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RESEARCH ARTICLE

Ruderals naturalize, competitors invade: Varying roles of plant adaptive strategies along the invasion continuum

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Abstract

1. It is increasingly recognized that the factors facilitating plant invasions depend on the stage along the introduction–naturalization–invasion continuum. Adaptative strategies, that is, combinations of functional traits that represent overall fitness in the face of one or more selection pressures, have shown promise in explaining plant invasions. However, whether adaptive strategy patterns change with stages of plant invasion is not yet known.
2. Using the Pladias Database of the Czech Flora and Vegetation, we explored how Grime's adaptive strategies (competitors, stress-tolerators, ruderals; CSR) and introduction pathways (deliberate vs. accidental) relate to plant invasion along the introduction–naturalization–invasion continuum.
3. Phylogenetically corrected ANOVAs showed that naturalized species (referring to non-invasive naturalized species in this study) were mostly R-selected, whereas invasive species tended to be C-selected. The results of phylogenetic regression analysis further confirmed that across the deliberately and accidentally introduced species, R- and C-selection were positively related to naturalization and invasion success respectively. We also found that deliberate introduction was negatively related to naturalization success and grid-cell occupancy of naturalized species, likely due to the different CSR strategies of deliberately and accidentally introduced aliens.
4. Our study provides empirical evidence that different adaptive strategies are associated with species that have reached different invasion stages and confirms the usefulness of the CSR strategy framework for understanding plant invasion. This has implications for predicting and preventing potential high-impact invaders. For example, our results show that naturalized C-selected species have a higher probability of becoming invasive than naturalized R-selected species.

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Therefore, management actions are essential to prevent further introductions and spread of competitors.

KEYWORDS
alien species, Grime's adaptive strategy, introduction pathways, introduction–naturalization–invasion continuum, invasion stages

1 | INTRODUCTION

Untangling why certain alien species successfully invade while others fail has been a central topic in ecology for decades. It has been increasingly recognized that multiple factors, such as species traits (Divíšek et al., 2018; Dostál et al., 2013; Montesinos, 2021) and human support (e.g. increased propagule pressure due to intentional and repeated introduction of ornamentals; Dehnen-Schmutz & Touza, 2008; van Kleunen et al., 2018) interact to codetermine invasion success. Additionally, growing evidence suggests that the effects of these factors depend on the invasion stage, from introduction through naturalization to invasion (Pyšek, Jarošík, et al., 2009; Pyšek, Křivánek, & Jarošík, 2009, Moodley et al., 2013).

Many studies have linked species traits to the invasion success of plants. For example, van Kleunen et al. (2010) found that invasive plants generally allocate more resources to shoot growth and possess advantageous physiological traits such as higher photosynthetic rates and water use efficiency. Apart from these individual functional traits, adaptive strategies, that is, combinations of functional traits representing overall fitness in the face of one or more selection pressures, have been employed to understand plant invasion. For example, Guo et al. (2018) demonstrated, using a global dataset of 3,004 vascular plant species, the usefulness of Grime's adaptive strategy scheme (Grime, 1974, 1977; Grime & Pierce, 2012) in explaining plant naturalization.

Grime's framework is delineated by three fundamental adaptive strategies, that is, competitors (C), stress-tolerators (S) and ruderals (R), reflecting the trade-offs among traits representing adaptations to environmental selection pressures. In brief, C, S and R percentages represent the relative investment between leaf resource economics and size functions (sensu the 'global spectrum of plant form and function'; Díaz et al., 2016). Theoretically, competitors can survive in relatively stable and productive habitats by investing resources into continued vegetative growth and forming large individuals with large organs to secure resource pre-empting. Stress-tolerators are adapted to variable, resource-poor environments by storing resources in dense and persistent tissues, allowing relatively consistent metabolism in the face of inconsistent external factors. In contrast, ruderals can maintain populations despite repeated biomass destruction events (disturbances) by investing a large proportion of resources in propagules and quickly completing the life cycle (Grime & Pierce, 2012). Guo et al. (2018, 2019) found that C- and R-scores are positively, whereas S-scores negatively related to naturalization success. Moreover, they demonstrated that CSR strategies are strongly associated with the native and naturalized range sizes and horticultural usage of species (and thus introduction and opportunity to become naturalized), indicating a significant role of the CSR strategy in invasion success.

The introduction pathway of aliens is another important factor affecting plant invasions (Pyšek et al., 2011). Previous studies found that deliberately introduced plants have a higher probability of becoming naturalized than accidentally introduced plants (e.g. Riera et al., 2021). In addition, species with multiple introduction pathways (e.g. direct release into nature, escape from cultivation, contamination of grain imports) are more likely to have an ecological impact (e.g. negative effects on biodiversity of the recipient community) because they have higher propagule pressure (the number of introduced individuals and introduction events), resulting in a higher probability of establishment (Pergl et al., 2017). Understanding the effects of different introduction pathways on biological invasions is considered a central component of invasion ecology and key to the effective management of alien species (Donaldson et al., 2014; Saul et al., 2017).

