used
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20 181 the C, S, and R scores calculated by Pierce *et al.* (2017) for 3004 species in combination with
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22 182 data from the Global Naturalized Alien Flora database (GloNAF; van Kleunen *et al.* 2015a;
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24 183 Pyšek *et al.* 2017). We asked if (i) the incidence and (ii) the extent of naturalization of alien
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26 184 plant species are associated with their specific C, S and R score, as calculated by this method
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28 185 (and while accounting for phylogeny). In addition, since plant functional traits are closely
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30 186 linked to life form (Faber-Langendoen *et al.* 2015; Pierce *et al.* 2017), which also influences
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32 187 naturalization success (e.g., Razanajatovo *et al.* 2016), we included species life form (short-
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34 188 lived herb, long-lived herb, shrub, tree) in our models to test whether they interact with
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36 189 calculated C, S and R scores to affect the incidence and extent of naturalization. Furthermore,
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38 190 as previous global studies revealed that geographic regions and habitats differ as donors and
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40 191 recipients of naturalized species (Pyšek *et al.* 2003; van Kleunen *et al.* 2015a; Kalusová *et al.*
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42 192 2017; Pyšek *et al.* 2017), we also included information on the biome of the species' native
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44 193 range as a covariate.
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50 195 **Methods**

51 52 53 196 54 55 197 **Global database compilation**

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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 km², with a mean of 1.3×10^5 km² 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).

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3 222 Naturalization success was first measured as the *incidence of naturalization*, i.e.,
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5 223 whether a species was listed as a naturalized alien in the GloNAF database. Of the 3004
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7 224 species, 1515 were reported to be naturalized alien species somewhere in the world. As a
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9 225 second measure of naturalization success (for the subset of naturalized species), we estimated
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11 226 the *extent of naturalization* as the number of GloNAF regions for which the species is
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13 227 recorded as naturalized. The extent of naturalization could also be measured as the cumulative
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15 228 area of the regions in which the species is naturalized. However, because a species does not
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17 229 necessarily occur in all parts of a region, and because the number and cumulative area of
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19 230 regions are strongly correlated (Pyšek *et al.* 2017), we used only the number of regions.

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22 231 Data on the life history and growth form of each species were taken from Table S1 of
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24 232 Pierce *et al.* (2017). Due to low numbers of biennial species (only 83 naturalized alien and 11
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26 233 non-naturalized species), we combined annuals and biennials in the group of *short-lived*
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28 234 species, and perennials formed the group of *long-lived* species (Figs. 1 & S3). The species
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30 235 originally belonged to seven growth forms (as classified in Pierce *et al.* 2017), but as some
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32 236 groups consisted of only a few species (e.g., liana, herbaceous vine), which could limit
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34 237 statistical power, we created a broader classification of four life forms. These life-form
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36 238 categories largely correspond to those of Raunkiær (1934), and include *short-lived herbs*
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38 239 (annual and biennial herbs, which merges the graminoid, forb, herbaceous vine and aquatic
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40 240 categories of Pierce *et al.* 2017), *long-lived herbs* (perennial graminoids and forbs), *shrubs*
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42 241 (shrubs and lianas) and *trees* (as used in FGDC, 1997; Qian *et al.* 2017).

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44 242 The native distribution range of species was assigned to geographic continents
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46 243 following the Biodiversity Information Standards TDWG (TDWG level 1; Brummitt 2001).
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48 244 Geographic continents were assigned using several online databases: the World Checklist of
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50 245 Selected Plant Families (WCSP, <http://apps.kew.org/wcsp/>), the Germplasm Resources
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52 246 Information Network (GRIN, <http://www.ars-grin.gov/cgi-bin/npgs/html/index.pl>). The
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3 247 Global Biodiversity Information Facility database (GBIF, <http://www.gbif.org>) was used for
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5 248 some non-naturalized species, if no other distribution data were available. To account for a
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7 249 potential effect of species' biogeographic origins, we further assigned each species' native
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9 250 distribution range to biomes, i.e., biogeographic units of representative habitats and species
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11 251 assemblages (*sensu* Olson *et al.* 2001). We obtained species' biome information from Pierce
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13 252 *et al.* (2017). The native ranges of the 3004 species investigated in this study covered eight of
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15 253 the nine TDWG continents (Antarctica was not covered; Fig. S4), and covered all the 14
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17 254 world biomes (Pierce *et al.* 2017). The 1489 non-naturalized species belonged to 50 orders
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19 255 and 160 families, and the 1515 naturalized alien species belonged to 53 orders and 141
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21 256 families (Figs. S1 & S2).
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258 **Phylogenetic tree**

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31 260 To account for phylogenetic relatedness in our statistical analyses, we constructed a
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33 261 phylogenetic tree of the 3004 species in our final dataset. This was done using a dated
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35 262 supertree initially constructed by Zanne *et al.* (2014), and corrected and extended by Qian and
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37 263 Jin (2016). This tree includes 31,749 species and was generated based on several genetic
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39 264 markers. Qian and Jin (2016) also provided an R function, *S.PhyloMaker*, to generate
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41 265 phylogenies for subsets of species. Following their recommendations, we used their Scenario
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43 266 3 approach, which adds absent species to their families or genera using the same approach as
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45 267 used in Phylomatic and BLADJ (Webb *et al.* 2008). The phylogenetic tree was visualized
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47 268 using the *ggtree* package (Figs. S5 & S6; Yu *et al.* 2017).
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270 **Statistical analysis**

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3 272 All analyses were done in R 3.3.3 (R Core Team 2017). We used the *ggtern* package
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5 273 (Hamilton 2015) to visualize the triangular plots of the **C, S, and R scores** of species. We
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7 274 standardized the C-, S-, and R-scores to means of zero and standard deviations of 1 to
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9 275 facilitate comparisons between models (Schielzeth 2010). We used phylogenetic logistic
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11 276 regression (Ives & Garland 2010, 2014), as implemented in the R package *phylolm* (Ho &
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13 277 Ane 2014), to analyze the relationships between naturalization incidence and each of the C-,
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15 278 S- and R-scores, while accounting for phylogenetic relatedness. We included species' life
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17 279 form (i.e., short-lived herb, long-lived herb, shrub and tree) and its interaction with each of
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19 280 the three CSR-strategy scores to test if the relationship between each strategy score and
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21 281 naturalization incidence was different for species in different life-form categories. We ran a
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23 282 similar set of models to test for associations between naturalization extent and each strategy
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25 283 **score**, and the interaction of life form with each of the three strategy scores using
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27 284 Phylogenetic Generalized Least Squares regression in the *phylolm* package (Ho & Ane 2014).
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29 285 We included biome and its interactions with each strategy score in both the naturalization-
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31 286 incidence and naturalization-extent models. For each predictor variable in each model, Wald
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33 287 tests were performed to determine if its main effect or interactions were significant, using the
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35 288 *aod* package (Lesnoff & Lancelot 2012). To show the general effect of biome and its
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37 289 interactions with the **C, S, and R scores**, we ran Wald tests for the 14 biomes. We calculated
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39 290 R^2 to assess the amount of variation explained by each regression model using the *rr2* package
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41 291 (Ives 2017).
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48 293 **Results**

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53 295 The C, S and R scores were all negatively correlated to each other (Pearson's correlations, C
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55 296 vs S: -0.47; C vs R: -0.32; S vs R: -0.68; all $p < 0.001$). Without accounting for life form,
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3 297 biome and phylogeny, the naturalized species had, compared to the non-naturalized species,
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5 298 higher R (mean \pm SD: $39.2 \pm 25.4\%$ vs $26.6 \pm 25.0\%$) and lower S scores ($29.3 \pm 26.7\%$ vs
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7 299 $42.2 \pm 27.7\%$), whereas the C scores were similar ($31.5 \pm 21.8\%$ vs $31.2 \pm 21.6\%$) (Fig. 2a).
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9 300 Among the naturalized alien species, those with high C and R scores occupied a greater
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11 301 number of regions outside of their native range (i.e., had a larger naturalization extent),
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13 302 especially when compared to species with high S scores (Fig. 2b).