In this study, we used the Pladias Database of the Czech Flora and Vegetation (www.pladias.cz; Chytrý et al., 2021), which contains comprehensive information on native and alien plants, to explore how the different stages of the invasion process relate to CSR strategies and introduction pathways (deliberate vs. accidental introduction). We first used phylogenetic ANOVA models to assess whether each of the CSR strategy scores differs between native and alien species, and depends on whether the latter is a casual, naturalized (referring to non-invasive naturalized species in this study) or invasive species (see Table 1 for detailed definitions). Then, we ran phylogenetic regression models relating CSR scores and introduction pathway to naturalization and invasion success and occupancy of grid cells by native species and alien species at different stages of invasion. We asked (a) whether specific adaptative strategies and (b) introduction pathways (deliberate vs. accidental) are associated with plant naturalization and invasion success and grid-cell occupancy.

2 | MATERIALS AND METHODS

2.1 | Compilation of species list and invasion-status data

Data were obtained from the Pladias (Plant Diversity Analysis and Synthesis) Database (www.pladias.cz; Chytrý et al., 2021). This database contains more than 120 plant characteristics, including traits

TABLE 1 Glossary of selected terms used in this study

Used terms	Definitions
Casual species	Alien species that do not form self-sustaining populations in introduced areas and whose persistence depends on repeated introductions of propagules (Pyšek et al., 2012; Richardson et al., 2000)
Naturalized species	Alien species that form self-sustaining populations over several life cycles without or despite human intervention, often recruit offspring freely, usually close to adult plants, and whose persistence does not depend on the continuous input of propagules (Pyšek et al., 2012; Richardson et al., 2000). In this study, naturalized species do not include invasive species
Invasive species	Alien species that form self-replacing populations over many life cycles, produce reproductive offspring, often in very large numbers and at considerable distances from the parent and/or site of introduction, and have the potential to spread over long distances (Pyšek et al., 2012; Richardson et al., 2000)
Grid-cell occupancy	The number of grid cells (10 min of longitude and 6 min of latitude) of the Central European flora mapping in which a species has been recorded in the Czech Republic (Chytrý et al., 2021; Wild et al., 2019)
Introduction pathway	Alien species were classified according to whether they were deliberately or accidentally introduced into the Czech Republic (Pyšek et al., 2012). The deliberate introduction refers to direct release into the wild (e.g. landscaping) or as an escape from cultivation (e.g. horticulture), whereas accidental introduction includes import through contamination of a commodity or as a stowaway in human transport. See Hulme et al. (2008) and Pyšek et al. (2012) for details
CSR theory	The competitor, stress tolerator, ruderal (CSR) theory was developed by Grime (1974) and updated by Grime and Pierce (2012). The C, S and R strategies represent the extremes of a continuous spectrum of viable trait combinations that occur under conditions of competition, abiotic growth limitation or periodic biomass destruction respectively (Pierce et al., 2017). For each species, CSR scores were calculated as a trade-off between 'resource economics' and the size traits based on specific leaf area (SLA), leaf area (LA) and leaf dry matter content (LDMC), following the method of Pierce et al. (2017)

and environmental associations, for native and alien plant species occurring in the wild in the Czech Republic. Of the 3,878 species in the database, information on CSR scores of 1,660 species could be compiled. Of these 1,660 species, 499 were alien (archaeophytes or neophytes) to the Czech Republic (Pyšek et al., 2012). The alien species were classified into three invasion stages, that is, casual, naturalized and invasive (Table 1), describing how far species have progressed along the introduction–naturalization–invasion continuum (Blackburn et al., 2011; Richardson et al., 2010). It should be noted that invasive species is a subset of naturalized species (Richardson et al., 2000), and in this study, naturalized species exclude invasive species. In addition, since casual species are less common than naturalized and invasive species in the Czech Republic, they were excluded from the grid-cell occupancy analysis (see Section 2.2).

2.2 | Species occupancy and introduction pathway

Species occupancy was estimated as the number of grid cells in which a spontaneous (i.e. not planted) occurrence of the species has been recorded in the Czech Republic. Each grid cell measures 10 min of longitude and 6 min of latitude, corresponding to an area of approximately 12.0 km × 11.1 km (133.2 km^2). A total of 679 cells cover the territory of the country, including incomplete cells on the borders (Wild et al., 2019).

For each alien species, information on the deliberate or accidental introduction (as defined by Hulme et al., 2008) into the country was compiled from Pyšek et al. (2012) and coded as a binary explanatory variable (1 for deliberate introduction, 0 for accidental introduction) for use in the analyses.

2.3 | Compilation of CSR scores

Most of the CSR scores were obtained from Guo et al. (2019), who expanded the database of Pierce et al. (2017) by including species from the China Plant Trait Database (Wang et al., 2018). Additional trait data on leaf area (LA), leaf dry matter content (LDMC) and specific leaf area (SLA) were obtained from other studies (Bjorkman et al., 2018; Dayrell et al., 2018; Tavşanoğlu & Pausas, 2018). When multiple trait values were available for a species, the mean values were used to calculate CSR with the 'StrateFy' calculator (Pierce et al., 2017).