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15 303 When life form, biome and phylogeny were accounted for, the results were slightly
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17 304 different. Averaged across the four different life forms, the C score was significantly
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19 305 positively related to naturalization incidence and extent, and the S score was significantly
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21 306 negatively related to naturalization incidence and extent (Table 1, Fig. 3). The R score was
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23 307 significantly positively related to naturalization incidence, but had no significant effect on
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25 308 naturalization extent (Table 1, Fig. 3). However, the effects of most scores on naturalization
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27 309 differed significantly among the four life-form categories (Table 1, Fig. 3). This reflects in
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29 310 particular that for trees, none of the C, S and R scores was significantly related to
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31 311 naturalization incidence and extent (Fig. 3). On the other hand, for short-lived herbs, long-
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33 312 lived herbs and shrubs, having a relatively high C score or having a relatively low S score was
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35 313 associated with increased naturalization incidence and extent (Fig. 3). For long-lived herbs
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37 314 and shrubs, having a relatively high R-score increased the naturalization incidence (Fig. 3a).

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39 315 Species' native biome significantly affected naturalization incidence and extent, and
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41 316 species originating from certain biomes had a higher naturalization success than those from
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43 317 other biomes (Table 1, for details see Tables S1 & S2). Moreover, the effects of the S-score
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45 318 on naturalization incidence and extent, and the effect of the R-score on naturalization
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47 319 incidence varied among biomes (Table 1).

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50 321 **Discussion**

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323 Based on a large dataset of 3004 vascular plant species of different life forms, we used the
324 CSR-calculation method of Pierce *et al.* (2017) – which is in agreement with the theoretical
325 context of Grime’s (1974, 1977) adaptive strategy scheme – to test the relationships between a
326 species’ C-, S- and R-scores and its naturalization incidence (i.e., whether or not it has
327 naturalized somewhere) and extent (i.e., in how many regions of the world it is naturalized).

328 While previous studies, using Grime’s CSR categories, revealed some general trends at the
329 regional scale (Pyšek *et al.* 2003; Lambdon *et al.* 2008; Dainese & Bragazza 2012; Alexander
330 *et al.* 2016), our study using quantitative C, S and R scores provides the first global test for
331 these relationships, and of the relative importance of the different adaptive-strategy axes.

332 Across different plant life forms, C scores were positively and S scores negatively associated
333 with naturalization incidence and extent, whereas R scores had positive effects on the
334 naturalization incidence only. These effects of the strategy scores were, however, weak or
335 even absent for tree species. Our results thus demonstrate the divergent associations between
336 adaptive strategy spectra and naturalization success among life forms.

337 Interpreting our results from the viewpoint of key traits typical for each plant strategy
338 (Grime 1979; Grime & Pierce 2012), competitors and ruderals are both characterized by rapid
339 growth, a short leaf life-span, a high flowering frequency, and nutrient-rich leaves (thus
340 having a higher photosynthetic rate; Wright *et al.* 2004; Reich 2014). All of these traits are
341 frequently associated with invasive plant species (Pyšek & Richardson 2007; van Kleunen *et al.*
342 2010). These features are also sought after for certain kinds of cultivation activities (e.g.,
343 ornamental horticulture, bioenergy crops; van Kleunen *et al.* 2018). This implies that
344 competitive and ruderal species might have been more likely to be introduced early and
345 frequently by humans, which would have increased their probability of naturalization. The
346 higher propagule pressure and longer residence time in the introduced ranges, together with

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3 347 higher frequency of reproduction, may in turn result in greater naturalization extent to those
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5 348 kinds of species (Pyšek & Jarošík 2005; Proches *et al.* 2012; Pyšek *et al.* 2015). However,
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7 349 such an ‘introduction bias’ (van Kleunen *et al.* 2015a; Maurel *et al.* 2016) could result in
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9 350 spurious associations between plant adaptive strategies and naturalization success, and should
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11 351 be accounted for in future studies.

12
13 352 Theoretically, a high nutrient content of tissues should make competitors and ruderals
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15 353 prone to higher rates of herbivory (Grime 1979, 1988; Grime & Pierce, 2012) and impair their
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17 354 naturalization success. As a plant’s specialist herbivores are often absent in its new range
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19 355 (Enemy Release hypothesis; Keane & Crawley 2002; Liu & Stiling 2006), having a strategy
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21 356 of fast growth and low defense, instead of slow growth and high defense, may pose stronger
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23 357 advantages to alien species in their naturalized than in their native range (the Resource Enemy
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25 358 Release hypothesis, Blumenthal 2006). In addition, a high degree of morphological plasticity
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27 359 typical of competitors and ruderals (Grime 1979, 1988) can also provide an advantage for
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29 360 being able to grow in a wider range of environments (Richards *et al.* 2006; Hulme 2008).