2.4 | Phylogeny

To account for the potential phylogenetic relatedness of the species, a phylogenetic tree was constructed for the 1,660 species using the V.PhyloMaker package (Jin & Qian, 2019; Smith & Brown, 2018; Zanne et al., 2014). The default settings of the function (node = 'build.nodes.1' and scenarios = 'S3') were used to build the final tree, that is, species that were missing from the backbone tree were added as polytomies in the middle of the branch of the species' genus or, if not available, the species' family.

2.5 | Data analysis

All data analyses and visualizations were done in R v4.0.2 (R Core Team, 2020).

To examine whether each of the three CSR scores varied between native and alien species, and between native species and the three invasion stages, phylogenetic ANOVA models were used (function *phylANOVA* in R package phytools; Garland et al., 1993; Revell, 2012). This method was also used to test whether deliberate or accidental introductions were related to grid-cell occupancy by naturalized and invasive species. *p*-values were determined by phylogenetic simulation (i.e. simulating the trait on phylogeny using the Brownian motion model) with 10,000 runs. Bonferroni correction was used to adjust *p*-values for multiple comparisons.

The relationships between introduction pathways and naturalization and invasion success were examined using Chi-square tests. To assess how CSR scores, introduction pathways and their interactions relate to plant invasion along the introduction–naturalization–invasion continuum, we used phylogenetic logistic regression to test their associations with native versus alien species, casual versus naturalized species and naturalized versus invasive species. For each of the three comparisons, the first was coded 0 and the second 1. The introduction pathway, which only applies to alien species, was included in the models for naturalization and invasion success. We also performed phylogenetic linear regression to test for associations between C-, S- and R-scores and the introduction pathways (for alien species only), and the grid-cell occupancy of native, naturalized and invasive species. Since CSR scores for each species sum to 100 (%), we ran separate models for each score to avoid multi-collinearity. Prior to analyses, species occupancy was log-transformed, and all numeric variables, for example, CSR strategy scores and grid-cell occupancy, were standardized to a zero mean and unit variance to provide standardized coefficients for comparisons between and within models (Schielzeth, 2010). These phylogenetic regression models were run using the R package phylolm with default settings (Tung Ho & Ané, 2014), that is, logistic maximum penalized likelihood estimation optimization method for phylogenetic logistic regressions (i.e. naturalization and invasion success) and the Brownian motion model for the error term for models with continuous response variables (i.e. grid-cell occupancy). To show the general relationships between CSR scores and plant invasion, we also ran models for deliberately and accidentally introduced aliens separately whenever possible (e.g. regressions on naturalization success).

Rather than using *p*-values to provide dichotomous justifications for results, for example, significant versus non-significant, we used the 'language of evidence' proposed by Muff et al. (2022). Briefly, *p*-values were considered as continuous measures of statistical evidence and reported as concrete values along with the estimate and associated uncertainty whenever possible. Consequently, results were described with evidence-based language, for example, there was very strong/strong/moderate/weak/little evidence that *X* was associated with *Y*.

3 | RESULTS

3.1 | Summary of the dataset

In the final dataset, 499 of 1,660 species were alien, of which 216, 237 and 46 were casual, naturalized and invasive respectively (Figure 1). The percentages of deliberately introduced species were 62.5%, 34.6% and 54.3% for casuals, naturalized and invasive species respectively.

3.2 | Differences in CSR scores

Overall, native and alien species occupied different areas of the CSR triangle (Figure 2a; Figure S1a). Specifically, alien species had greater C-scores ($M \pm SD$ for alien vs. native species: 35.7 ± 22.13% vs. 28.7 ± 21.63%, p = 0.017) and smaller S-scores (21.6 ± 24.17% vs. 29.6 ± 28.07%, p = 0.032) than native species, whereas R-scores (42.7 ± 24.31% vs. 41.7 ± 25.22%, p = 0.805) were similar to each other (Figure S1b–d).

CSR scores also showed substantial differences between native species and the three groups of alien species with different invasion stages (Figure 2a–d and Table S1). For C-score, native species (28.7 ± 21.63%) had the lowest values and invasive species (43.5 ± 25.66%) had the highest values, with intermediate values for casual (36.0 ± 22.34%) and naturalized (34.0 ± 20.93%) species (Figure 2b). For S-score, naturalized species (18.6 ± 21.48%) had the lowest values, and native (29.6 ± 28.07%) and casual (25.0 ± 26.84%) species had the highest values, with intermediate values for invasive species (18.6 ± 21.48%; Figure 2c). For R-scores, casual species (39.0 ± 23.77%) had the lowest values and naturalized species (47.5% ± 23.94%) had the highest values, with intermediate values for native (41.7 ± 25.22%) and invasive (35.2 ± 24.33%) species (Figure 2d).