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31 361 Our results also showed that the R scores of short-lived herbs had no association with
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33 362 naturalization success. In theory, even though typical ruderals usually establish very quickly,
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35 363 flower more frequently, allocate a large proportion of resources to seed and form a persistent
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37 364 seed bank (Grime 1979; Gioria *et al.* 2012; Grime & Pierce 2012), their ability to compete is
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39 365 much weaker in undisturbed habitats. In addition, under continuous, moderate disturbance, the
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41 366 seed production of ruderals does not compensate for the mortality rate, and ruderals
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43 367 eventually fail to establish (Grime 1979, 1988). Therefore, short-lived herbs with R-selection,
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45 368 unlike long-lived herbs and shrubs, did not relate to the incidence of naturalization. In our
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47 369 dataset, however, naturalized alien long-lived herbs and shrubs tending towards a more
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49 370 ruderal strategy are mostly Mediterranean evergreen microphyllous species (e.g., *Santolina*
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51 371 *chamaecyparissus*, *Retama sphaerocarpa*), indicating that they may have adapted to relative
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3 372 stressed and human-dominated (highly disturbed) environments in the native Mediterranean
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5 373 range (Lambdon *et al.* 2008). Moreover, our results indicate that a Mediterranean origin was
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7 374 positively related to a species' naturalization success (Tables S1 & S2).

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9 375 We found that species with a **greater S-score** were less likely to become naturalized,
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11 376 which supports the findings of previous studies showing that stress-tolerators were under-
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13 377 represented among naturalized alien plants (Pyšek *et al.* 2003; Alexander *et al.* 2016). In
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15 378 theory, stress-tolerators are generally very long-lived, have a long leaf life-span, grow slowly,
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17 379 fruit late and produce fewer seeds **with respect to competitors and ruderals** (Grime 1979;
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19 380 Grime & Pierce 2012). All these traits are the opposite of those commonly reported to be
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21 381 associated with successful invaders (Pyšek & Richardson, 2007; van Kleunen *et al.* 2010),
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23 382 and could also make stress-tolerators less likely to be selected by humans **for introduction as**
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25 383 **horticultural plants**. In general, stress-tolerant plants rely heavily on **vegetative instead of**
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27 384 **sexual** reproduction and rarely show a high morphological plasticity, which limits their **spread**
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29 385 **potential** (Grime 1979, 1988). In addition, the chance of a stress-tolerant plant being
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31 386 introduced into an environment with a stress regime comparable to **the one** it is adapted to in
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33 387 its native range is relatively low, given that stressful environments are relatively rare in
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35 388 general (Alexander *et al.* 2011).

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39 389 **In contrast to the other life forms, naturalization incidence and extent of trees were not**
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41 390 **or only weakly affected by their C-, S- and R-scores (Fig. 3)**. Tree species with high R-scores
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43 391 do not appear to exist (Pierce *et al.* 2017). The absence of a clear association of naturalization
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45 392 success of trees with the C score could be caused by the overall lower representation of
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47 393 naturalized trees in our dataset (13% of all naturalized species were trees; Fig. 3). Trees are
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49 394 also less numerous in the global pool of naturalized plants compared to herbs (Pyšek *et al.*
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51 395 2017), most likely because the global pool of tree species is much smaller than that of herbs
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53 396 (Beech *et al.* 2017). The lesser representation of trees and their non-significant associations of
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3 397 C, S, and R scores with naturalization success may be related to the long periods needed for
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5 398 establishment, long generation times, the relatively low proportion of resources invested in
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7 399 seed production (Grime 1979), and the long time lag following introduction to new ranges
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9 400 (Kowarik 1995; Pyšek *et al.* 2017).