The results also showed that CSR scores differed between deliberately and accidentally introduced aliens (Figure S2). Among the casual species, the deliberately introduced species had lower C-scores than the accidentally introduced species (27.8 ± 19.33% vs. 40.9 ± 22.65%, p = 0.012), but similar S-scores (27.0 ± 28.07%

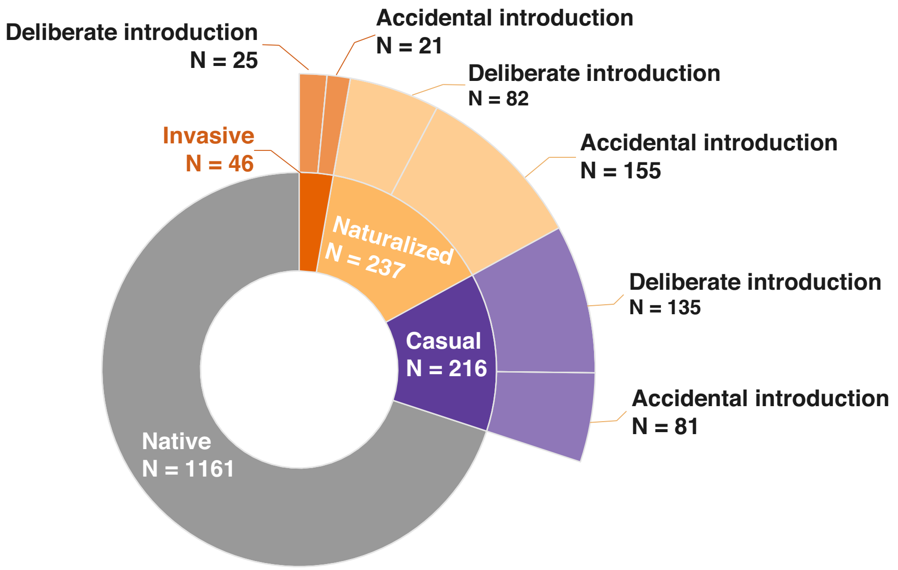

FIGURE 1 The numbers of native and alien species by introduction pathway (deliberate vs. accidental introduction). The inner donut chart shows the numbers of native, casual, naturalized and invasive species, while the outer donut shows the numbers of deliberately and accidentally introduced alien species.

vs. 23.9 ± 27.17%, p = 0.673) and R-scores (45.2 ± 25.22% vs. 35.3 ± 24.69%, p = 0.103). Among naturalized species, there was strong evidence that deliberately introduced species, compared to accidentally introduced ones, had greater C-scores (41.4 ± 21.36% vs. 30.0 ± 19. 66%, p = 0.003) and S-scores (24.1 ± 24.20% vs. 15.6 ± 19.34%, p = 0.036) but smaller R-scores (34.5 ± 22.35% vs. 54.4 ± 21.87%, $p \leq 0.001$). Among invasive species, deliberately introduced species also had greater S-scores (29.9 ± 25.20% vs. 11.0 ± 12.24%, p = 0.015) and smaller R-scores (23.9 ± 13.24% ± 48.8 ± 27.70%, p = 0.003) than accidentally introduced species, while C-scores (46.3 ± 24.04% vs. 40.2 ± 27.71%, p = 0.539) were similar.

3.3 | Relationships between CSR scores, introduction pathways and naturalization/invasion success

Logistic regression analyses of alien versus native status provided strong evidence that C-scores were positively (estimate = 0.30, 95% confidence interval, hereafter CI = [0.20, 0.39], $p \leq 0.001$) and S-scores were negatively (estimate = −0.26, CI = [−0.36, −0.15], $p \leq 0.001$) related to the likelihood that a species was alien. Furthermore, there was moderate evidence of a positive association between R-scores (estimate = 0.10, CI = [−0.02, 0.18], p = 0.046) and the likelihood that a species was alien (Figure 3a; Table S2).

A Chi-square test for casual versus naturalized species showed very strong evidence that deliberately introduced species are less likely to become naturalized than accidentally introduced species (χ^2 = 34.14, $p \leq 0.001$). However, a Chi-square test for naturalized versus invasive species found moderate evidence that deliberately introduced naturalized species were more likely to become invasive (χ^2 = 5.58, p = 0.018) than accidentally introduced species. Logistic regressions for naturalization and invasion success showed that the interaction terms between CSR scores and introduction pathway had effects on naturalization and invasion success in several models (Figure 3b,c; Table S2). This suggests that the relationships between CSR scores and naturalization or invasion success vary between accidentally and deliberately introduced alien species. Nevertheless, on average across the two introduction pathways, there was no evidence that C-scores were related to naturalization success, but there was weak to strong evidence that R-scores were positively related to naturalization success (Figure 3b; Table S2). In contrast, there was weak to moderate evidence that C-scores were positively associated and R-scores were negatively associated with invasion success.