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11 401 The model estimates of associations between S-score and naturalization extent showed
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13 402 a gradual increase from short-lived herbs to trees (Fig. 3b), indicating that among the more
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15 403 stress tolerant species, long-lived, big woody species tend to be naturalized in more regions
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17 404 than short-lived, small herbs. A possible explanation could be that stress-tolerant trees live
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19 405 longer than other plants, allowing them to accumulate the necessary resources to survive,
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21 406 grow and establish in a habitat that can be unproductive due to extreme climatic conditions or
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23 407 low nutrient availability (Grime 1979). In addition, increased propagule pressure resulting
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25 408 from forestry can significantly increase the odds of successful naturalization of trees
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27 409 (Křivánek *et al.* 2006; Bucharová & van Kleunen 2009; Pyšek *et al.* 2009b; Proches *et al.*
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29 410 2012), thereby masking, or compensating for the effects of species characteristics, such as
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31 411 their adaptive CSR strategy. Furthermore, alien trees with a stress-tolerant strategy are often
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33 412 evergreen angiosperms (e.g., *Quercus* spp. in our data set, Table S3) or conifers (Pierce *et al.*
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35 413 2017). The latter are represented by several *Pinus* species in our data set (Table S3), a genus
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37 414 which is known to include many invasive species (e.g., Richardson *et al.* 1994; Richardson &
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39 415 Rejmánek 2004; Essl *et al.* 2011; Pyšek *et al.* 2017).

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43 416 Previous studies have also tested the associations of the three leaf traits used to
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45 417 calculate the C, S, and R scores (i.e., SLA, LA and LDMC) with naturalization and invasion
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47 418 success of alien plants. SLA, the most widely-examined trait among the three, is generally
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49 419 higher for naturalized and invasive species compared to non-naturalized species (Hamilton *et*
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51 420 *al.* 2005; Pyšek & Richardson 2007; Gallagher *et al.* 2015). However, this trend is not
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53 421 universal as studies have also found lower SLA for invasive species compared to non-invasive
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3 422 species (e.g., McDowell 2002). In addition, a recent study did not find a direct causal
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5 423 relationship between SLA and naturalization success, when accounting for cultivation in the
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7 424 introduced ranges, other species traits, propagule pressure and residence time in a path
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9 425 analysis (Pyšek *et al.* 2015). Studies that tested for the associations of LA and LDMC with
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11 426 naturalization success usually did not find any either (Pyšek & Richardson 2007; Gallagher *et*
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13 427 *al.* 2015; Pyšek *et al.* 2015). In our study, however, the C, S and R scores obtained from the
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15 428 trade-off among the three traits showed clear relationships with naturalization success,
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17 429 indicating that it is the combination of viable trait values that is associated with success. This
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19 430 is in agreement with the concept of adaptive strategies, and shows that the estimation of
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21 431 strategy scores can help to potentially explain the ability to invade.
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26 433 **Conclusions**

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31 435 With a global dataset, a dated species-level phylogeny, and accounting for life forms and
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33 436 species' biomes, we demonstrate that plant C, S and R scores play an important role in alien
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35 437 plant naturalization. This also suggests that the CSR theory has a great potential to facilitate
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37 438 understanding of the determinants of invasion success. For example, by taking into account
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39 439 the residence time of naturalized species, it should be possible to estimate, using the CSR
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41 440 scheme, how quickly a species can establish in the new range. Due to the ease of obtaining C,
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43 441 S, and R scores, the scheme can rapidly identify species with a high naturalization potential,
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45 442 and thus can be used in risk-assessment systems to warn and prevent future plant invasions.
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48 443 With ongoing accumulation and increased accessibility of field data for the relevant traits (i.e.,
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50 444 SLA, LA, and LDMC) it will be possible to validate the generality of these results for regions
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52 445 and life forms that were less represented in our data set (e.g., trees), and address in greater
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3 446 detail the biogeographic differences in the role plant strategies play in alien species'
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5 447 naturalization.

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643 **Table 1** Results of regression models of C-, S-, or R-score, life form, biome, and interaction terms in
 644 affecting naturalization incidence (n = 3004) and naturalization extent (n = 1515). Naturalization
 645 incidence models were run as phylogenetic logistic regressions, naturalization extent models were run
 646 as phylogenetic generalized least squares models, and then the significance of each variable was tested
 647 with the Wald test. Phylogenetic signal $\alpha = 0.1352, 0.1258, 0.1336$ for the three phylogenetic logistic
 648 regressions, respectively; and $\lambda = 0.3137, 0.3360, 0.3374$ for the three phylogenetic generalized least
 649 squares models, respectively.
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Variable	df	Naturalization incidence			Naturalization extent		
		X^2	<i>p</i>	R^2	X^2	<i>p</i>	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	