3.4 | Relationships between CSR scores, introduction pathways and grid-cell occupancy

Phylogenetic linear regression analysis of grid-cell occupancy of native species (Figure 4a; Table S2) showed that there was strong evidence (all $p \leq 0.001$) that R-scores (estimate = 0.51, CI = [0.46, 0.56]) were positively associated while C- (estimate = −0.31, CI = [−0.38, −0.24]) and S-scores (estimate = −0.72, CI = [−0.80, −0.63]) were negatively associated with grid-cell occupancy.

The results of phylogenetic ANOVA revealed that among naturalized species, there was very strong evidence that deliberately introduced species occupied a smaller number of grid cells than accidentally introduced naturalized species (Figure S4a; 205 ± 191 vs. 317 ± 204, $p \leq 0.001$). By contrast, among invasive species, deliberately and accidentally introduced species occupied similar numbers of grid cells (Figure S4b; 347 ± 178 vs. 360 ± 191, p = 0.917). In addition, a phylogenetic regression analysis including both CSR scores and the introduction pathways revealed moderate to strong evidence that their interaction terms had effects on the occupancy of naturalized and of invasive species (Figure S5a,b; Table S2). For accidentally introduced naturalized species, there was moderate

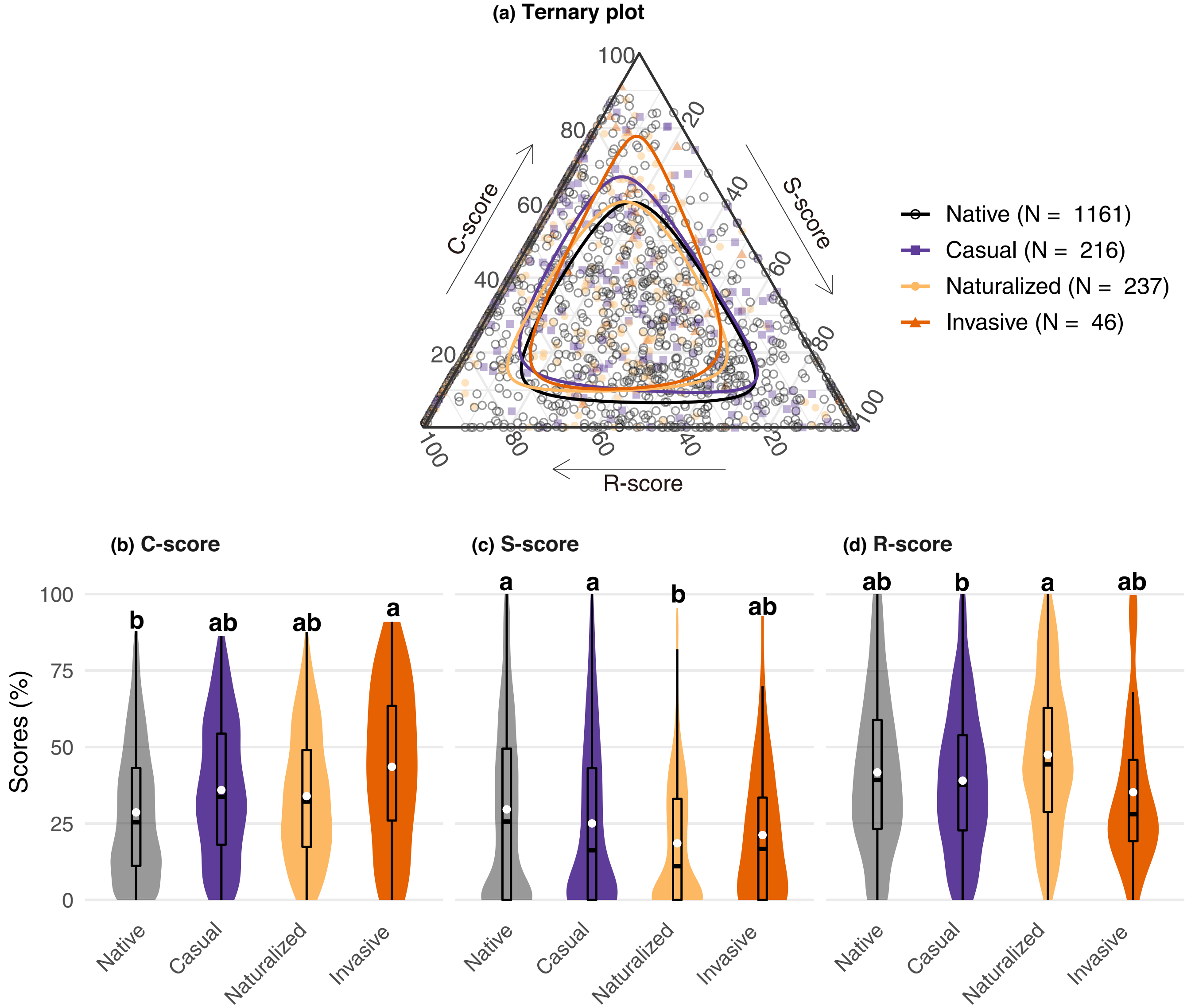

FIGURE 2 Ternary plot showing native, casual, naturalized and invasive species within the competitive, stress-tolerant and ruderal (CSR) adaptive strategy triangle (a). The triangles inside the plot represent the 50% confidence regions, calculated as Mahalanobis distance (Hamilton & Ferry, 2018). Differences in (b) C-score, (c) S-score and (d) R-score between native species and the three invasion stages of alien species (casual, naturalized and invasive) were further tested using phylogenetic ANOVA models, and the results are presented as violin plots, showing the distribution of the data. For the boxplots inside each violin plot, the horizontal line represents the median, the white dot represents the mean, the box represents the interquartile range (IQR) and the whiskers represent 1.5 times the IQR. Different letters above the boxes indicate that there was moderate to very strong evidence for the tested differences. See Table S1 for *p*-value of each comparison