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3 653 **Figure captions**

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5 655 **Fig. 1** Summary of naturalized and non-naturalized species numbers by life forms in the dataset used
6 656 (n = 3004 species). The original seven categories of growth form in Pierce *et al.* (2017) were grouped
7 657 into three categories: herb (including aquatics, forbs, graminoids and herbaceous vines), shrub
8 658 (including lianas and shrubs) and tree. According to the duration of the life span, herbs were further
9 659 divided into short-lived (annual and biennial) and long-lived (perennial). This resulted in a four-level
10 660 life-form category, i.e., short-lived herb, long-lived herb, shrub, and tree.
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15 662 **Fig. 2** Naturalization incidence (a) and extent (b) within the CSR strategy triangle. (a) Competitor (C),
16 663 stress-tolerant (S) and ruderal (R) scores of 1515 vascular plant species that are naturalized (orange
17 664 dots) in at least one of 843 global regions outside of their native range, and of 1489 vascular plant
18 665 species that are not naturalized anywhere (blue dots), according to the GloNAF database. The orange
19 666 and blue triangles from interior to outward are 50%, 90% and 95% confidence levels, respectively.
20 667 The black arrow indicates the shift of means from non-naturalized species to naturalized alien species.
21 668 Along each axis of the ternary plot, a boxplot of the respective strategy score displays the median (line
22 669 in the middle of boxes), the mean (black dot), the interquartile range (boxes), ± 1.5 times the
23 670 interquartile range (whiskers), and outliers (circles) for each group of species. (b) Naturalization extent
24 671 (number of regions where naturalized) of the 1515 naturalized alien species. Data were $\log(x + 1)$
25 672 transformed. Along each axis of the ternary plot, a heatmap shows the mean number of regions for
26 673 every 10% bin of the respective strategy score.
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29 675 **Fig. 3** Effects of each C-, S-, or R- score on (a) naturalization incidence and (b) naturalization
30 676 extent of alien plant species for each life form. Estimates of the effects and their standard errors
31 677 were obtained from phylogenetic logistic/generalized linear regression models. Detailed results of
32 678 models are shown in Tables 1, S1, S2.
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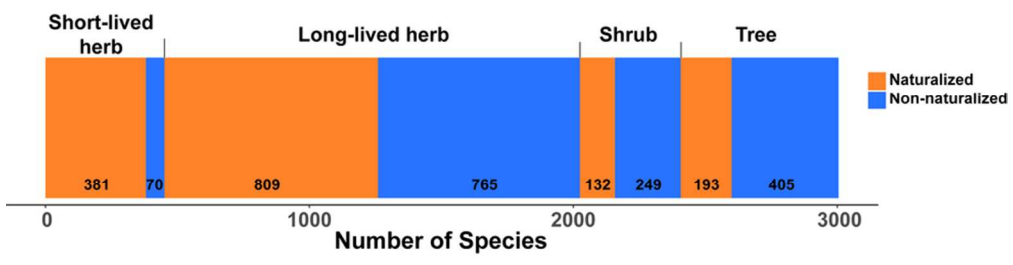


Fig. 1 Summary of naturalized and non-naturalized species numbers by life forms in the dataset used (n = 3004 species).