to strong evidence (all $p \leq 0.022$) that C-scores were negatively, while S- and R-scores were positively related to their occupancy. Conversely, for deliberately introduced naturalized species, there was strong evidence that C-scores were positively, whereas S-scores were negatively associated with their occupancies. For accidentally introduced invasive species, there was no evidence (all $p \geq 0.488$) that CSR scores were associated with the occupancy of accidentally introduced species. However, for deliberately introduced invasive species, there was moderate to strong evidence (all $p \leq 0.025$) that C- and R-scores were positively, and S-scores were negatively associated with their grid-cell occupancy.

4 | DISCUSSION

This study, based on a dataset of 1,660 plant species from the Czech Republic, examined how CSR scores and introduction pathways are related to plant invasions as alien species progressing along the introduction–naturalization–invasion continuum. Although this is of great importance in both theoretical and applied ecology, relatively few studies (e.g. Banerjee et al., 2021; Divíšek et al., 2018; Moodley et al., 2013) have addressed the main factors associated with the different stages of the invasion continuum. Here, we found that native and alien species of the three invasion stages occupy

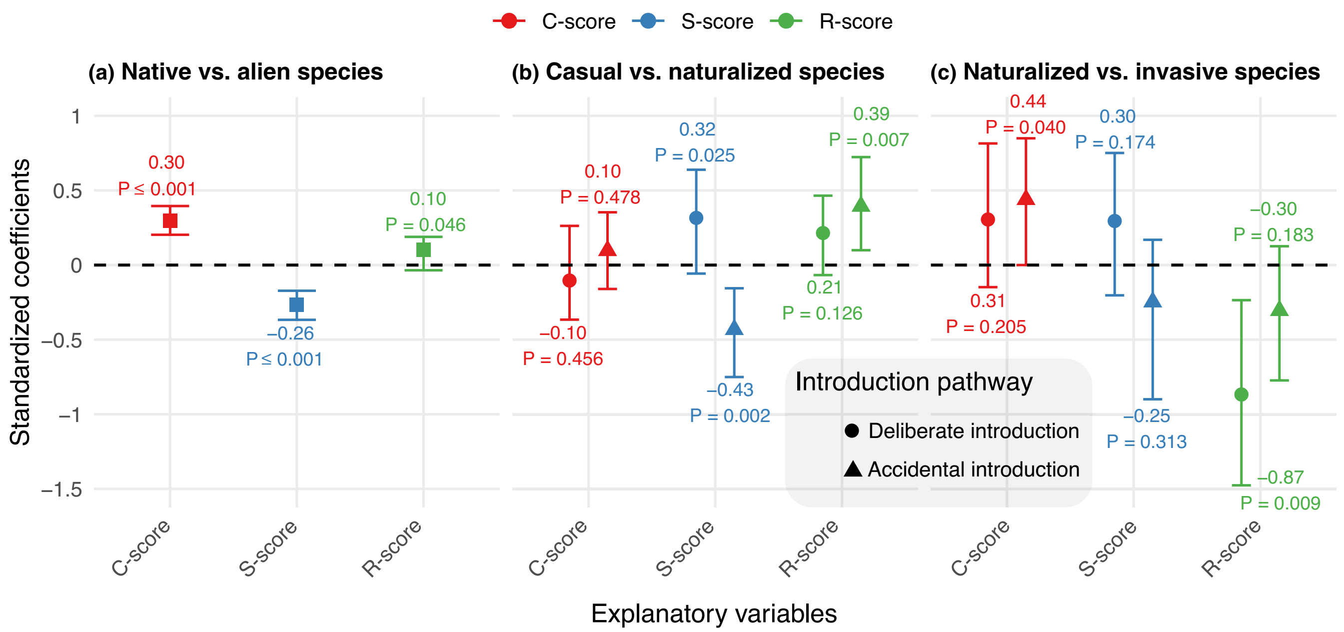

FIGURE 3 Standardized phylogenetic logistic regression coefficients (±95% confidence intervals) of each CSR score for (a) native versus alien species, (b) casual versus naturalized species and (c) naturalized versus invasive species. For these comparisons, the former was coded 0 and the latter 1. For naturalization and invasion success, models were run for each introduction pathway. The estimated coefficients of the explanatory variables and the corresponding *p*-values are indicated above or below each point.

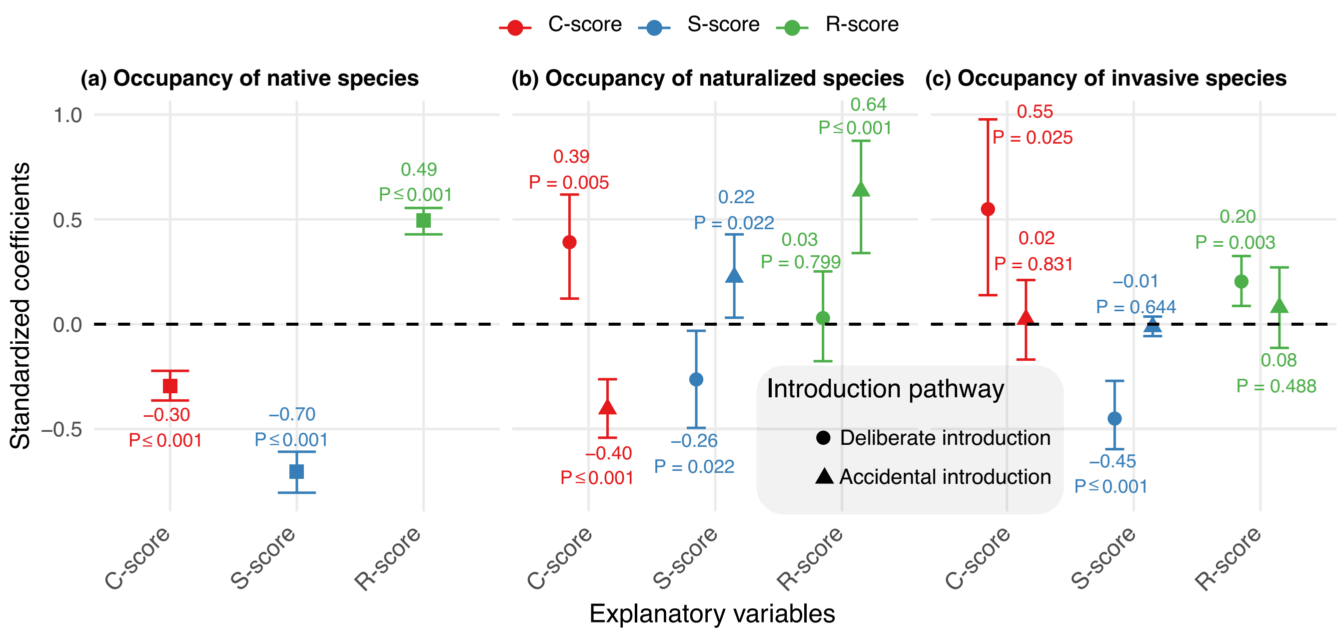

FIGURE 4 Standardized phylogenetic regression coefficients (±95% confidence intervals) of each CSR score on the grid-cell occupancy of (a) native, (b) naturalized and (c) invasive species. For occupancy of naturalized and invasive species, the models were run separately for deliberately and accidentally introduced aliens. The estimated coefficients of the explanatory variables and *p*-values are shown above or below each point.

different areas of the CSR triangle, suggesting the changing roles of CSR strategies in facilitating plant invasions along the continuum. Such changing roles were confirmed by phylogenetic regressions, which showed that R- and C-selection were positively associated with plant naturalization and invasion success, respectively, across deliberately and accidentally introduced aliens.

Few studies have included casual species in the investigation of factors associated with plant invasion, mostly because these species are less widely distributed than naturalized and invasive species (Divíšek et al., 2018). Here, our results showed that casual species occupied a similar area in the CSR triangle as invasive species, that is, there was no evidence that CSR scores differed between the two species groups (Figure 2a,d; Table S1). We also found weak evidence that casual species had higher C-scores than native species, which is surprising given the competitive superiority of C-selected species. In contrast, based on a national dataset from India, Banerjee et al. (2021) demonstrated that casual species had smaller specific leaf area (i.e. representative of S-selected species) than invasive species. This discrepancy could reflect the importance of climate in regulating plant invasion (e.g. Guido et al., 2016; Irl et al., 2021), that is, even though casual species in theory are competitors, the unfavourable climate in the introduced range prevents their successful establishment. In addition, such discrepancy also highlights the unpredictable ecology of casual species. Moreover, Banerjee et al. (2021) showed that casual species had shorter minimum residence times than both naturalized and invasive species and less economic uses than invasive species, suggesting that casual species are more strongly related to human-introduced attributes but only weakly related to inherent characteristics of species. Taken together, these results indicate that the inclusion of casual species can provide important insights into the stage-wise determinants of plant invasions, but caution is needed in interpreting the results.