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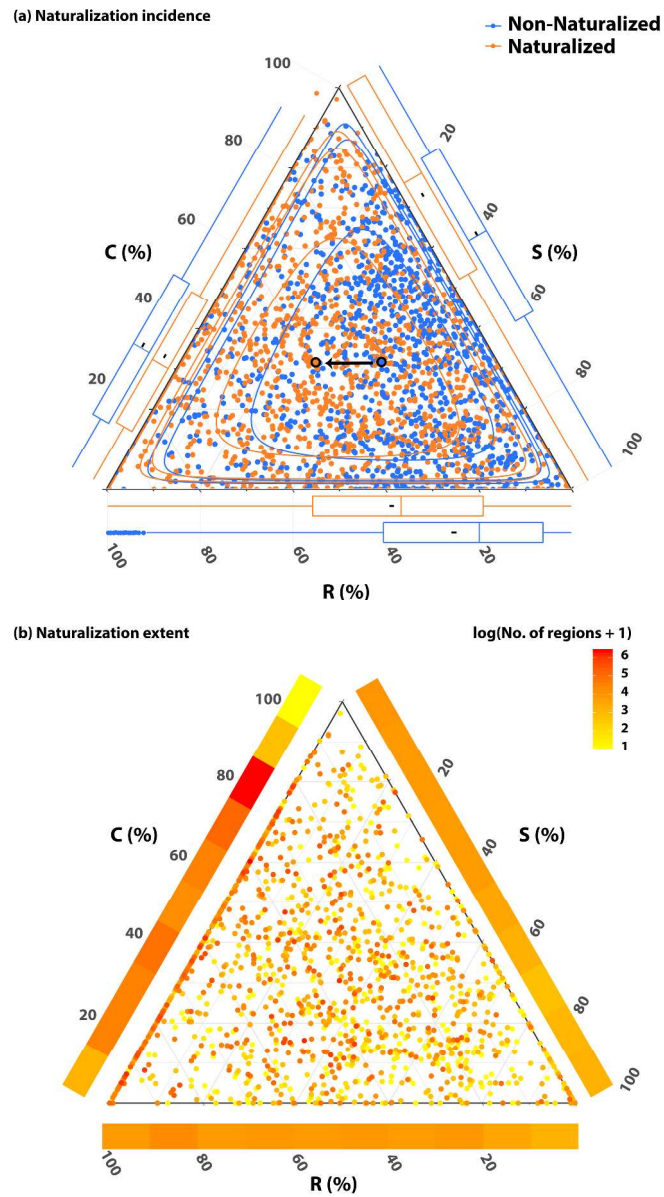


Fig. 2 Naturalization incidence (a) and extent (b) within the CSR strategy triangle.

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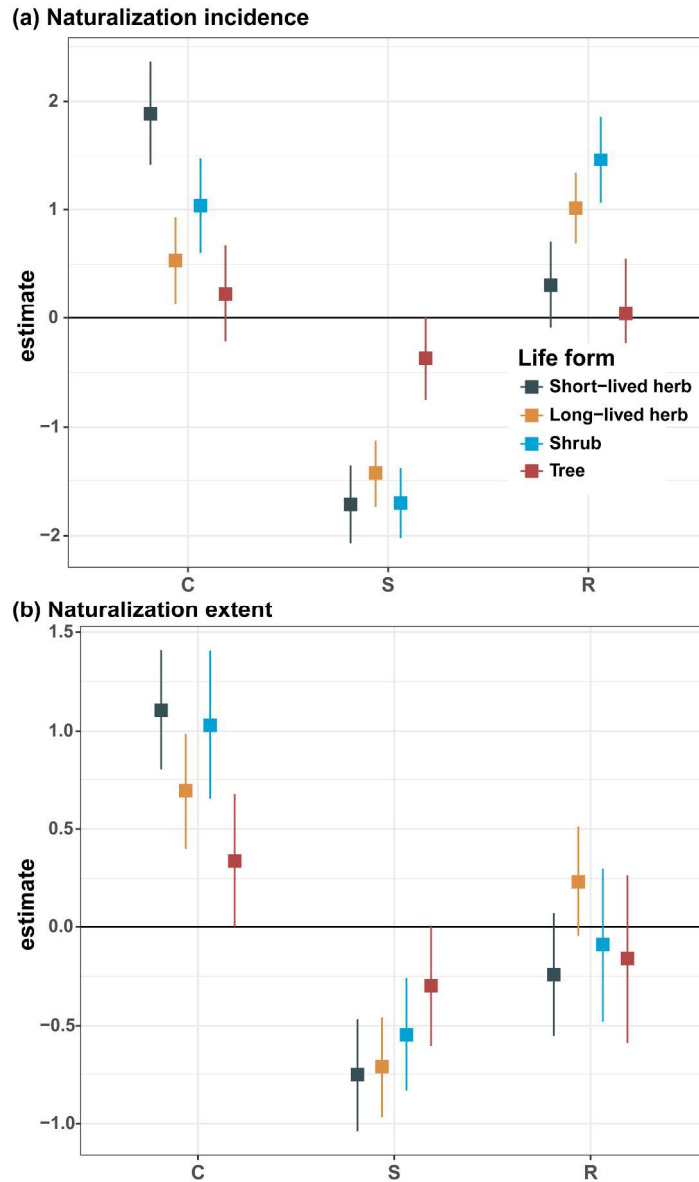


Fig. 3 Effects of each C-, S-, or R- score on (a) naturalization incidence and (b) naturalization extent of alien plant species for each life form.

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