The positive association between R-scores and naturalization success across deliberately and accidentally introduced aliens (Figure 3b) highlights the role of R-selection in promoting naturalization success. This confirms the findings of a global-scale study by Guo et al. (2018), which additionally found that competitors are also more likely to naturalize than stress-tolerators. However, our results showed no evidence of such an association between C-scores and naturalization success. It is possible that this apparent discrepancy reflects that the plant species used in this study are a subset of the global dataset used by Guo et al. (2018), and that species classified as native in the Czech Republic are naturalized or invasive elsewhere in the world (e.g. Pyšek et al., 2015; Pyšek, Jarošík, et al., 2009; Pyšek, Křivánek, & Jarošík, 2009). In addition, invasive species were excluded from the group of naturalized species in our analyses, and the results showed that naturalized and invasive species occupy different areas of the CSR triangle. Specifically, naturalized species were more likely to be characterized as ruderals, whereas invasive species were better characterized as competitors (Figure 2b–d), which may further explain the discrepancy between the two studies.

There is strong evidence that invasive species tend to have traits that provide competitive advantage compared to the average traits of non-invasive species. For example, van Kleunen et al. (2010) showed that invasive species had significantly higher values of performance-related traits such as growth rate and size compared to non-invasive (both alien and native) species. In our study, comparisons between native and alien species at the three invasion stages showed a gradual increase in C-scores from native to invasive species (Figure 2b), which is consistent with the results of van Kleunen et al. (2010). In addition, phylogenetic regression models showed that C-scores were positively and R-scores were negatively related to invasion success, regardless of the introduction pathway (Figure 3c). These results suggest that successful invasive species are characterized by competitive superiority over most native species, which has also been reported by Pyšek et al. (1995) and Dalle Fratte et al. (2019). Our findings highlight the changing roles of CSR strategies at different stages of the introduction–naturalization–invasion continuum. Ruderals, characterized by rapid growth and life cycle completion, have a higher probability of becoming naturalized. In contrast, the higher competitive ability of naturalized aliens compared to native species favours invasiveness once the self-sustaining population is established.

Unexpectedly, we found that deliberate introduction was negatively related to naturalization success and the occupancy of naturalized species (Figure S4a). These results contrast with previous findings that deliberately introduced aliens are more likely to become naturalized than accidentally introduced species (Pyšek et al., 2011; Riera et al., 2021). This discrepancy could be due to the different adaptative strategies possessed by deliberately and accidentally introduced aliens—deliberately introduced casual and naturalized species had lower R-scores (which showed positive associations with naturalization success) than accidentally introduced species (Figure S2c,f). This difference also explains the different (and even opposite) associations between CSR scores and the occupancy of deliberately and accidentally introduced aliens (Figure 4b,c; Figure S5); for example, C-scores and R-scores were positively related to the occupancy of deliberately and accidentally introduced naturalized species respectively. Nevertheless, the positive associations between R-scores and the occupancy of native species (Figure 4a) are consistent with previous findings at the global scale (Guo et al., 2019; Liao et al., 2021) and likely reflect that ruderals can rapidly establish self-sustaining populations due to abundant seed production and rapid life cycle (Grime & Pierce, 2012).

The negative effects of the deliberate introduction on plant naturalization also contrast with previous findings that horticulture (which corresponds to the deliberate introduction in this study) plays an important role in promoting naturalization success (Guo et al., 2019; van Kleunen et al., 2018). This could be due to the different spatial scales of the datasets, that is, the national scale in this study versus the global scale in the previous studies. Combined with the aforementioned discrepancy of the absence of associations between C-scores and naturalization success in this study versus positive relationships in Guo et al. (2018, 2019), our results also highlight the need to consider spatial scales (e.g. global vs. regional) in understanding stage-specific determinants of plant invasions.

5 | CONCLUSIONS

Based on a national-scale dataset and detailed information on species status along the introduction–naturalization–invasion continuum, we found that (a) native and alien species at the three invasion stages along the continuum occupy different areas of the CSR triangle, with naturalized species tending to be ruderals and invasive species tending to be competitors; (b) deliberate introduction was negatively related to naturalization success and the grid-cell occupancy of naturalized species, likely because deliberately and accidentally introduced aliens have different CSR strategies. Our study not only confirms the usefulness of the CSR strategy framework in understanding plant invasions but also provides empirical evidence of the stage-dependent drivers of such complex processes. Consequently, it has significant implications for predicting which alien species could become invasive and have serious negative impacts. For example, naturalized species with high C-scores are expected to have a higher probability of becoming successful invaders. Based on these results, management measures can be derived to prevent the further introduction and spread of alien species with potentially negative impacts.

AUTHOR CONTRIBUTIONS

K.G., P.P., M.C. and W.-Y.G. conceptualized the research; P.P., M.C., J.D., Z.L. and M.K. provided the data; K.G. and W.-Y.G. analysed the data and drafted the manuscript; P.P., M.C., J.D., Z.L., M.v.K. and S.P. contributed to the revising of the manuscript. All authors gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and scripts used to obtain the results of this study are available in https://doi.org/10.5061/dryad.zkh1893c0 (Guo et al., 2022).

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